Chapter 32

Biodiversity Loss and the Maintenance of Our Life-Support System

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Early global change research focused on the interactions between environmental changes (mainly climate change), ecosystem functioning and human societies. When biodiversity was added to the picture, it was to the extent that it is affected by these other components of global change (Fig. 32.1). But why does biodiversity matter to us? There are at least three classes of reasons why it does. First, it provides us with a number of goods that have direct economic value, such as food, new pharmaceuticals, genes that improve crops, and organisms that perform biological control. Second, it is intricately linked to human well-being for aesthetic, ethical, cultural and scientific reasons. And third, it may contribute to the provision of ecological services that are generally not accounted for in economic terms, such as primary and secondary production, the regulation of climate, the maintenance of atmosphere quality, the regulation of the hydrological cycle, the maintenance of water quality, and the maintenance of soil fertility. During the last decade, the effects of biodiversity on the other components of global change have received increasing attention (Fig. 32.1). In particular, there has been an explosive growth of research into the potential effects of biodiversity loss on ecosystem functioning and thereby on the provision of ecological goods and services to human societies (see review in Loreau et al. 2001).

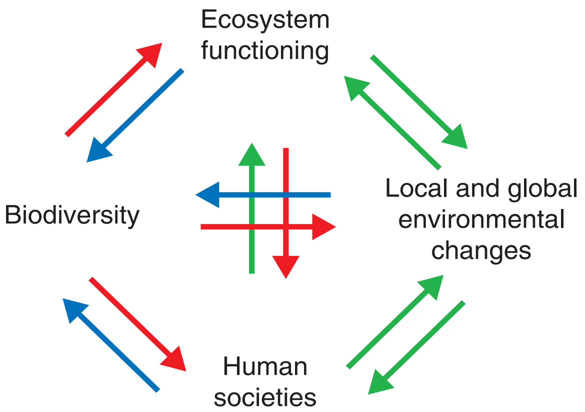

Fig. 32.1. Early global change research focused on interactions between environmental changes, ecosystem functioning and human societies (*green arrows*). When biodiversity first entered the picture, it was to the extent that it is affected by the other components of the Earth System (*blue arrows*). During the last decade, new research has focused on how biodiversity itself affects the other components, in particular how it influences ecosystem functioning and the provision of ecological goods and services to human societies (*red arrows*)

32.1 How Does Biodiversity Affect Ecosystem Functioning at Small Scales?

To investigate the effects of biodiversity on ecosystem processes, a new wave of experimental studies has manipulated species diversity using synthesised model ecosystems in both terrestrial and aquatic environments. While the first study that experimentally manipulated diversity did so across several trophic levels (Naeem et al. 1994), later studies focused mainly on effects of plant taxonomic diversity and plant functional-group diversity on primary production and nutrient retention in grassland ecosystems (e.g., Tilman et al. 1996, 1997a; Hooper and Vitousek 1997; Hector et al. 1999). Because plants, as primary producers, represent the basal component of most ecosystems, they represent the logical place to begin detailed studies. Several, though not all, experiments using randomly assembled communities found that plant species and functional-group richness both have a positive effect on primary production and nutrient retention. The largest of these experiments to date, the BIODEPTH project, showed a consistent positive effect of diversity on plant aboveground biomass production across eight sites with widely different soils and climates in Europe (Hector et al. 1999; Fig. 32.2). Each halving of the number of plant species reduced productivity by approximately 80 g m^{-2} on average, a figure that might not look spectacular on a m^2 basis, but that does when extrapolated to the total surface area covered by European grasslands (about 48 million t). Similarly, the omission of a single functional group reduced productivity by approximately 100 g m^{-2} on average.

It is fair to mention, however, that the interpretation of these experiments has been controversial (e.g., Huston et al. 2000; Hector et al. 2000), because their results can be generated by different mechanisms. These mechanisms may be grouped into two main classes (Loreau 1998, 2000). First are local deterministic processes, such as niche differentiation and facilitation, which increase

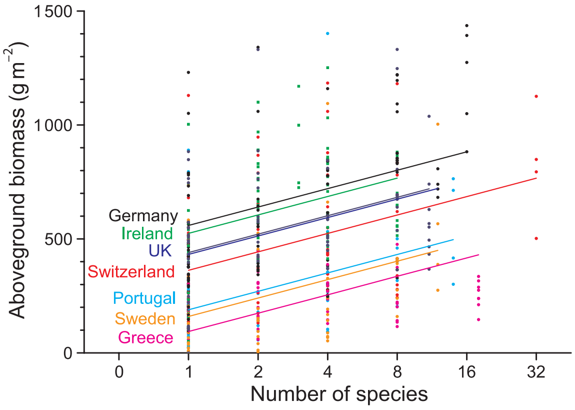

Fig. 32.2. Aboveground biomass production on average increases with plant species richness in grassland ecosystems. Results from the second year of the BIODEPTH experiment across eight sites in Europe (modified from Hector et al. 1999)

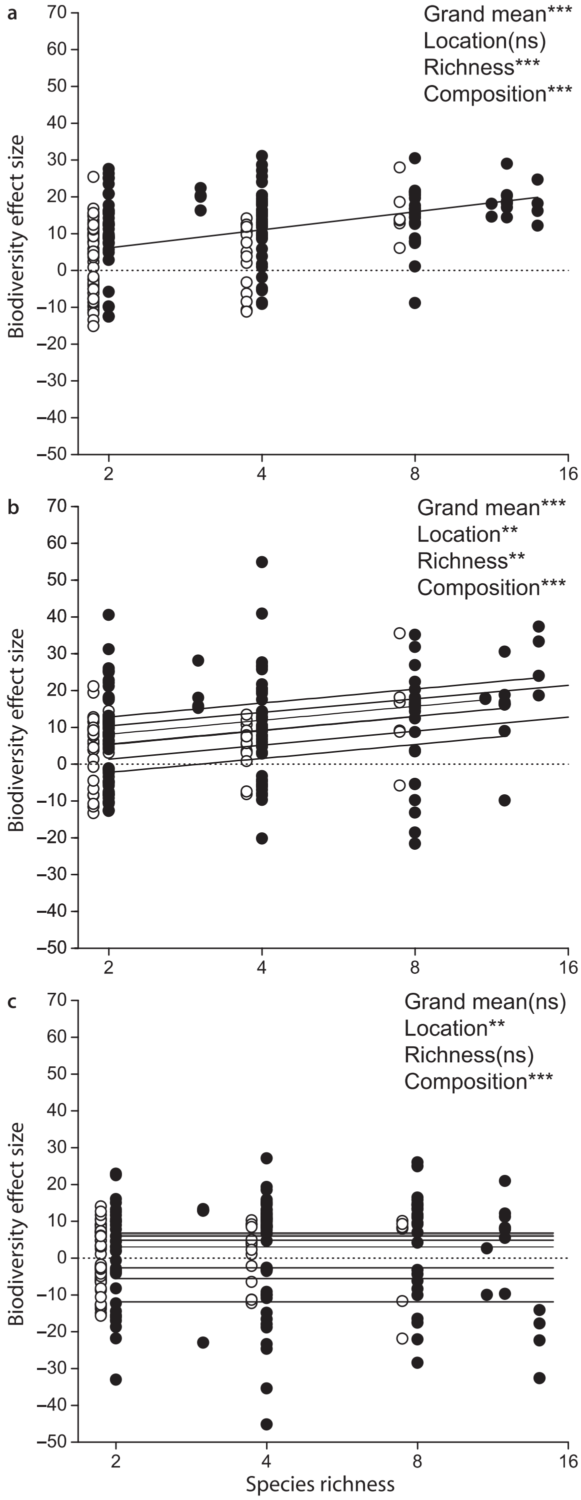

Fig. 32.3. Partitioning of biodiversity effects in the results from the BIODEPTH experiment (Fig. 32.1). **a** Net, **b** complementarity and **c** selection effects are based on comparisons of mixture yields and monoculture yields. Their values (in g m^{-2}) are square-root transformed but preserve the original positive and negative signs. *Open circles* are plots that do not contain any legume species; *filled circles* are plots that contain legumes. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ (modified from Loreau and Hector 2001)

the performance of communities above that expected from the performance of individual species grown alone. I shall subsume them under the term "complementarity". Second are local and regional stochastic processes involved in community assembly, which are mimicked in experiments by random sampling from a species pool. Random sampling coupled with local dominance of highly productive species can also lead to increased average primary production with diversity, because plots that include many species have a higher probability of containing highly productive species. As sampling processes were not an explicit part of the initial hypotheses, they have been viewed by some as "hidden treatments" (e.g., Huston 1997), whereas others have viewed them as the simplest possible mechanism linking diversity and ecosystem functioning (e.g., Tilman et al. 1997b).

New theoretical advances are making the resolution of this controversy possible. First, it is becoming clear that complementarity and sampling are not mutually exclusive mechanisms as previously thought. Communities with more species have a greater probability of containing a higher phenotypic trait diversity. Ecological "selection" of species with particular traits that leads to dominance and complementarity among species with different traits are two ways by which this phenotypic diversity maps onto ecosystem processes (Loreau 2000). These two mechanisms, however, may be viewed as two poles on a continuum from pure dominance to pure complementarity. Intermediate scenarios involve complementarity among particular sets of species or functional groups, or dominance of particular subsets of complementary species. Any bias in community assembly that leads to correlations between diversity and community composition may involve both dominance and complementarity.

Second, a new methodology now exists to partition the net effect of biodiversity into a selection effect and a complementarity effect, using comparisons between the yield of a mixture and its expected value based on monoculture yields (Loreau and Hector 2001). Application of this methodology to the data from the BIODEPTH experiment showed that the selection effect was variable, ranging from negative to positive values in different localities, but was zero on average (Fig. 32.3). Therefore it can be rejected as the sole mechanism explaining results from this experiment. In contrast, there was a consistent positive complementarity effect. This supports the hypothesis that plant diversity influences primary production through local biological processes such as niche differentiation and facilitation. Similar conclusions have been obtained from long-term data in another large-scale biodiversity experiment at Cedar Creek, Minnesota (Tilman et al. 2001).

Thus, there is little doubt that plant species diversity does affect ecosystem processes such as primary production and nutrient retention in grassland ecosystems, even at the small spatial and temporal scales considered in recent experiments. What remains unclear, however, is how many species are involved in these effects. And what is still largely unexplored is whether similar effects of diversity also occur at other trophic levels, and in other ecosystems, such as forests, and freshwater and marine ecosystems.

32.2 Scaling Up in Time: Biodiversity As an Insurance Against Environmental Changes

Even when high diversity is not critical for maintaining ecosystem processes under constant or benign environmental conditions, it might nevertheless be important for maintaining them under changing conditions. The insurance hypothesis proposes that biodiversity provides an “insurance”, or a buffer, against environmental fluctuations, because different species respond differently to these fluctuations, leading to functional compensations between species and hence more predictable aggregate community or ecosystem properties (McNaughton 1977; Yachi and Loreau 1999). A number of studies have recently provided theoretical foundations for this hypothesis (e.g., Doak et al. 1998; Yachi and Loreau 1999; Lehman and Tilman 2000). Several empirical studies have found decreased variability of ecosystem processes as diversity increases, despite sometimes increased variability of individual populations, in agreement with the insurance hypothesis (Fig. 32.4). The interpretation of these patterns, however, is complicated by the correlation of additional factors with species richness in these experiments, which does not fully preclude alternative interpretations (e.g., Huston 1997). Experiments in which both diversity and environmental fluctuations are controlled are needed to perform more rigorous tests of the insurance hypothesis.

The important message here is that time adds another dimension to the potential for complementarity among species and hence for biodiversity effects on ecosystem properties. Species that appear to be functionally redundant for an ecosystem process at a given time may no longer be redundant through time, because their variations in abundance or metabolism compensate each other. Society depends on the steady and predictable input of ecological services; biodiversity may provide greater stability in the production of these services, such as timber production, pollination levels, biomass production, and nutrient cycling. Functional compensations may be particularly important in a world that is changing in many ways at an unprecedented rate. Biodiversity loss may reduce the ability of natural and managed ecosystems to cope with other global changes. As an example, some recent experiments showed significant effects

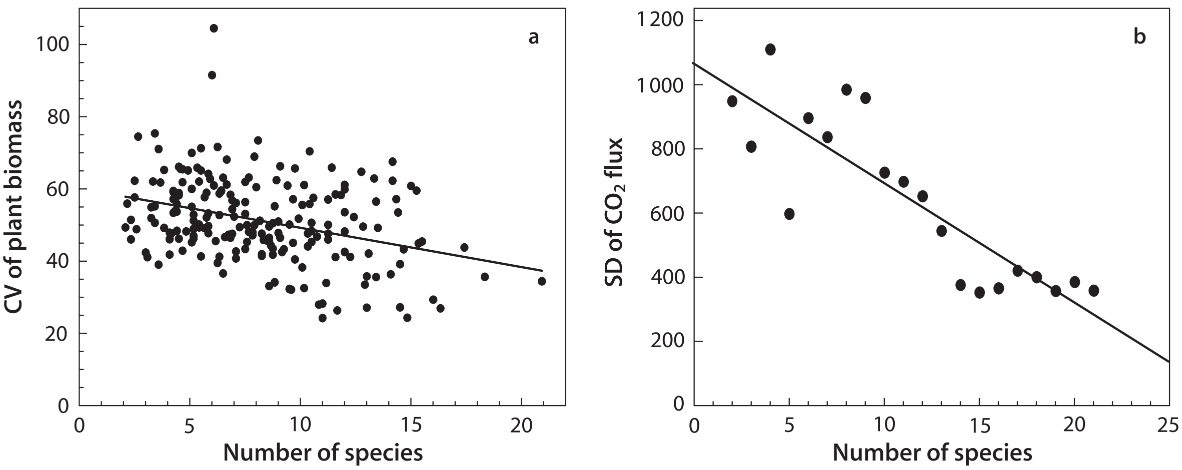

Fig. 32.4. Variability of ecosystem processes decreases as species richness increases. **a** Adjusted coefficient of temporal variation (*CV*) of annual total plant biomass (in g m^{-2}) over 11 years for plots in experimental and natural grasslands in Minnesota (reproduced from Tilman 1999a with permission, Ecological Society of America). **b** Standard deviation (*SD*) of CO_2 flux (in μl per 18 h) from microbial microcosms (reproduced with permission from Nature; McGrady-Steed et al. (1997) Nature 390:162–165, ©1997 MacMillan Magazines)

of plant diversity on the responses of grassland ecosystems to elevated atmospheric CO_2 concentration and nitrogen deposition (e.g., Reich et al. 2001). Thus, short-term experiments are very likely to underestimate the importance of biodiversity for the maintenance of ecosystem processes and services.

32.3 Scaling Up in Space: Biodiversity Effects at Landscape and Regional Scales

Small-scale experiments are equally likely to underestimate the functional significance of biodiversity. Many species that coexist locally occupy similar ecological niches at small scales because the niche differences that allow them to coexist are situated at larger scales, in their habitat differences from the scale of the landscape to that of the region. Just as diversity allows functional compensations between species through time, it allows functional compensations through space. Species replace each other along environmental gradients, because different species have different optimum abilities along these gradients. The larger the spatial scale, the greater the environmental heterogeneity, and the higher the biological diversity needed to take full advantage of these environmental differences. Species richness typically increases with surface area as a power function (Rosenzweig 1995). These species–area curves have been used to extrapolate the diversity that is needed at larger scales to perform the ecosystem processes that have been studied at small scales (Tilman 1999b).

There are good reasons to believe that these estimates are underestimates of the actual importance of biodiversity at large scales. Habitat shifts and fragmentation following land-use and climate changes are transforming, and will increasingly transform landscapes into patch mosaics. Accordingly, spatially continuous communities are being broken up into "metacommunities", i.e., isolated local communities connected by dispersal fluxes. Since many species from stable natural ecosystems are poor dispersers, habitat shifts and fragmentation will increase recruitment limitation of the appropriate set of complementary species that best perform given ecosystem processes in each site, and thereby amplify the effects of biodiversity loss on ecosystem functioning. Another way of seeing this is through species-area curves. Isolation at both ecological or evolutionary time scales typically has the effect of increasing the exponent of the power function relating species richness to surface area (Rosenzweig 1995). This implies that an even higher diversity is needed at large scales to ensure a given level of diversity at small scales, or, equivalently, that biodiversity loss at regional scales increases the extent and impact of biodiversity loss at local scales.

32.4 Conclusions

Recent theoretical and experimental work provides clear indications that biodiversity loss can have profound impacts on the functioning of the Earth System and the maintenance of our life-support system. Biodiversity can both enhance some ecosystem processes, such as productivity and nutrient retention, and act as a biological insurance against potential disruptions caused by environmental changes. Therefore biodiversity can no longer be ignored in global change and environmental issues.

Despite the explosive growth of the biodiversity-ecosystem functioning area during the last few years, knowledge of the functional consequences of biodiversity loss is still limited. The main challenges that lie ahead of us are:

1. To extend current knowledge on plant-based processes in temperate grasslands to other organisms (animals and microorganisms), other trophic levels (herbivores, predators and decomposers) and other ecosystems (forest, tropical, fresh-water and marine ecosystems);
2. To understand impacts of biodiversity change at larger temporal and spatial scales in interaction with other environmental changes, in particular land-use change;
3. To extend current research beyond a basic science perspective and focus on impacts on the provision of ecosystem goods and services of relevance to human societies.

This science agenda is that of the joint project of *Diversitas* and IGBP-GCTE on Biodiversity, global change and ecosystem functioning. *Diversitas*, as the international programme on biodiversity science, further aims to integrate this research on the functional and societal impacts of biodiversity change into a broader picture that includes the causes and processes of biodiversity change as well as the ways by which biodiversity can be conserved and used in a sustainable manner.

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