

BIODIVERSITY AND ECOSYSTEM FUNCTIONING: BASIC PRINCIPLES

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Summary

Since the mid 1990s, ecologists have intensified their efforts to describe and quantify the effects that biodiversity can exert on the various processes within ecosystems. Both theoretical and experimental work has shown that within a habitat, changing diversity has profound effects on biomass production, nutrient retention, and other ecosystem characteristics such as stability. In most experiments, a positive relationship between plant diversity and productivity has been found, while the level of unconsumed resources was inversely related to diversity. The diversity of functional groups in general had more pronounced effects than the number of species, emphasizing the importance of functional traits of species. As underlying mechanisms, niche differentiation leading to complementary resource use, facilitative interactions among species, and probabilistic sampling effects have been identified. For management or conservation purposes, it is crucial to distinguish results obtained from within-habitat manipulative experiments, from those of observational studies comparing across-habitat patterns of diversity and ecosystem functioning. As the understanding of the biodiversity-ecosystem functioning relationship progresses, conservation and management will more and more benefit from these basic insights into how communities and ecosystems function.

1. Introduction

‘Does biodiversity matter for the functioning of ecosystems?’ or ‘Does it make any difference to the processes within an ecosystem if there are many or only a few species?’ These are the central questions that arise when one is looking at the many ecosystems on earth differing very much in their biological richness, but which all have a similar basic set of energy-, matter-, and information-fluxes. For example, both tropical forests with their overwhelming richness in flora and fauna, and extremely species-poor systems such as lichen communities in Antarctica, fix carbon through photosynthesis of the plant compartment, and organic matter is decomposed by microorganisms into mineral components, which are partly taken up by the primary producers again. Although admittedly simple, this example shows that processes central for the functioning of ecosystems might be maintained by many or very few organisms, which suggests the question whether there is any relationship between biodiversity and ecosystem functioning. The answer to this question is not only of pure academic interest, but it becomes more and more relevant as the loss of biodiversity is dramatic and globally accelerating. From a human point of view, the key question may thus be formulated: ‘Does biodiversity matter for the provision of ecosystem services?’, which are the benefits people obtain from ecosystems.

This contribution focuses on the relationship between biological diversity and two aspects of ecosystem functioning: resource dynamics at a given point in time such as primary production or nutrient cycling, and long-term stability in the face of environmental change. The anthropocentric ‘value’ of biodiversity and its importance for the ecosystem services that humanity obtain are dealt with in *The Value of Biodiversity* and is in the focus of another large international initiative, the Millennium Ecosystem Assessment (MA 2003, www.millenniumassessment.org).

2. A historical perspective

It was not until the beginning of the 1990s that, alarmed by the increasing loss of biodiversity, scientists started to systematically seek answers to the basic question outlined above. Before that time, a related topic was discussed mainly from a theoretical perspective: the relation between diversity and stability of food webs. While early theory predicted more stable properties in more complex food webs of producers and consumers, later models predicted less stable population dynamics (see also section 5). Therefore, the notion that diversity may influence ecosystem processes in a ‘positive’ way was not apposite. In addition, research from agronomy demonstrated that mixtures of crop species were often less productive than the best monoculture. Experience from agriculture also showed that in the course of intensification of production, productivity increased through higher input of fertilizers and pesticides, while diversity within fields decreased.

However, the ‘biodiversity crisis’ again raised interest in the question whether diversity has effects on ecosystem functioning or not. The launch of the Scientific Committee of Problems of the Environment (SCOPE) program of 1991 entitled ‘Ecosystem Functioning of Biodiversity’, initiated the recent rapid development in this field of research. This program helped to bridge the gap between two disciplines in ecology that

had followed separate ways in studying ecosystems, namely ‘population or community ecology’ and ‘ecosystem ecology’. The former discipline accumulated knowledge on the distribution and abundance of species as a function of abiotic (physical and chemical) and biotic (interactions among species such as competition) conditions. The latter discipline has studied the flow of energy and the fluxes and pools of elements within ecosystems, without explicitly considering the diversity of organisms involved and their functional roles. In the first product of that SCOPE program, a hypothesis-based and comprehensive framework on how biodiversity may affect ecosystem processes was expressed for the first time (see Schulze & Mooney 1993, section 3).

In the second half of the SCOPE program, an in-depth exploration of the functional role of biodiversity in various biomes was published in three books (Mooney *et al* 1996, Solbrig *et al* 1996, Orians *et al* 1996). This effort was largely based on the evaluation of observational studies comparing communities with different levels of diversity, e.g. species poor temperate forests of mid-Europe with species rich ones of East Asia. Quickly it became obvious that such correlational studies could hardly detect any causal mechanisms of biodiversity effects due to co-varying factors (see section 3.2. for more details) and that they have to be complemented by experimental approaches. Parts of that program were then included into the Global Biodiversity Assessment (GBA; Heywood & Watson 1995), an independent, peer-reviewed analysis of the biological and social aspects of biodiversity, commissioned by the United Nations Environment Programme (UNEP). This assessment was done to fulfill the need of a comprehensive review of current knowledge in the framework of the United Nations Convention on Biological Diversity (CBD).

Based on the insight gained from correlational studies and on the formulation of the early hypotheses, a first generation of experiments were conducted that sought to reject the null hypothesis of no relationship between biodiversity as an independent variable and ecosystem functioning as the dependent variable (see examples listed in the bibliography). All those experiments adopted a basic common design: establishment of a gradient in biodiversity (most often plant species richness or the number of functional groups), while keeping extrinsic conditions (e.g. climate, fertility, land use history) as constant as possible. They were conducted in microbial microcosms, in controlled environmental facilities, or in the field. A variety of ecosystem processes were monitored as response variables, with a focus on biomass production (primary productivity). For very practical reasons, these experiments used fast-growing, small sized, mainly early successional model systems such as grasslands. In essence, most studies reported a positive, but asymptotic relationship between diversity and ecosystem processes, wherein the loss of species from an ecosystem initially has only a weak effect, but which accelerates as the system impoverishes. More diverse systems consistently had higher biomass production, higher nutrient uptake and consequently lower leaching losses to the groundwater, and they were more resistant against invasion by other species (see *Biodiversity and Ecosystem Functioning: Experimental Systems*). More recently, experimental work on the biodiversity–ecosystem functioning relationship increased strongly in number and many different ecosystem types such as wetlands, marine systems or forests were tackled. In addition, more mechanistically driven experiments were initiated, focusing on nutrient dynamics, trophic interactions, population dynamics or below/above-ground interactions, for instance. Parallel to the

empirical work, theoretical studies began to explore the functional significance of diversity, building upon concepts of intercropping theory from agriculture and upon models of resource competition and niche differentiation.

These experiments have spurred a tremendous controversy among ecologists about the importance of biodiversity for ecosystem functioning. The debate focused on the validity of the experimental designs, on the relevance of several distinct mechanisms responsible for the observed diversity effects (see section 3.3.), and on the relevance of the findings for interpreting biodiversity loss in natural ecosystems. In part, this controversy arose from the apparent discrepancy between the results obtained from the artificially assembled model communities and observational studies (for details see sections 3.2. and 4., and also *The Role of Above- and Below-ground Linkages in Ecosystem Functioning*).

After almost a decade of intensive research, two conferences held in 1999 and 2000 under the auspices of the International Geosphere-Biosphere Program – Global Change and Terrestrial Ecosystems (IGBP-GCTE) and the international program of biodiversity science DIVERSITAS summarized and synthesized the empirical findings and theoretical concepts. The resulting books are another two landmarks in the fast-growing area of research addressing biodiversity and ecosystem functioning (Kinzig et al. 2002; Loreau et al. 2002), providing both thorough reviews of all relevant studies and perspectives and challenges for future work. A recent article by Hooper and colleagues summarizes these issues too (Hooper et al. 2005). Recently, a synthesis book explicitly focused on the role of insects for ecosystem functioning (Weisser and Siemann 2004), whereas another one extended the biodiversity-ecosystem functioning issue to the temperate and boreal forest realm (Scherer-Lorenzen *et al* 2005).

Interestingly, the first ecological experiment documented that was analyzed by Darwin and mentioned in *On the Origin of Species* (1872, p. 113) had a similar aim as the manipulative biodiversity experiments of the last decade: to determine which species growing in monoculture or in mixtures make the most productive grasslands on different soil types. From that experiment Darwin concluded that mixtures of several distinct plant genera produce higher yields than species grown in monocultures, which essentially was endorsed by the modern experiments.

3. A new paradigm in ecology: the ‘Biodiversity-Ecosystem Function Paradigm’

The recent advances made in functional biodiversity research led to a new synthetic ecological framework, which has even been denoted as a new paradigm of ecology. While biodiversity has historically been seen as a response variable that is affected by climate, nutrient availability and disturbance, this new emerging paradigm, called ‘Biodiversity-Ecosystem Function Paradigm’ (Naeem 2002), sees the environment primarily as a function of diversity, underlining the active role of the biota in governing environmental conditions. It does not deny, of course, the influence of the environment on organisms. More specifically, within this framework, a specific ecosystem function is thus seen as a function of (i) biodiversity and the functional traits of the organisms involved, (ii) associated biogeochemical processes, and (iii) the abiotic environment.

This is not only of pure academic interest, but it has important implications for the conservation and sustainable management of biological diversity (see section 6).

3.1. Hypotheses

At the beginning of the 1990s, three main hypotheses were formulated concerning how species richness as a surrogate for biological diversity (as the independent treatment variable) may affect ecosystem processes (as the dependent response variable); namely that diversity shows (i) no effect ('null hypothesis'), (ii) a linear relationship between diversity and ecosystem processes, or (iii) an asymptotic relationship where species at higher levels of diversity might be redundant in their function. These early hypothetical relationships have been expanded since then (see Figure 1 for examples) and they represent a variety of underlying mechanisms. However, they can be classified into three classes:

- *Species are primarily redundant:* Loss of species is compensated for by other species with a similar function. Conversely, the addition of such species adds nothing new to the system. The graphical presentation shows an asymptotic relationship in which a major proportion is insensitive to changes in diversity. The basis for this view is a classification of species into functional groups where those species within one group have a similar function in the system. For the maintenance of ecosystem functioning, a minimal set of functional groups is essential, but species within a group are at least partially substitutable and thus 'redundant' (Lawton and Brown, chapter 12 in Schulze and Mooney 1993). While this might be true under stable environmental conditions, such 'redundant' species might replace species that are lost under changing conditions such as disturbance events or climate change. In consequence, the 'insurance hypothesis' predicts more stable ecosystem functioning with higher diversity under fluctuating environmental conditions (Yachi and Loreau 1999, see also section 5.), highlighting the context-dependency of the 'redundancy hypothesis'. Related to this class of hypotheses is the so-called 'rivet hypothesis' that compares the role of species with rivets holding together a machine: some rivets (species) are redundant in their function, increasing the reliability of the system. However, after the number of rivets drops below a certain threshold, the system fails.
- *Species are primarily singular:* Loss or addition of species causes detectable changes in ecosystem process rates, i.e. species make unique contributions to ecosystem functioning. The graphical presentations have a positive (or negative, depending on the process under study) slope. Cases of singular species with extreme impacts are 'keystone species' or 'ecosystem engineers', the former being species with disproportionate effects on ecosystems relative to their abundance (e.g. predators controlling dominance of other species), the latter being species that modify the resource availability for other members of the community through modification of the habitat (e.g. dam-building beavers) (Lawton 1994).
- *Species impacts are context-dependent and therefore idiosyncratic:* The impact of loss or addition of species depends on environmental conditions (e.g. community composition, fertility, disturbance regime), so that a species makes different contributions to ecosystems depending on conditions. The graphical presentation shows a variety of different slopes over different proportions of their trajectory

and shows no clear trend. The ‘idiosyncratic response hypothesis’, however, does not mean that there is no effect of diversity (i.e. the ‘null hypothesis’), but that it is rather difficult to predict the effects due to the complexity of species’ roles in ecosystems.

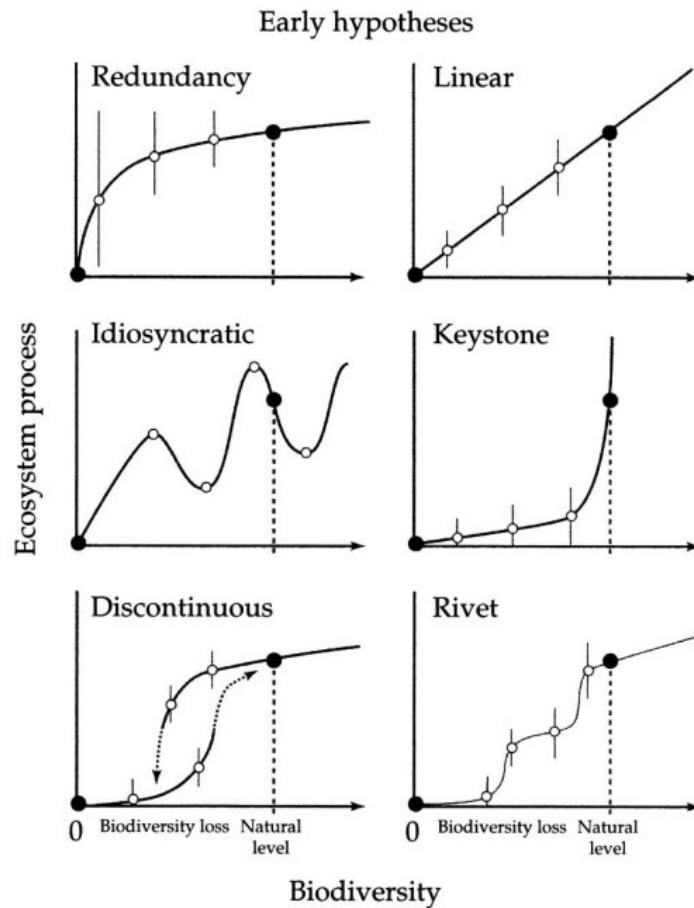


Figure 1. Graphs of early hypotheses considering the relationship between biodiversity and ecosystem functioning. Source: Naeem *et al.*, in Loreau *et al* 2002.

3.2. Approaches

If one is interested in answering the question how biodiversity affects ecosystem functioning, certainly the first approach coming to one’s mind would be to search for communities differing in one aspect of biodiversity, and to compare these in terms of a variety of ecosystem processes. For example, two types of forests with different number and composition of plant species would be sampled, following this comparative approach. However, unless site conditions are extremely similar, such across-habitat or across-locality comparisons may hide any potential effects that diversity exhibits within a site, because of environmental differences between the sampled sites. These environmental factors themselves determine the diversity of an ecosystem. Thus, comparative studies or sample surveys can be used to document any correlations between diversity and ecological processes, but they can never be used to establish causality or underlying mechanisms of this relationship. For example, Caspersen and

Pacala (2001), using forest inventory data from the USA, plotted the number of tree species in the canopy against stand growth. They found an asymptotical increase of growth with increasing tree species (Figure 2). One conclusion from that could be that a higher diversity of trees enhances productivity due to functional differences between species leading to higher resource exploitation and, hence, higher growth. This argumentation would follow the niche complementarity hypothesis outlined in detail below (3.3.1.). However, causality could also run the opposite way: more productive stands may simply permit the coexistence of more species. Thus, cause and effect cannot be disentangled from observational and comparative studies.

As a first experimental approach, so-called 'removal experiments' have been used where certain aspects of diversity (species, functional groups) are removed from intact, natural systems, thus creating a gradient in diversity levels ranging from natural to depauperate. These experiments can be very useful under certain circumstances, although the question of proper control treatments is rather difficult. In addition, other drawbacks have to be accounted for, such as large disturbance effects, changes in density, or spatial segregation of species. Díaz *et al* (2003) present a good overview on this approach.

Due to these difficulties, experimental approaches were initiated during the early 1990s, as described above that randomly allocate diversity treatments to plots within one site, keeping environmental conditions as constant as possible. Only by adopting this 'synthetic community approach', can within-habitat effects of diversity be detected unequivocally. In *Biodiversity and Ecosystem Functioning: Experimental Systems*, the most important aspects of these biodiversity experiments are described, focusing on grassland ecosystems.

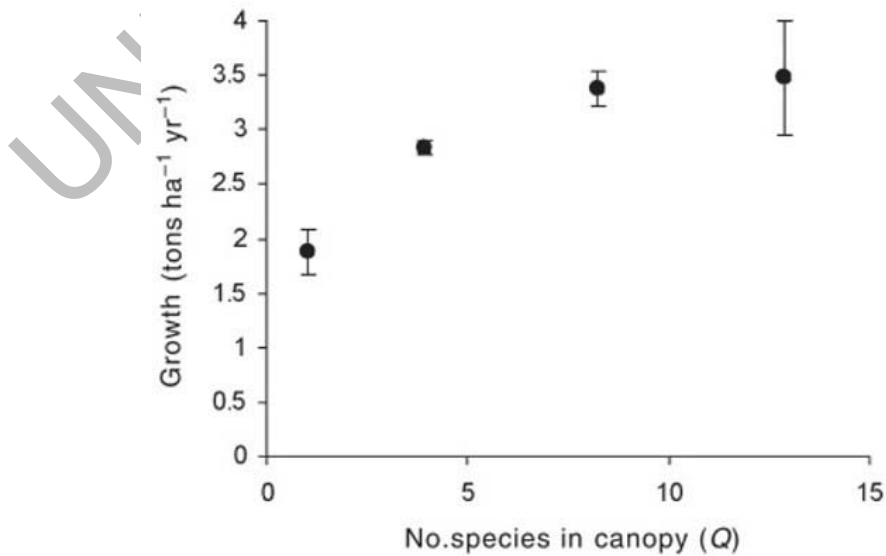


Figure 2. Relationship between tree species richness and stand growth in North American forests. Source: Caspersen and Pacala, 2001.

However, it is clear that for many ecosystems, one still has to rely on observational studies, simply because experimental manipulation of diversity is difficult to perform (e.g. forests, although there have been experiments established recently). Careful site characterization and large numbers of study sites are then needed to come to a reasonable ‘signal-to-noise’ ratio. In addition, among-site abiotic variation has to be adequately accounted for by including these ‘third’ variables as covariates in statistical analyses.

3.3. Mechanisms

What are the potential mechanisms to explain a causal relationship between biodiversity and ecosystem processes? For simplicity, in the following biodiversity will be restricted to one trophic level (plants as producers) and to the level of species, while ecosystem processes will be restricted to short-term resource dynamics, e.g. primary productivity. Ecological theory developed at least three potential mechanisms which can be grouped into two distinct classes.

3.3.1. Niche complementarity

Local deterministic processes, such as niche differentiation or resource partitioning, can lead to increased yield and nutrient retention in mixtures compared to that of the corresponding monocultures. These ‘niche complementarity’ or ‘niche differentiation’ effect models have their roots in theories about coexistence of species in competitive situations. Differences among species in their requirements for different resources will cause complementary interactions so that a combination of species could obtain more resources than could any species living by itself. This will result in higher biomass production and lower levels of unconsumed resources. Typical examples for resource-use complementarity are mixtures of plants with shallow and deep roots, of warm-season and cold-season grasses, of sun-adapted trees in the overstory and shade-tolerant species in the understory. Such species have also been called species with good ‘ecological combining abilities’, because they face less competition in combination with other species than when growing only with conspecific neighbors. The principle of resource complementarity has been successfully adopted in intercropping or agroforestry to increase yields per unit land area, for instance. In these cases, species with markedly distinct functional properties have been chosen to produce higher yields in mixtures than in monoculture, a phenomenon which has been called ‘overyielding’.

From a theoretical viewpoint, a possible mechanistic explanation of niche complementarity could be the following: consider a habitat with spatial or temporal heterogeneity of two factors, which are limiting plant growth, such as temperature and soil pH. Each species would occupy a certain region within this 2-dimensional niche space (Figure 3 A). It would perform best at a certain combination of temperature and pH, and it would be the superior competitor at this combination. By adding more and more species, the heterogeneous habitat or the available niche space would be covered more completely, thus the available resources would be used more completely and productivity would rise. If species are chosen randomly in a mathematical model, total community biomass increases asymptotically with increasing species richness until the resource pool is used up completely (Figure 3 B). Similar theoretical niche

complementarity models all yield the same basic relationship between plant diversity and ecosystem processes.

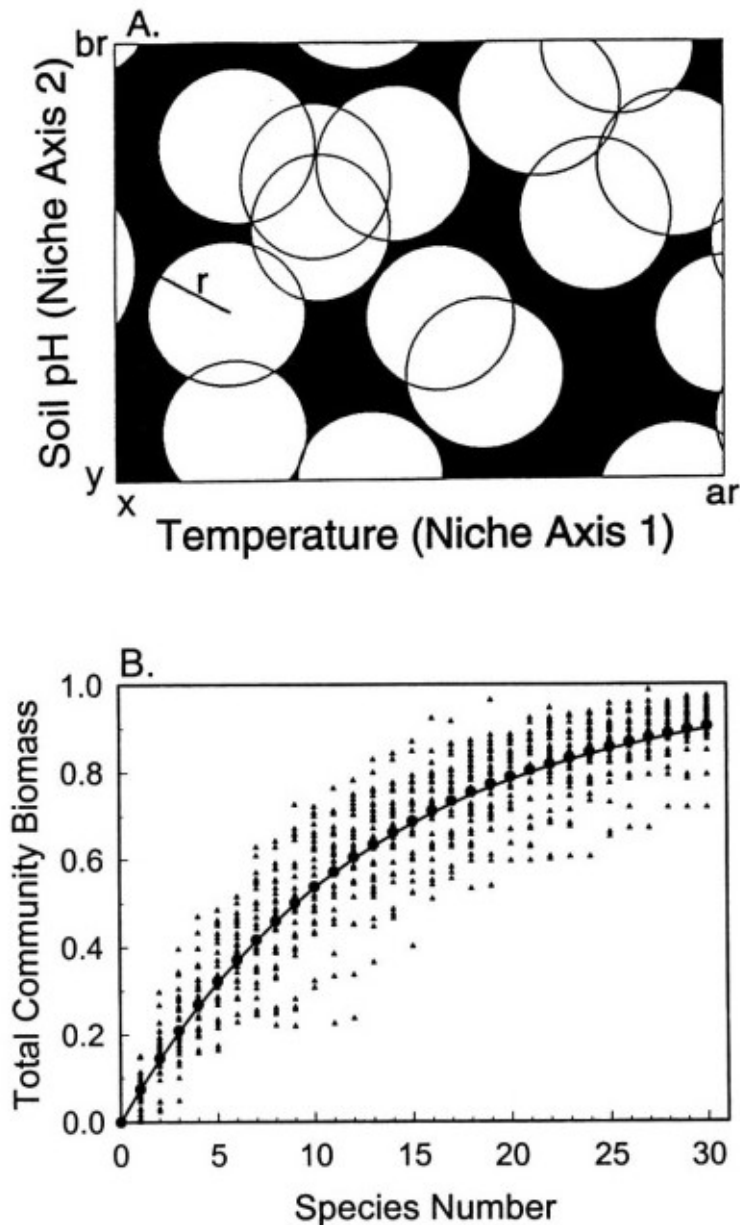


Figure 3. Niche differentiation in response to spatial heterogeneity of two limiting factors (temperature and soil pH). A: One circle represent the physical conditions under which a species can survive, at the centre of the circle, that species performs best. B: Modeled dependence of total community biomass on number of species capable of living somewhere in this heterogeneous habitat. Source: Tilman & Lehmann, chapter 2 in Kinzig *et al* 2002.

3.3.2. Facilitation and mutualism

Plants living in close proximity to each other commonly make demands on the same resources and therefore compete with each other. However, plants may also benefit from their neighbors through amelioration of the physical and biotic environment. Such

positive interactions among different species can also generate a positive relationship between biodiversity and ecosystem processes. For example, the ability to symbiotically fix atmospheric nitrogen by some plant groups, such as legumes, increases the overall availability of nitrogen to the whole community so that more biomass can be produced than in the absence of legumes. This effect is commonly applied in intercropping to increase yields, e.g. by mixing a crop species (e.g. corn) with a nitrogen-fixing legume such as beans.

Because it is difficult to distinguish facilitative or mutualistic interactions from niche differentiation—in fact there are many transitions between them—both aspects are often included in a general concept of complementarity.

3.3.3. Sampling or selection effects

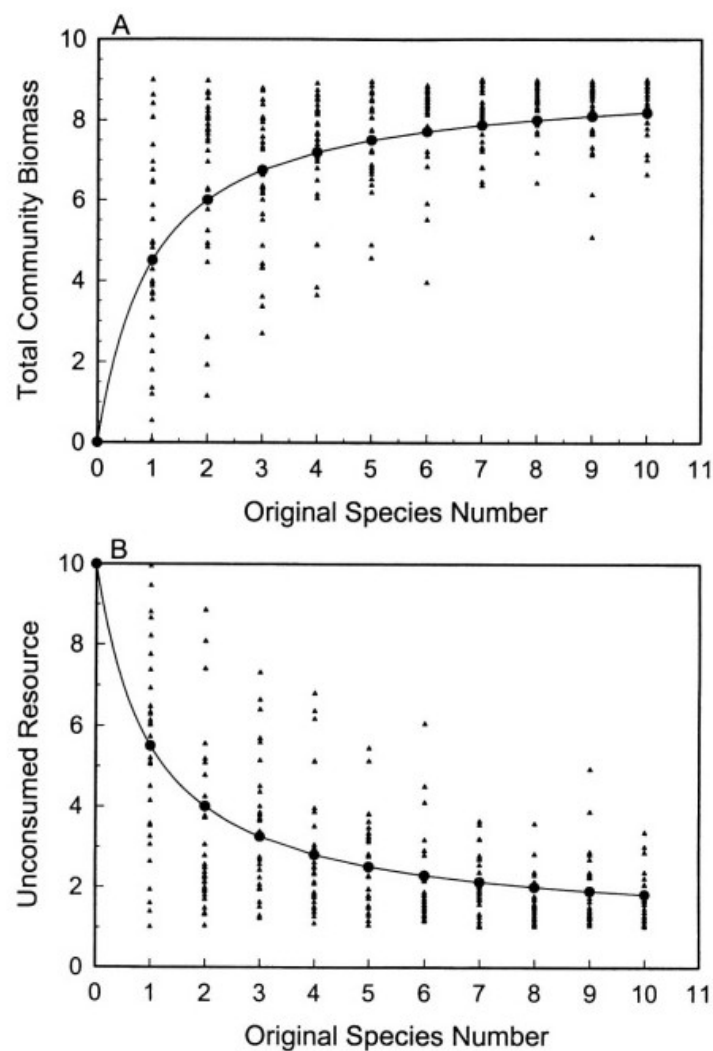


Figure 4. Sampling effect model where a single species is the best competitor and displaces all other species at equilibrium. A: Dependence of total community biomass at equilibrium on original species number. B: Effect of species number on the level of unconsumed resources.

Triangles show results from different simulation runs, large dots show the means.
Source: Tilman & Lehmann, chapter 2 in Kinzig *et al.*, 2002.

The second class of mechanism that can explain a positive relationship between biodiversity and ecosystem processes is related to the statistical chance of having a species in a mixed community, or not to have it. Consider a community assembled randomly from a fixed pool of species. Then, the probability of the presence of species with particular important traits increases with increasing species richness. For example, if the pool consists of ten different species, the probability to have species A in a monoculture is one tenth, or 0.1. In a five-species mixture, this probability is 0.5, and it is 1.0 at the ten-species level (where species A is always present, of course). Thus, it is more likely for that species to have been 'sampled' from the pool at higher diversity. If the presence of this particular species influences ecosystem functioning to a great extent, e.g. because it is a dominant competitor, or because it is a very high yielding species and so on, the system should—on average—tend to take the functioning imposed by that species. These stochastic processes involved in community assembly can lead to a similar pattern of diversity-productivity relationships as those produced by niche complementarity models (Figure 4). While some scientists view sampling effects as experimental artifacts or hidden treatments, others have argued that they constitute the simplest possible mechanism linking diversity and ecosystem functioning.

3.3.4. Distinguishing between complementarity and sampling

Discussions about the interpretation of early biodiversity experiments mainly centered on the question of whether the observed patterns could be explained by niche complementarity or by the sampling effect. It is now clear that these two classes of mechanisms are not mutually exclusive and that they can occur simultaneously. In addition, in most experiments sampling effects prevail during the early phases due to exponential growth of species that develop quickly and dominate mixed plots initially. Later in the course of the experiment, competitive dynamics take over and niche complementarity effects are getting stronger. In *Biodiversity and Ecosystem Functioning: Experimental Systems*, a mathematical approach is presented showing how the net observed biodiversity effect can be separated into the complementarity and the sampling or selection effect. A simple visual inspection of the diversity-functioning patterns found in experimental studies, however, also reveals whether complementarity or sampling prevails: as a good diagnostic for the sampling effect, the upper bound of the composition-dependent variation in productivity is a flat line. Thus, there is no single combination of species which is more productive than the most productive monoculture, i.e. there is no 'overyielding' (Figure 4). In contrast, an increasing upper bound indicates that some mixtures perform better than the monocultures, which can only be explained by complementarity or positive interactions among species in mixture (Figure 3).

Clearly, both niche complementarity and sampling effects are not only relevant for experimental situations, but they are also responsible for patterns observed in nature. The importance of each mechanism, however, will change with environmental conditions, with stronger relevance of sampling in small habitat patches and areas of

high resource availability, whereas complementarity should be more relevant in areas of high heterogeneity of resource availability, for instance.

3.3.5. Trait differences are responsible

Irrespective of the class of mechanisms responsible, trait differences among species are the underlying causes of any biodiversity effects on ecosystem functioning. In the debate about the relevance of results from manipulative experiments, a distinction was often made between effects of species numbers and species identities (i.e. their functional traits). Many studies have shown that the identity of species within a mixture is more important than the number of species *per se*. However, because no two species are identical in their characteristics (e.g. growth rate, size, nutrient use efficiency, leaf lifespan, etc.) it is impossible to manipulate species richness without selecting species with different characteristics. Thus, it becomes clear that there is no ‘magic effect of numbers of species *per se*’ and that any effect will arise from functional differences between species and from species interactions. There cannot be any relationship between species richness and ecosystem processes without these functional differences between species. All theoretical models of diversity-functioning relationships also include assumptions concerning differences in species’ traits, and there is no theoretical mechanism that would produce any relationship between species richness and ecosystem processes with identical species. Therefore, the characteristic traits of species and thus the diversity of functions these species perform are important determinants for ecosystem processes. In consequence, the number of functional groups is normally a stronger determinant of ecosystem functioning than the number of species.

Depending on the process of interest, not all species are equally important due to these trait differences. For example, if the pool size of soil nitrogen is measured in response to changing levels of diversity, symbiotically fixing plant species such as legumes play a key role. In addition, the relative abundance of these species is important too. In many plant communities such as temperate grasslands or forests, the proportion of biomass is highly inequitable, with few species contributing the most (dominants) and many sub-dominant or rare species contributing less. Therefore, the traits of the dominants are usually the key drivers for ecosystem functioning.

4. Combining old and new concepts

In the previous sections, the emergence of the new ‘Biodiversity-Ecosystem Function Paradigm’ and its key features has been described. In essence, diversity is seen as the treatment variable, whereas ecosystem processes such as productivity are seen as the response variables. In most cases, an increase of diversity led to an asymptotic increase in productivity. In contrast, community ecology traditionally has seen diversity as a response to site characteristics such as fertility (which determines productivity). In field surveys, the so-called ‘humped-backed’ relationship has often been observed, showing highest levels of diversity at intermediate levels of productivity. So, cause and effect are reversed in both concepts. This has often led to the notion that recent biodiversity experiments would contradict the findings from field surveys. However, both aspects are perfectly reconcilable, as clearly demonstrated by Schmid (2002): First, the area below the humped-backed line is most often filled with data points so that the line might

be better seen as the upper bound of an envelope of points rather than a line of fitted average values (Figure 5a). Therefore, the trajectories of manipulative biodiversity experiments do not cross 'forbidden territory' in the productivity-diversity plane (Figure 5b). Second, site fertility and productivity are often correlated in observational studies; so if site fertility is introduced as a third axis in a 3D graph, the humped-backed line can be drawn above the diagonal between fertility and productivity (Figure 6). This diagonal reflects maximum productivity at a given level of fertility when the species pool is intact. Because fertility does not change in experimental studies (the aim of which is to assess the within-site effects of diversity by keeping environmental conditions constant), their diversity-productivity curves will be constrained to rectangular planes (A and B in Figure 6). The two curves thus represent the effects of random species loss at two levels of site fertility, with maximum site productivities following the humped-backed curve.

The distinction between observational studies focusing on the diversity-functioning relationship across different habitats and the experimental approaches working at the within-habitat scale is also crucial for interpreting these findings in the context of ecosystem management (see section 6).

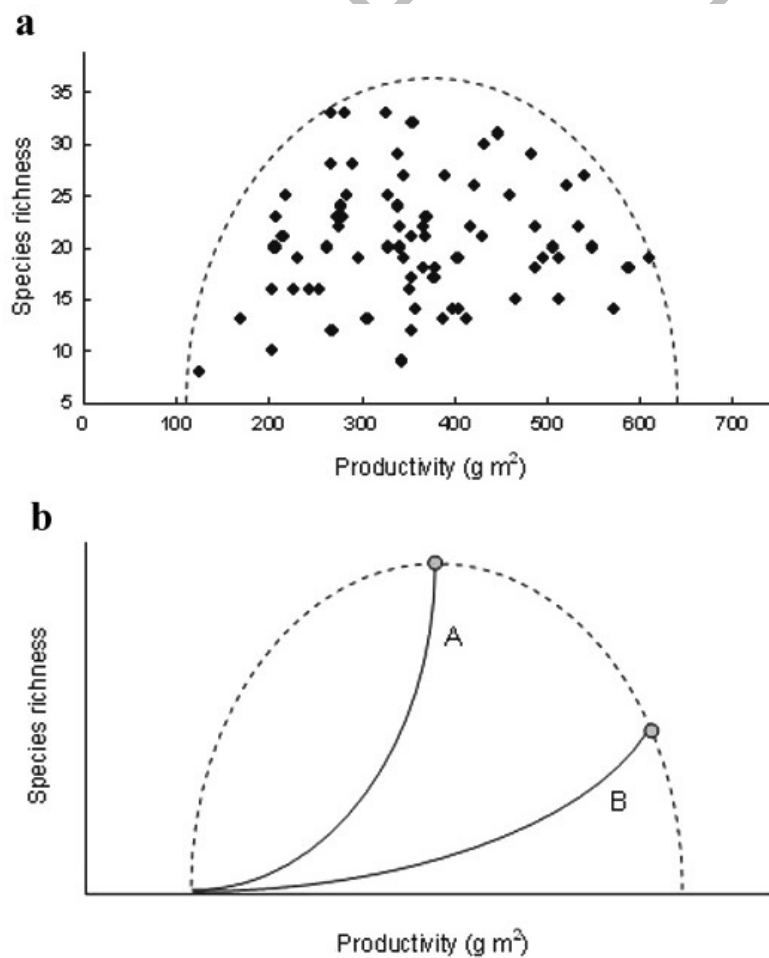


Figure 5. The relationship between plant productivity and plant species richness in grassland ecosystems. a) Example of results from an observational study of montane

grasslands in the Thuringian Schiefergebirge, Germany (data taken from Kahmen *et al.* 2005). The dashed line is the upper envelope over the point cloud, following the humped-backed model. b) Conceptual model showing how the trajectories from experimental studies fit within the humped-backed model. The dashed line is the humped-backed envelope curve of observational studies; the solid lines A and B are trajectories typically obtained in experimental studies that simulate random species loss. Modified after Schmid 2002.

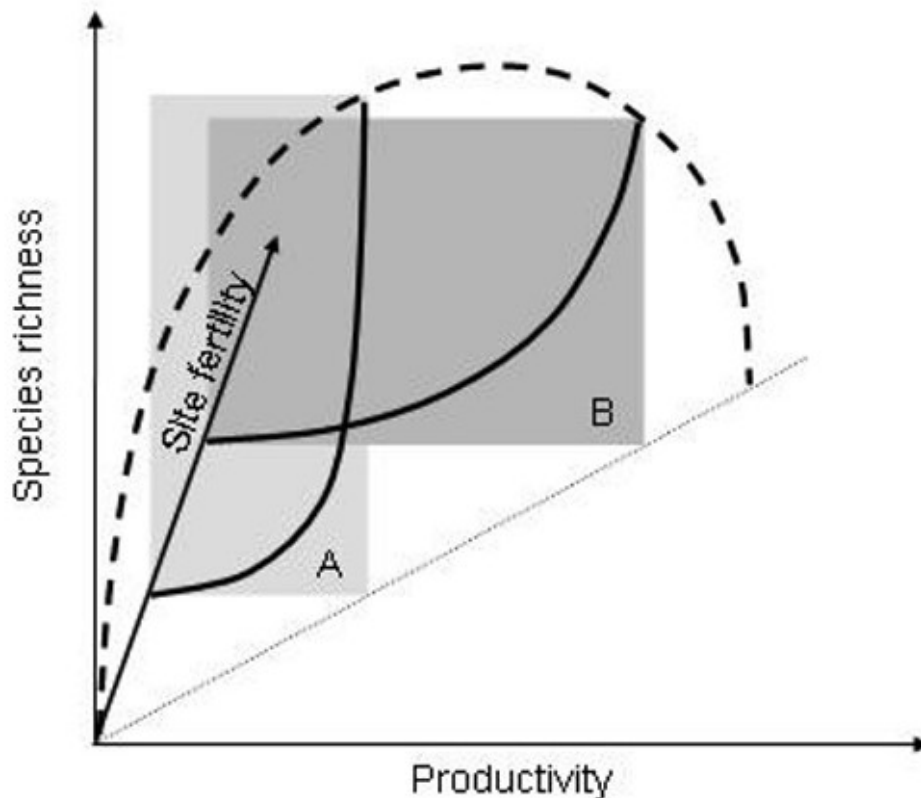


Figure 6. 3D representation of the humped-backed relationship with site fertility as a third axis, indicating the correlation between fertility and productivity found in observational studies. The dashed and solid lines correspond to those in Figure 5b. The rectangles A and B represent the planes to which the diversity-productivity curves are constrained due to non-changing fertility levels in experiments. Modified from Schmid 2002.

5. Biodiversity and stability

The question whether biodiversity is related to ecosystem stability is a very old one in ecology, and it has been discussed controversially. Ecosystem stability is often divided into three aspects: (i) persistence, i.e. the tendency of a system to exist in the same state through time; (ii) resistance, i.e. the capability of a system to remain unchanged in the face of external pressures such as disturbances; (iii) resilience, i.e. the ability of a system to return to its original or equilibrium state after it has been displaced from it by external pressures. In addition, temporal variability is often used as an inverse measure of resistance. As response variable, community composition (identities of species,

abundances) is used most often, although other community characteristics such as biomass production or nutrient pool sizes are used too.

Early work in the 1950s and 1960s by famous ecologists such as MacArthur, Elton, Odum or Margalef suggested that more diverse communities and food webs are more stable and more resistant to invasion by other species, constituting the 'diversity-stability hypothesis'. Theoretical work done by May in the 1970s with simple models of interspecific competition then showed that communities became less stable as the number of interacting species increased. This led to the widely accepted rejection of the diversity-stability hypothesis, although it was solely based on theory and not on empirical tests. In the 1980s the question was re-examined again and empirical studies in the 1990s again supported the notion that diversity begets stability, reviving the debate again.

One way that biodiversity can influence ecosystem stability is through statistical averaging: the summed variance of a series of random variables becomes lower when more variables are included. This effect has been called the 'portfolio effect' in analogy to economics: on average, the relative fluctuation in a diversified portfolio of financial investments is smaller than the relative fluctuation in the constituent stocks (Lehman and Tilman 2000). Similarly, greater species richness increases the temporal stability of the entire community (total community biomass) while the stability of the individual species (species biomass) decreases. Community biomass is stabilized because a decrease of abundance of one species allows its competitors to increase, partially compensating the initial decrease. The individual species' biomass is slightly destabilized with increasing diversity because a higher number of interactions between species and feedback loops may cause change in abundance of one species to impact on many more other species in a competitive network (Tilman 1996). This theory provides a resolution to the old diversity-stability debate: diversity increases stability at the community or ecosystem level, but decreases stability at the population level, thus each side of the debate was correct. While there is some empirical evidence for this theory in temperate grasslands, it seems not to be correct for the most species-rich communities in the tropics.

The same principles are also a basis for the so-called 'insurance hypothesis' which proposes that biodiversity buffers ecosystem processes against environmental changes such as global warming, because different species respond differently to such changes. This will result in functional compensations among species and hence more stable community properties. From that it becomes clear that also the number of species within a functional group is crucial for overall stability in the face of environmental fluctuations: the more species performing similar functional roles, the more likely there are to be some that respond differently to such changes, keeping overall ecosystem performance stable. In contrast, if there are only few species within a group, the probability is much higher that none of them survives the pressures and that the whole functional group is lost. As stated above, the loss of an entire functional group normally has much more pronounced effects than the loss of species out of many groups. This stabilizing mechanism has been called the 'functional redundancy hypothesis' (see section 3.1.).

There are now experimental and observational studies available that study the influence of biodiversity on ecosystem stability (reviewed in Loreau *et al*, chapter 7 in Loreau *et al* 2002; see also Schmid *et al*, chapter 6 in Kinzig *et al* 2002). Mostly, these studies analyzed the effects of some sort of external perturbation (e.g. drought), and they essentially support theory: plant species diversity had a positive effect on the resistance of above-ground biomass production. However, they not always adequately incorporated the influence of other confounding factors in the analyses, such as fertilization gradients. Evidence for diversity effects on resilience is even weaker.

Many studies manipulating the diversity of the resident community experimentally focused on another aspect of stability, namely invasion resistance. The majority of them report of a positive relationship between plant species richness or the number of functional groups and resistance against invading plants. Better resource utilization in fully established high diverse systems may result in no vacant niche that could be occupied by an invading plant. In contrast, large-scale comparative studies most often find that native species diversity is positively correlated to exotic species diversity. Probably, the factors that influence diversity and coexistence of native species, such as resource supply, intermediate levels of disturbance, habitat heterogeneity, also favor the occurrence of invasion. However, both findings are not necessarily contradicting: while the positive effect of diversity on invasion resistance operates at the neighborhood-scale, factors correlated with diversity may be more important in driving the community-wide patterns (Figure 7).

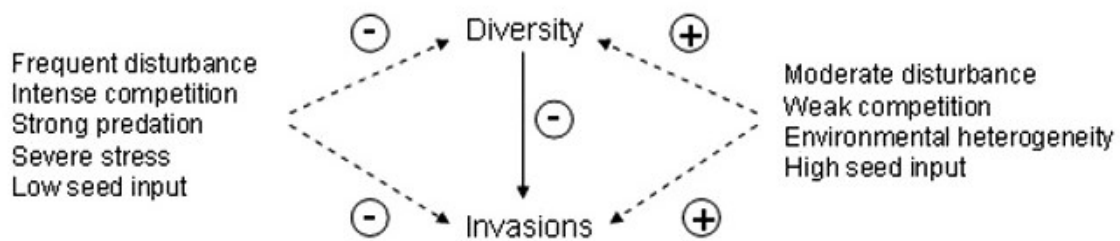


Figure 7: Synthetic framework for reconciling natural patterns of diversity and invasion with results from theory and experiments. The direct solid line between ‘Diversity’ and ‘Invasion’ represent the causal effects of diversity on invasion resistance operating at the neighborhood scale. In contrast, the correlations between diversity and invasibility across entire communities also result from effects of factors covarying with diversity (dashed arrows). Modified from Levine *et al.*, chapter 10 in Loreau *et al.* 2002

6. Implications for ecosystem management and conservation

From the review of current knowledge about the effects of biodiversity on ecosystem processes it became clear that many aspects are of importance for ecosystem management and conservation. However, the implications of these results mainly coming from highly artificial experiments are debated intensively among the scientific and conservation community (see overview by Lawler *et al*, chapter 13 in Kinzig *et al* 2002). Conservationists, ecosystem managers and politicians should keep the following points in mind when considering these scientific results for their purposes.

A first general point is that high biodiversity is not always an appropriate conservation goal, because there are many ecosystems that are species poor naturally, such as boreal forests. These low-diverse systems do not necessarily have depauperated ecosystem functioning as the low-diverse systems in experimental communities, which are mostly artificially maintained. However, in many cases ecosystems have experienced high rates of diversity loss, so conserving or augmenting diversity in those systems might be reasonable (see also *Halting Biodiversity Loss: Fundamentals and Trends of Conservation Science and Action* and *Application of Ecological Knowledge to Habitat Restoration*).

Second, it is crucial to recognize the different scales where diversity effects have been studied: within-habitat effects (simulated by experimental approaches) versus across-habitat effects analyzed in comparative studies with biodiversity being the manipulated treatment variable in the first case and being the response variable in the second case, respectively (see sections 3.2. and 4.). This may lead to confusion, for example in the context of extensification schemes in agriculture: the measures taken aim to reduce productivity so that diversity increases, following the humped-backed model of productivity and diversity. But the results from the experiments suggest that this increase in diversity should be accompanied with an increase in productivity again. Schmid (2002) proposes a conceptual model, how both views can be reconciled and that both recommendations make perfect sense (Figure 8).

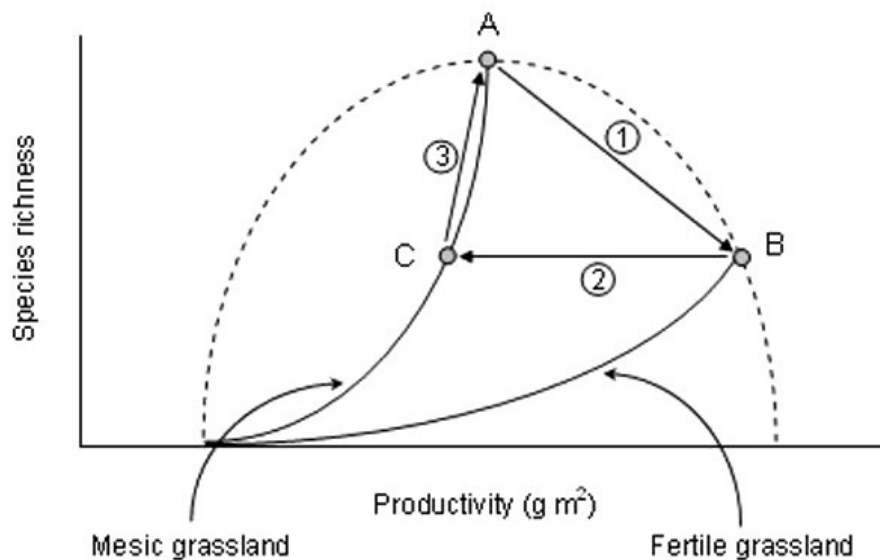


Figure 8. The relationship between productivity and species richness, showing processes that can occur during land use changes typical for European grasslands. The dashed line is the humped-backed curve from figure 5, the solid lines are the diversity-productivity relationships observed in biodiversity experiments. Fertilization of mesic, species-rich grasslands (A) leads to an increase in productivity and to a loss of species (arrow 1). Extensification reduces productivity but may not increase diversity if the species lost during intensification are not present in the wider region any more (arrow 2). In another restoration step, species have to be added to increase diversity, which will then increase productivity too (arrow 3). Modified from Schmid 2002

If mesic, species rich grasslands are intensified through fertilization, biodiversity declines while productivity increases (step 1). During extensification (step 2), e.g. through mowing and hay removal, productivity declines again, although species richness may remain low (point C) because the species lost during step 1 are not present in the wider region any more, so propagule import might be limited. Note that point C can also be reached directly if species loss is simulated in experiments. To restore a highly diverse community again, management should add species lost during intensification, which will increase both diversity and productivity (step 3). In essence, extensification alone might not be sufficient to increase grassland diversity.

Third, in most ecosystems, the loss of biodiversity is caused by major external impacts induced by man, such as disturbance and fragmentation, nutrient input, or land use change. These changes influence ecosystem processes also directly. Within-habitat effects of biodiversity are thus expected to be relatively small in comparison to such major impacts. For instance, increased nutrient input is one major factor responsible for species loss in many ecosystems because nutrient-demanding, fast-growing species outcompete other species adapted to low nutrient levels (corresponding to step 1 in the example of land use change of meadows stated above). This loss of species, however, is connected with increased, rather than decreased productivity.

In summary, results from biodiversity experiments may lead to misleading recommendations to conservationists or ecosystem managers if taken uncritically. However, the information accumulated until now should help to understand the potential consequences of losses in biodiversity and to develop successful conservation strategies. Lawler *et al.* very nicely summarize the main points of this issue:

“To conclude, preserving reliable ecosystem functions may prove to be an excellent reason to conserve biodiversity locally, regionally, and globally. However, more studies are necessary to characterize the relationships between diversity, particular functional groups, and various ecosystem functions. While biodiversity experiments are not intended to provide justification for protecting particular species or ecosystems, they are important to conservation because they provide information needed to protect and maintain viable communities. Studies of biodiversity and the interplay of community structure and ecosystem function are the cornerstone of applied conservation, even when the motivation for preserving nature is spiritual, ethical, aesthetic, or economic. This is because biodiversity studies will be crucial to understand how communities and ecosystems function, and conservation will not succeed without such knowledge.” (Lawler *et al.*, chapter 13 in Kinzig *et al.* 2002, p. 313)

Glossary

- Biodiversity:** number, abundance and composition of genotypes, populations, species, functional types and landscape units in a given system.
- Complementarity:** A positive interaction among organisms caused by differences among species in their resource use. This allows mixed communities to obtain more resources than any species by itself.

- Ecosystem functioning:** activities, processes or properties of ecosystems that are influenced by its biota.
- Ecosystem services:** benefits people obtain from ecosystems, including provisioning services (e.g. food, fiber, genetic resources), regulating services (e.g. erosion control, climate regulation, pollination), cultural services (e.g. spiritual and religious, recreational, educational), and supporting services (e.g. soil formation, primary production, nutrient cycling).
- Functional groups (= functional types, = guilds):** sets of organisms that affect ecosystem properties or processes in a similar way (functional effect groups); and/or that respond to changes in the environment (functional response groups) in a similar way.
- Keystone species:** A species whose impact on the community is disproportionately large relative to its abundance or biomass.

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Biographical Sketch

Dr. Michael Scherer-Lorenzen was born in September 1968 in Rottweil (Germany). He is married and has one son. He finished his studies in Biology at the University of Bayreuth (Germany) in 1995 with a master thesis on impacts of land use changes on biodiversity in Chile. During his PhD (University of Bayreuth) he investigated the effects of plant species loss on ecosystem functioning. This work was done within the European BIODEPTH project. After that, he held positions as Research Assistant at the German Advisory Council on Global Change (WBGU) and as Executive Director of the Institute of Biodiversity Network (IBN) in Germany. He did a post-doc at the Max-Planck-Institute for Biogeochemistry in Jena, Germany, and is now Senior Scientist at the Institute of Plant Sciences at the Swiss Federal Institute of Technology Zurich (ETH). In 2000, he won the International Horst-Wiehe Award for the Promotion of Ecological Sciences of the Ecological Society of Germany, Austria, Switzerland and Liechtenstein. One year later, he was finalist, with the BIODEPTH project, of the Descartes Prize of the European Union.

His research interests are related to the central question: "Does biodiversity matter for ecosystem functioning, and the provision of goods and services?" Within this huge field, he focuses on the relationship between biodiversity (focusing on plants) and ecosystem processes, with special emphasis on productivity, soil nitrogen dynamics, nitrogen allocation within and among plants, decomposition, mineralization and other soil processes. He is especially interested to elucidate the mechanisms behind diversity effects on these processes, such as resource use complementarity and facilitation.

He is working in mid-European grassland systems, and in afforestation in temperate and tropical regions, using experimental approaches to manipulate plant diversity. In addition, he is now expanding this work into natural alpine grasslands differing in biodiversity due to land use changes.

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