13 Ecological importance of species diversity

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Introduction

Understanding the ecological importance of biodiversity

Understanding the ecological importance of biodiversity for ecosystem functioning and ecological services to mankind requires us to relate the diversity of ecosystem properties to the diversity of species performances in space, in time, in biotic interaction and under changing environmental conditions. Before discussing ecosystem functioning, we therefore explore three basic properties of ecological systems related to energy, matter and information, three fundamental aspects of biodiversity related to quantitative, qualitative and functional aspects, and knowledge on functional traits of species. We then review emerging theory on the role of biodiversity for ecosystem functioning, including functions such as productivity, stability, nutrient retention, resistance against invasion, and the temporal performance of communities. We further extend our scope to the benefits and services of biodiversity for human societies at large and discuss possible implications of losing biodiversity. Finally, we present prominent experimental methods, modelling and conceptual approaches in biodiversity science, thereby reviewing the most important biodiversity hypotheses, which are still under debate. Concluding, we point to emerging challenges related to key functions, historical contingency, cross-scale and cross-system research, and the implications of spatio-temporal dynamics for the performance of biodiversity under changing environmental conditions.

Currently, an extensive and controversial debate is questioning the effects that are expected to follow the decline of plant species diversity (Mooney *et al.*, 1996; Grime, 1998; Kaiser, 2000; Schmid, 2002). This debate stimulated ecological theory and methodology (e.g. Risser, 1995; Wardle *et al.*, 1997; Lawton, 1999; Loreau, 2000; Bednekoff, 2001; Naeem and Wright, 2003). Initially, opposing standpoints were developed concerning functional implications of species richness (Huston, 1997; Hector *et al.*, 1999, 2000b). The progress in biodiversity research during recent years is thus a consequence of the engagement of various international research groups with differing approaches and perspectives. Scientists began to realize that no general unified mechanism can be found that could be applied to every ecosystem (or site), nor are individualistic restrictions per se responsible for patterns and processes. Today, paradigms are shifting (Loreau *et al.*, 2001;

 Plant Diversity and Evolution: Genotypic and Phenotypic Variation in Higher Plants (ed. R.J. Henry)

Naeem *et al.*, 2002). Based on the critical analyses of data and experiments, new challenges and research issues are emerging in biodiversity science (Loreau *et al.*, 2001). In addition, the recent insights contribute to a better understanding of the potential effects of global changes for human society.

It is obvious that local and regional biodiversity is strongly influenced by human land use and its alteration in many landscapes (Machlis and Forester, 1996). The threat to biodiversity during the next century will be caused mainly by changes of land use. At the global scale, climate change, depositions of nutrients and toxic compounds, and invasive species will be less important (Sala *et al.*, 2000). This adds the human factor to the complexity of systems as humans act within ecosystems and control many functions directly. Anthropogenic action may influence biodiversity as well as key ecosystem functions. If we are interested in the effects of biodiversity loss on ecosystem functioning, direct and indirect effects of human influences will have to be considered.

Properties of ecological systems

In principle, there are always three different aspects or properties of ecological systems that are controlled or maintained by the assemblage and diversity of organisms: the flow and cycling of (i) energy, (ii) matter and (iii) information. In addition, storage and transformation occurs. Organisms are influencing these flows, transformations and storages in a non-stochastic, directed way. They regulate ecological processes and functions. This regulation cannot be predicted on the basis of physical laws or chemical processes only. The genetic information of species becomes ecologically effective as regards, for example, life-history traits, metabolisms and their plasticity under changing environmental conditions (Fig. 13.1).

As there is a limited range of ecological niches in any ecological system, species diversity is believed to be limited too (Cornell and Lawton, 1992). The diversity of coexisting species can probably be understood by considering their functional capabilities. Organisms have differentiated their functional traits and niche occupation during speciation (e.g. Cody, 1991). Their coexistence is a reflection of functional specialization and niche complementarity. Although redundancy of functions may occur in various species at a certain focus of interest, each species generally performs unique mechanisms and functions within an ecological system. Therefore, a correlation between species diversity and functional diversity is probable but is not necessarily a causal explanation (Tilman *et al.*, 1997b) (Fig. 13.2).

Still, the ecological implications of species diversity are more complex. Ecological systems and species assemblages are influenced by stochastic processes. Species combination and diversity is not deterministic and also not directly connected to a given environment. Additionally, plant species that contribute to the diversity and functioning of ecosystems differ in many aspects: for example in size, longevity and metabolisms. This indicates that the ecological importance of species diversity must be related to specific communities and ecosystems. For mankind, it has been shown early that there is a relationship between biodiversity and the rise of highly developed ancient cultures (Vavilov, 1935). For instance, the centres of old cultures and the origins of many crops are closely linked to the global 'hot spots' of biodiversity (Myers, 1988; Barthlott *et al.*, 1996). The decline of such cultures is very probably an effect of non-sustainable use of resources and biodiversity. Kim and Weaver (1994) even predict that the survival of mankind depends on the preservation of biodiversity.

The diversity of biodiversity

Initiated by Wilson's (1985) alert on the 'crisis of biodiversity' and the Rio Conference, intensive research on biodiversity topics emerged, followed up by an incredible number of publications ('The diversity of publications on diversity is overwhelming', van der Maarel, 1997). Public and political awareness occupied the theme as well.

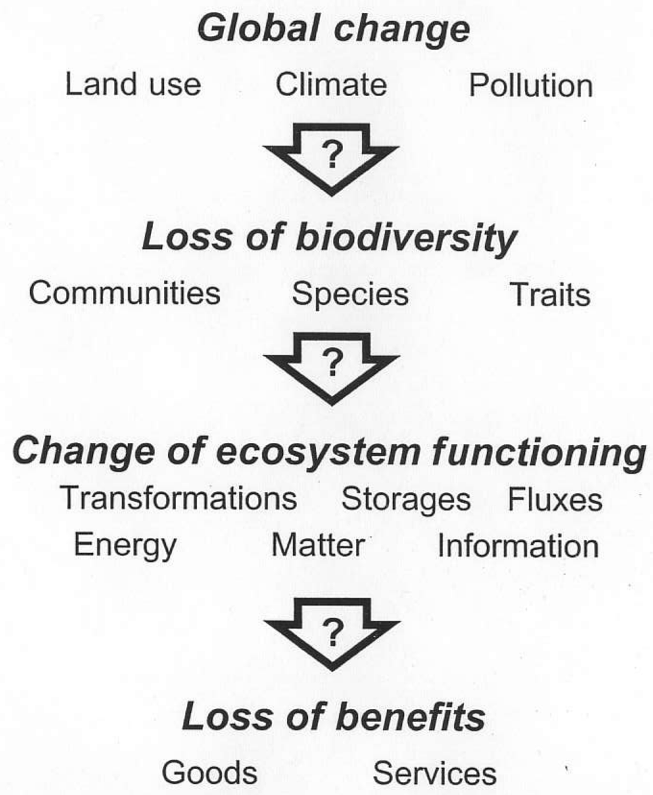

Fig. 13.1. Hypothetical consequences of environmental and land-use changes. The subsequent loss of biodiversity is likely to be followed by functional changes and shifts of ecological complexity. Some of these changes result in a decline in human benefits. Note that there are many unclear connections and unsolved questions between these levels.

Looking closer, many research projects are continuing traditional approaches under the label of biodiversity just to gain funding. Perhaps more problematic is the lack of theory and concepts, which is a source of confusion and misinterpretation of results.

Different opinions and views of biodiversity research simply reflect the fact that the concept of biodiversity summarizes and integrates various aspects of biotic variability at different levels of organization (Bowman, 1993). Organisms are just one of these levels. Other levels are genes, populations, communities or ecosystems. Thus, species diversity is just one part of biodiversity. Yet, it does not inform about abundance, dominance patterns or equitability.

Generally we can distinguish: (i) qualitative variability from (ii) quantitative richness of a community, an ecosystem or an area. In addition, different degrees of (iii) functional interactions create varying ecological complexity. With the focus on plants, this means that phytodiversity integrates the variability between plants, their number and their functional differences. Most attention is concentrated on the number of species, because this is easy to measure. However,

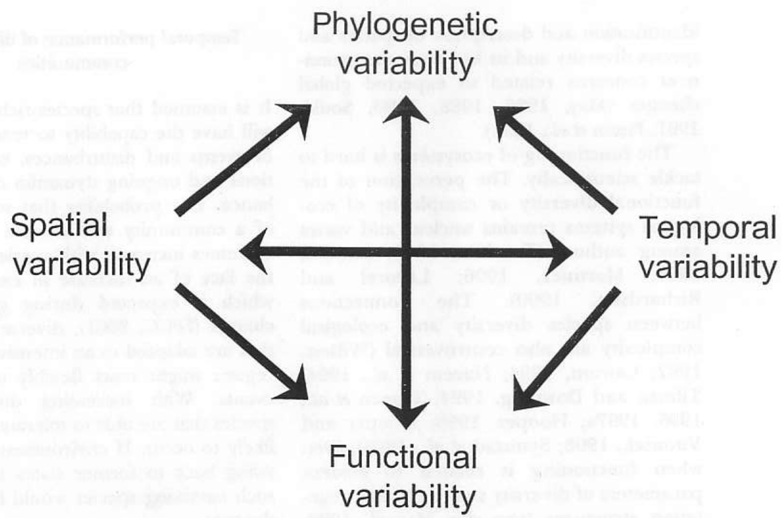

Fig. 13.2. Four aspects of biotic variability. Biodiversity occurs at all categories (spatial, temporal, phylogenetic and functional). Even if the performance of functional variability or diversity is influenced by spatio-temporal restrictions and reflects genetically fixed traits, it cannot merely be explained or predicted on the basis of one single criterion such as species diversity, but has its own quality.

we should keep in mind that taxonomic units such as species are just one possibility for the classification of plants. In this case, the types are based on phylogenetic relatedness. Other criteria could be applied as well, such as growth form or seasonality, and then other classes and units result. This in turn would influence the number of types to be counted.

There is no single index or value for all different aspects of biodiversity. Consequently, effects of biodiversity on ecosystem functioning have to be clearly related to the particular aspects of biodiversity considered in a study.

Functional traits and types

Based on approaches that concentrate on the functional response of species to certain environments (Grime, 1977), different functional groupings have been developed in vegetation science (Körner, 1993). However, guilds and functional groups have been generally more prominent in animal ecology (Hawkins and MacMahon, 1989). Another functional perspective in plant ecology is derived from population biology, where the regeneration of species is seen as a key factor for the maintenance of species diversity (Grubb, 1977). This approach concentrates only on the reaction of populations to functional processes.

The concept of plant functional types (PFTs) or functional groups deals explicitly with functional diversity (Smith *et al.*, 1993; Woodward and Cramer, 1996; Westoby and Leishman, 1997; Woodward and Kelly, 1997). This classification approach is based on functional traits (Walker *et al.*, 1999). In turn, the classification of individual species depends on those functional criteria applied. PFTs are very helpful if global forecasts of effects of climate change are undertaken, because they are both specific and coarse enough to show global patterns and processes (Smith *et al.*, 1993; Diaz and Cabido, 1997). It is not realistic to work at this level with species diversity. The same is true for changes in global biogeochemical cycles and land-use changes.

Functional attributes and traits focus on properties of plant organs or their metabolism. This approach is more flexible and clearly related to criteria such as fluxes of carbon or storage of water. Several functional species traits have been used to classify plants in ways that relate either effect or response to the environment (Noble and Slayter, 1980; Pavlovic, 1994). Now, the functional perspective concentrates on the effects of species, in particular of species diversity, *on* ecological functions (Lamont, 1995; Grime, 1997; Hector *et al.*, 1999). It is evident that the response to changes in the environment is likely to be shifts in the functional composition of a community (Aiguar *et al.*, 1996). If the 'importance' of plant diversity in a changing world is questioned, the concept of functional types is obviously successful (Boutin and Keddy, 1993; Chapin, 1993; Golluscio and Sala, 1993; Diaz, 1995; Box, 1996; Chapin *et al.*, 1996; Diaz and Cabido, 1997; Gitay and Noble, 1997; Diaz *et al.*, 1998). However, the numerical diversity of functional types (alpha-diversity) depends on the selection of certain key functions; it differs for the same real community with different criteria applied. It seems very much more concise to concentrate directly on specific functional traits (Leishman and Westoby, 1992; Solbrig, 1993).

Functional traits are properties of an organism that are considered to be important according to the response to or to the effect on the environment. Functional traits may be reflected in the morphology of plant organs (e.g. leaf size, seed structure) or in morphological capabilities (e.g. resprouting, clonal growth) (Kindscher and Wells, 1995). Other traits or attributes are related to the life cycles of plants. Their 'vital attributes' (Noble and Slayter, 1980) or 'life-history attributes' (McIntyre *et al.*, 1995) and the quantitative contribution of such strategies to communities help to predict their responses to disturbance events. The composition of temporal traits reflects the long-term disturbance regime at the community level (White and Jentsch, 2001). However, important ecophysiological metabolic or mutualistic properties (C3/C4 grasses, nitrogen fixers) are not evident in many cases.

Functional traits can be defined not only by the optimum conditions for species responses, but also by the range of their tolerance and the shape of their response curves to a particular factor. Indeed, most species have plastic responses to the environment, and their role in, for example, post-disturbance recovery is a function not only of their optima but also of the competitive environment they encounter. For example, even shade-tolerant, slow-growing species respond to added light with accelerated growth, but at a slower rate than light-demanding species (Brokaw, 1985; White *et al.*, 1985). The problem is even more complex: the species of a particular ecosystem, and thus the range of responses in that ecosystem, have functional traits that were shaped by past exposures to environmental processes. Thus, there is a twofold historical contingency in responses of species diversity. First, in ecological time, only those species with access to the site can participate in recovery (this access can be influenced by prior disturbance) and, second, in evolutionary time, species adaptations reflect previous evolution. Both determine the diversity of functional responses within an ecosystem.

Whittaker's classification (1972) into alpha-, beta- and gamma-diversity can only be partly applied to this concept, because it does not consider functional diversity (Hooper *et al.*, 2002) or – in a systemic perspective – ecological complexity. Alpha- and gamma-diversity are just an index for the number of objects (species) in a certain subset. They depend on the scale of observation and the number of records. Beta-diversity may be seen as an index for qualitative differences between objects. However, it is mainly applied at the level of communities and then characterizes the resemblance or floristic distance or turn-over between samples. It can be applied to identify spatial heterogeneity and temporal trends. New genetic techniques would allow the calculation of the similarity or dissimilarity (contrast) between organisms. However this approach is as yet uncommon.

Ecosystem Functioning

Processes, mechanisms and functions

Functional aspects of biotic communities are characterized as 'ecosystem processes' (Odum, 1993), 'biogeochemical processes' (Schlesinger, 1991) or 'ecosystem functions' (Schulze and Mooney, 1993). We would like to make a distinction between biotic functions and processes. Processes are mechanisms such as photosynthesis, pollination or nitrogen fixation. Their properties do not depend on the object. In contrast, functions are a relation between processes and objects. We may find functions *of* an object according to a certain process, for example high capability of nitrogen fixation for nutrient retention in soils, or identify a function *for* an object via the same or another mechanism, for example nutrient retention in storage organs of plants.

As already mentioned, there is a difference between functions that affect an organism and those that are the effect of an organism. Some morphological properties of an organism may not easily be attributed to one or the other way of functional interaction. In plants, for instance, the reaction to a given environment (drought) may lead to certain growth. These structural properties, however, may also be genetically fixed and the occurrence of a certain species or ecotype will just indicate the competitiveness of certain functional traits under these site conditions. Functions may also result from different processes.

To ensure the persistence of ecological functions in plant communities in the face of disturbance, functional adaptations of species generally underlie two mechanisms of ecosystem response: complementarity and redundancy (Loreau and Hector, 2001). First, species have evolved a diverse spectrum of abilities relative to disturbance. After a particular disturbance, some species increase or invade, while others decrease or retreat (Vogl, 1974). Thus, ecosystem response is, in part, a result of niche complementarity. Second, when dominant species are primarily the ones affected by disturbances, other species may increase after a disturbance, even if their functional traits are similar to the previously dominant species. This has been expressed by the resilience hypothesis (Walker *et al.*, 1999). Dominant and minor species in the same functional groups are similar with respect to the contribution to ecosystem function, but they differ in their environmental requirements and tolerances and, thus, in their ability to respond to disturbances. Dominant and less dominant species switch in abundance under changing environmental conditions allowing functional stability. Thus, species diversity including functional redundancy is important in ensuring the persistence of ecosystem function under changing environmental conditions and in ensuring resilience in response to a disturbance. Moreover, apparently redundant species may operate on different spatial and temporal scales (Peterson *et al.*, 1998), thereby reinforcing function across scales.

Both complementarity and redundancy can be mechanisms that contribute to overall ecosystem stability. For example, Marks (1974) showed that fast-growing, early-successional trees are able to take up dissolved nitrogen after a disturbance, thus preventing nitrogen export to groundwater and streams. Vitousek's (1984) general theory of forest nutrient dynamics suggested that early-successional species immobilize limiting nutrients quickly after a disturbance.

Ecosystem functioning as a system property will be the integral of all different processes going on between the members of the community. Some of these functions (e.g. carbon cycling) may be relevant to objects (e.g. humans) outside the system (Reich *et al.*, 2001).

Initiated by DiCastri and Younès (1990) and then strongly supported by Chapin *et al.* (1992) and Schulze and Mooney (1993), functional aspects became a major focus of biodiversity research from the 1990s onwards (Baskin, 1994; Mooney *et al.*, 1995a,b; Chapin *et al.*, 1997, 1998; Tilman *et al.*, 1997c, 1998; Schläpfer *et al.*, 1999; Wall, 1999; Loreau *et al.*, 2001; Kinzig *et al.*, 2002; Mooney, 2002; Schmid *et al.*, 2002b). The

identification and description of species and species diversity and its loss were the prominent concerns related to expected global changes (May, 1986, 1988, 1990; Soulé, 1991; Pimm *et al.*, 1995).

The functioning of ecosystems is hard to tackle scientifically. The perception of the functional diversity or complexity of ecological systems remains unclear and varies among authors (Franklin, 1988; Lawton, 1996; Martinez, 1996; Lavorel and Richardson, 1999). The connections between species diversity and ecological complexity are also controversial (Wilson, 1992; Lawton, 1994; Naeem *et al.*, 1994; Tilman and Downing, 1994; Tilman *et al.*, 1996, 1997a; Hooper, 1998; Hooper and Vitousek, 1998; Symstad *et al.*, 1998), even when functioning is related to evident parameters of diversity such as spatial vegetation structures (van der Maarel, 1986, 1988; Pacala and Deutschmann, 1996), plant species composition (Hooper and Vitousek, 1997; Tilman, 1997b) or dominance patterns (Grime, 1987; Smith and Knapp, 2003).

As animals depend directly on vegetation structure and composition, herbivores and other trophic groups have been correlated to plant species diversity (Asteraki *et al.*, 1995; Siemann *et al.*, 1998; Koricheva *et al.*, 2000). Further on, there are correlations between plant diversity and the diversity and functioning of soil bacteria and fungi (Spehn *et al.*, 2000b; Stephan *et al.*, 2000). There is evidence that plant species diversity positively affects key ecosystem processes such as decomposition via its influence on microbial functioning (Hector *et al.*, 2000a; Knops *et al.*, 2001; Mikola *et al.*, 2002). Another important type of interaction is direct mutualism between plants and fungi. Here as well, hints of positive correlations between plant diversity and fungal diversity are found, but methodological constraints have hindered further insights (van der Heijden and Cornelisson, 2002). Generally, the linkage between above-ground diversity and dynamics and below-ground processes and aspects (Wardle and van der Putten, 2002) is one of the important research gaps that has to be filled.

Temporal performance of diverse plant communities

It is assumed that species-rich communities will have the capability to react to a variety of events and disturbances, ensuring functions and ongoing dynamics despite disturbance. The probability that some members of a community will be able to cope with extremes increases with species richness. In the face of an increase in extreme events, which is expected during global climate change (IPCC, 2001), diverse communities that are adapted to an intensive disturbance regime might react flexibly to trends and events. With increasing diversity, plant species that are able to tolerate extremes are likely to occur. If environmental conditions swing back to former states in the future, such surviving species would be already on the spot.

Nevertheless, current biodiversity research is facing the dilemma that changing environmental conditions are accelerating, and that anthropogenic pressures on biodiversity are of global extent (Sala *et al.*, 2000). Obviously, the organismic potential to change its current location by large-distance migration or fast alteration of life-history cycle and growth form will offer survival mechanisms in the face of global change for a certain fraction of species (Higgins *et al.*, 2003). Still, the slow alteration of distribution areas (decades, centuries) will most likely cover only short distances, and evolutionary adaptation mechanisms will most likely take many generations (millennia). The expected spatio-temporal dynamics of global change clearly exceed such low-speed and short-range developments of most species. Hence, there is a sensitive threshold to the ongoing speed of change. As soon as species cannot cope with the speed or the spatial extent of environmental change, they are likely to become extinct. A decrease in local biodiversity is to be expected if the spatio-temporal mechanisms of migration, phenotypic plasticity and dispersal, meta-population dynamics or evolutionary development do not meet the scales of global change (Jentsch *et al.*, 2002; Jentsch and Beierkuhnlein, 2003). Consequently, ecosystem functioning may be permanently altered with respect to biotic feedback, material and energy cycles.

High species diversity is likely to go along with a diversity of ecological rhythms, which can also contribute to stability of ecosystem functioning. For instance, in high mountain ecosystems, a few dominating species reach very long life spans of several hundred to several thousand years. Most of them are trees, dwarf shrubs or clonal grasses such as *Betula nana*, *Pinus longaeva* or *Carex curvula*. Such long-lived, slow-growing species may neither be able to react to changing environmental conditions, nor die owing to some unfavourable decades or centuries. They represent ecological inertia in the face of altering conditions or competitive pressure by new species (Jentsch and Beierkuhnlein, 2003). This can mean both risk and potential for the future of biodiversity.

The risk of not being able to cope with changing environmental conditions by adaptation or migration is simply the fate of extinction (Ehrlich and Ehrlich, 1981). On the other hand, evolutionary inertia or the 'persistent niche' (Bond and Midgley, 2001) may provide temporal refuges in cyclically changing environments. The potential of enduring novel conditions via long-term survival is an option for 'a better future', in which conditions may become favourable again, although this strategy does not seem currently adequate. Species with very long lifespans exhibit genetic stability through time. They do not respond to novel conditions. When trends of alteration return to past conditions, their particular traits may be most successful and even ensure the persistence of these species through cyclic alterations. Populations of some tree species perform prolific resprouting after being cut or blown down.

Diversity and the stability of functions

One of the 'evergreen' topics of ecology is the relationship between diversity and stability of ecosystem functions (Tilman *et al.*, 1994, 2002a; Levine and D'Antonio, 1999; Loreau *et al.*, 2001, 2002; Tilman, 2001). This debate has to be seen as a modern reflection of the idea of the balance of nature, which has been a general paradigm since the 19th century. Now it has shifted to whether and how plant diversity influences ecosystem functioning.

Stability includes the persistence of functions despite disturbance or despite change of environmental conditions. Examples are persistence of productivity, nutrient retention, carbon sequestration, air and water purification and slope stability, and the avoidance of erosion, desertification, and other forms of degradation. The constancy of species composition and abundance patterns, and finally of biodiversity, then reflects the functional continuity of an ecosystem in the face of disturbance impacts (Tilman, 1993; McIntyre *et al.*, 1995). McGrady-Steed *et al.* (1997) demonstrate the positive role of biodiversity for the control and predictability of ecosystems. Naeem (1998) points at the role of redundant species in changing ecosystems for maintaining their functioning ('reliability').

Based on the hypotheses from Connell and Orias (1964) about the expected feedback between species diversity and stability, a theoretical consideration of such mechanisms developed (e.g. Margalef, 1969; Goodman, 1975). May (1972) pointed early on at the restrictions according to the connection of the state of a system (diversity) and its ongoing processes (stability) and suggested replacing diversity by complexity. He postulated that with increasing complexity the variability of whole systems will be lower than the variability of species populations. Lehman and Tilman (2000) also found that diversity stabilizes the community but destabilizes individual populations.

To date much research has been directed towards the interrelation between stability and diversity, because this connection is both theoretically and practically attractive (McNaughton, 1977, 1978; Thierry, 1982; Kikkawa, 1986; Frank and McNaughton, 1991; Johnson *et al.*, 1996; Tilman, 1996; Doak *et al.*, 1998; Tilman *et al.*, 1998; Loreau and Behara, 1999; White and Jentsch, 2001). Decreases in population size as a consequence of resource partitioning in diverse stands may lead to higher sensitivity against stochastic fluctuations.

There is fundamental significance of multi-trophic dynamics for ecosystem processes such as stability, with primary producers in a key role (Raffaelli *et al.*, 2002). Increasing the number of species without increasing the food-web linkages within an ecosystem is not likely to increase the stability (Leigh, 1965).

The purpose of species diversity for stability and maintenance of functions within ecosystems has been discussed in a community-based approach by Walker *et al.* (1999). This paper proposed that persistence in ecosystem function under changing environmental conditions and resilience against disturbance are ensured by functional similarities among dominant and minor species. According to the resilience hypothesis, major and minor species switch in abundance during times of stress or disturbance, thus maintaining ecosystem function. Abundant species contribute to ecosystem performance at any particular time (and are functionally dissimilar from each other). However, minor species contribute to ecosystem resilience during times of stress (Mulder *et al.*, 2001) or disturbance (and are functionally similar to dominant species and could increase in abundance to maintain function if dominant species decline or disappear). Peterson *et al.* (1998) indicated that apparently redundant species operate at different scales and thus reinforce function across scales. It may be shown with the help of model ecosystems, that diversity–stability relationships are likely to occur (Doak *et al.*, 1998).

The answer to the question of whether diversity and stability are related varies with the community or ecosystem that is dealt with. On the other hand, stability concepts differ. Grimm and Wissel (1997) identify four primary stability concepts (persistence, resistance, resilience and constancy). Diversity will influence such different qualities specifically.

Tilman and Downing (1994) demonstrate a linear relationship between species diversity and the recovery of grassland after severe drought. Givnish (1994) doubts the higher stability of diverse stands because of their dependence on certain site conditions and nutrient availability. This indicates that in natural ecosystems both diversity and site effects will have to be considered. Huston and McBride (2002) also hint at the relative importance of both factors for the control of ecosystems. Wardle *et al.* (2000) suggest the importance of above-ground functional group richness and composition, which may dominate stability effects.

Species in turn are capable of changing their own environment. Mutualistic interrelationships between legumes and rhizobia strongly modify the nutrient status of a site (Spehn *et al.*, 2002). Such species are indirect ecosystem engineers, such as termites or ants (Jones *et al.*, 1994).

Species are idiosyncratic in their response to environmental constraints or disturbance regimes. Some species are keystone species that influence ecosystem dynamics more than others (Naeem *et al.*, 2002). For instance, the fuel provided by a dominant understorey grass is critical to the fire regime, species diversity and pine regeneration in longleaf pine forests in the south-eastern United States (Christensen, 1981).

Diversity and productivity

The effects of biodiversity on the productivity of stands are of crucial importance and are closely linked to economic perspectives (Tilman, 1999). Early studies found a positive correlation (Connel and Orias, 1964; Pianka, 1966; MacArthur, 1969). Others came to opposing conclusions (Margalef, 1969). It depends on the system whether effects of diversity per se or of certain parts of the community such as productive species emerge even if an increase in productivity is theoretically to be expected (Tilman *et al.*, 1997b). Guo and Berry (1998) could not find clear effects of species number and biomass at different sites. Nevertheless, many studies detect a positive relationship between plant species richness and ecosystem processes, especially regarding above-ground primary production, and especially in species-poor communities (Schläpfer and

Schmid, 1999; Schwartz *et al.*, 2000; Spehn *et al.*, 2000a; Troumbis and Memtas, 2000; Bergamini *et al.*, 2001; Hector, 2002; Schmid *et al.*, 2002b; Tilman *et al.*, 2002b). Not many studies are able to separate site effects that are controlling both biodiversity and productivity. There is also an interrelation between productivity and functional stability (Lehman and Tilman, 2000; Pfisterer and Schmid, 2002).

The probability of the occurrence of highly productive species grows with increasing species richness (Aarssen, 1997). Additionally species that promote nutrient availability, such as legumes (Spehn *et al.*, 2002), or influence the ecosystems as ecosystem engineers in a positive way are likely to occur in species-rich stands. In Hooper's (1998) experiment biomass varied more within certain levels of diversity than between them. This also hints at the individual functional importance of certain species. Huston (1997) criticizes experimental approaches that ignore the possibility of 'hidden treatments' through the ecophysiological differences in species assemblages. Hooper and Vitousek (1998) find a better use of resources in species-rich stands. This reflects the paradigm of higher efficiency of diverse communities due to niche partitioning.

Not many approaches are able to separate such effects from mere biodiversity effects. Van Ruijven and Berendse (2003) find positive effects of plant species richness on the productivity of communities even in the absence of legumes.

In restoration ecology, it is of crucial importance to determine both the presence of particular functional traits in plant communities and the species diversity as a pool of complementary regeneration mechanisms for community assembly. For instance, diversity can affect initial productivity correlated with soil resources in several ways: the greater the diversity of present response groups to a disturbance, the higher the initial rates of establishment, growth and productivity. The greater the abruptness and magnitude of an increase in resources, the greater the initial selection for rapid colonization and the higher the initial growth rates, leading to critical uptake of soil elements that are otherwise vulnerable to leaching. The greater the productivity, the greater is the differentiation of successional roles and the greater the amount of successional turnover during assembly (White and Jentsch, 2004). This is reflected in changes in life-history traits: resource use efficiency, longevity and age at sexual maturity increase, while relative investment in reproduction decreases. As resources become immobilized in biomass and organic detritus, present diversity creates a filter for further establishment.

In this context, it is remarkable that the greater the resource supply in a diverse community, the greater the importance of disturbance to increase turnover by removal of inhibition (White and Jentsch, 2004). Whereas, the greater the stress or disturbance, the greater the importance of facilitation and mutualism within the species community (Temperton *et al.*, 2004).

Nutrients, soil and relief

In the context of global climate change it is assumed that diverse ecosystems will have better capabilities to adapt to novel conditions and environmental constraints by shifting dominances (Peters and Lovejoy, 1992; Peters, 1994).

Following mechanical ground disturbances, the mineralization of nutrients would lead to nutrient leaching, as demonstrated for dry acidic grasslands in the lowland area of central Europe (Jentsch, 2004). If nutrients become available after disturbance, temporal aspects of species diversity increase in significance. Early colonists are able to store those resources rapidly. When resources become available after disturbance, such as in forest blowdowns, colonizing ability and growth rate are important and can have a lasting impact on ecosystem composition and structure. Rapid establishment supports rapid uptake of resources and stabilization of soil. Such mechanisms have been shown to be important in the tropics. However, generally, biodiversity and its temporal performance may play a decisive role in nutrient cycling.

Hooper and Vitousek (1998) could not prove lower leaching of nutrients in diverse stands. In contrast, Scherer-Lorenzen (1999) and Scherer-Lorenzen *et al.* (2003) found lower levels of nitrate in the leachate under grasslands when their species diversity was high, although plots with legumes showed higher nitrate values and the probability of the occurrence of legumes increased with species diversity. Even in non-fertilized plots without legumes, high concentrations of nitrate occurred due to atmospheric deposition and mineralization. This was only the case in species-poor communities. In rich stands, critical levels of nitrate in the leachate could not be measured.

On steep slopes, soil stability is an important property and also a service for the protection of human settlements and infrastructure. Soil stability is highly dependent on plant cover and rooting patterns. The more diverse the root growth forms, the less likely it is that extreme events will promote soil erosion. The loss of diversity could alter the sensitivity to soil erosion and slope stability in high mountains (Körner, 1999). This can also be perceived in terms of the insurance hypothesis (Yachi and Loreau, 1999).

Combating desertification and degradation is another of the most important international activities in the scope of sustainable development (UNEP, 1992). The problem is mainly caused by increasing human populations and overexploitation in developing countries. In semi-arid climates with high natural variability of drought and rainfall, sites could be negatively influenced by species loss. Species-rich plant communities are likely to be able to shift in abundance or dominance patterns and to preserve ecosystem functioning under stress. At higher scales, multi-patch vegetation patterns are likely to control the process of desertification (von Hardenberg *et al.*, 2001). Spatial heterogeneity or evenness becomes effective for the maintenance of ecosystem functions in terms of promoting or hindering small-scale reactions to ecosystem changes (Wilsey and Potvin, 2000; Wilsey and Polley, 2002). However, this broad topic cannot be completely covered in this review.

Biodiversity and the invasibility of communities

Biodiversity is not constant in time. At the regional scale and within the temporal scales of ecosystems there are fluctuations. Dispersal and succession occur. Species composition may shift. Biodiversity is also influenced by invasive species and vice versa (Palmer and Maurer, 1997; Prieur-Richard and Lavorel, 2000). Due to the increasing connectivity of isolated habitats by anthropogenic vectors, species become introduced and thereby extend their former distribution. Competitive neophytes are initially adding to the flora of a region. As soon as they contribute to the local extinction of several less competitive indigenous species, negative effects on species diversity can follow, especially in biodiversity hot spots (Stohlgren *et al.*, 1999).

High diversity was found to act as a barrier against or at least have a negative influence on ecological invasions and delay them in some communities (e.g. Tilman, 1997a; Crawley *et al.*, 1999; Naeem *et al.*, 2000; Prieur-Richard *et al.*, 2000; Kennedy *et al.*, 2002). Field experiments support the role of diversity in controlling invading plants (Knops *et al.*, 1999; Hector *et al.*, 2001a). However, there are also some contraindications in dynamic systems with high turnover and short-lived species (Robinson *et al.*, 1995; Palmer and Maurer, 1997). Wardle (1999, 2001) is sceptical about findings that support diversity effects because the control of invasion can be species specific and then is related to diversity via the sampling effect.

Even if Dukes (2001) did not find an effect of species diversity in grassland microcosms on the establishment of alien *Centaurea solstitialis*, he observed a stronger suppressed growth of species-poor stands by this invasive species. This means that biodiversity did not prevent invasion but affected the stability of previous ecosystem properties. On longer timescales, this might produce negative feedback. Meiners *et al.* (2004) stress the fact that species-specific aspects and sampling effects are important and overlay diversity effects. Furthermore, it is important to understand species-specific interactions and the mechanisms of competition and mutualism that occur in a given community.

Stohlgren *et al.* (1999) and van Ruijven *et al.* (2003) point out that there is a scale dependence of diversity effects. Such mechanisms are likely to occur only at the community level. At larger scales, other factors (e.g. disturbances, heterogeneity of resource availability) are more decisive (see also Levine, 2000; Wardle, 2001).

However, also at the scale of the community, there is an influence of short-term disturbances that will affect invasibility (Rejmánek, 1989). The problem is that such disturbances and their effects have a short duration. Thus, it is absolutely necessary to look at spatio-temporal patterns. This is true not only for competition-free space but also for the performance of biodiversity that may differ over short distances and time steps (e.g. seasons). In some ecological zones, disturbances and temporal variability can foster invasions owing to environmental constraints. In the Mediterranean, temporal variability strongly controls the diversity of plant communities. The co-occurrence of therophytes, geophytes, dwarf-shrubs and bushes simply reflects the fact that there are temporal niches that are occupied. Even there, an effect of diversity on invasibility can be detected (Lavorel *et al.*, 1999). However, it is important to realize that disturbance may promote diversity. In many cases species-rich stands are frequently disturbed. The invasibility then is controlled by disturbances but these promote the initial diversity as well. This is the case in floodplains and riparian sites (McIntyre *et al.*, 1988; Planty-Tabacchi *et al.*, 1996).

The most sensitive phase is the establishment of invaders and thus the existence of competition-free safe sites. Such conditions can be delivered by disturbances (Burke and Grime, 1996), and this explains why dynamic systems are more prone to invasion than stable ecosystems. As we have seen for the Mediterranean vegetation, dynamic communities are often also rich in species. It will be important to separate effects of diversity and effects of temporal variability in invasion research. Diversity effects have to be differentiated into effects of species number per se and effects of functional diversity (Prieur-Richard and Lavorel, 2000), the latter being more likely to be important (Symstad, 2000).

Human Threats and Benefits

Crisis of biodiversity

The current species-extinction period is mainly caused by human impact, and is estimated to happen at a rate 1000 times greater than the natural rate of extinction (Primack, 1993). Recently, various global change scenarios have been developed that address the effects on biodiversity caused by atmospheric warming, altered precipitation patterns, land-use changes, increased fragmentation, urban expansion and other human activities (Sala *et al.*, 2000). Ongoing discussions among natural and social scientists (Jentsch *et al.*, 2003) have been further alerted by the last report of the Intergovernmental Panel on Climate Change (IPCC, 2001), stating an accelerated speed of change of environmental conditions. The upcoming IPCC report will emphasize the crucial role of extreme events for driving biodiversity patterns.

This 'crisis of biodiversity' as a consequence of human impacts has brought much attention and many repercussions in society, not only because of ethical responsibility and aesthetic interests. More than that, the fear of losing ecosystem functions and especially those that are of societal importance (Ehrlich and Wilson, 1991) characterize such functions as 'ecological services' (Daily, 1997; Daily *et al.*, 1997). This perception is the reason for political attention and societal awareness. Society is afraid that benefits could be lost that are delivered from nature for free. This would mean economic constraints as a follow-up of species decline (Jentsch *et al.*, 2003). The direct use of natural resources (plants) or the direct protection that is given by them (pure water, preservation of soil, protection against avalanches and landslides, etc.) is not the only concern; there is also the loss of potential benefits (e.g. pharmaceutical traits; Cragg and Newman, 2002) that have not yet been identified (Farnsworth, 1988). In this perspective biodiversity per se is regarded as a resource (Plotkin, 1988; Nader and Mateo, 1998).

Biodiversity, however, may also contribute to threats to human health and welfare (Dobson, 1995). Vectors may distribute toxic plants as well as diseases. Public awareness concentrates on human pathogenic microorganisms. Pathogenic microorganisms and insects that are distributed by trade and traffic can affect plants as well. Then species diversity and genetic variability within populations may contribute to the regulation of outbreaks of disease and the severity of such outbreaks (Mitchell *et al.*, 2002). It is mainly because of such assumed capabilities, which are not easy to prove, that biodiversity has a positive image.

Goods, Services and Values

The benefits that society gains from biodiversity are differentiated into use values (extractive benefits) and non-use values (e.g. ethical, non-extractive benefits). Goods and services represent direct or indirect use values. Goods are directly related to an economic profit. Services represent the functioning of ecosystems (van Wilgen *et al.*, 1996; Williams *et al.*, 1996). Services of biodiversity include preservation and renewal of soil fertility, air and water purification, nutrient recycling, carbon uptake, waste detoxification and decomposition, moderation of disturbances and maintenance of genetic diversity for agricultural improvements, as well as control of agricultural pests and human diseases (e.g. Randall, 1994).

It is clear that the value of biodiversity to mankind has many aspects. The ethical value and the heritage that we must preserve for future generations represent a moral duty for society. The aesthetic values are evident as well (Heerwagen and Orians, 1993); some of them may be economically important. However, these values may only be identified and evaluated in the course of an inter-subjective participatory discussion. Biologists are no more competent in these fields than other groups of society.

Meanwhile, the socio-economic value of ecosystem services is widely acknowledged (Costanza *et al.*, 1997). Biodiversity, especially functional biodiversity, is increasingly recognized as decisive for maintaining these services (Hooper and Vitousek, 1997; Hector *et al.*, 2001b). Still, it remains a fundamental challenge to assign economic and ethical attributes to particular species, communities or to ecological functions, in order to propose conservation measures where the obtained benefits exceed the costs necessary for action (Jentsch *et al.*, 2003). Nevertheless, there are some approaches to calculate services and goods derived from ecosystem functioning at a monetary scale (Huston, 1993; Buongiorno *et al.*, 1994; Pearce and Moran, 1994; Montgomery and Pollack, 1996; Costanza *et al.*, 1997; Pimentel *et al.*, 1997; Rickleffs, 1997). As money is an efficient tool to make things comparable and to communicate the value of a subject, it may serve as a powerful argument for the preservation of biodiversity (Perrings, 1995). It may also contribute to finding solutions in conflicts between ecology and economy (Gowdy and Daniel, 1995).

Balmford *et al.* (2002) estimate, based on conservative assumptions and using a broad range of evaluation techniques such as hedonic pricing, contingent valuation and replacement cost methods, that there is a tremendous underinvestment in nature reserves. After their calculations and review, the benefit:cost ratio of reserve systems is around 100:1. Still, the value of biodiversity is most appreciated in a crisis, and in crises its value is extraordinary.

To determine monetary values of biodiversity that are not reflected in current market prices is an important task from an economic perspective (Jentsch *et al.*, 2003). These values include: (i) non-consumptive use values, such as the benefits that species richness provides to tourism; (ii) indirect use values for ecosystem stability or functions, such as the provision of clean water; (iii) option values, such as future use in pharmaceuticals; (iv) existence; and (v) bequest values (Perrings, 1995; Costanza *et al.*, 1997; Fromm, 2000; Heal, 2000; Dasgupta, 2001). A debate has evolved that elaborates the conditions under which economic valuation of biodiversity is sensible (Hampicke, 1999; Seidl and Gowdy, 1999; Nunes and van den Bergh, 2001). Limiting factors include the non-substitutability of the natural resource, the fact that societal preferences for the natural good to be valued cannot be represented by individual preferences, and that institutional structures significantly influence the results of the monetarization.

As biodiversity conservation typically causes costs at the local level while producing a global public good, special attention is paid to developing well-defined mechanisms for compensating local communities and land users (Ring, 2002). Hence, research on global biodiversity governance further includes the investigation of incentive structures and policy instruments (OECD, 1999; Barbier, 2000).

We can only briefly mention that, even if most authors focus on biodiversity-related economic evaluations on positive aspects of diversity and genetic resources and benefits (e.g. ten Kate and Laird, 2002), invasive non-indigenous species – which may add to species diversity – are causing enormous costs and hazards (e.g. Pimentel *et al.*, 2000). Some invasive aliens such as giant hogweed (*Heracleum mantegazzianum*) in Central Europe (Pysek and Pysek, 1995) may even cause severe health problems.

If invasibility is reduced by biodiversity, as has been indicated above, then the risks that are related to non-indigenous plants will be reduced in species-rich stands. However, we have demonstrated that factors other than diversity decide whether a community is prone to invasion. In the case of giant hogweed, no effect of species diversity could be demonstrated but the disturbance regime was of crucial importance.

Heuristic Methods and Approaches

Theoretical considerations and diversity hypotheses

Theoretical considerations on the importance and mechanisms of species diversity are a challenging field in ecology (Naeem *et al.*, 2002; Tilman and Lehman, 2002). Vitousek and Hooper (1993) initially identified three major possible relationships between biological diversity and ecosystem-level biogeochemical functions: no effect, linear correlation and asymptotic approximation of a maximum level. The third was regarded as reflecting species redundancy by Lawton and Brown (1993). It has to be stressed that these concepts focus on 'species richness' only, even if graphical representations are often simplified to 'biodiversity' (Naeem *et al.*, 2002). Functional diversity, which is not necessarily correlated to species richness, is rarely explicitly addressed (Wardle *et al.*, 2000).

Since those initial theoretical concepts, many other views and hypotheses were published (review in Schläpfer and Schmid, 1999). Within the group of hypotheses that describes the occurrence of positive effects, perhaps the linear hypothesis (complementarity hypothesis) and the idiosyncratic hypothesis represent extreme positions. The first assumes that each species adds a comparable part to ecosystem processes. The reason for such a pattern is seen in the assumed complementarity of species (Hector, 1998; Hooper, 1998). We have already pointed out that, because of their ecological traits, species perform specifically. An equal contribution of each species to ecosystem functioning is unlikely.

Nevertheless, there is an indication that a close relationship between particular ecosystem processes and species diversity occurs. This does not imply general mechanisms. Species diversity might be relevant only within a given frame. Most experiments have been conducted within rather species-poor communities, and it is not surprising that within a set of just a few species a correlation of increasing number of species to functioning will be proven. The response of ecosystem functions to diversity is often controlled by restrictions of resource availability. Such restrictions will be effective in one case but not in another. If effective, increasing diversity would not influence the functioning of the system.

Biodiversity effects, such as higher biomass production with increasing species diversity in experimental grasslands (e.g.

Hector *et al.*, 1999), can occur per se as an effect of ecological complexity and functional complementarity (Hector, 1998) (Fig. 13.3). However, they can also be a result of probability. A critical perspective on biodiversity effects, the sampling hypothesis, says that with increasing numbers of species (or other objects) the probability arises that single powerful (e.g. productive) species will occur and contribute to the function of interest (Huston, 1997). Those species that are lacking in species-poor stands can be key species, which play decisive roles in diverse communities. This problem is hard to tackle. However, it seems possible to separate sampling and biodiversity effects (Loreau, 1998b).

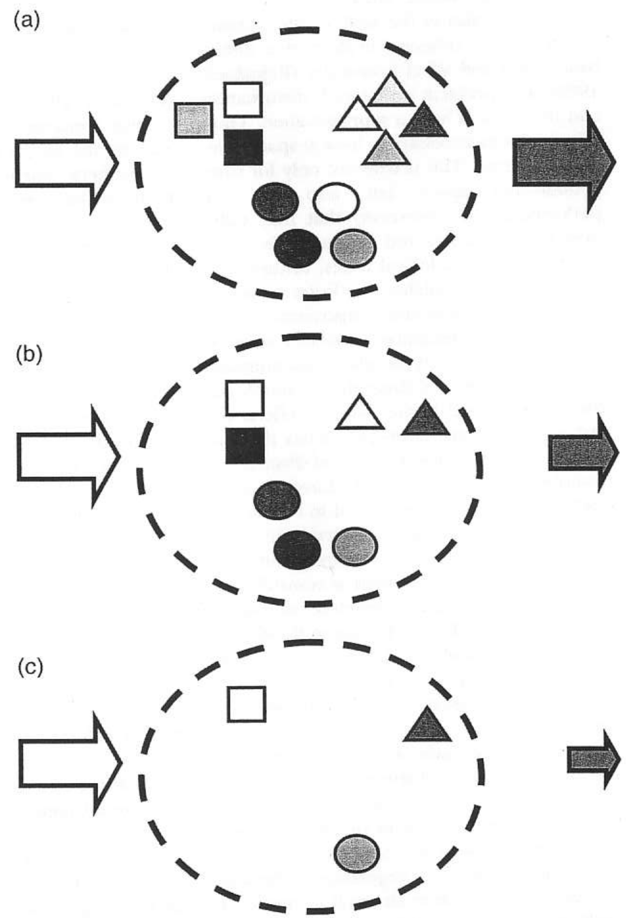

Fig. 13.3. According to the *complementarity, rivet* or *linear hypotheses,* the loss of species diversity is assumed to lead to a loss of functioning or output (dark arrows) of the community (dashed lines). This example simulates a loss from 11 (a) to 3 (c) species (objects) that belong to three functional groups (symbols). Every species contributes to the functioning of the community.

The rivet hypothesis (Ehrlich and Ehrlich, 1981) says that some species contribute additionally to the functioning of ecosystems. The hypothetic trajectory along a diversity gradient is then more stepwise than linear. However, it is inconsistently interpreted. Some views are close to the complementarity hypothesis rather than the keystone hypothesis.

A modification of the complementarity or linear theory is the redundancy hypothesis (Walker, 1992; Lawton and Brown, 1993; Gitay *et al.*, 1996). This consideration predicts that the cumulative contribution of species in diverse communities will show an asymptotic distribution. When transformed to log scale, the data become linear. For a given diversity, each additional species contributes or adds in a different way to the functioning of this system. Just recording the number of species therefore ignores the individual response capabilities of species depending on the number of species that are already there. In any ecosystem, there are limits to the performance of certain functions. There are maximum values or thresholds that can be achieved. In less-diverse communities, any additional species is important, but after a certain threshold new species will not add remarkably to ecosystem functioning (Fig. 13.4). This hypothesis has been criticized from a nature conservation perspective because it implies that some species are unnecessary and their extinction would not cause negative effects.

The importance of redundancy effects depends on the dynamic trend of the community. The increase or decrease in functioning can be influenced by the direction of the development (Naeem *et al.*, 2002). It matters whether species are added or lost. Non-linearity and hysteresis is possible and even likely to occur. The response of ecosystem functioning will differ for the same level of species diversity (Fig. 13.5). Another source of redundancy may be rareness. If organisms are rare or afford little space, they will not interact. Then, it is possible that the same ecological niche is occupied by different species. They will contribute to the species diversity of the community but not increase its complexity ('functional analogues' after Barbault *et al.*, 1991). The taxonomic similarity between species (e.g. their assignment to a genus or family) does not necessarily hint at functional resemblance. Nevertheless, closely related species or representatives of one life form are quite often regarded to be functionally redundant. This is due to the fact that some morphological or ecological traits are restricted to a limited set of genetically related taxa.

The idiosyncratic hypothesis takes into account that the response of an additional species depends on the complexity of the community that is already established. Unpredictable interactions occur (Fig. 13.6). There is no clear linear or non-linear trend but more or less chaotic behaviour of the system. This cannot be explained by keystone species because here the functioning of a species is not regarded as independent. This theory does not state that there is no effect, but that the effects are individualistic and not to be predicted only by the number of species.

The unequal contribution of species to functioning is reflected by other hypotheses. The fundamental difference is that the following hypotheses assume that the contribution of a species is genetically fixed. Hence, its functional performance does not depend on the diversity of the community. Consequently, some species would be more efficient than others under certain site conditions.

If only a few or one single effective species occur, they can be regarded as 'keystone' or 'key species'. Functioning of the community will more or less exclusively depend on this species. In most cases, there will be more than one species that is strongly effective. With increasing species diversity the probability of the occurrence of effective species increases as well ('sampling effect') (Fig. 13.7).

Hector *et al.* (2002b) have tested the sampling effect hypothesis (Aarsen, 1997; Huston, 1997; Tilman *et al.*, 1997b). Although diverse communities are strongly influenced by some dominant plant species, it could not be shown that species with highest biomass in monocultures were also most efficient in mixtures. Yields from mixtures

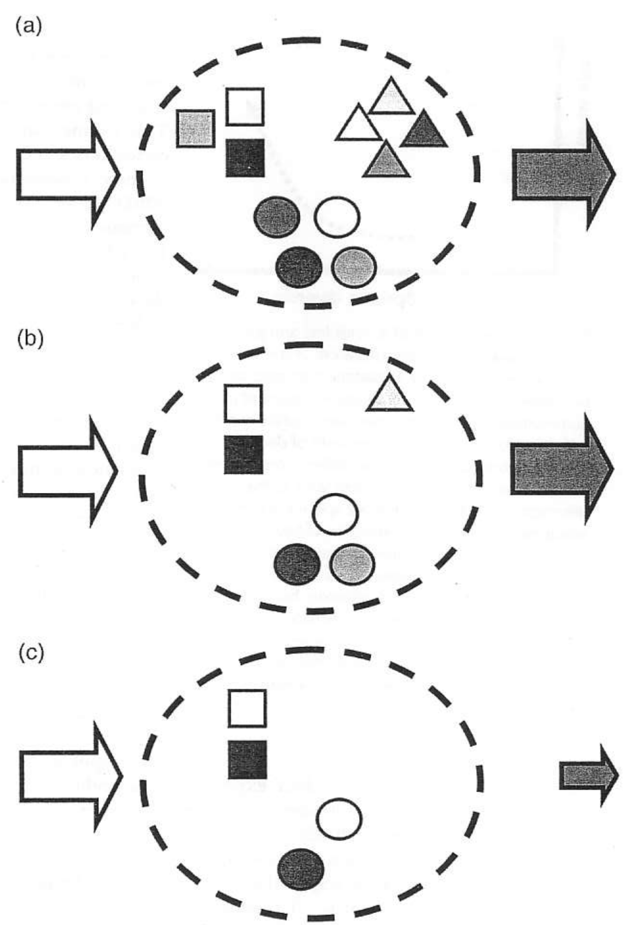

Fig. 13.4. The *redundancy hypothesis* predicts that there are redundant species within a functional group, which contribute only to species diversity but not remarkably to the functioning of a community (dashed lines) (a, b). Only if complete functional groups are lost (c) will reductions of functionality occur and the output of key functions (dark arrows) decline. Species diversity is reflected by the number of objects and functional diversity (functional groups) by different symbols.

were generally higher than the monoculture yield of dominant species within these mixtures. Pacala and Tilman (2002) support a shift from the sampling hypothesis to the complementarity hypothesis.

If there is a stronger effect of an increase in species diversity than expected from stochastic mixtures, 'overyielding' is detected. For instance, there are higher common values than might result from adding the values for single species derived from monocultures. In agricultural communities, it has also been found that certain combinations of species in polycultures had

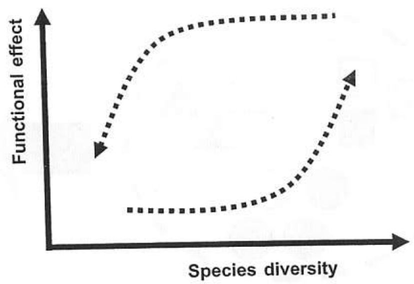

Fig. 13.5. The direction of species loss and gain is likely to cause different repercussions at the same level of species diversity. Hysteretic processes and non-linear response curves are mainly relevant in communities with low turnover rates and for species with high longevity. At the same level of diversity, saturated communities will then differ strongly from pioneer stages. Initial mechanisms such as the selection of functionally relevant species (e.g. in seed mixtures) will differ from extinction of key species. In communities with high turnover rates, both curves will be rather close. As ecosystem functions are not directly connected to species diversity but influenced more by ecological complexity, the redundancy of species is a matter of the direction of temporal processes such as invasion or extinction and of the time that is available to strengthen functional interactions such as competition.

higher biomass production than expected when reducing initial species diversity (Vandermeer *et al.*, 2002). However, Vandermeer *et al.* point out that overyielding does not necessarily imply that interspecific facilitation occurs. It could be related to species-specific capabilities in the use of resources.

Biodiversity is considered to be a potential resource that might become effective in the future. Rare species of today could play more important roles under the expected new environments of tomorrow. The different abilities of species to tolerate and react, to survive and to disperse are some sort of insurance against changing conditions in heterogeneous landscapes (Loreau *et al.*, 2003). They could become relevant even when no evident functional diversity *within* a group of plants can be detected under recent conditions. With increasing numbers of species within such a group, the probability grows that the functions that are attributed to this group will be maintained in a changing environment (Chapin *et al.*, 1996). This means that redundancy under certain conditions will deliver the potential to react to new conditions (Fonseca and Ganade, 2001). The 'reliability' of communities increases with species diversity (Naeem and Li, 1997; Naeem, 1998). Based on such thoughts, Yachi and Loreau (1999) have developed the insurance hypothesis (Fig. 13.8).

The above-mentioned theories do not consider the influences of site conditions and especially of resource availability. Complementarity is most likely to occur when the participating species are not limited, for example by nutrient availability. At poor or dry sites, individuals of different species may exist in low abundances without any interaction. Adding or losing species will produce stochastic reactions within the limited frame of the environment. On the other hand, it can be observed that when resource availability is high, for example on fertilized or wet sites, only few specialists will be competitive and abundant. There, redundancy is common. In conclusion, we emphasize that the type of response depends very much on the availability of resources such as light, nutrients or water (Fig. 13.9).

Experimental Approaches

Removal experiments

It is strikingly simple to follow this approach and to exclude some species from formerly diverse communities in order to simulate the loss of plant species diversity. Most of the removal experiments in the literature are applied to animals and focus on food-web complexity. A critical point about removal experiments with plant communities is the impact on nutrient cycling. This is a problem even if no soil disturbances are affected or if no dead biomass or litter is left. After cutting a plant or destroying it with herbicides, its remaining root biomass will be mineralized. This leads to temporarily enhanced nutrient values in the soil (Jentsch, 2004). In consequence, these nutrients will promote the remaining specimens from other species to be more productive. This effect then could be interpreted as a positive signal due to less competition whereas in fact it is a hidden fertilizing effect. Such processes are hard to avoid and even harder to quantify. This may explain why species-removal experiments have been widely neglected, whereas synthetic experiments have had a strong impact in the scientific community.

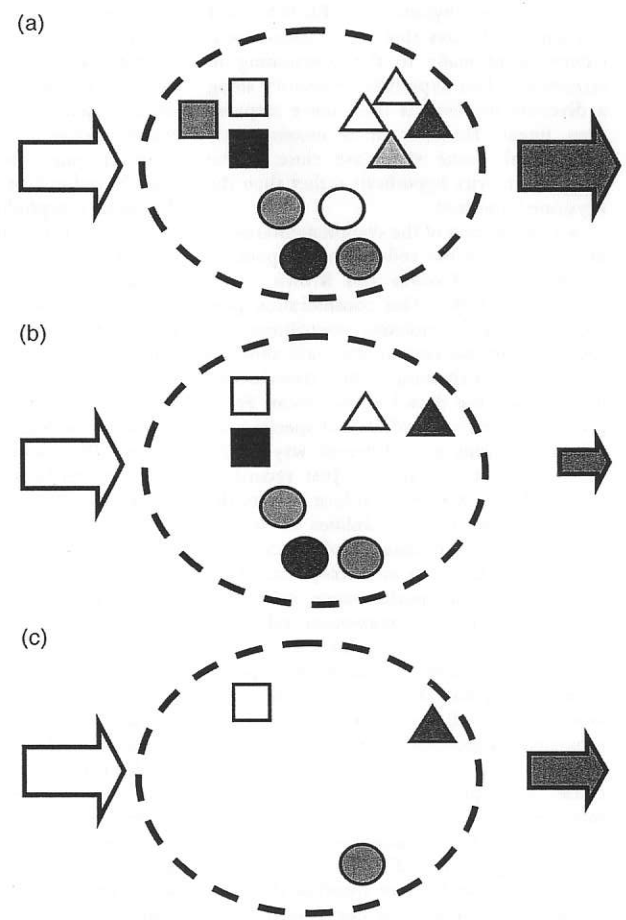

Fig. 13.6. The *idiosyncratic response hypothesis* implies that it is almost impossible to predict the effects of a decline of functional complexity that accompany species loss. Non-linear chaotic responses may occur. An initial decrease in the functioning (dark arrows) of a community (dashed lines) (a, b) can be followed by increases due to changing interactions (e.g. the removal of competitive but slow-growing species) during ongoing losses of species (objects) (c).

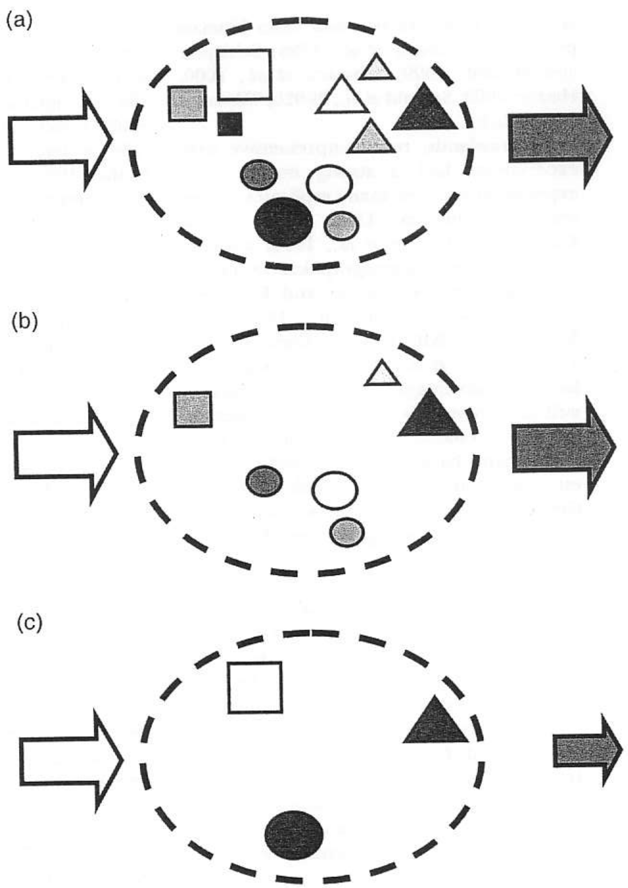

Fig. 13.7. The *sampling hypothesis* points at the lower probability of the occurrence of strongly influential species (represented by larger objects), according to the function of interest (e.g. biomass production) (dark arrows), with decreasing species diversity (a, b). It is difficult to avoid such effects in synthetic/additive experiments. Only some key species contribute substantially to the functioning of the community (dashed lines). If key species representing important functional groups (symbols) are preserved, there will be no negative effects of species loss to functioning (c).

Symstad and Tilman (2001) showed, in a 5-year removal experiment on abandoned agricultural fields, that there is a strong effect of the functional groups remaining in the community. The ability to occupy the space and to make use of the resources that have been required by the former competitors is unequally distributed across functional types. With this approach, traits have been identified that might become important in the course of species extinctions. Synthetic experiments with all species starting at the same time after the experiment has been installed are not able to simulate such spatio-temporal aspects.

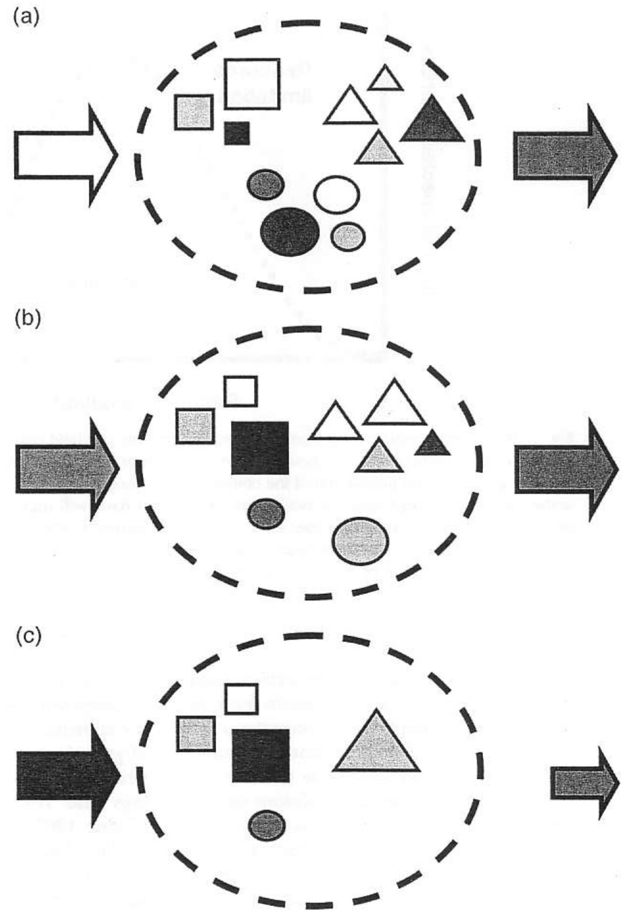

Fig. 13.8. The *insurance hypothesis* hints at the higher probability of flexible functional responses and adaptations to novel environments in species-rich communities (dashed lines). Shifts in abundance or dominance of species and in their relative contribution to the functioning may compensate for restrictions or the decline of sensitive species (a, b). If a negative threshold of diversity is surpassed, further changes in the environment will not be answered adequately (c).

Wootton and Downing (2003) point out that the results of species removal are highly idiosyncratic and therefore impossible to forecast. They suggest combining targeted species removals with general diversity manipulation. This approach could be helpful to find out which effect is related to key species (Mills *et al.*, 1993) and how biodiversity contributes via complex interactions between species to ecosystem functioning or buffers environmental extremes (Hughes *et al.*, 2002).

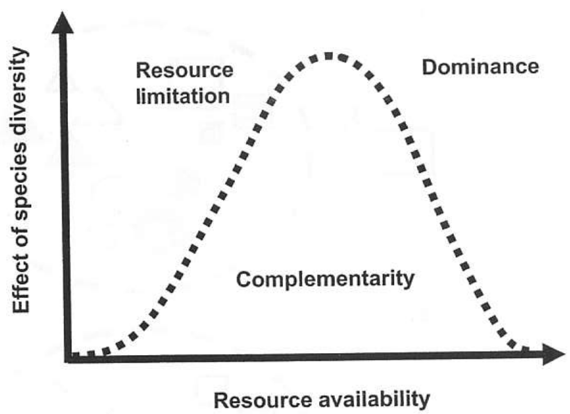

Fig. 13.9. Controversial findings from different experiments and field research can probably be explained by underlying effects of resource availability. An increase or loss of species diversity will hardly have any effect (e.g. on biomass production) if the community is strongly limited in resource supply (e.g. nutrients, water and energy). High resource availability on the other hand will support the predominance of a few or one specialized and competitive species (K species). Additional species will not be important. Only under intermediate conditions (for the ecological scale of the community) will complementarity be found and is species diversity likely to be functionally effective.

Synthetic experiments

During the search for interrelationships between biodiversity and ecosystem functions, experiments in simple model ecosystems were much supported. The reduction of complexity in these systems as well as their strongly controlled environmental conditions (see also Fukami *et al.*, 2001) would allow us to identify effects of changing variables such as species diversity (Schmid *et al.*, 2002a). In addition such experiments can be carried out within rather short timeframes. Their results can be validated by means of replicates. Furthermore, specific experimental designs can be repeated at different sites (Hector *et al.*, 2002a,c). This helps to identify generality behind individual experimental results.

One of the first influential projects in this field was the ECOTRON microcosm experiment (Naeem *et al.*, 1994, 1995, 1996; Hodgson *et al.*, 1998; Lawton *et al.*, 1998; Thompson and Hodgson, 1998). This approach was still very artificial. It was carried out in isolated chambers. However, it prepared the way for more natural field experiments.

Most experiments with plants focus on short-lived species (grasses, forbs) or are carried out on artificial substrates to reduce site heterogeneity and noise. The simplification of the approaches leads to a gap in the validation of gained results versus natural communities. Critical voices point at many other shortcomings and restrictions of such experiments (Grime, 1997; Huston, 1997; Fridley, 2002).

The heuristic value of experiments is clear. Functional consequences of biodiversity loss and causal effects can be detected – if just under the restricted conditions of an experiment. This helps to support or falsify hypotheses that have been developed theoretically. In nature many factors are interacting. It is impossible to separate them and to relate observed phenomena to selected site conditions directly.

Many recent experiments and manipulations that deal with biodiversity effects concentrate on plants because they are non-mobile and in many cases easy to control and to establish. In addition, they represent only one trophic level. Most of these research projects find positive correlations between species diversity of plants and key

ecosystem functions (in most cases biomass production) (Hector *et al.*, 1999; Schläpfer and Schmid, 1999; Schwartz *et al.*, 2000; Hector, 2002; Schmid *et al.*, 2002b; Tilman *et al.*, 2002a,b).

In grasslands, two comprehensive field experiments had a strong impact. One experiment featured many replicates on one site in Minnesota, USA (Cedar Creek Experiment; Tilman *et al.*, 1996) and the other followed biogeographical gradients across Europe (Biodiversity and Ecosystem Processes in Terrestrial Herbaceous Ecosystems – BIODEPTH; Diemer *et al.*, 1997; Hector *et al.*, 1999). Grasslands do have the advantages of being spatially as well as economically important and they are easy to establish in a short time. Experiments have also been installed in forest communities (e.g. in Finland and in Germany). These will continue until stable conditions have developed, then the results will be published.

Due to the complexity of natural and anthropogenic ecosystems and landscapes, the monitoring of the loss of diversity is rather time consuming and will only deliver good results for selected examples and areas. There, it will be necessary to prove the generality of the results and to identify the causes of the decline, if it occurs at all. However, local species diversity may even increase because of new vectors and invading species at the same time as global extinctions occur, even in the same area, when rare species are lost.

Some important insights into ecological functions of biodiversity and driving factors for the decline of endangered species have been gained through the recent use of experimental designs at the landscape level (e.g. Caughley and Gunn, 1996). Results from experimental manipulations predict that high biodiversity will enhance ecosystem responses to elevated carbon dioxide and nitrogen deposition (Reich *et al.*, 2001; Catovsky *et al.*, 2002). Reich *et al.* (2001) show that current trait-based functional classifications alone might not be sufficient for understanding ecosystem responses to elevated carbon dioxide.

Nevertheless, experimentally proven correlations between biodiversity and ecosystem functions must be related to temporal and spatial scales (Oksanen, 1996; Rapson *et al.*, 1997; Bengtsson *et al.*, 2002; Levine *et al.*, 2002). Small-scale effects are not necessarily valid at larger scales (Waide *et al.*, 1999; Weiher, 1999; Chase and Leibold, 2002).

To apply a functional perspective and to identify the repercussions of changes in species diversity on the complexity of ecosystems will be almost impossible in most natural ecosystems. This is why reductionist models and experiments with defined conditions and environmental interactions became prominent during the past decade, when forecasts on the effects of species loss on key ecosystem functions were discussed.

Modelling approaches

Another promising heuristic approach for investigating the relationship between diversity and functioning is the application of ecological models (Loreau, 1998a). Models allow us to simulate interactions and multi-species diversity effects without being prone to the restrictions and noise of field investigations and experiments. In addition, they are not restricted to short-lived species. However, most models are still extremely simple and cannot cope with the reality of ecological complexity.

Doak *et al.* (1998) found that statistical averaging would result in greater stability of ecosystem functioning at high levels of diversity. Tilman *et al.* (1998) demonstrated that statistical averaging is not a necessary consequence of high diversity, but depends on the system that is investigated. The 'portfolio effect' may lead to a limited stabilization of the community due only to statistical grounds. The term is derived from economics, where experience shows that a diversified portfolio will be less endangered by stochastic market processes.

Lehman and Tilman (2000) compared different types of ecological models (mechanistic models, phenomenological models and statistical models). They showed that, even if the models perform differently, the general reactions of the simulated systems according to the stability of the communities are comparable: the variability of the entire communities decreased and the variability of the contributing populations increased.

Yachi and Loreau (1999) formulated the insurance hypothesis based on biodiversity models. Their model proves that the maintenance of key ecosystem functions as a reaction to temporal variability of the environment is more likely to occur in species-rich stands. Other ecological models that are dealing with insurance and related research questions have produced comparable results (Fonseca and Ganade, 2001; Petchey and Gaston, 2002).

Generally, ecological modelling can be used as a tool for integrating scientific results from various experimental and observational analyses as well as scenarios of changing environmental or socio-economic conditions. Spatially explicit grid-based models (De Angelis and Gross, 1992; Grimm, 1999) show that spatio-temporal correlations are a key to understanding system dynamics, their vulnerability or resilience (stability). There is growing evidence that such correlations are the currency to understand not only spatio-temporal dynamics of ecological systems, but also general mechanisms of biodiversity and species-specific functions and traits (Wiegand *et al.*, 1999).

Recently developed ecological–economic models are promising techniques for the integration of social and natural sciences. They are pioneering approaches for economic assessments of different ecological management options (e.g. Frank and Ring, 1999; Johst *et al.*, 2002). For instance, the modelling approach establishes the relationship between economic parameters of disturbance-management alternatives and the ecological effects on biodiversity properties.

Conclusion

Looking at certain key functions that are thought to be important, we do have to keep in mind that primary ecological factors such as water and nutrient cycling, energy in- and output and secondary or integrated abiotic constraints such as soils, relief and climate are strongly influencing ecosystem processes. The direct effect of such mechanisms will be much more important in many cases than biodiversity effects. In addition, direct human impact (e.g. pollution) may have consequences for biodiversity and ecosystem functioning. Cause and effect of changes in ecosystem functioning are then difficult to separate.

Nevertheless, plant species diversity plays a significant role for the control of ecosystem processes and overall functioning. In some cases, the effects will be related to complementarity of functional traits of species, in others just to the occurrence of key species (e.g. productive ones or ecosystem engineers). Today, the impact of biodiversity on ecosystem functioning can be neither predicted nor neglected.

Species are not similar. The historical and evolutionary background of each species may have a strong influence on the performance of entire ecosystems. Traits control the reaction pattern and metabolic capabilities of plant species. It is not possible to conclude general principles simply from the response of a given set of species. Mooney (2002) points at the fact that there is no simple solution to the controversial standpoints of whether the number of species or the variability of functional traits determines ecological functioning.

From a methodological point of view, it is absolutely necessary to link controlled but artificial experiments not only with models but also with standardized monitoring techniques. It is promising that the communication and exchange of results gained with different approaches will contribute to a better understanding of ecological mechanisms. In this field of cross-cutting research, enormous gaps still have to be filled.

Another challenge is the transfer or the validation of results across systems and communities. What has been found for the relationship between biodiversity and productivity in Central European grasslands (Minns *et al.*, 2001; Hector, 2002) may be true for North American grasslands (Tilman *et al.*, 2001, 2002a,b) but will be hard to apply to deciduous forests or even subtropical or tropical ecosystems.

Most of the diverse and threatened ecosystems of the world are poorly productive (e.g. the South African fynbos; Davis *et al.*, 1994). Other mechanisms and functional interrelations will be important in these communities and may be reduced or modified by biodiversity loss. The key functions (e.g. inflammability and proliferation of fire as a key disturbance for the maintenance of diversity) are largely to be identified. On the other hand, rather species-poor ecosystems such as mangroves might suffer severe functional restrictions with plant species losses (Field *et al.*, 1998).

The ecological importance of biodiversity can be subdivided into aspects that are relevant for ecosystem functioning and others that are, in addition, important to human society. Some aspects are exclusively relevant to humans (aesthetical and ethical values), but these have to be discussed at a broad societal level.

The paradox of depending on biodiversity and threatening it at the same time is one of the phenomena in complex human societies that are difficult to cope with. The human contribution to the processes that maintain and threaten biodiversity works at different scales. The regional diversity in Europe is to a major part dependent on anthropogenic disturbances and structures. If land use was stopped, biodiversity would be lost. Some species have even evolved with close dependence on land-use techniques and crops. At the global scale, land-use change today is the major driver for the irreversible loss of genetic variability (Sala *et al.*, 2000). This is due to the speed of transitions and to the technical and chemical intensity that is applied to fulfil social and economic requirements.

The same is true for the benefits that can be derived from biodiversity. Services at one spatial or temporal scale may be accompanied by a non-sustainable use of such benefits. The awareness of the risk of economic restrictions in connection with the loss of biodiversity might strongly support action to slow down or even stop this development.

Sustainable, long-term use and development is only possible if crucial ecological compartments and objects are maintained. Biodiversity is a complex resource that is hard to define and to analyse with respect to its functional effects. However, there is strong support for the idea that it contributes to the maintenance of ecosystem functioning, which is fundamentally important for human beings. Some of the potential uses of biodiversity have not yet been discovered because of the large number of unknown species and our limited knowledge of the functional traits of plant species at the global scale.

Implicitly, the loss of biodiversity has been regarded as an indication of the loss of quality of life since the publication of Rachel Carson's book in 1962. In more recent decades this development has been perceived to be negative. However, it has actually speeded up in recent years. Short-term economic interests are more prominent and the survival of growing human populations in marginal habitats has to be ensured. Obviously, those socio-economic forces are powerful drivers for the loss of biodiversity. On the other hand, this ongoing loss is very likely to be followed up by violent negative feedback. Profits from the use of the global stock of biotic resources and ecosystems could be endangered in the future. Then, short-term individual economic gains would be followed by long-term societal economic losses.

Natural scientists tend to ignore normative social or economic values. In the case of biodiversity it would be foolish not to cooperate with socio-economic scientists in order to both identify the driving forces of extinctions and forecast and evaluate their effects. This chapter concentrates on the ecological part of the problem. Economists have developed methods to scrutinize the value that is given to natural subjects by people. One method is to ask for the 'willingness to pay'. However, this willingness is strongly influenced by knowledge, and knowledge on biodiversity is still fragmentary.

Ecological complexity, meaning the functional interactions between biota and their abiotic environment, can be seen as the most important aspect of biodiversity for human society as it controls the services and goods that can be derived from ecosystems. The biota does not exist in isolation from abiotic site conditions (extrinsic factors) but influences them and is influenced by them. This is crucially important for basic ecological research as well. The functional interactions between single elements of ecological systems such as organisms or soil or water bodies are still not completely understood. The web of interactions and reactions is woven at different levels of time (from osmotic responses to evolutionary patterns) and space (from cells to landscapes). Systemic features emerge from the non-stochastic interactions between species under specific site conditions and disturbance regimes resulting in comparable assemblages and structures. Such structures and their resource character from the human perspective are nothing less than the effect of ecological complexity. Thus, only a better understanding of ecological complexity will help us to save and manage biotic resources and functioning. Former experiences and knowledge have to be adapted to novel circumstances in the face of climate change.

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