
Biodiversity experiments – artificial constructions or heuristic tools?

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1 Introduction

Biodiversity experiments are important tools for basic research. Here, we discuss their scientific basis, some major hypotheses and review the most prominent results according to the role of biodiversity in productivity, invasion and nutrient cycling. Progress in methods and insights is documented. Shortcomings and restrictions of recent approaches are identified. Finally, we point out research perspectives.

At the global level, the loss of rare species is recorded. Regional extinctions of populations are also documented. Communities are becoming more and more uniform due to standardized management techniques and increased dispersal of ruderal species. Alien and invasive species are contributing at the regional scale to an increase in species diversity whereas rare species may be lost from the same area. Changes of biodiversity have many facets at different scales. The mechanisms that are responsible for the ongoing changes are generally being identified, with rapid land use changes being the most prominent (Sala et al. 2000). Early biodiversity research concentrated on the detection and description of taxa and their diversity within certain ecosystems or regions and on their loss or decline (e.g. Ehrlich and Ehrlich 1981). Due to the complexity of natural and anthropogenic ecosystems and landscapes, monitoring of such changes is rather time consuming and will deliver sound results only for selected case studies and areas.

Science has to analyse the mechanisms of change and to contribute to coping strategies through predictive conclusions. The long-term preservation of sound ecosystems is needed. Strategies that consider biodiversity and ecosystem functioning are requested (Schwartz et al. 2000; Hector et al. 2001b). One category that adds complexity to the system is the interaction between biotic compartments, and between biotic and abiotic compartments differing from stand to stand. As early as in the 1920s the recognition of this fact led to the development of the individualistic concept by Gleason

(1926). Even if this variability can be reduced and categorized, it is an obstacle to the identification of general rules in ecology. What holds true for one community does not necessarily do so for another one. The role of diversity in the functioning of ecosystems was not recognized as a highly important scientific issue until the end of the twentieth century. However, recently the relationship between (plant) species diversity and ecosystem functions has been highlighted in many studies. Observational case studies yielded varying results depending on the respective system, spatial scale and time frame. Thus, an urgent need for experimental studies became obvious to close the gap of knowledge when comparing theory and reality (Schmid and Hector 2004).

During the last decade, there was a controversial debate about the relevance of biological diversity for ecosystem functioning (e.g. Schulze and Mooney 1993; Naeem et al. 1994, 1995; Mooney et al. 1996; Tilman et al. 1996; Grime 1997; Naeem and Li 1997; Chapin et al. 1998; Hector et al. 1999; Wall 1999; Chapin et al. 2000; Ghilarov 2000; Hall et al. 2000; Huston et al. 2000; Kaiser 2000; Loreau 2000; Wardle et al. 2000b; Fridley 2001; Loreau et al. 2001; Huston and McBride 2002; Loreau et al. 2002a; Mooney 2002; Naeem et al. 2002; Schmid 2002; Schmid et al. 2002b; Vandermeer et al. 2002; Symstad et al. 2003; Beierkuhnlein and Jentsch 2005; Hooper et al. 2005; Schläpfer et al. 2005). Some aspects of the discussion had already been raised decades ago, the diversity–stability debate initiated by MacArthur (1955) being the most prominent one (e.g. Leigh 1965; May 1972). The loss of interest in the diversity–stability relationship in the 1970s was due to difficulties in defining stability, diversity and – closely connected to these issues – complexity. Global environmental changes and the uncertainty about their consequences ignited this discussion again (Tilman and Downing 1994; Johnson et al. 1996; Tilman 1996; McGrady-Steed et al. 1997; Naeem and Li 1997; Doak et al. 1998; Tilman et al. 1998; Ives et al. 2000; Lehman and Tilman 2000; McCann 2000; Wardle et al. 2000a; Fonseca and Ganade 2001; Loreau et al. 2002b; Pfisterer and Schmid 2002; Tilman et al. 2002b; Wardle and Grime 2003). Stability in a strict sense does not exist in ecosystems. It is ecologically neither positive nor realistic and there are no standard ways to measure or calculate it (Grimm and Wissek 1997). Recent approaches aim to produce as clear results as possible on the basis of specific and measurable parameters. This is one reason why much emphasis is put on aboveground biomass production. The net biomass that is produced per area and in a defined time is a prominent trait of ecosystems, and comparable data can be achieved across different ecosystems.

The perception of environmental problems as well as the lack of explanatory and predictive scientific capacity stimulated the debate. Wrong conclusions could result in serious consequences (Tilman 1999;

Chapin et al. 2000). Direct connections to global change ecology have been pointed out (Reich et al. 2001; Lloret et al. 2004; Thomas et al. 2004; Hooper et al. 2005). Effects of increasing nutrient inputs and global climate change on diversity and on ecosystem processes are expected (see Hartley and Jones 2003), respectively. For example, experimental results support predicted interactions between the loss of species and an increased CO₂ concentration in the atmosphere (Stocker et al. 1999; Reich et al. 2001; He et al. 2002). Further, there is an indication that not only trends in average values will occur, but extreme climate events will become more frequent (Meehl et al. 2000). It is assumed that species-poor communities will be less resilient when disturbance frequency increases (White and Jentsch 2001) or when single events of extreme magnitude occur (White and Jentsch 2004). Stochastic short-term events are important historical factors that contributed to invasion and determine present-day species composition (Davis and Pelsor 2001).

Biodiversity research is not only a fascinating scientific discipline but is also of high socio-economic importance and political relevance (Gowdy and Daniel 1995; Perrings 1995; Montgomery and Pollack 1996; Jentsch et al. 2003). It has been the subject of a great deal of attention in society at large and political bodies not only because of the ethical responsibility of mankind or of aesthetic needs. More than that, the fear of losing ecosystem functions, and especially those which are of societal importance, are the reasons for political concern and societal awareness. Most biodiversity experiments focus on element cycling, nutrient use and biomass production, because these ecological parameters are of socio-economic relevance (e.g. Spehn et al. 2000; Tilman et al. 2002b; Roscher et al. 2004).

From agricultural systems it is well known that the cultivation of species mixtures (intercropping or multiple cropping) may increase productivity, in comparison with monocultures, via positive interactions (Trenbath 1974, 1976; Mead and Willey 1980; Chetty and Reddy 1984; Willey 1985; Vandermeer 1989). Indirect effects occur if suboptimal site conditions are improved, resources are made available or microclimatic conditions are modified in a way that prevents plant pathogens or restricts herbivores (Altieri 1994; Bertness and Callaway 1994; Hooper and Vitousek 1997). Mainly on resource-limited sites or under low input conditions, at least one of the components in a mixture may benefit as a result of facilitation that does not restrict the productivity or performance of the dominant species. Combinations of trees and annuals in agro-forestry systems have increased stand productivity remarkably (Schroth 1999). Nevertheless, there are obvious limits to extrapolating results from agronomy to biodiversity research. Plants in land use systems are planted and supported

(by weeding, fertilizing and specific management techniques). In many cases, the plants are extremely different (e.g. trees and annuals). But above all, only a few species are included, even in intercropping systems, compared to the diversity of natural ecosystems or biodiversity experiments (Swift and Anderson 1993; Vandermeer et al. 2002). In addition, it can be assumed that there are even more species in these systems (weeds) which are ignored because they are not of any economic interest.

The basic thought behind biodiversity experiments is that ecosystems have evolved a characteristic diversity of species and that this diversity contributes to their functioning. In managed systems, the influence of humans on environmental conditions and the disturbance regime via management of diversity and functioning will be strong and overwhelm the potential influence of diversity (Fig. 1). But if human impacts are kept constant, a change in diversity would thus be accompanied by changes in ecosystem functions (central arrow, Fig. 1). In most experiments, establishing communities with varying diversity tests this relationship. The main aim of biodiversity experiments is to understand the nature of this relationship and identify general trends. Experiments are considered to be of value as examples, and their results may be applied to various other ecosystems. In this article, we will discuss the findings of the types of experiments outlined and try to identify important results, shortcomings and future applications.

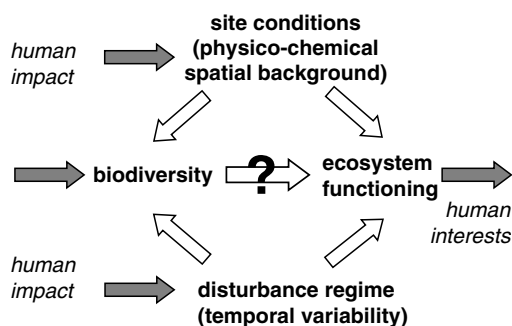


Fig. 1. Humans are altering the environment and nature in many ways. The effects of such activities can hardly be differentiated. Pollution and environmental change may directly affect ecosystem functioning but also biodiversity. Land use change modifies the temporal variability of ecosystems and this will have repercussions for biodiversity and ecosystem functioning. Changes in biodiversity can result from direct and indirect human impacts. This web of cause and effects implies that it is necessary to separate the various processes experimentally. As a consequence, it is almost impossible to detect and measure the impact of biodiversity loss on ecosystem functions in natural ecosystems

2 Some Philosophical and Basic Aspects of Ecology and Diversity Research

Ecology deals with complex systems, especially when communities and ecosystems are studied. Ecology is considered a precise natural science (or “hard” science), but workers recognise that ecological units cannot be characterized completely due to the complexity of the subject, and this creates tension. Decisions have to be made by ecologists on how to proceed with research, which aspect should be focused on, and what has to be ignored. The complexity and the spatio-temporal heterogeneity of ecological objects provoke simplifications, such as reductionism, or generalisations, such as holism. In any case, there is a necessity to concentrate or filter the scientific topic. Either parts are taken out of their context and investigated in detail, or the whole system is considered to be one unit. It is impossible to cope comprehensively with an entire ecosystem. The variety of paradigms and methodological approaches that are partly complementary, partly competing, reflects the range of the theoretical and philosophical background of ecologists. Research aims of ecology have shifted from descriptive studies, including sampling and monitoring of field data (which is still urgently needed), i.e. from “what, when, where” questions, to analytical investigations of cause and effect (“why” questions) (Fridley 2001). Thus ecology has become progressively theory-oriented.

The quality of pure science depends on the standard of theory. Theory is used to search for general rules or even laws. Such rules have to be empirically proven and the aim is to understand the mechanisms that give rise to certain phenomena. When a new gap in knowledge has been identified, when patterns or processes cannot be explained or predicted, and when an urgent need to find an answer to a question is felt, the appropriate approach is to formulate hypotheses which are reasonable as well as innovative. Hypotheses comprise testable predictions about cause and effect. In ecology this is not an easy task, even if regular structures are evident. The complexity of interactions between organisms (see Connell 1983), but also between biotic and abiotic processes, inevitably leads to a high variance in data. This “noise” is an integral part of the subject. As a matter of fact, it creates restrictions to statistical analyses and tests. Simberloff (1980) illustrates this ambiguity of ecology in a comparison with other fields of natural science “physicists may view it as noise, but it is music to the ecologist”.

Does this vagueness and uncertainty exclude the application of criteria of hard sciences, such as the search for theories and laws with predictive and/or explanatory power (Loehle 1987)? Certainly not! However, restrictions have to be considered. The hypothetico-deductive approach requires an elaborated

theoretical framework. Its appropriateness varies according to the maturity of a theory. Biodiversity research is a young discipline and, as we will show, many divergent theories and hypothesis have been worked out. This can be taken as an indication of immaturity, and if this were true, it is difficult to conduct conclusive tests (Loehle 1988). Data and results are then related to a certain approach or even paradigm (see also Naeem 2002b). Predictions will be vague or even contradictory.

According to Popper (1959, 1963), only the falsification of a hypothesis can be regarded as a sound result. However, if a hypothesis is based on previous knowledge, if it is intelligent, innovative and reasonable, it is hard to accept that it is wrong. Scientists tend to defend their ideas. If the hypothesis has to be rejected, this means that it is based on false assumptions or theory or that it is valid only under certain circumstances, which were not given in this specific case. Results that confirm a theory do so only under certain constraints and are never able to support a general truth of it or, in the worst case scenario, may be just a result of artefacts and autocorrelations but not of any causal importance at all. Coming back to the ecological complexity of nature and to the point that this goes hand in hand with a certain individuality of ecological communities, we are thus faced with essential logical, if not philosophical, frontiers. When can we be sure that a hypothesis is falsified or verified? When can an explanation be accepted as adequate? To which degree are we allowed to or even have to generalize, classify and sweep aside differences between ecological units?

One way to find a solution is to accept the fact that observations in natural systems, as exactly measured as they may be, “only” serve as a source for generating theories and hypotheses but are not adequate for their approval. Observations and descriptions are necessary and essential to identify problems, regular patterns or remarkable exceptions. Field data will stimulate scientists to think about reasons for their structure. Such thoughts can be compared with existing knowledge and if there are conflicts, this is an indication that there is a need for more research. Nonetheless, the falsification of theories can only be successful with the support of models and experiments (Fig. 2). In addition, there is no absolute truth in theory, especially not in ecological theory. Theoretical considerations, as necessary as they are, are nothing more than idealized approaches. They serve as tools for a better understanding of complex phenomena. Like ideal gases they simulate the exclusion of interfering factors. This is helpful when considering isolated interactions, but it often fails to explain the variation of data in reality.

In biodiversity research we are confronted with a mixture of assumptions (that are not tested but taken for granted) and hypotheses. Science requires that researchers agree about their objects. Terminological conventions have

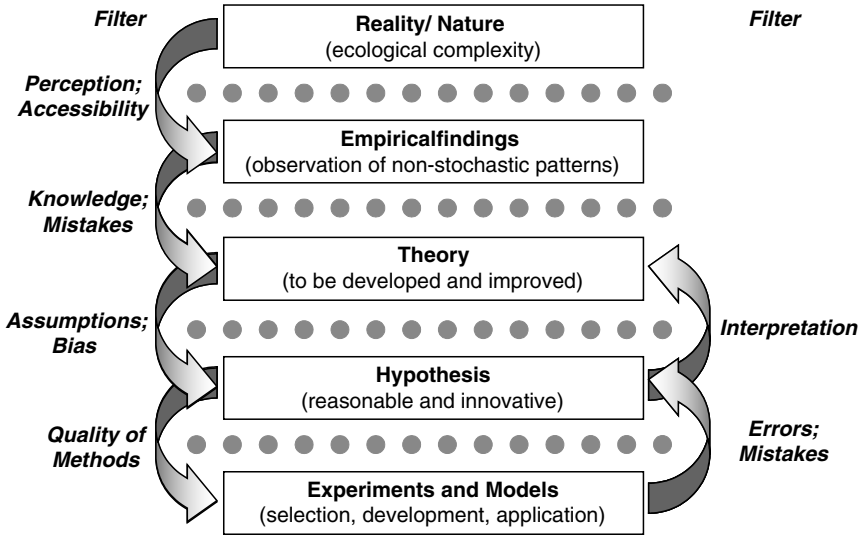


Fig. 2. The progress of knowledge and the solving of theoretical problems are always subject to various filters. For example, we can detect only a narrow range of radiation and sound waves, and many natural phenomena are simply not within our range of detection. In addition we are limited in terms of temporal and spatial scales. Our lifetime sets the limit for our individual access to resources and space, and important habitats are simply out of our reach, either being too high (forest canopies), too deep (oceans) or too hidden (soils). The creation and the further development of theoretical concepts, definitions and models for a better understanding of nature are at the heart of any scientific approach. When we aim to prove their validity, hypotheses have to be formulated which are both logical on the basis of previous findings and novel in terms of their focus. Technical and scientific progress constantly lead to improvement in methods. The interpretation of results is influenced by paradigms, knowledge and creativity. The progress which is achieved will always be a relative and transient one. Note that empirical findings merely stimulate the development of theories but can never be used to prove hypotheses!

to be created, such as the concept of species and their nomenclature. However, taxa differ a lot according to their within-species divergence or variability. Species are not discreet units that integrate the same amount of variance. A basic assumption, which is implied if species are stochastically mixed, is that species are functionally different due to niche complementarity (see also Grime 2002; Fargione et al. 2003), and even more that they are more or less equally different. However, between-species dissimilarity also differs. Species vary gradually according to their morphological similarity and phylogenetic proximity, longevity, life cycles and reproductive turnover, but also according to the importance of sexual reproduction within certain taxa (e.g. Weiher et al. 1999; Poschlod et al. 2000; Thompson et al. 2001; Craine et al. 2002; Lavorel and Garnier 2002). Clonal or apomictic

species underlie very different operating mechanisms than species for which the focus is sexual reproduction and selection (Dietz and Steinlein 2001). Distances between the units (species) are not regular and will differ in magnitude according to the criteria that are applied. Ignoring functional dissimilarity between organisms creates problems, but so does a priori classification when selecting species for an experiment. Many dimensions and parameters would have to be considered. However, very presumably, positive interactions and facilitation are more effective if species differ noticeably. And, competition is likely to be strongest when species are quite similar. Assuming that the evolution of species is mainly triggered by selection and niche occupation, taxonomic diversity has to be related closely to functional divergence. Biodiversity will strongly reflect biocomplexity (Reich et al. 2003). This view ignores the fact that evolution is related to other temporal scales than present-day ecological processes.

As operational units species are related to human perception and the definition of taxa. This is indicated by the fact that taxa undergo permanent modification due to increasing knowledge and access to molecular methods. Although using species is a widely used approach when working with biota, they may be not the best tool for biodiversity investigations when ecosystem functioning is the subject under investigation. If we accept species as a concept and not as a reality there is no problem with this, but if we integrate this construct into units of a higher hierarchy, as is done in diversity experiments, an awareness of the concept of species is required, it being merely a very successful and pragmatic approach, which levels out a large part of the diversity within and between species.

Hypotheses about community performance have to consider site-dependent limits in the supply of energy, water and nutrients, too. Site-specific constraints, which cannot be exceeded, have to be taken into consideration. Thus, knowledge, for instance on the carrying capacity of a stand, is needed as an extensive variable, which is not dependent on fixed species traits (Fig. 3). If this value can be exhausted by one single species, e.g. during competitive-exclusion experiments, then mixtures and biodiversity are irrelevant. If intrinsic mechanisms within the community are able to slightly modify the site and increase its capacity, this is a question of temporal scale and no longer within the scope of the investigated system.

The shortcomings of various approaches used to identify repercussions of changes of species diversity can only be superficially touched upon here. However, the arguments needed to develop reductionistic models and experiments with defined conditions and environmental interactions are clear, as are the restrictions of such approaches. Theoretical considerations and experiments are mostly based on unrealistic simplifications. Nevertheless,

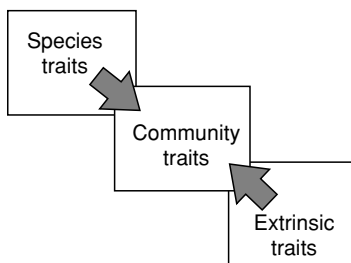


Fig. 3. Assembly experiments in biodiversity research focus on the community level. When aiming to explain the community performance at different levels of diversity, the discussion concentrates on the species level (composition, complementarity, dominance, selection, functional attributes, niches). However, some inconsistent results can be put down to external variables such as plot size, nutrient availability or climatic site conditions

they are crucial for the development of knowledge as they concentrate on specific arguments, assumptions or aspects of interest and thus will provoke a willingness to identify the limits of their validity. This will deepen and extend our fundamental theories.

3 Hypotheses and Concepts Addressing Biodiversity and Ecosystem Functioning

The purest hypothesis addressing the relation between species diversity and ecosystem functioning is based on theoretical niche occupation. It states that each species plays a specific additive functional role and no two species share exactly the same function within a community. High species diversity then would be associated with efficient use of resources and high performance of the whole system. However, this assumption mixes evolutionary and current processes. Ehrlich and Ehrlich (1981) compare the species of an ecosystem with the rivets of an airplane. Each one has a function, and the security of the plane will be reduced if one after the other is lost. Even if this does not directly lead to a crash, however, the risk of severe damage increases with the loss of units (rivet hypothesis). The focus of the rivet hypothesis is on saturated systems with large populations. In contrast to this, many examples of communities exist where several ruderal species occupy the same niche with few individuals without any interference. In addition, ecological niches are multidimensional. When looking at ecosystem functions, mostly only one parameter, such as biomass production, is selected. Coexisting species are in most cases to some degree complementary (Hector 1998) but not necessarily so according to the parameter that is

selected as a dependent variable. Just recording the number of species ignores the individual importance of different species. The taxonomic relation between species (e.g. their affiliation to a genus or family) does not necessarily provide information about their functional relatedness or resemblance. However, in many cases, traits are restricted to a limited set of phylogenetically related taxa (Reich et al. 2003).

When classifying types according to specific ecosystem functions, this leads to the concept of functional redundancy. Here, complementarity is related mainly to functional groups and not to single species. The occurrence of various groups then is important and the diversity within these groups contributes less or minimally to ecosystem performance. Species within one group are redundant (Walker 1992; Gitay et al. 1996). They are able to replace each other without a decline of ecosystem functioning. Reactions of the system occur only if one group is lost or strongly reduced. A high diversity of functional groups or types is considered to be decisive (Diaz and Cabido 2001).

The next approach is to look more closely at single species, which may be well adapted, powerful, competitive or highly efficient in their use of resources. In the long term, this could be the successful *K*-selected species, but such important species can also be identified in a short time period. Many communities are regularly dominated by certain species, which control overall functioning (Smith and Knapp 2003). In the first biodiversity experiments, such observations were ignored to some degree. Bias was avoided and all species were regarded as equally important. However, it is just a question of statistics that the probability of occurrence of certain powerful (e.g. highly productive) species will increase with species richness in stochastic mixtures of species (Aarssen 1997; Huston 1997; Loreau 1998b; Wardle 1999; Deutschman 2001). Huston (1997) calls this the “sampling effect”. It corresponds to the “selection probability effect” (see Van der Heijden et al. 1998; Wardle 1999). If this was true, a tendency for an increase in productivity with species richness could be related to the occurrence of single species which tend to be lacking in species-poor mixtures. They represent only one of many monocultures. Mean values obtained from various monocultures will not make the potential of single species obvious. After the first debate on this topic, statistical methods were developed to separate complementarity effects from sampling effects (Spaěková and Lepš 2001; Loreau and Hector 2001).

Up until now, all hypotheses concentrate on contributions made by species either via complementarity, redundancy or species-specific characteristics. When ecosystem functioning is related to ecological complexity, we additionally have to integrate direct interactions between species such as

competition or facilitation (Cardinale et al. 2002; Bruno et al. 2003). If such interactions take place, and this is highly probable, we can expect effects which are related to the occurrence of certain pairs or combinations of species that cannot be explained just by species numbers or by the presence of specific traits. If system behaviour is related to species number, it may give the impression of being chaotic ("idiosyncratic response effect") (Lawton and Brown 1993). Such communities are sensitive to and react to the addition or loss of certain interacting groups of organisms.

Finally, biodiversity can be considered to have just a potential value. According to findings on certain ecosystem functions, many species may behave as if redundant today. They can be rare and quantitatively unimportant. Nevertheless, the possibility exists that the dominant and successful species in recent communities could be challenged by novel environmental conditions. In the case of climate change, there are the first hints that temperature increase might favour insect outbreaks in monodominant forests. If there are no other species that could replace the formerly dominant tree species, this leads inevitably to a crash of the system. Redundancy can be considered to contribute to stability or "reliability" when environmental conditions are changing (Naeem and Li 1997; Naeem 1998). The theoretical concept is called the "insurance hypothesis" (Yachi and Loreau 1999). It integrates aspects of redundancy and sampling effects. The higher the number of species with comparable requirements and functional traits, the higher is the probability that environmental hazards will not necessarily cause a loss of the community and its contribution to ecological functioning (Chapin et al. 1998). Higher resilience of diverse communities is predicted (Naeem and Li 1997; Peterson et al. 1998; White and Jentsch 2004). In the face of global climate change, some authors expect that diverse ecosystems will have the capacity to shift dominances within certain communities and to better adapt to novel conditions (Peters 1994).

Nevertheless, the effects of rapid changes in ecosystems are ambiguous (Van der Maarel 1993; Mackey and Currie 2000). Nonlinear interactions are highly probable. Such disruptions (e.g. drought) may be buffered by diversity but they will impact diversity and functioning themselves. For many systems it is not clear which intensity or magnitude of environmental change will cause irreversible effects (Sprugel 1991; Fay et al. 2000). The debate remains controversial in this respect. Models seem to confirm the theory (Yachi and Loreau 1999; Fonseca and Ganade 2001; Norberg et al. 2001), but are strongly simplified in comparison with nature. However, it is evident that biodiversity or other biotic aspects can influence the behaviour of a system to a certain degree (Hooper et al. 2005). There are thresholds and strong physico-chemical influences that render biotic processes marginal. Without

considering the abiotic compartments and fluxes, biodiversity experiments will remain as reduced artificial constructs and perhaps irrelevant.

4 Experiments in Community Ecology and Biodiversity Research

4.1 The Role and the Value of Experiments

Methodological concepts of natural science differentiate between theoretical considerations, hypotheses and models on the one hand and field work, measurements and observations on the other hand. Experiments are placed somewhere in between, as they closely relate to theoretical considerations but apply and test these with the support of real objects. The gap between statistical requirements, such as replication or randomisation, and reality is a fundamental one. Experience, recognition and observation are important scientific skills. However, if potential problems are identified that might become important in the future, field work and the monitoring of developments is not a very helpful approach. It has only limited predictive power. Processes and effects will not be detected until they occur. Models are able to make significant contributions, but they share the restriction that they simply cannot be better than the knowledge that is entered into them. The problem with ongoing global changes and with biodiversity loss is that no comparable development has ever been recorded.

Experiments may contribute to a simulation of future conditions of ecological communities. As we do not know how systems will behave under novel circumstances (e.g. at higher temperatures, with less species), experiments are always not only reductionistic but also actualistic. A decisive advantage of the experimental approach is that abiotic site conditions are controlled. This limits the “noise” of other processes. The value of experiments and their explanatory power depends strongly on the rigour of their experimental design. It has to integrate controls, replicates, random distributions and interspersions (Hurlbert 1984). Theoretical and conceptual problems and suggestions regarding the design of biodiversity experiments have been extensively discussed (e.g. Allison 1999; Naeem 2002a; Schmid et al. 2002a). Non-adequate design can easily lead to systematic errors that cannot be erased later on. Efficient experiments aim at minimizing the variance of the SE in the statistical analyses, but this requires good level of knowledge about plant traits and their contribution to heterogeneity via specific spatial and temporal performance. This knowledge is mostly implicit and based on experience, and only rarely on hard data. On the other hand, special care has to be taken to avoid effects that are attributed to certain species (Benedetti-Cecchi 2004).

However, with increasing complexity of the experiment, the number of plots becomes very large (Table 1) if the experiment is based on a random draw of species in a mixture from a given pool (Huston and McBride 2002). The required surface area becomes large and the workload to maintain it becomes high.

Many ecological experiments concentrate on rather limited research questions, such as autecological or ecophysiological questions or on competition, and investigate them on the basis of simple and species-poor experimental setups (Scheiner and Gurevitch 1993; Underwood 1997). Experience from competition experiments is helpful for diversity studies, but limits are obvious according to methodological transfer. The quality of an experimental analysis depends on whether the effective variables are really considered. In complex experiments, the key variables are often superimposed by other factors that have not been considered in the experimental design. Huston (1997) criticises experimental approaches, which ignore “hidden treatments” in species assemblages. Being confronted with this problem in biodiversity experiments contributed enormously to improving experimental methodology.

4.2 Historical Experiments

The first documented experiment which considered the importance of species diversity in ecological communities was set up at Woburn Abbey in Bedfordshire, England, at the beginning of the nineteenth century. This

Table 1. Number of possible treatments in biodiversity experiments [five types and a maximum (*Max.*) of six diversity levels]. Statistical analyses would require three replicates and thus increase the numbers threefold. *Level 1* Monocultures

Max.	Level of species diversity					
	1	2	4	8	16	32
32	32	496	35,960	10,518,300	601,080,390	1
16	16	120	1,820	12,870	1	–
8	8	28	70	1	–	–
4	4	12	1	–	–	–
2	2	1	–	–	–	–

experimental garden was documented for the first time in 1816 (Hector and Hooper 2002). In addition to a varying diversity of species, different substrates were also applied. In total, 242 plots, each 4 square feet, were set up. Even though this experiment had several obvious methodological shortcomings (e.g. species-poor stands and monocultures were sown and diverse plots were transplanted from nature), it remains impressive. Obviously, the aim was to find out the role of diversity and under which circumstances diversity is important. This question, which was apparently new to ecologists at the end of the twentieth century, had clearly already been addressed almost 200 years earlier.

This historic experiment is indirectly referred to by Charles Darwin in his work *The Origin of Species*, when he says “it has been experimentally proven that, if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised” (after Hector and Hooper 2002). The first part of Darwin’s conclusion can hardly be proven, as in these communities of mostly clonal grasses apparently only the number of tillers and not the number of plants was meant by “number”. The second part anticipates the recent discussion on the relationship between species diversity and productivity of a stand. Once again, the discovery of this old treatment reveals the importance of bibliographic sources. During the twentieth century, diversity experiments were rarely applied and when they were, focussed on the effects *on* diversity and not *of* diversity.

4.3 Modern Experiments

Since the formulation of essential research needs regarding the relationship between diversity and ecosystem functioning (Schulze and Mooney 1993), numerous experiments have been designed, performed and analysed in different systems, using different designs, on different spatial and temporal scales and regarding different ecosystem functions, during the last decade. Such concerted activity is unprecedented in ecology. Beginning in the early 1990s, research groups started with mesocosms, glasshouses and chamber experiments to exclude external influences due to small-scale differences in site conditions (Naeem et al. 1996; Symstad et al. 1998). The ECOTRON experiment (Naeem et al. 1994; Lawton et al. 1998) at the Centre for Population Biology in Silwood close to London aimed to investigate the importance of ecological complexity and not only species diversity. In isolated chambers, where the water, light, nutrient, wind and temperature regime was controlled, mixtures of two, five and 16 plant species were established. In addition, a diversity

gradient of invertebrates simulated diversity at higher trophic levels. In total, 31 species (among them 15 invertebrates) were cultivated in 16 chambers. The numbers of replicates per level of diversity differed. The fact that the replicates were composed of exactly the same species combinations was criticized as producing pseudoreplicates (Hurlbert 1984, 2004). In such cases, diversity effects and effects of certain combinations of species or of species identity cannot be separated (but see Oksanen 2001). Field experiments with model ecosystems are an efficient tool with which to simulate biodiversity loss under semi-natural conditions (Lawton 1995; Tilman et al. 1997b; Hooper and Vitousek 1997; Schläpfer and Schmid 1999). Results from these experiments have already been subject to extensive reviews (e.g. Schläpfer and Schmid 1999; Schmid et al. 2002a; Tilman et al. 2002b; Spehn et al. 2005).

However, such experiments in the field are associated with many restrictions (Lamont 1995; Grime 1997; Huston 1997; Allison 1999). They are more representative of nature than microcosms or mesocosms in the laboratory or greenhouse. Nevertheless, they can hardly be compared with natural communities even if their diversity resembles one in nature, because their composition of species has to ignore natural combinations due to statistical requirements. Although their environment (water and nutrient availability, climate) is strongly standardized and small-scale differences are not to be expected, it remains difficult to link the processes and data that are recorded to the diversity gradient. Uncontrolled influences, such as small-scale differences in soil biota and nutrient status, cannot be avoided completely. If the soil remains undisturbed, it is difficult to measure fluxes of gases and liquids. In any case, the site conditions have to be manipulated and this creates deviations from conditions in natural grasslands. Pre-experimental site preparation includes the application of herbicides (e.g. methyl bromide) in some cases, in order to reduce unintentional contributions by the soil seed bank. Herbicides can disrupt microbial activities in the upper soil horizons and even eliminate soil biota.

Technical problems have to be understood. In contrast to greenhouse research, field experiments are exposed to unplanned extreme events, such as heavy rainfall, drought, or to unintended biotic impacts, such as herbivory. If the whole experiment is affected in the same way, non-linearity may be integrated as part of the work; if this is not the case, the entire experiment may be lost. The direct simulation of the loss of diversity by the removal of species (e.g. Hobbie et al. 1999; Symstad and Tilman 2001; Berlow et al. 2003; Diaz et al. 2003; Bret-Harte et al. 2004) is accompanied by direct effects of the manipulation itself. Root decomposition and nutrient fluxes are affected (McLellan et al. 1995; Wardle et al. 1999). In this case, the artefact of increased short-term production would respond a reduced functioning of the system.

The removal is accompanied by either mechanical disturbances or by the application of toxic compounds. We can better differentiate between controlled diversity experiments (with installed communities under controlled and comparable site conditions) and biodiversity manipulation experiments (e.g. exclusion of species from natural communities or artificial increase of diversity). The terminology here is not always clear (Hector et al. 2002b). The quality of seeds gave rise to problems in many biodiversity experiments. Limited availability of large numbers of seeds from natural varieties is a consequence of the low demand for and limited longevity of seeds. They are economically unimportant. On the other hand, cultivars which can be obtained from commercial traders, cannot be used in experiments which are aimed at simulating natural grasslands. Harvesting of seeds is time consuming and need not be carried out by highly skilled scientists. However, distinguishing sub-species, identifying adequate ecotypes and even distinguishing species (e.g. in the case of many grasses) is not a trivial matter. Some experiments (Cedar Creek, BIODDEPTH) partly suffered due to single seed portions that were contaminated with plants from other origins.

The largest portion of field experiments focuses on herbaceous plant communities on a plot scale ranging from 0.5 m×0.5 m up to 20 m×20 m and with a regular duration of 1–3 years. In some cases, this timeframe is exceeded, e.g. at the Cedar Creek field experiment in Minnesota (Tilman et al. 2001), or at some of the BIODDEPTH sites (Pfisterer et al. 2004; Nesshöver et al., submitted). Some experiments are undertaken for even shorter time scales (Garnier et al. 1997; Fridley 2002, 2003). Only recently have experiments been designed and established that manipulate tree species diversity and thus cover a longer time span (Scherer-Lorenzen et al. 2005a). In this article, we focus on results from the most comprehensive grasslands experiments, Cedar Creek (e.g. Knops et al. 1999, 2001; Tilman et al. 1996, 1997a, 2001, 2002a) and BIODDEPTH (e.g. Hector et al. 1999, 2002b; Spohn et al. 2005).

The Cedar Creek biodiversity experiment in Minnesota started in 1993. It had a strong impact on the scientific debate. It was set up within the Cedar Creek Natural History Area on a nutrient-poor sandy soil. The topsoil was removed from a surface area of 9 ha and a strong herbicide applied to avoid germination of the existing soil seed bank. The soil was superficially mixed and seeds were sown at a standardized number of seeds per plot in a stochastic design in 168 out of 342 available plots, 9×9 m each. The diversity gradient ranged from one (39 plots), to two (35), to four (29), to eight (30), to 16 (35) species. All species were cultivated in monocultures as well. Species mixtures were defined on the basis of a random draw from a pool of 18 selected species. They reflect the composition of natural grasslands

nearby and represent various functional groups such as C3 grasses, C4 grasses, legumes, herbs and woody plants. The plots were continuously weeded to make sure that no additional species could invade the plots. The fulfilling of basic statistical requirements and the high number of plots and replicates were the major innovative contributions of this experiment.

In 1996, the BIODDEPTH project was launched (Biodiversity and Ecosystem Processes in Terrestrial Herbaceous Ecosystems) (e.g. Diemer et al. 1997; Hector et al. 1999; Minns et al. 2001; Hector 2002; Spohn et al. 2005). The project was run for a 3-year period. It made reference to the Cedar Creek experiment. For instance, the same diversity gradient was installed. However, at some sites, the highest level of 16 species could not be reached. On the other hand, an additional 32-species level experiment was installed in Lupsingen, Switzerland. Its novel contribution was that this multi-site experiment applied the same experimental design to eight sites following biogeographical gradients across Europe, from Portugal to northern Sweden and from Ireland to Greece (Hector 2002; Hector et al. 2002b). So, the experiment was carried out with the same design in each country, but under very different environmental conditions across Europe. However, regional species pools had to be considered. Of course, it was impossible to use the same species everywhere. The plots (2×2 m) were weeded during the 3 years of the experiment. The questions which can be answered with this approach, are whether diversity effects are site-specific and arise only when certain environmental conditions are met or if they are a common phenomenon. On the BIODDEPTH sites in Switzerland and Germany, the investigation of the field plots was continued after the end of the project in 1999, leading to additional insights into the relationship between diversity and productivity. At both sites, the maintenance of the original diversity gradient was stopped and species not present in the plots were able to invade giving some idea about the stability of species compositions and diversity patterns (Pfisterer et al. 2004; Nesshöver 2004).

In 2002, a new experiment was installed in Jena, Germany, which also focuses on grasslands (Roscher et al. 2004). Ninety plots (20×20 m) were established. Diversity levels followed the Cedar Creek and BIODDEPTH experiment (one, two, four, eight, and 16 species) with additional, extremely diverse 60-species plots being composed by stochastic mixtures. The species pool of 60 species adapted to moist meadows was classified according to morphological, phenological and physiological traits and four functional groups (grasses, small herbs, tall herbs, and legumes) were distinguished. The experimental design is based on four blocks to eliminate soil heterogeneity within this rather large area. First results are available, but the experiment is designed to continue for 10 years.

Many diversity experiments are based on rather simple communities with short-lived (or at least assumed to be) species. Results are obtained within several months (e.g. Garnier et al. 1997) or within the first years. However, for many herbaceous species, their optimal performance in time is not known. The experiments assume that this is achieved when the plants are established. Experiments are set up in pots or on artificial substrate (e.g. Sheffield in the BIODDEPTH experiment). Other sites used widely undisturbed developed soil. To reduce weeding effort either steam sterilization or the application of methyl bromide is carried out. The latter may have effects on soil organisms such as fungi or bacteria. These artificial environments have often been criticized (Grime 1997; Huston 1997; Fridley 2002), but their artificial nature goes along with the advantage of delivering well-known and, first of all, comparable site conditions. This allows for replicates and comparisons.

Many experiments are based on grassland communities. Grasslands can easily be established in a short time and their structure is simple compared to other perennial communities such as forests. Grasslands have a rather constant performance in time (compared with fields and ruderal communities). According to the disturbance regime, most experiments simulate mowing, because this allows a more precise experimental approach and aboveground biomass can be harvested at defined stages. Pastures and grazing would afford much more spatial and temporal heterogeneity in biomass, trampling and local nutrient hotspots. Grasslands share the advantage of being spatially as well as economically important. Under continental climates, they represent the natural vegetation. In more oceanic climates grasslands are a major land use type. Besides being a food supply for ruminants, grasslands are also relevant for water cycles and atmospheric gas fluxes. There are many indices showing that the diversity of European grasslands has declined during the twentieth century. Technical advances – especially physical (drainage) and chemical (fertilization) improvements of the sites as well as efficient mowing facilities – are responsible for this development.

5 Advances and Frontiers – Insights into Mechanisms and Processes

5.1 The Biodiversity–Productivity Relationship

One major focus of modern diversity experiments has been on the relationship between species richness and measurable abiotic ecosystem functions, especially aboveground productivity. The BIODDEPTH plots show in general

a positive logarithmic relationship between species richness as well as functional richness (number of plant functional types) and aboveground productivity (Hector et al. 1999; Spehn et al. 2005). The strength of this relationship varied between sites as well as between the years of observation within the 3-year period of measurements (Spehn et al. 2005). Partitioning this effect into a complementarity and a sampling component showed that species richness complementarity was significant and positive at most sites (Loreau and Hector 2001) and increased over time (Spehn et al. 2005). The sampling effect was more variable between sites and within time. One important factor for the species richness–productivity relationship at some sites was the presence of legumes in the seed mixture and their positive influence on productivity (Spehn et al. 2002). Besides high productivity of the legume species themselves, a complementarity effect between legumes and other species was also detected (Scherer-Lorenzen 1999; Spehn et al. 2002). At the German BIODDEPTH site, this effect was strongest and even continued for 5 years after weeding had been stopped (Fig. 4a; Nesshöver et al., in review). Since legume abundance strongly decreased over time (see the graph of *Trifolium pratense* data in Fig. 4b), this effect was driven by the facilitation of other species due to the early legume development. For other ecosystem functions, such as light use and aboveground space use, similar effects were found indicating greater resource use by niche differentiation (Spehn et al. 2000, 2005). The experiments at Cedar Creek showed similar patterns in the relationship between diversity and productivity (Tilman et al. 1996, 1997a, 2001, 2002a). There, it was shown that the diversity effect increased over time. Complementarity effects were believed to be responsible for this (Tilman et al. 2001). It was found that few species or functional groups play a major role in this process, although an additional influence of richness remained (Lambers et al. 2004).

In contrast, various publications support the low importance of facilitation and complementarity or even no effect of diversity on productivity at all (Kenkel et al. 2000). An experiment carried out at different sites across Europe, where different seed mixtures were added to the natural secondary succession, showed no consistent effect of richness on productivity during 3 years (Van der Putten et al. 2000; Lepš et al. 2001). The response was mainly triggered by single species and their traits. A short-term experiment by Fridley (2002, 2003) suggests that resource availability may influence productivity more than species richness. This is not surprising, as the experimental communities were mainly composed of annual grasses and herbs. The species composition of communities and the presence of single species were more important than richness per se. This experiment was carried out with very small raised-bed plots (50×50cm). Edge effects make facilitative

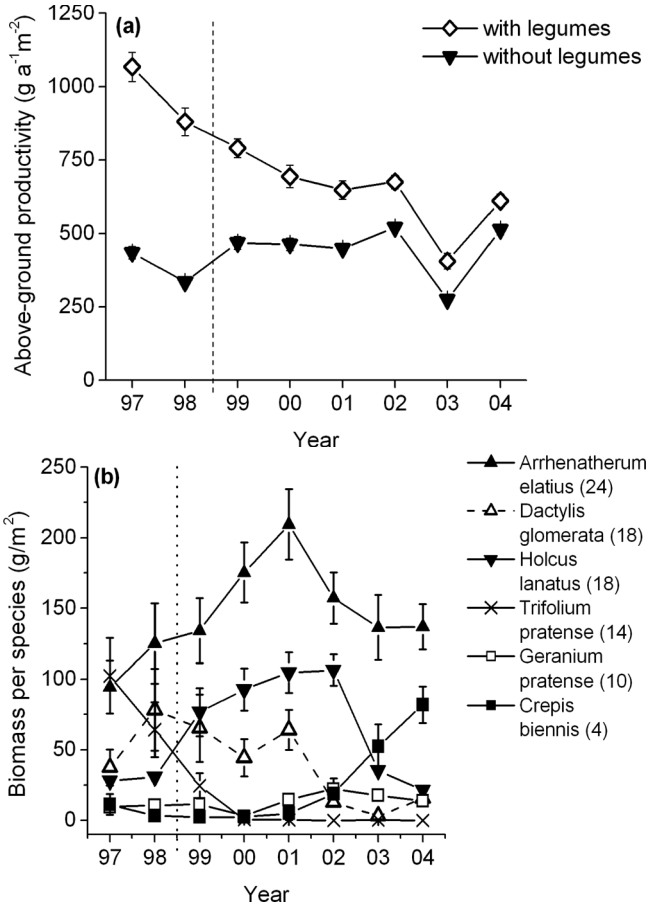


Fig. 4a, b. Development of above ground biomass production in the BIODEPTH experimental field site in Bayreuth, Germany. The vertical dotted line indicates cessation of weeding after the BIODEPTH experiment terminated. Species were then able to immigrate into plots in which they had not been sown. **a** Total above ground productivity per year separated by plots with and without legumes in the seed mixtures, **b** mean biomass production of single species in summer harvest. Numbers in parentheses indicate the number of plots in which the species were present in 1997 and 1998; after that, the species shown also immigrated into other plots. See text for further explanation and also Nesshöver (2004), Nesshöver et al. (in review). Means \pm SE are shown

interactions between species less probable. Only ten species were used. Polley et al. (2003) found negative complementarity and selection effects in an experiment with annual grasses and herbs on small plots of 1×1 m. However, the short-term development of annual species on small plots can hardly be taken as a proof for general mechanisms in vegetation. It is strongly influenced by resource availability and founder effects.

When multi-species assemblages are compared to species-poor communities or even monocultures, it has to be noted that it makes a difference whether the mean values for monocultures or the maximum yield of the most successful monoculture are taken (Garnier et al. 1997; Huston et al. 2000). To test the second aspect would require monocultures of all the species that are used in the mixtures available. This is not the case in many experiments (e.g. BIODDEPTH). Garnier et al. (1997) conclude that there are only rare cases where superior productivity of multi-species assemblages as compared to monocultures has been clearly shown.

If mixtures show higher productivity than species-poor stands or monocultures, this is called "overyielding" (Hector 1998; Loreau 1998b). Pretzsch (2005) analyses forest experiments with tree species mixtures and finds that overyielding can occur if early and late successional species are combined or if the trees are considerably different in their light use strategy or seasonal culmination (e.g. *Larix decidua* and *Picea abies*). Mixtures of such species can yield higher biomass than pure stands. However, most mixtures do not reach the yield of the best performing species. When species were competing for the same resources, total yield was reduced by up to 30%. Several analyses on overyielding in grassland experiments were performed (e.g. Hector et al. 2002a; Hooper and Dukes 2004; Roscher et al. 2005). Hector et al. (2002a), analysing the BIODDEPTH results, found a low explanatory power of the overyielding effect based on the monocultures of the most productive species (but see Drake 2003). Hooper and Dukes (2004) analysed the results from an 8-year experiment in serpentine grassland and find that overyielding effects got stronger with time and varied with the functional characteristics of the included species and the abiotic conditions. Combining two different sets of experimental plots on different spatial scales in the Jena experiment, Roscher et al. (2005) also found an overyielding effect mainly caused by complementary effects. Lambers et al. (2004) point out that both positive and negative interspecific interactions determine whether species-specific overyielding occurs.

To summarize the discussion on the diversity–productivity relationship, apparently two sets of mechanisms, sampling and competition on the one hand, and niche complementarity and facilitation on the other hand, are effective at varying levels of importance in most ecosystems. Their relative importance may vary depending on the life stages of individuals and populations (Walker and Vitousek 1991; Tilman and Lehman 2002), physiological attributes (Callaway et al. 1996; Holmgren et al. 1997) and abiotic stressors (Bertness and Callaway 1994). It has further become apparent that species richness per se is not the main driver behind the diversity effects, but rather a combination of different diversity parameters, including the composition of

the communities and the presence of single functionally important species (Hooper et al. 2005). Ecosystem engineers (Jones et al. 1994) deliver improved conditions to other species such as shading, higher nitrogen supply or favourable soil structures. Various studies indicate that the productivity of diverse grasslands depends more on the occurrence (not their abundance or quantitative share) of *certain* functional types than on their diversity (Hooper and Vitousek 1997; Hooper 1998; Scherer-Lorenzen 1999; Nesshöver 2004). Our results on the lasting effect of originally sown legumes on productivity are a good example of this (Fig. 4a; Nesshöver et al., submitted) So, the question is, whether comparisons with stochastic combinations of functional types or species are adequate, or if the best-adapted type should be used as a standard? The degree of overyielding is strongly dependent on the specific traits of the species used in mixtures, which is in contrast to the Grime's "mass-ratio" hypothesis (1998).

5.2 Plant Species Diversity, Invasibility and Community Dynamics

In the context of biodiversity loss, the question that is raised is: does enhanced diversity stabilize community structure and thus hinder the invasion of alien species (e.g. Levine and D'Antonio 1999)? The resistance against invasion becomes increasingly important due to efficient dispersal vectors. This topic is even more complex than the biodiversity–productivity discussion. Not only the qualities of the invaded communities (of different diversity) but also those of the invading organisms or populations have to be considered. Generally, invasion, or more general immigration, is an indication of species turnover. This mechanism is also important for native species within the community, but there it is less obvious. Mouquet et al. (2004) have experimentally investigated the contribution of seed rain to biodiversity and found that it affects communities differently depending on the competitive abilities of the present species. The authors suggest that the mechanisms which control species dynamics in grasslands are a mixture of colonization–extinction processes and a competitive weighted lottery.

It has been documented by various authors that species diversity seems to control the invasibility of communities. Most experimental approaches found a negative relationship between species and/or functional diversity and invasion (e.g. Tilman 1997; Knops et al. 1999; Naeem et al. 2000b; Prieur-Richard et al. 2000; Symstad 2000; Kennedy et al. 2002; Fargione et al. 2003; Pfisterer et al. 2004). Species-rich communities are supposed to possess a higher resistance against invasion and to be more stable in their composition (Sankaran and McNaughton 1999; Hector et al. 2001a; Kennedy

et al. 2002). But results of other studies diverged from these findings (e.g. Robinson et al. 1995; Palmer and Maurer 1997; Crawley et al. 1999; Lavorel et al. 1999). In general, experimental studies tend to find negative correlations, while observational studies more often find no significant or positive correlations, between diversity and invasibility (reviews in Prieur-Richard and Lavorel 2000; see also Hector et al. 2001a; Meiners et al. 2004). Fox (1987) formulated the assembly rule, that a decrease or lack of certain functional groups will facilitate the invasion of species which belong to this specific group. Given a certain pool of species and functional types there should be a correlation between functional diversity and invasibility. Symstad (2000) and Dukes (2001a) found negative relationships between the functional diversity of experimental grassland plots and the success of an invasive annual weed.

Some experimental findings indicate that species composition (certain species-specific traits or interactions) determines invasibility more strongly than richness per se (Crawley et al. 1999). There, species identity matters more than richness in determining the number and the biomass of invaders. Other case studies point at the role of dominance patterns (here of C4 grasses) for the control of invasion by exotic plants rather than at the diversity of the stands (Smith et al. 2004). The latter would indicate that sampling effects might conceal diversity effects. With the experiment's duration, with increasing invasion and decreasing dissimilarity between plots, the diversity effects (complementarity) on productivity tend to become less significant (Pfisterer et al. 2004).

Hector et al. (2001a) report the influence of diversity on invasion by analysing the number of species and individuals weeded out during the experiment. They found a clear, positive relationship between number of sown species and invasion resistance. Confounding effects appear due to the fact that the weeding of species-poor communities causes higher disturbances than weeding of species-rich ones. During long-term observation on the Swiss BIODDEPTH site, the number of species invading after the end of the weeding period showed a negative log-linear relationship with the numbers of sown species (Pfisterer et al. 2004). The results from Bayreuth showed the same pattern (Nesshöver 2004). We additionally analysed whether this effect was triggered by species richness or rather by compositional effects. Since the most productive species (*Arrhenatherum elatius* and *Holcus lanatus*) had a strong influence on the biomass of invaders, selection effects have to be considered (Fig. 4b). Similar trends were found by Crawley et al. (1999), Van der Putten et al. (2000) and Van Ruijven et al. (2003). In this respect, Wardle (2001a) criticises studies which find a positive relationship between species richness and invasion resistance. He states that no study was able to separate the richness

effect from effects triggered by single species. In addition to this, individual immigrating species might react differently towards species richness of communities (Meiners et al. 2004).

The importance of richness versus compositional effects in this context may further be altered by the influence of environment and management. The German BIODDEPTH site was relatively nutrient-rich, although the plots were not fertilized (Scherer-Lorenzen 1999). According to the hump-shaped model (Grime 1973), the dominance of single species was relatively strong (Nesshöver 2004) and thus influenced invasion. Davis and Pelsor (2001) also find that resource availability affects competition intensity and that this restricts invasibility. These authors point at the role of history when discussing invasion processes. Short-term stochastic disturbances may locally reduce competition and allow for invasion (White and Jentsch 2001). Van der Putten et al. (2000) detected in their multi-site comparison across Europe a dependence of invasion success on the overall productivity.

Invasion and invasibility have to be considered as source and sink models. But again, experiments which integrate differences in diversity at the multi-patch scale have not yet been set up. Up until now, only a few experiments have been carried out that manipulate the genetic diversity within species of recipient plant communities. Weltzin et al. (2003) could not find an effect of genotypic richness of *Arabidopsis thaliana* on invasion success, emergence and survivorship of *Arabidopsis suecica*.

Some studies have been conducted which analyse the influence of plant species diversity on the diversity, performance and biomass of other trophic levels (Mulder et al. 1999; Knops et al. 1999; Koricheva et al. 2000; Naeem 2002b; Holt and Loreau 2002). Andow (1991) finds a lower probability that specialised herbivores are successful in diverse stands. In addition, predators of herbivores are supported. In contrast to this, Hanley (2004) could not identify effects of plant species diversity on the herbivory of seedlings by molluscs in experimental grasslands which compared three, six, and 12 species mixtures of seedlings. There seemed to be even a slight increase in seedling mortality with increasing diversity. Obviously, facilitating effects are unimportant in the seedling phase. Using field experiments in moorlands and the ECOTRON facility, Hartley and Jones (2003) conclude that the effects of climate change on diversity and indirect effects on herbivores are likely to be strongly site specific. Initial community structures and dominant species are important. It is most likely that belowground factors such as the composition of soil biota are more important than species diversity. On the other hand, structures that provide microclimatic shelter can reduce insolation and deliver wind protection and this can improve the water use efficiency during photosynthesis (Vandermeer 1989). The better regulation of

fungal plant diseases with increasing diversity was documented by Mitchell et al. (2002). However, again, species richness correlates with biomass, and thus, a direct influence is hard to prove.

5.3 Influences of Species Diversity on Element Cycling

Plant species diversity is also proclaimed to contribute to a higher efficiency in resource use in the rhizosphere (Tilman et al. 1997b; Loreau 1998a). Tilman et al. (1996) report elevated nitrogen uptake from soil in diverse stands via complementary resource use. This was confirmed in various investigations (see Schläpfer and Schmid 1999). Hooper and Vitousek (1998) found a better use of resources and increased nitrogen and phosphorous uptake at higher levels of species diversity but no effect on nitrate leaching. Only when nitrogen fixers were present did nitrate leaching occur. Scherer-Lorenzen (1999) and Scherer-Lorenzen et al. (2003) show, based on the experimental plots of the BIODDEPTH experiment in Bayreuth, Germany, that stands of low diversity may intensify nitrate leaching without being fertilized. Enhanced values were mainly found in soil depths below 15 cm, hinting at the possible impacts on ground water. Even in the absence of legumes, at certain times critical concentrations of nitrate occurred in species-poor communities.

A decrease in unconsumed soil nitrate with increasing richness was found in Cedar Creek (Tilman et al. 1996, 2002b). However, the latter effect could be attributed to the presence of certain functional groups (legumes and C4 grasses) and not to species richness per se. Knops et al. (2002) conclude in a review of plant species' impacts on nitrogen cycling that in the short-term no effect of plant species richness on nitrogen cycling can be expected, since the main driver is the microbial community within the system. Impacts of single species can be found, if they alter nitrogen inputs and losses directly (e.g. legumes).

However, the image we have of the diversity–function relationship is rather hazy, when looking at belowground processes (Naeem et al. 2000a; Wardle et al. 2000a; Van der Heijden and Cornelissen 2002; Wardle and Van der Putten 2002). The influence of legumes on the nitrogen pool may differ between sites and alter the relationship between diversity and soil nitrogen. At some BIODDEPTH sites, fixed nitrogen was transferred to non-legume species (Mulder et al. 2002; Spehn et al. 2002), and thus, diverse communities could profit from increased nitrogen availability. Plots without legumes showed no coherent reaction of diversity to soil nitrogen (Scherer-Lorenzen

et al. 2003). Decomposition of cotton strips and wood was found to be generally unaffected by species richness and only slightly affected by functional group richness (Spehn et al. 2005). In addition to plant diversity, small-scale site conditions, such as microclimate, are decisive for leaf litter decomposition (Hector et al. 2000a).

Zaller and Arnone (1999) report a linear decrease in lumbricid populations together with decreasing plant species richness. In contrast, Wardle et al. (1997, 1999) could not find a positive effect of species diversity such as enhanced activity of decomposers (Collembola, lumbricids). Stephan et al. (2000) detected positive effects of plant diversity on bacterial diversity. Zak et al. (2003) could experimentally prove significant increases in microbial community biomass, respiration and fungal abundances with increasing plant species diversity, but could not separate biomass from diversity effects.

It is assumed that niche complementarity will support the efficient use of resources and thus enhance productivity in diverse communities (Tilman and Downing 1994; Hooper and Vitousek 1997; Hector 1998; Dukes 2001b). Excluding legumes, Van Ruijven and Berendse (2003, 2005) experimentally demonstrated complementarity effects. They attribute this effect to increased nutrient use efficiency in species-rich stands. This can be explained by species-specific root morphology (Kutschera et al. 1992a, 1992b), rooting depth (Sullivan and Zedler 1999) and turn-over as well as by physiological complementarity in the use of the variety of chemical molecules and linkages. Structural heterogeneity produces micro-hotspots (nutrient patches) in soils, which – depending on symbiotic partners – some plant species are able to utilize and others are not. Plants differ in their capability to release protons, chelates or other compounds. This may explain coexistence and complementary resource use. Nutrient uptake by plants is correlated with the biodiversity of mycorrhizal fungi in grasslands (Van der Heijden et al. 1998). Hyphae of mycorrhizal fungi have access to smaller soil pores and the nutrients therein. The diversity of mycorrhizal fungi is in turn correlated with plant species diversity (Van der Heijden et al. 1998). Thus, indirect effects in carbon and nitrogen turnover in the soil can be expected (Hooper and Vitousek 1998). Bardgett and Shine (1999) point to the role of plant litter diversity in microbial activity and biomass in temperate grasslands. The significance of tree species diversity for litter quality and decomposition is reviewed by Hättenschwiler (2005). Only few studies focus on diversity effects, and here results are inconsistent. There is some indication of specific effects of chemical compounds, which are more likely to occur in mixtures, but research is still in its infancy in this area.

6 Developments in Methods and Approaches

6.1 Functional Types, Traits and Attributes

A major point that is raised in the context of biodiversity–ecosystem functioning experiments is, whether diversity should be treated at the species level, or on the basis of functional characteristics (Lavorel and Garnier 2002; Hooper et al. 2002). The common application of functional characteristics is to identify plant functional types or functional groups (see Gitay and Noble 1997; Westoby and Leishman 1997; Woodward and Kelly 1997) as groups of species which have a similar response to disturbance or a similar effect on ecosystem properties. Functional types are considered to be a promising approach to cope with functional diversity and ecological processes and to assess the consequences of biodiversity loss. When using plant functional types, we have to keep in mind that this reduces the information according to a continuous gradient of functional diversity (set by the functional traits) to a few groups. Furthermore, the individual decision on which functional traits are used as criteria for the classification of groups, is in most cases a subjective one (Smith et al. 1997; Lavorel and Garnier 2002). It can lead to circular reasoning when using functional groups to characterize functionality (Beierkuhnlein and Schulte 2001). Especially in grassland experiments, the categorization is simple. Growth type (grasses vs. herbs), nitrogen-fixing ability (legumes vs. non-legumes) and carbon-metabolism (C3 vs. C4 grasses) may serve as examples. The consistency of the approach is lost when groups are mixed that have been classified on the basis of different criteria (e.g. herbs, grasses and legumes).

Besides functional redundancy, one source of redundancy may be rareness. There are only some hints that the loss of rare species might interfere with ecosystem functioning (Lyons and Schwartz 2001). If organisms are rare or afforded little space, they normally will not interact strongly. Then, the same ecological niche can be occupied by different species within one community. Even if edge effects and transient emergence are excluded, dynamics of species turnover in microsites, non-uniform seed dispersal and spatio-temporal site heterogeneity will support such co-occurrences (Shmida and Ellner 1984). They will contribute to species diversity in the sense of “functional analogues” (Barbault et al. 1991) but not enhance the complexity of the system.

Functional traits are derived from direct functional properties of organs or from specific forms of metabolism. “Response traits” are attributes which determine how individuals (or species) will react to environmental changes (Walker et al. 1999). “Effect traits”, in contrast, influence certain ecosystem

properties (Lavorel and Garnier 2002). Especially the latter ones are interesting for biodiversity–ecosystem functioning studies. With regard to biodiversity loss scenarios, response traits also become important (Hooper et al. 2002). The trait approach is more flexible and also more specific than the functional type approach. It can be directly linked to specific processes, such as fluxes of carbon or water. For some ecosystem properties, effect and response traits may be tightly linked (Weiher et al. 1999). Functional traits are not always strictly based on certain mechanisms but on merely structural or temporal attributes. In such cases, it is better to stay with the established terminology of morphological traits, and then use the classification of growth forms or life forms or – when time is the scale – life-history traits (Poschlod et al. 2000), but not functional types. Phenological complementarity may contribute to the functional performance of ecosystems (Loreau and Behara 1999; Stevens and Carson 2001). Depending on the ecosystem function under consideration, the relevant functional traits are specific too. Thus, on a functional level, it is difficult to design experiments with proper gradients of functional diversity if various traits are investigated. Furthermore, we are often not provided with satisfying information about the relevance of functional traits for a certain function. For many species, important functional traits are not documented (see Weiher et al. 1999).

A data-defined analysis of functional diversity and species diversity measures based on data from the BIODDEPTH experiment demonstrated that only few functional characteristics – in this case the presence of legumes – explain the biodiversity–ecosystem functioning relationship best, and that simple functional groups, i.e. only grasses, herbs and legumes, also serve this purpose well (Petchey et al. 2004). Thus, it may be concluded that simple measures of functional diversity, such as functional types, are good surrogates for the description of the biodiversity–ecosystem functioning relationship, at least in grasslands, where the functional diversity gradient of species is not very broad (Nesshöver 2004). However, the role of structural or functional diversity is still less emphasized than the importance of species diversity.

In experiments including functional diversity as well as species diversity, autocorrelation between the different measures may occur (Fig. 5; Tilman et al. 1997a; Naeem 2002a; Petchey and Gaston 2002; Naeem and Wright 2003). Depending on the design of the experiment, it can be impossible to separate their effects (Schmid et al. 2002a). Functional diversity and species diversity is tightly linked due to evolutionary constraints (Reich et al. 2003). Species diversity might be, as well as functional type diversity, a rather good surrogate for the more complex diversity of functional traits.

Additionally, it has to be asked whether it is applicable to separate effects of different richness components, such as richness of species and plant functional

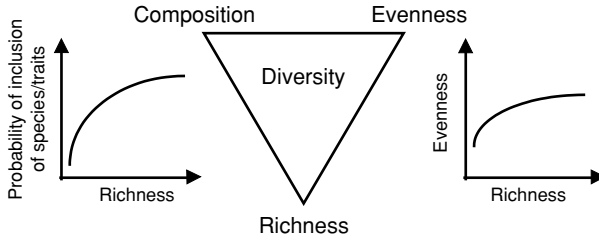


Fig. 5. Scheme of general relationship between different diversity parameters. The diversity of elements can be seen as a combination of their richness (number of elements), their composition (if certain elements are included or not) and their evenness (their abundance in the community). All three parameters will be more or less tightly correlated (graphs on the *right* and the *left*), leading to the inevitable consequence of autocorrelation in experiments

types, and to ignore other diversity components (Schmid et al. 2002b)? On an abstract level, separation of effects should be attempted between richness, evenness and composition effects. Richness will in most cases be correlated with evenness – the more species, the more even distribution of abundance might be expected (Fig. 6, right) – and compositional effects; the probability of a species included in a mixture will increase with higher richness, the sampling or selection effect. Instead of trying to statistically separate effects of single diversity parameters within one analysis, e.g. species and functional type richness and mixture effects in an ANOVA of a multiple regression, it might

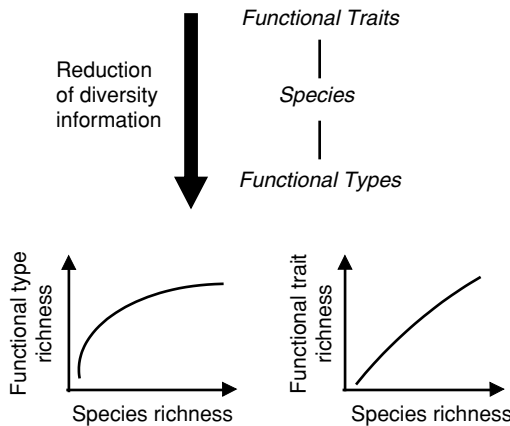


Fig. 6. Different diversity levels used in diversity experiments. From the functional trait to the species and the functional type level, the information within the level is reduced, leading to specific correlations between the levels (*bottom graphs*)

be more applicable to accept that the different parameters have to be considered jointly, e.g. by using them in a principal component analysis to derive independent orthogonal factors from them. These factors can help us to analyse the relationship between diversity and functioning (Naem 2002a; Nesshöver et al., in review). However, one still has to choose which diversity parameters should be included in such an analysis (Nesshöver 2004) or use randomised bootstrapping techniques for analysis (Petchey et al. 2004).

6.2 Individuality, Assembly Rules and Non-Stochastic Extinction

In order to statistically test hypotheses, data have to be as appropriate as possible, and tests make only sense when replicates are included. However, after some years of a study, it becomes obvious that even if there are still similarities, the development of each plot is unique. The quality of replicates thus depends on time and is better in the beginning of an experiment. In addition, at the beginning of an experiment, stochastic events, such as the effects of pioneer species, and the role of slight differences in the mechanical disturbance during the setting up of the experiment, are relevant. They become less important during the development of the stands, when biotic interaction and space-filling takes place.

Due to the target of identifying general tendencies or rules, biodiversity experiments use a specific species pool. They mix species for certain diversity levels. This mechanistic approach does not reflect the assembly rules and population dynamics in natural communities (see Lepš 2004; White and Jentsch 2004). Biodiversity experiments tend to ignore the coevolved and non-stochastic inter-relationships between species. When the consequences of extinction are derived from assembly experiments, it cannot be neglected that simulated random loss of species is not realistic (Fonseca and Ganade 2001; Schlöpfer et al. 2005). Causing species loss by highly intensive land use and then allowing regeneration, Schlöpfer et al. (2005) show that highly productive monoculture species were most persistent when subjected to community disturbance. However, these species were not superior to others during the regeneration phase. Species do not react equally to environmental stress. Their identity plays a role in their resilience. Predictions of consequences of plant species loss have to consider both specific extinction probabilities and post-extinction development (Schlöpfer et al. 2005). When knowledge about species traits, such as extinction risk, is available (Pimm et al. 1988; Stöcklin and Fischer 1999; Thomas et al. 2004), this can be integrated into the design of diversity experiments. Non-random extinctions can disproportionately affect the invasibility of communities (Zavaleta and

Hulvey 2004). Ives and Cardinale (2004) stress the fact that the community performance after non-random extinctions depends strongly on food web interactions. When simulated extinctions are random and conclusions are based on mean values, the findings will deviate strongly from observation. Models indicate that the high importance of competition increases differences between random and ordered extinctions, but mutualisms reduce the differences (Gross and Cardinale 2005).

6.3 The Importance of Temporal and Spatial Scales

According to temporal scales, there are some fundamental problems inherent in experimental approaches. Compared to the development of natural ecosystems, biodiversity experiments aim to produce results within a very short time period. Thus, they are composed of rather short-lived or pioneer species. For many of them, a 3-year period is rather short to attain optimal performance. In addition, such short periods can hardly ensure that adapted mutualistic communities of soil biota can develop. Another temporal problem is synchrony. Experiments start on the same date with species characterized by different life cycles. It is technically almost impossible to ensure from the beginning a diversified age structure within the populations of different species in mixtures: juvenile, adult and senescent individuals in comparable proportions for different species with different potential age and development. As a consequence, the dominance structures change as experiments continue. It may take years until late successional species, such as *Arrhenatherum elatius* in European grasslands, gain their natural importance (Fig. 4b). Organisms which respond slowly, such as most characteristic competitive species of natural communities, which follow the strategy of resource allocation to storage organs, need some time to play the role that is attributed to them in nature. This can be ignored if a comparable proportion of species is aimed at. However, this target can hardly be achieved at any time of an experiment. Extrapolations of short-term experiments to natural processes and responses are naïve if they ignore this. However, there seems to be an influence of diversity on temporal variability of the community (Cottingham et al. 2001). At the very least, hysteresis can occur. The loss and the addition of species can produce contradictory results. Starting from low diversity and complexity this can slowly contribute to increased community performance, and the loss of species, starting from diverse communities can be compensated for (Fig. 7). If such mechanisms are effective, additive experiments have to be tested against removal experiments.

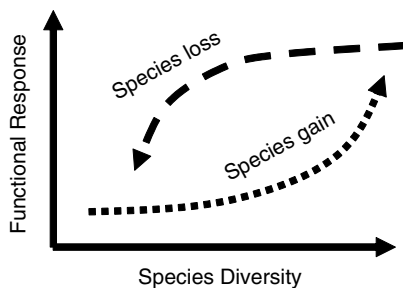


Fig. 7. Experiments manipulate species diversity in order to simulate the consequences of species loss. The better experimental reliability (replicates, controlled communities) of an additive set up compared to species removal is the reason why most experiments rely on additive approaches. However, there can be hysteresis in the system. The direction of the development, species gain or loss, can be related to a delayed response or functional persistence. It takes time until facilitative interactions are built up and the loss of complexity may be temporarily compensated for (after Beierkuhnlein and Jentsch 2005)

Bommarco (2003) demonstrates in a meta-analysis that herbivore and predator abundance depends on available space. For many reasons, the scale of experimental plots will influence results where biocoenotic interferences are concerned. Cardinale et al. (2004) simulated changes in spatial scale and could not find an effect on diversity–productivity relationships. However, as discussed earlier, such simplified models cannot replace experiments because they are based on unrealistic simplification. Whittaker and Heegard (2003) found scale-dependency of the species richness–productivity relationship in observational studies. Up until now, only few experimental studies have focussed on spatial aspects. Varying soil depth and rooting space yielded a remarkable influence on the performance of plant species diversity–productivity effects (Dimitrakopoulos and Schmid 2004). These authors found a linear increase in the magnitude of positive diversity effects on aboveground as well as belowground biomass with increasing availability of space and access to resources.

Biodiversity experiments are not comparable in size to natural communities due to logistic restrictions. This affects not only the population dynamics within the plots and treatments but has also an influence on microclimate and on biotic interactions with herbivores. This is because there will be side-effects by neighbouring and mostly structurally different plots, or side-effects at the edge of the experiment. This problem has been broached in the Jena experiment, but still, the size of the plots is not comparable to grassland communities found in the cultural landscape. One approach used to take into account the heterogeneity within communities of

differing diversity is to look at evenness (Mulder et al. 2004). However, if the scale of investigation is increased to the landscape scale, the role of diversity in the system can be expected to change completely with respect to increased abiotic heterogeneity (Bengtsson et al. 2002).

6.4 Separation of External Factors and Intrinsic Factors – Multi-Site Experiments and the Connection Between Experimental and Observational Studies

Site productivity and resource availability control strongly the performance of entire communities. Many experiments (e.g. Cedar Creek) were carried out on sites where nutrients or other resources were limited. Consequently, small differences in habitat carrying capacity may alter the relationship between diversity and functioning (Huston and McBride 2002; Aarssen et al. 2003). On a gradient of natural communities with different habitat carrying capacity (or site productivity), this leads to the observed hump-shaped curve first identified by Grime (1973). The results from the experiments using a logarithmic relationship between diversity and productivity seemed to contradict these findings (Mittelbach et al. 2001). The BIODEPTH experiment tried to identify general mechanisms across a wide spatial range in Europe with different environmental conditions. Differences in climate and soil conditions between the sites were part of the design that considered transects from oceanic to continental and from boreal to Mediterranean climates.

Schmid (2002) approached this by applying a three-dimensional model to separate habitat carrying capacity from community productivity (Fig. 8a). With differences in resource supply, the plane of an observed relationship moves from plane A to plane B. According to the hump-shaped model, which restricts the possible combinations, the planes change their extension. The results from different experiments with given species numbers are reflected by trajectories within the planes A and B (Schmid 2002). Projected back into the two-dimensional diversity–productivity model, this predicts specific trajectories within the hump under specific environmental conditions (Fig. 8b, curves 1, 2, 3). This is found when comparing different BIODEPTH sites (Schmid and Hector 2004). The question in this context is, how can the observed experimental relationship be related to natural conditions? Schmid and Hector (2004) argue that, if the weeding is stopped, diversity as well as productivity will shift along the observed trajectories towards an optimised state within the hump (arrows, Fig. 8b), as was observed at the Swiss BIODEPTH site (Pfisterer et al. 2004).

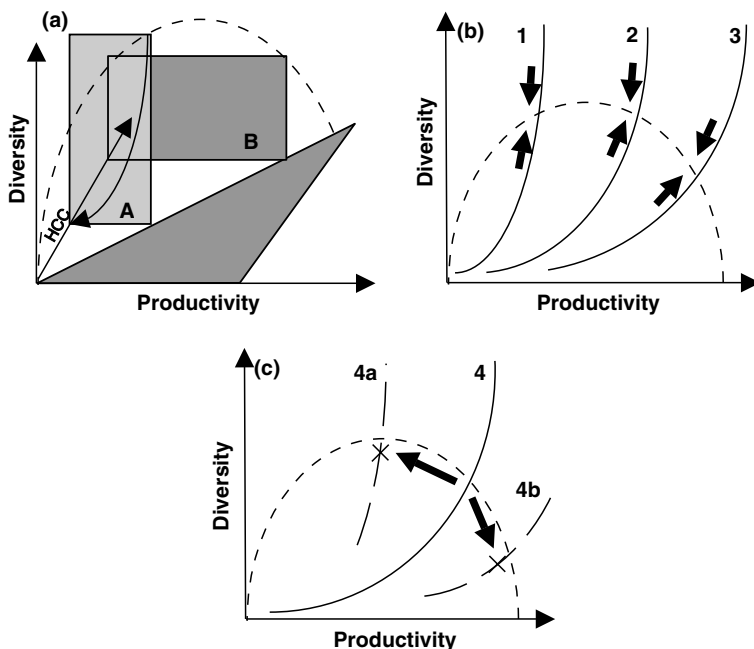


Fig. 8a–c. Schematic relationship between diversity, stand productivity and habitat carrying capacity (HCC). **a** Three-dimensional relation of diversity, productivity and capacity, **b** schematic visualisation of the logarithmic relationship found in experiments under different HCC (*graphs 1–3*, e.g. the different sites of the BIODEPTH experiment). The *arrows* indicate the potential development of productivity and diversity towards a convergence point along the hump (*dotted line*) if the diversity gradient is not maintained (compare Schmid and Hector 2004). **c** If the HCC is altered, alternative convergence points might be approached, leading to either increased or decreased diversity. See text for further explanation

Nevertheless, this effect will only appear if the carrying capacity of the site remains constant over time. For the German BIODEPTH site with the strong influence of legumes on the nutrient status of the stands, an additional shift was observed, since carrying capacity decreased with the decreasing abundance of legumes. Thus, an unexpected additional shift towards less productive and more species-rich stands was found (Fig. 8c, curves 4, 4a). Since the gradient of diversity is shortened as a consequence of immigration and succession, the hypothetical relationship (dashed line, Fig. 8c) is no longer found. All plots converge towards one point within the hump (cross, Fig. 8c). Another hypothetical question is: what would happen if the carrying capacity were strongly increased (e.g. by fertilization; Schmid 2002)? Then, diversity can decrease, since dominant species out-perform others, and productivity can rise at the same time (Fig. 8c, curve 4b).

7 Outlook

Biodiversity experiments are obviously both artificial constructs and heuristic tools, and there is compelling evidence that these qualities are tightly linked. The particular value of experiments lies in their contribution to an examination of causal effects. They can be designed in a way which aims to falsify specific hypotheses. Natural communities do not offer this opportunity. They share unobservable and immeasurable factors that have previously influenced their present-day condition. In addition, there are many measurable factors which interact at each site at different intensities.

Biodiversity experiments mainly involve rather simple or simplified communities – and if only annuals are concerned, they are often far too simplified to yield valuable results. Up until today, most approaches have used the community scale. Only the ECOTRON chamber experiment integrated higher trophic levels. The realization of more natural experiments, meaning systems that show a higher degree of complexity, is a major challenge in ecology (Belovsky et al. 2004). Large-scale experiments with higher complexity and with higher longevity of organisms are required – perhaps even across different ecosystems. Such experiments would be more representative of natural mechanisms and give us more information about the real effects of biodiversity loss. However, it would take years until relevant results could be achieved. Plantation experiments have been installed recently in forests around the world (e.g. Finland, Germany, Panama, and Borneo) with a varying diversity of tree species and genera (Scherer-Lorenzen et al. 2005b). At the global scale, the contribution of forests to ecosystem functioning and biodiversity loss is outstanding. Their structural diversity but also the integration of long-term site conditions, management, and natural disturbances have strong impacts on data (Pretzsch 2005). Up until now, silvicultural experiments have concentrated on tree species and ignored shrubs, dwarf shrubs and grasses, which might benefit from tree species diversity. This is reasonable from an economic point of view but limits their relevance for ecology. In the future, entire forest communities should be investigated. This means also looking, for instance, at epiphytes and cryptogams. Nevertheless, manipulating diversity in forests is an enormous step towards experiments which are of a more realistic scale and representative of nature.

Despite partly contradictory results from different case studies, there is more and more consensus in the scientific community regarding the effects of biodiversity loss (Hooper et al. 2005). Obviously, it depends on the system under consideration whether effects of diversity per se or of certain parts of the community, such as productive species, emerge in additive experiments (Tilman 1997). There is some indication of the higher probability of selection

of highly productive species with increasing species richness, but a sophisticated experimental design allows us to cope with this. Not forgetting the initial motivation of combating species loss, a more decisive question is, which species are prone to extinction? In nature, it is obvious that the risk of becoming extinct is not randomly distributed. In this case, non-random selection means selecting those which have the highest extinction probability, e.g. short-lived seeds, low competitive ability (Stöcklin and Fischer 1999), not the ones with the greatest contribution to ecosystem functioning, to simulate biodiversity loss (Lepš 2004). As there is a reason for their being under threat, such species are often difficult to cultivate in experiments.

Productivity is a prominent ecosystem function and the most widely considered variable in many experiments. However, a large proportion of the diverse ecosystems of the world is not very productive (e.g. South African Fynbos vegetation). Thus ecosystem functions other than productivity might be of more relevance in these cases. The role of structural diversity as habitat quality or as a factor to prevent soil erosion can matter. Until now, most biodiversity experiments have been carried out in the temperate region, and have concentrated on grasslands. However, biodiversity at the global scale is mainly threatened in tropical and subtropical areas. There, many structural and logistic constraints have to be considered when planning experiments. The first biodiversity experiments have only recently been installed in tropical areas (Scherer-Lorenzen et al. 2005b). More of them are urgently needed.

In order to evaluate the results that have been obtained experimentally, it seems inevitable that biodiversity models will become more complex on the one hand and that these data will need to be related to natural ecosystems on the other. Up until now, convincing concepts devised to calibrate experimental data according to real world data, do not exist. In our opinion, only the combination of various methodological approaches will deliver the insights required into the functioning of ecosystems. Any approach has its methodological restrictions and constructs. To broaden the validity of results from within experiments to within natural communities, data from various sources have to be adjusted. It would be most welcome if it were planned from the beginning that experimental results should be integrated into meta-analyses, in order to separate site-specific effects from general trends. Single-site experiments just add another unit to a large puzzle. What has been found for northern European grasslands does not necessarily hold true for the Mediterranean macchia (see Wardle 2001b; but also Troumbis and Memtsas 2000). In the case of biodiversity studies, this affords not only comparable levels of diversity but also a standardized experimental design. This was applied in the scope of the BIODDEPTH project, but also independent experiments could follow such a rationale.

One major reason for confusion in biodiversity experiments is the multi-dimensional nature of biodiversity. There is no concept of biodiversity that concentrates merely on one aspect, such as species diversity. Diversity includes richness, evenness and composition components. Most experiments still concentrate on species richness as it is easily established. Nevertheless, community heterogeneity is of increasing importance, if larger plot sizes are used, as clumped aggregations (Stoll and Prati 2001) and small-scale hot spots of functional effects become more probable.

Experiments on biodiversity and its changes in ecosystems cannot be solely restricted to species diversity and its decline. Changes of diversity occur at various scales as do qualities. The total extinction of a genetic pool of a species is only one facet. The local or regional loss of populations may be another one and can result in a decrease in local alpha diversity. However, this may locally be (over-) compensated for in numbers by alien or even invasive species (Sax and Gaines 2003). Present approaches consider invasibility as an effect of declining diversity. Such experiments are not designed to work out the effects of invasion and of a conceivable increase in diversity on ecosystem functioning.

A local increase in species richness, nevertheless, can be accompanied by extinction of rare or specialized species. Again, we do have to consider scale and ask which communities profit and which suffer. As an effect of such changes, the dissimilarity (beta diversity) between communities (see also Fukami et al. 2001) and between areas may decrease. This will lead to a loss of biodiversity at the landscape level that cannot be characterized by numbers of species. Many biodiversity experiments focus on alpha diversity – no matter if referring to species or functional groups. The loss of dissimilarity between stands has not been identified as an experimental research objective. One of the probable effects is a lower colonization rate by new species from neighbouring communities, as these are more similar, and thus less temporal turnover in species composition. In the face of global changes, this can mean lower resilience and adaptational capability. Even less is known about the consequences of modified turnover and age structure diversity within given communities or levels of species diversity.

Functional traits have been found to be a good tool with which to characterize the functioning of communities. However, according to temporal traits, observational knowledge that can be used in the design of experiments is only satisfactory for tree species. The population dynamics and life cycles are only understood for few species. It matters for metabolism and functioning, whether the individuals within an experiment are juveniles or adults, but as long as we cannot differentiate them, which is the case for many grasses and herbs, this cannot be considered. Up until now, many

mechanisms which are known to occur according to interactions between organisms, have not been applied to diversity experiments. The diversity of interactions is still largely unknown. The role of allelopathy, mutualisms of various kinds, interactions via promoted or suppressed soil organisms, are widely unknown. Many of these important functional processes will be species specific. Theoretical considerations help us to develop hypotheses; however, these have to be proven or withdrawn. The intrinsic epistemological problem of biodiversity research is that it is almost impossible to carry out in the vast majority of natural ecosystems. One reason for this restriction is to be found in the complexity of biotic interactions across and within trophic levels and functional groups. Species play a variety of roles, and there are many of these, including competition, facilitation and mutualism.

One factor limiting our ability to analyse biodiversity loss is the contribution of historic factors to ecosystem patterns and traits which have emerged. Recent aspects and structures are often attributed to past processes (see Davis and Pelsor 2001). Historical site conditions and ecosystem performance can be documented by storage matter or informational qualities such as patterns of behaviour. Connell (1980) stressed that the “ghost of competition past”, evolutionary forces that are not necessarily effective today, have often had repercussions not only on the behaviour, distribution or morphology of species but also on their performance. Past interferences and facilitation stimulated coevolutionary adaptation. If this is reflected in genotypes, which are not detectable by morphologic means, only experiments can prove its effect.

Various restrictions of biodiversity experiments have been discussed in this paper. What has been found to be true in one experiment (e.g. the positive correlation between productivity and species diversity by Hector et al. 1999) may not be confirmed when the scale of the investigation is changed (Waide et al. 1999; Bengtsson et al. 2002; Chase and Leibold 2002). This may be attributed to the fact that the emergence of biodiversity and of ecological complexity is strongly related to spatial scale. The size of experimental plots differs and larger plots are regarded as delivering more promising results. Experiments with varying plot size could help us to find answers to this technical problem (Roscher et al. 2005).

The aim to search for generality was an initial impetus of biodiversity–ecosystem functioning research. However, generality has still not been found here, and maybe this is not possible at all. Both of the terms, biodiversity and ecosystem functioning, turn out to be just too wide for testing by hypotheses. Functions, species and ecosystems integrate a huge amount of individuality and complexity. First conclusions based on single case studies had to be revised or at least restricted. Today, the focus is on more specific research

questions. It would be a commonly made mistake to accept or reject theories as units (Loehle 1988). Nevertheless, ecological experiments have contributed tremendously to a better understanding of the effects of biodiversity loss. Valuable insights have been gained, which are of great relevance for society and policy. The recognition of their limited validity and partly controversial results indicate the ongoing development of ecological insight.

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