

## Diversity and Ecosystem Function

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### 11.1 Introduction

It is generally supposed that species diversity is important for the stability and proper functioning of ecosystems and for ecosystem services. Indeed, the Shannon formula ( $H'$ ) for species diversity was introduced to ecology as a stability index (MacArthur 1955). The relation between diversity and stability is complex. For instance, population outbreaks are more common in species-poor boreal regions than in species-rich tropical communities, or in species-poor agro-ecosystems and planted tree monocultures than in the species-rich natural communities. This has led to the 'diversity begets stability' statement. However, the causality of observed patterns could be reversed: the tropics are so rich in species because they have experienced long-term environmental stability, which enabled survival of many species, or even both; stability and diversity can be dependent on similar sets of external characteristics, so that they are just statistically correlated, without any direct causal relationship.

Since the 1990s, the global loss of biological diversity has become a major concern. Could indeed the decline of biodiversity impair the functioning of ecological systems? And do we have sound evidence of ecological consequences of declining biodiversity? These are matters of concern and controversy (e.g. Naeem *et al.* 1999; Wardle *et al.* 2000; Grace *et al.* 2007), but also of a growing consensus (e.g. Loreau *et al.* 2001; Hooper *et al.* 2005). Pimm (1984) and others showed that there are many aspects of stability and diversity. The term ecosystem functioning includes a variable set of characteristics. In natural ecosystems, diversity is a 'dependent variable', i.e. it is a result of evolutionary and ecological processes, which affect community composition and also ecosystem functioning.

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If we want to study diversity and its effects, we must be able to quantify diversity, and we need to understand the factors that affect diversity in nature. Then, we will have to quantify the ecosystem functions that are expected to be affected. Next we must find interrelationships and find ways to test the causality behind statistical relationships.

## 11.2 Measurement of species diversity

Ecologists use various terms for diversity: species diversity, ecological diversity, richness, and recently biodiversity and complexity. However, the concepts underlying these terms differ among ecologists, and also, various terms are sometimes used for the same concept.

### 11.2.1 Which organisms to include

In most studies, the community is defined taxonomically. Many descriptions of plant communities are restricted to vascular plants, while in some studies, where bryological expertise was available, bryophytes are also included. However, the diversity of vascular plants is not necessarily related to the diversity of all the plant species, and the diversity of all plant species is not necessarily a good indicator of the richness of the whole ecosystem. Another restriction concerns the lack of below-ground data, notably about the seed bank. This might cause some problems, because a seed is a substantial part of the species' life-cycle, particularly in arid systems. For the study of some processes (e.g. response to certain perturbations), the seed bank can be very important. There is no general rule for what should be included in the analysis. Decisions are often made on pragmatic grounds. They may be decisive for the type of relationships found.

### 11.2.2 Number of species and diversity

Let us imagine a plant community being analysed on a given location. Its species number is not sufficient to characterize the community diversity. Two communities with the same number of species may differ in the variation in species abundances. This leads to the distinction between two components of species diversity: species richness and evenness. However, species richness is often called diversity as well. Several diversity indices have been devised, the two most popular being the Shannon index and the reciprocal or complement of the Simpson dominance index.

Let us call species number  $S$ , define  $p_i$  as the proportion of the  $i$ -th species, i.e.  $p_i = N_i/N$ , where  $N_i$  is the quantity of the  $i$ -th species, usually its abundance or biomass, and  $N = \sum N_i$ , i.e. the total quantity of all the species. The Shannon index is then defined as

$$H' = -\sum_{i=1}^S p_i \log p_i \quad (11.1)$$

The Shannon index is based on information theory; hence,  $\log_2$  was used. Later also natural log and  $\log_{10}$  have been used, but all three functions are called Shannon (or Shannon–Wiener, or Shannon–Weaver) index. Although nowadays natural log ( $\ln$ ) usually is used, it is necessary to indicate which logarithm was used to avoid confusion. The antilogarithm of  $H'$ , i.e.  $2^{H'}$ ,  $e^{H'}$  or  $10^{H'}$  for  $H'$  based on  $\log_2$ , natural log and  $\log_{10}$ , respectively, can also be used. This value can be interpreted as the number of species needed to reach diversity  $H'$ , when the species are equally represented. The value of  $H'$  equals 0 for a monospecific community, and  $\log S$  for a community of  $S$  equally represented species.

The second most frequently used diversity index is the reciprocal of the Simpson dominance index,  $1/D$ . The Simpson dominance index is defined as:

$$D = \sum_{i=1}^S p_i^2 \quad (11.2)$$

As for antilog  $H'$ , the minimum value of  $1/D$  equals 1 for a monospecific community, and its maximum is  $S$  for a community of  $S$  equally represented species. Sometimes,  $1 - D$  is used as measure of diversity; this value ranges from zero for monospecific communities to  $1 - 1/S$  in cases of maximum evenness. If  $p_i$  is defined as the proportion of *individuals* in an indefinitely large community, then  $1 - D$  is the probability that two randomly selected individuals will belong to different species.

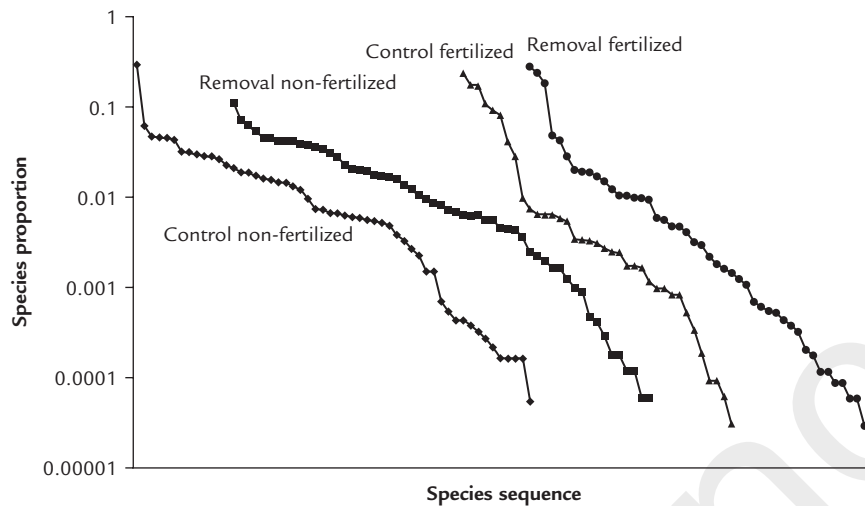
Hill (1973) has shown that the common indices of diversity are related to each other (and to Rényi's definition of generalized entropy) and suggested a unifying notation. His general diversity index can be written as:

$$N_a = \left( \sum_{i=1}^S p_i^a \right)^{1/(1-a)} \quad (11.3)$$

$N_a$  is a general numerical diversity of 'order'  $a$  – which should not be confused with  $N_i$ , the quantity of the  $i$ -th species in the community! By increasing  $a$ , an increasing weight is given to the most abundant species. The following series arises (in some cases as a limit of equation 11.3):

- $N_{-\infty}$  reciprocal of the proportion of the rarest species;
- $N_0$  number of species;
- $N_1$  antilog of  $H'$ , the Shannon index (asymptotically);
- $N_2$  reciprocal of the Simpson index,  $1/D$ ;
- $N_{\infty}$  reciprocal of the proportion of the most abundant species, also known as the Berger–Parker Index.

Evenness is usually expressed as the ratio of the actual diversity and the maximum possible diversity for a given number of species. More complicated evenness indices were also suggested. However, the interpretation of evenness indices is sometimes problematic (e.g. Magurran 2004).



**Fig. 11.1** Diversity–dominance curves for four plots in a wet oligotrophic meadow in Central Europe under different treatments (Lepš 1999), combining fertilization and removal of the dominant grass *Molinia caerulea*. Curves are based on pooled biomass values in three  $0.5 \times 0.5$  m quadrats, 6 years after the start of the experiment. The values of the reciprocal Simpson index are (from left to right) 9.2, 22.6, 7.0 and 5.9; the values of the antilogarithm of  $H'$  are 19.7, 30.0, 9.6 and 9.7; the numbers of species are 54, 57, 37, and 47, respectively.

The variation in species quantities can also be expressed graphically, using so-called dominance–diversity curves (also called rank/abundance curves; see Whittaker 1975). Species are ranked from the most to the least abundant and the relative abundance (proportion of community biomass, or of the total number of individuals) is plotted on a logarithmic scale against species rank number. In this way, we obtain a decreasing curve, which varies in shape and length, and characterizes the community (Fig. 11.1). For other possibilities of graphical representation, see for example Hubbell (2001) and Magurran (2004). Sometimes, various species abundance models are fitted to the data, notably the geometric series, the log series, the lognormal distribution and the broken stick model (e.g. Whittaker 1975; Hubbell 2001). Their parameters are also used as diversity indices (Magurran 2004).

The shape of the dominance–diversity curve often varies in a predictable way along gradients, or among community types. In the example of Fig. 11.1 the four curves reflect the effects of fertilization and removal of the dominant grass *Molinia caerulea* in a yearly mown wet meadow. The slope of the curve is much steeper in the fertilized plots, reflecting a higher degree of dominance, and the curves are shorter, reflecting fewer species. The non-fertilized, non-removal plots are strongly dominated by *Molinia*, but the remaining species occur in rather equal proportions. Six years after removal, none of the remaining species had developed a strong dominance in the non-fertilized removal plots. Comparison

of the curves with values of  $1/D$  and  $H'$  shows that the reciprocal Simpson index is much more affected by the presence of the single dominant than the antilogarithm of  $H'$ .

In most plant communities, regardless of their species richness, the community consists of relatively few dominant species and many subordinate species, most of which have a low abundance – and consequently have a small effect on community productivity or nutrient cycling. In the example in Fig. 11.1, 90% of the biomass was made up by 27 of 57 species (47%) in the non-fertilized plots with the dominant removed, by 12/47 (25%) in removal/fertilization plots, 23/54 species (42%) in non-fertilized control plots, and 8/37 (21%) in fertilized control plots. Unlike the dominants, the low-abundant species will have a limited effect on ecosystem productivity or nutrient retention (the mass ratio hypothesis of Grime 1998). On the other hand, even low-abundant species can support populations of specialized herbivores, for example monophagous insects in a wet alder forest (Lepš *et al.* 1998). Such species may thus be crucial for the maintenance of diversity at higher trophic levels.

### 11.2.3 Spatial characteristics of diversity

The preceding section dealt with communities occupying a delimited area. However, we usually sample only part of a much larger community. With an increasing area sampled in the community, the number of species will normally increase, at a rate that varies among communities. The dependence of the number of species  $S$  found on the size of the investigated area  $A$  is described by the species–area relationship. Mainly two functions are considered: the power curve (Arrhenius model), usually written as  $S = c \cdot A^z$  (and often fitted after log–log transformation  $\log S = \log c + z \cdot \log A$ ) and the semi-logarithmic (Gleason model) curve  $S = a + b \cdot \log(A)$ ;  $c$ ,  $z$ ,  $a$  and  $b$  are parameters estimated by the methods of regression analysis. The power curve starts in the origin – there are no species present at plot size zero;  $c$  is the species number in a plot of unit size;  $z$  measures the rate of increase: when doubling the plot size, the number of species increases  $2^z$  times;  $z$  usually ranges from 0.15 to 0.3. According to the semi-logarithmic curve, a sample plot of unit size contains  $a$  species, and when doubling the area,  $b \cdot \log(2)$  new species are *added*. The number of species at zero area is not defined; actually, for very small plot sizes  $S$  would become negative. Note that both  $c$  and  $a$  depend on the units in which area is measured, whereas  $z$  and  $b$  do not. Theoretical arguments supporting either of the relationships were suggested. For example, the Arrhenius model was advocated by Preston (1962) on the basis of his analysis of abundance distributions (distribution of commonness and rarity in his words). When used for real data, neither of the two is consistently superior. Hence usually both are tried and the function best fitting the actual data is chosen. Functions with three parameters were also suggested, but are seldom used. See further Rosenzweig (1995).

Species-area curves are used on widely varying spatial scales, from within-community areas of square centimetres to whole continents. However, each curve should be interpreted solely in relation to the scale at which it was derived,

and not for extrapolations. Indeed, it was shown (Rosenzweig 1995; Crawley & Harral 2001) that the slope of the relationship changes when based on different ranges of spatial scales. Lepš & Štursa (1989) showed that the estimate of the species number in the whole Krkonoše Mountains, as extrapolated from the within-habitat species area curve for mountain plains would be 30.3, and from avalanche paths 8225 species; the real value is *c.* 1220. Species–area relationships are governed by various mechanisms at various scales. At within-community scales, the increase of the number of sampled individuals is decisive, together with the ability of species to co-exist. The number of sampled individuals is negatively related to the mean size of an individual – a 1-m<sup>2</sup> plot may host thousands of individuals of tiny spring therophytes, but not a single big tree. With increasing area, the effect of environmental heterogeneity increases. This can be biotically generated heterogeneity – for example the variability between the matrix of dominant species and the gaps between them occupied by competitively inferior species – or small-scale heterogeneity in soil conditions at the within-habitat scale, or heterogeneity of habitats at the landscape scale. At continental scales the evolutionary differentiation between subareas starts to play a role. Fridley *et al.* (2006) demonstrated that similarly to the accumulation of species with increasing area, there is also a characteristic accumulation of species over time (i.e. when an identical plot is sampled repeatedly; see also the carousel model of van der Maarel & Sykes 1993) and that integration of these two processes can partially disentangle various mechanisms behind the species–area relationship.

To characterize the spatial aspects of diversity, the terms  $\alpha$  or within-habitat diversity and  $\beta$  or between-habitat diversity are sometimes used. Whereas  $\alpha$ -diversity can be measured by the number of species or any of the diversity indices within a limited area,  $\beta$ -diversity is characterized by differences between species composition in different (micro-)habitat types, or by species turnover along environmental gradients. A simple straightforward way for measuring  $\beta$ -diversity was suggested by Whittaker (1972; see Magurran 2004) as  $\beta_w = S/\alpha - 1$ , where  $S$  is the total number of species in the habitat complex studied (called sometimes  $\gamma$ -diversity) and  $\alpha$  is the  $\alpha$ -diversity, expressed as the mean number of species per fixed sample size. It would provide a good diversity estimate if we have a good estimate of  $S$ , the total number of species in the complex studied.

Usually, the number of all species in all quadrats is used as an estimate of  $S$ . This causes a problem: the mean number of species per quadrat is independent of the number of quadrats investigated, but the total number of species increases with the number of quadrats in the study, and thus  $\beta_w$  will increase with the number of quadrats used. A better approach to  $\beta$ -diversity is based on (dis)similarity measures. The distribution of (dis)similarity values between all pairs of samples is a good indication of  $\beta$ -diversity (Magurran 2004). We can base (dis)similarity measurements on both presence–absence and quantitative data.

As noted, the total richness of a community is usually not known because we are seldom able to investigate its entire distribution area. Usually a mean richness value can be obtained through analysis of sample plots of a size considered

representative. Nevertheless, information on species accumulation by increasing the number of sampled plots (which is affected by  $\beta$ -diversity) can be used for estimation of the total species richness of the community by extrapolation, provided that the sample plots are distributed across the whole considered area. Various methods are available; see the free EstimateS software (Colwell 2009).

#### 11.2.4 Species diversity, phylogenetic diversity and functional diversity

A community composed of four annuals will be less diverse from a functional point of view than a community composed of four species of different life-forms. This leads to the concept of functional diversity (Loreau 2000). Similarly, a community composed of four *Taraxacum* species is phylogenetically less diverse than one composed of four species from different genera. In several theories, the functional and phylogenetic differentiation within communities is more important than the plain number of co-existing species.

The traditional approach to functional diversity was based on the recognition of functional groups of species. Community diversity can be described in a hierarchical way – as diversity of functional groups, and as species diversity within functional groups. Similarly, phylogenetic diversity can be approached as diversity of genera, families, etc. The definition of functional group is crucial here, and there is a wide range of possible approaches (see Chapter 12). Clearly, by assigning individual species to usually broad functional types means a considerable loss of information. Recently, more quantitative approaches to functional and taxonomic diversity have been suggested. The most promising is the use of the Rao coefficient (e.g. see Botta-Dukát 2005; Lepš *et al.* 2006). In fact, it is a generalized form of the Simpson index of diversity (expressed as  $1 - D$ ). Using the same notation as for diversity indices, with  $d_{ij}$  being the (functional or phylogenetic) dissimilarity of species  $i$  and  $j$ , the functional (phylogenetic) diversity ( $FD$ ) has the form:

$$FD = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j \quad (11.4)$$

By definition,  $d_{ii} = 0$ , i.e. dissimilarity of each species to itself is zero. If  $p_i$  is the proportion of individuals of species  $i$  in an infinitely large community, then  $FD$  is the expectation of dissimilarity of two individuals, randomly selected from the community. If  $d_{ij} = 1$  for any pair of species (i.e. complete difference), then  $FD$  is the Simpson index of diversity ( $1 - D$ ), i.e.  $1 - \sum_{i=1}^S p_i^2$  (see e.g. Botta-Dukát 2005 for details).

The main methodical decision is how to measure species dissimilarity (see e.g. Lepš *et al.* 2006 for discussion). For functional diversity, the dissimilarity measure is usually some multivariate metric (e.g. Gower distance) based on *functional traits*, i.e. species properties believed to be important for species function.

However, because we need to know the trait values for all (or the vast majority of) constituent species, the calculation is usually based on easy to measure 'soft' traits (Lavorel & Garnier 2002). These are usually morphological characteristics, supposed to be correlated with functional properties. This is often supported by available data (see the discussion of specific leaf area, seed mass and plant height in Westoby 1998). Various soft traits are included in databases (e.g. Klimešová & de Bello 2009), which often cover most of the species in an area. As to phylogenetic diversity, the dissimilarity can be based either on classical taxonomy, or, preferably, on phylogenetic analyses, often based on DNA sequences (obtained usually from GenBank, as in Cadotte *et al.* 2008). Alternatively, the functional or phylogenetic diversity can be based on a hierarchical classification of species (using cluster analysis for functional traits or phylogeny reconstruction), and express the distance using the topology of the trees, e.g. total phylogenetic branch lengths connecting species together (Cadotte *et al.* 2008). We are not yet able to measure all functional traits or gene sequences for all species in a community; consequently we have to rely on databases. Here we will have to choose between widely available but less 'functional' traits and more functional traits which we have to approximate. As to not available gene sequences, we need to find a reasonable estimation of the dissimilarity, and also cope with the situation that different genes were sequenced for different species.

Both functional and phylogenetic diversity can be partitioned into their components, particularly  $\alpha$ - and  $\beta$ -diversity. By partitioning functional diversity, one can reveal trait convergence vs. divergence (de Bello *et al.* 2009), and suggest a mechanism of community assembly. If  $\alpha$ -diversity is lower than expected under a null model (i.e. species in a sampling unit are functionally more similar than expected in a random selection from the species pool), this would indicate trait convergence, which can be explained by environmental filtering, but also by elimination of weak competitors in a highly productive environment. Trait divergence may be interpreted as support for the limiting similarity hypothesis, i.e. competitive exclusion of species that are too similar (see Section 11.3.3).

### 11.2.5 Intraspecific diversity

Each population is composed of different genotypes. The genotype composition depends on the mating system in the population, on the clonality of plants, and also on population size. Recent studies suggest that the fitness of a population and its ability to cope with environmental variability can be dependent on its genetic structure. Population decline is usually correlated with a loss of genotype diversity (Alsos *et al.* 2012).

## 11.3 Determinants of species diversity in the plant community

### 11.3.1 Two sets of determinants

Species occurrence in a community is a function of arriving at the site and coping with the conditions in the community. Species diversity in a plant community is



thus determined by two sets of factors. The first is concerned with the species pool; the set of species propagules which is able to reach a site. The second comprises local ecological interactions; selecting species from the pool that are able to co-exist (Zobel 1992; Pärtel *et al.* 1996). In this ‘community filter’, both abiotic and biotic interactions operate. Abiotic conditions include physical conditions such as climate, soil, moisture, but also the disturbance regime (e.g. avalanches, fire). Biotic conditions include competitive relations, grazing pressure and effects of pathogens. In some cases, the absence of a species can be caused by the absence of a specialized dispersal agent, or absence of mycorrhizal fungi.

### 11.3.2 The species pool

The definition of species pool used here is broad; according to a narrower definition (e.g. Zobel *et al.* 1998) the pool will include species able to reach the site and survive. Recently, a conceptual synthesis was attempted by Vellend (2010), explaining community composition by four groups of processes: selection (deterministic fitness differences among species), drift (stochastic changes in species abundance), speciation, and dispersal. Dispersal is the basic factor influencing the composition of the species pool, whereas selection and probably also drift decide which species from the pool will finally form the community. Speciation, which is also affected by community processes, operates on a longer time scale and also affects the species pool.

The species pool is affected mostly by historical factors: the place where the species evolved, and whether they were able to migrate to a certain site. For example, many species migrated into boreal areas after the postglacial retreat of the ice sheets (Tallis 1991). The species pool is affected by the proximity of glacial refugia, and by migration barriers between the refugium and the site. The barriers are either physical (e.g. mountains), or biological. For example, the most important barrier for the dispersal of heliophilous mountain plants are forests in between the mountains, causing shade. The species pool is thus also affected by past and present competition (including competition that occurred on migration pathways). Also, postglacial micro-evolutionary processes modified species to make them better adapted to newly arising habitats, and new species also developed. Probably more species became adapted to postglacial habitats that were abundant (Taylor *et al.* 1990; Zobel 1992, Zobel *et al.* 2011).

For the sake of simplicity, the species pool is generally described as a fixed set of species. However, establishment of a single seed is highly improbable. The amount of seeds (or other propagules) needed for establishment of a viable population has to exceed a species-specific threshold. Not all populations are viable. Metapopulation theory (Hanski 1999) distinguishes source and sink populations; source populations are donors of propagules to other populations, sink populations are passive recipients of propagules. Sink populations, found in suboptimal habitats, need a constant influx of propagules from source populations to keep a stable population size (Cantero *et al.* 1999). Such ‘transitional

species' (Grime 1998) are probably not rare and may substantially increase the species richness of some communities. There is a mass effect occurring in the species pool: the probability that a species will pass through the community filter increases with the influx of propagules, which is related to its abundance in surrounding communities ('vicinism', see van der Maarel 1995). Another source of variation is in the dispersal ability of species. Good (e.g. anemochorous) dispersers can reach distant sites but many of their small propagules will be needed for a successful establishment, whereas bad (e.g. blastochorous) dispersers may need only a few propagules to establish, but will not reach far.

In relation to dispersal capacity, local and regional species pools are distinguished. This distinction is arbitrary, but can be useful when clearly defined. See also Chapter 6.

### 11.3.3 Species co-existence

Classical theory predicts that the number of co-existing species will not exceed the number of limiting resources. The competitive exclusion principle of Gause (see Chapter 7) states that two species cannot co-exist indefinitely in a homogeneous environment, if they are limited by the same resource. Nevertheless plant communities may consist of scores of species on a single square metre. This seems to contradict the competitive exclusion principle (Palmer 1994). There are many possible explanations for species co-existence. For example, Wilson (2011) counted 12 basic mechanisms suggested in the literature; he also noted that each realistic mechanism should include an 'increase-when-rare process'. Palmer (1994) suggested that mechanisms of species co-existence should be seen as a violation of assumptions of the competitive exclusion principle. The mechanisms are either equilibrium-based or not. Equilibrium-based explanations question the spatial homogeneity, i.e. species may use different parts of an existing resource gradient, or use resources in different ways: 'niche differentiation', for example different rooting depths, uses of light and phenologies. In order to co-exist, species should be functionally different (the limiting similarity concept; MacArthur & Levins 1967).

Non-equilibrium explanations challenge the assumption of permanence. If there is small-scale environmental variability and the rate of competitive displacement is low, competitive displacement may be prevented. For example, competitive hierarchies in grassland communities can change from year to year, depending on the weather (Herben *et al.* 1995). Recruitment of seedlings is more affected by heterogeneity, fluctuation and their interaction than the occurrence of established plants. The theory of the regeneration niche (Grubb 1977) assumes that co-existence is promoted through the differentiation of species requirements for successful germination and establishment. Many species are dependent on their recruitment in gaps in an otherwise closed canopy, in forests, or in grasslands. The gaps can be seen as highly variable resources; they differ not only in size, but also in the time of their creation – and plants differ in their seedling phenology (Kotorová & Lepš 1999). All this might lead to postponement of competitive exclusion and species co-existence. Indeed, the small-scale

species composition in a community patch changes in time, whereas the species composition on a larger scale is fairly constant (a key element in the carousel model of van der Maarel & Sykes 1993; see Chapter 3).

The above explanations are partly based on the effects of organisms from higher trophic levels. In particular, pathogens and specialized herbivores may have greater effects on dominant species: the denser a host population, the higher the probability that a specialized herbivore or pathogen spreads in the population. This idea was behind the Janzen–Connell hypothesis (Janzen 1970), which explains the extraordinary diversity of tropical forests. No tree would become dominant, because specialized seed predators close to a parent tree would prevent establishment of seedlings around the parent tree. Although this hypothesis has not received sufficient empirical support, particularly concerning insect or vertebrate herbivores, similar mechanisms may support species diversity through specialized pathogens, particularly in soil, and not only in the tropics (Wills *et al.* 1997; Petermann *et al.* 2008).

Hubbell (2001), using mathematical models, demonstrated that species coexistence could be maintained under the species ‘neutrality’ hypothesis – i.e. when all the species have the same competitive abilities, in case there is some constant influx of new species (by immigration, or by speciation). However, because species differ in their competitive abilities, it is difficult to see how such neutral models can be ecologically realistic. Still, the role of ‘lottery recruitment’, implying that the identity of a species entering a gap is determined at random (which is one of the bases of Hubbell’s model) is increasingly accepted. The chances to be the winner, however, differ among species, and a ‘weighted lottery’ (Busing & Brokaw 2002) is probably a more realistic model.

#### 11.3.4 Distinguishing the effect of the species pool from local ecological interactions

The relative importance of historical factors (as reflected in the species pool) vs. that of local ecological factors is often discussed, but it is difficult to separate these effects, particularly because the actual species pool is also affected by local species interactions. A positive correlation between the actual species richness of a community and the number of species able to grow there has been demonstrated. However, the set of species able to grow in a habitat is determined by the species which actually occur in the communities, and hence by local ecological factors (Herben 2000). For example, calcareous grassland communities in Central Europe may be rich in species because there is a large pool of species adapted to these conditions. But it can also be argued that the large species pool is a consequence of the richness of calcareous grasslands, which is consequence of local ecological factors that promote species coexistence.

Probably the best way to separate the effects of local ecological interactions and general historical effects is to compare the patterns of species richness between geographical regions. Schluter & Ricklefs (1993) suggested a procedure for the decomposition of variance in species richness into parts attributable to habitat, geographical region and their interaction. The method is analogous to the decomposition of the sum of squares in two-way ANOVA. Repeated patterns

in geographical regions differing in their history suggest the effects of local conditions, while differences indicate the effects of history.

Some patterns in species richness occur in various geographical regions; they are probably based on local mechanisms. For instance, tropical rainforests are always much richer in species than adjacent mangroves. This can be understood because of the physiologically extreme conditions in mangroves. On the other hand, mangroves in West Africa are poor in comparison with the richer mangroves of Malaysia. This difference may have historical reasons.

Experiments have shown that species which are missing in a community may be able to establish a viable population there, when their propagules are introduced. In this way we may get an indication whether limitation of diversity is related to species pool (dispersal) limitation, or to local ecological interactions, even though results of similar experiments must be interpreted with caution (Vítová & Lepš 2011). However, a successful experimental introduction should be followed by checking that none of the resident species was outcompeted from the community. An increasing species pool need not necessarily lead to increasing richness of a plant community. The introduction of a successful invasive species (i.e. increase of the species pool by a strong competitor) usually causes a reduction in diversity (see Chapter 13).

## 11.4 Patterns of species richness along gradients

### 11.4.1 Introduction

Ecologists have long since known that species richness of plant communities changes along environmental gradients in a predictable way (reviews in Huston 1994; Rosenzweig 1995). The decrease of species diversity from the equator to the poles is one of the most universal patterns in nature. This decrease does not only hold for species, but also for higher taxonomic levels (genera, families). Fossil records show that this pattern can be traced back at least to the Cretaceous (Crane & Lidgard 1989). At present, tropical rainforests are the richest plant communities on Earth at larger spatial scales; also, they are unsurpassed regarding their functional and phylogenetic diversity. Typical numbers of tall tree species are 100–300 ha<sup>-1</sup>. For example, in the Lakekamu Basin alluvial plot in Papua New Guinea, 182 species belonging to 104 genera and 52 families were identified (Reich 1998). Typically, many species had a low abundance; 86 species (47%) were found with one single individual. There is little doubt that the high number of tropical species has historical reasons – the historically relatively stable environment minimizes extinction rates. Although glacial periods also affected the tropics, rainforest regions pertained through all the ‘full-glacial’ periods in the tropics of Africa, South America, South-east Asia and Oceania (Tallis 1991).

How are these hundreds of tree species able to co-exist? Many explanations have been suggested (e.g. reviewed by Hill & Hill 2001). The high photon flux enables the diversification of the tree canopy (emergent trees, several canopy layers), supporting niche differentiation. The decreasing species pool in forests

further away from the tropics reflects both the historical reasons (e.g. the decreasing richness of genera and families), but also the increasing harshness of the environment (decreasing richness of life-forms). Nevertheless there are also extremely species-rich communities in various parts of the subtropical and temperate zones. For example, at finer scales temperate grasslands in various parts of the world, or even semi-deserts are among the most species-rich communities, with close to 100 vascular plant species per m<sup>2</sup> (e.g. Cantero *et al.* 1999). However, none of these communities is comparable to tropical rainforest for functional diversity and the diversity of higher taxonomic units, and also to species diversity at larger spatial scales.

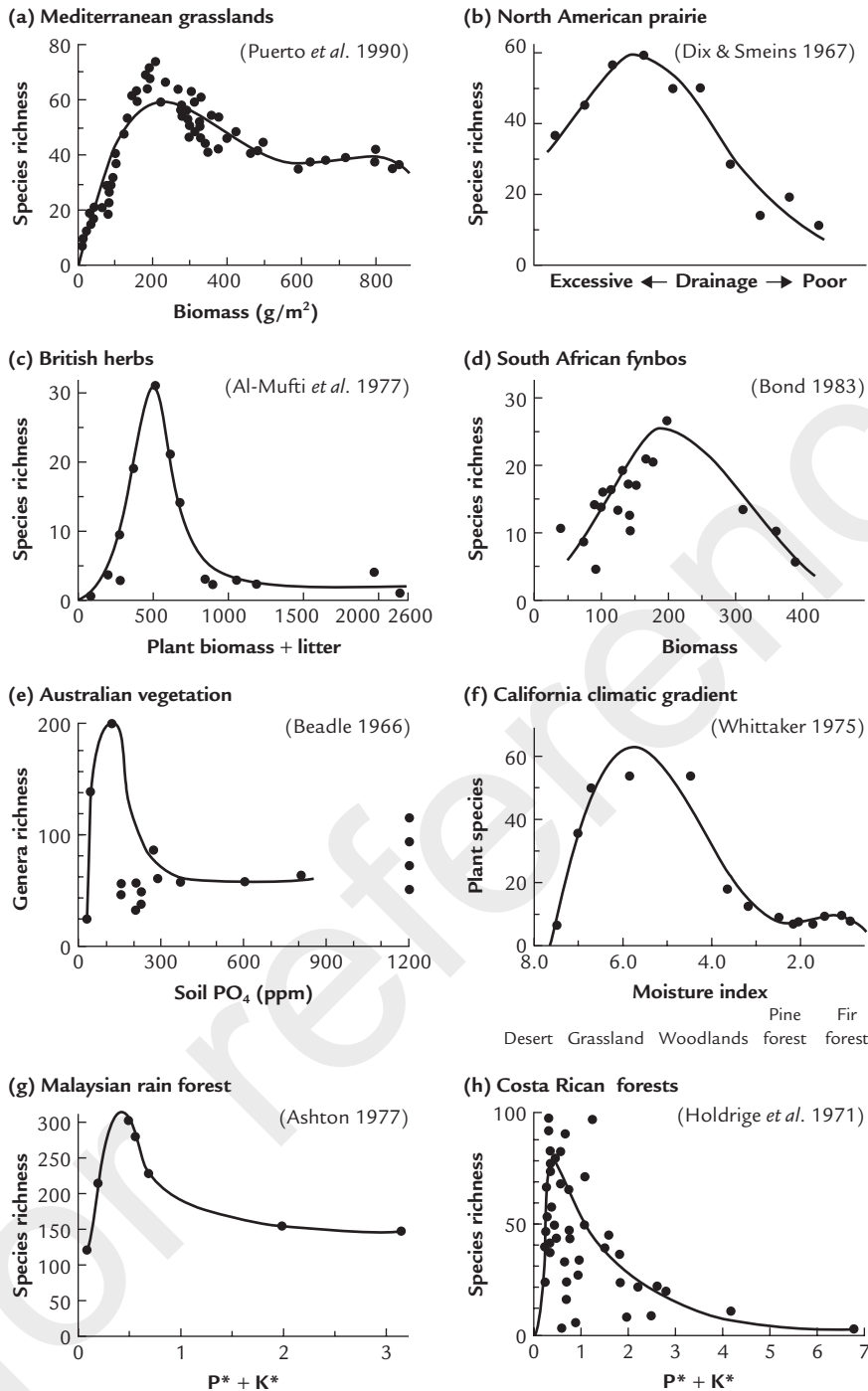
Here, we will discuss the diversity response to productivity, and to disturbance. These two gradients are considered to be the most important axes determining the habitat templet (Grime 2001; Southwood 1988).

#### 11.4.2 Relations between species richness and productivity

At the global scale, the productivity of terrestrial vegetation decreases from the equator to the poles, and species richness is positively correlated with productivity. At the local scale, however, unimodal (humped) relationships have often been found (Fig. 11.2). Meta-analyses of published studies (e.g. Mittelbach *et al.* 2001; Gillman & Wright 2006) have shown that unimodal relationships are common, but not ubiquitous. The validity of these meta-analyses have been questioned (see Forum in Ecology, *Ecology* vol. 91, e.g. Whittaker 2010 vs. Mittelbach 2010); the unimodal relationship is scale-dependent, i.e. it depends on the focal scale (size of plots included in the analyses) and also extent (total area, in which the samples were taken). The focal scale is particularly important because the shape of the species–area curve (the value of the  $z$  exponent in  $S = c \cdot A^z$ , see 11.2.3) often changes with the prevailing species strategy and with the size of the individuals of the constituent species, which in turn change with productivity or disturbance (Lepš & Štursa 1989). The productivity data (e.g. in g·m<sup>-2</sup>) should however be independent of plot size. Still, the pluriformity of the relationship species richness–productivity is clear; it seems that with increasing focal scale, the relationship changes from unimodal or negative to more positive. The situation is further complicated by selection of productivity measure (see various possibilities in Fig. 11.2), and also, by selection of community types (e.g. Gillman & Wright 2006 excluded from their meta-analysis all mown and grazed plots).

The impact of low productivity on richness can be adverse where the environment is so unproductive or otherwise extreme that no organism would survive. An increase in richness with increased productivity is then rather obvious. On the contrary, ecologists are puzzled by what happens at the other side of the hump (or in negative relationships): why does species richness decrease at high productivity levels.

Unimodal relationships between species diversity and standing crop, with a peak in richness at a moderate level and a decrease towards productive environments, have been found in many temperate grasslands, both natural and semi-natural (Fig. 11.2). A more rapid decline was also found in fertilization



**Fig. 11.2** Examples of unimodal relationships between species richness and measures of habitat productivity in plant communities.  $P^*$  and  $K^*$  are normalized concentrations of soil phosphorus and potassium, which were summed to give an index of soil fertility. (From Tilman & Pacala 1993, where also references to the original sources can be found.)

experiments (see Fig. 11.1). However, the unimodal relation was also found in woody vegetation (Fig. 11.2). Generally, eutrophication, an increased nutrient load, is considered one of the most important factors in the recent loss of diversity in European grasslands.

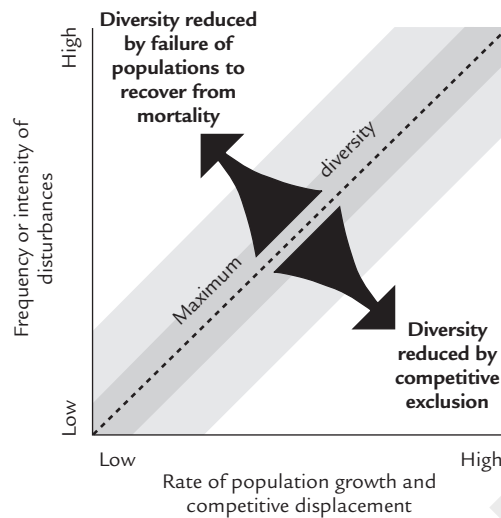
The reduction of species diversity in oligo- and mesotrophic grasslands and small sedge communities at increased nutrient levels may be caused by outcompetition of species by species increasing their growth rate faster (competitive displacement, Huston 1994). This has been confirmed by experiments where the faster growing species had been removed. Under increased soil productivity, competition for nutrients shifts to competition for light and the taller species take advantage. Competition for light is more asymmetric than below-ground competition. Soil heterogeneity, together with varying supply rates and varying rooting depth of plants may allow more niche differentiation and less asymmetric competition (Lepš 1999). Tilman & Pacala (1993) also suggested that the effective heterogeneity decreases when plant size increases.

#### 11.4.3 Relations between species richness and disturbance

Similarly to the response to productivity, species richness also often exhibits a unimodal response along an axis of disturbance intensity, with the maximum found in the middle of the axis (or in the intermediate successional stages). The following discussion will be based on Grime's (2001) concept of disturbance: partial or complete destruction of plant biomass. Impacts of avalanches, fire, windstorms, but also grazing and mowing are all types of disturbance (and succession can be seen as a response in time since the last major disturbance event). There are at least three features that characterize the disturbance regime: *severity* (what proportion of biomass is destroyed), *frequency* (how often the disturbance occurs) and *spatial extent*. Again, it is easy to understand that at high disturbance levels, the species richness decreases with further increasing levels of disturbance, until no plant species will survive. The focus of attention is on diversity at medium disturbance levels, where the disturbance positively affects species richness.

The 'medium disturbance hypothesis' (Huston 1979), demonstrated that in systems where a competitively strong species prevails in the absence of disturbance, a medium frequency of disturbance leads to an increase in species richness, while under a higher frequency of disturbance, only fast growing species will survive. Huston (1994) demonstrated that the impact of medium disturbances depends on the system's productivity (i.e. on the growth rates of the prevailing species); in a more productive environment maximum diversity occurs at a higher disturbance level (Fig. 11.3).

As to possible mechanisms of response to disturbance, Huston (1979) showed that the destruction of a constant proportion of each species could postpone competitive exclusion. However, disturbance often harms the dominant species more, particularly those superior in competition for light, which leads to a 'increase-when-rare process' (Wilson 2011). The disturbance by mowing a grassland is more destructive to the taller species because a larger proportion of their biomass is removed (Klimešová *et al.* 2010). One of the effects is that



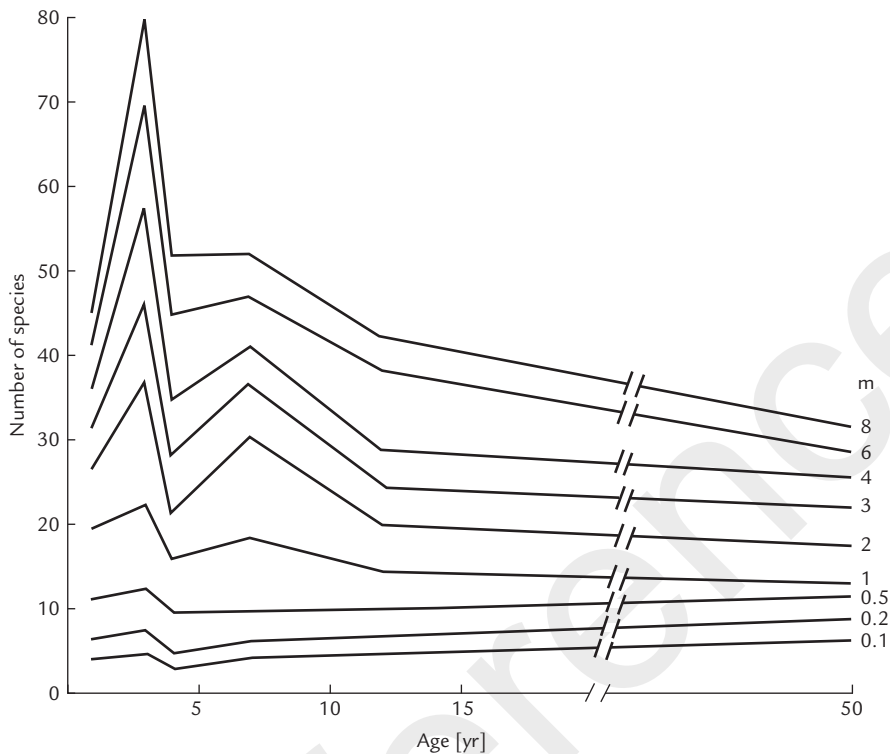
**Fig. 11.3** Conceptual model of domains of the two primary processes that reduce species diversity. Diversity is reduced by competitive exclusion under conditions of high rates of population growth and competitive displacement and low frequencies and intensities of disturbance. Diversity is also reduced by failure of small and slowly growing populations to recover from mortality under conditions of low population growth rates and high frequencies and intensities of disturbance. Note that the frequency or intensity of disturbance supporting maximum diversity increases with population growth rate (i.e. with system productivity). (From Huston 1994.)

low-growing species are no longer outcompeted for light. An avalanche will destroy existing trees on its path and affect occurring shrubs, but it will usually not disturb the herb layer too much. Further, several forms of finer-scale disturbance may be spatio-temporally heterogeneous, which again promotes species co-existence. For some types of disturbance, e.g. windstorm damage, the spatial extent of the disturbance and the average time between two subsequent events are inversely related (single tree falls appear often, large windbreaks may happen only once in many decades). Medium disturbance leads to a mosaic community structure, with patches of various successional stages – and the resulting complex community is species-rich. In communities with many species dependent on regular seedling recruitment, disturbance provides the ‘safe sites’ for seedling recruitment.

Each community type has its typical disturbance regime. Changes in the intensity and type of a disturbance regime of an adapted community will often lead to a decrease in species richness: typical examples are fire suppression in North American forests (e.g. Hiers *et al.* 2000), and cessation of grazing and/or mowing in species-rich meadows (Lepš 1999).

The development of species diversity during a secondary succession often shows a similar pattern as described for the relation of diversity to productivity





**Fig. 11.4** Changes in species richness during an old-field succession, measured on various spatial scales. The numbers on the right side are sizes of sampling plots expressed as the lengths of the quadrat side. (From Osbornová *et al.* 1990.)

and disturbance: there is a rapid increase in species richness during the early years towards a maximum in intermediate stages, followed by a slow decrease. This is shown for an old-field succession (Fig. 11.4, which also elucidates the scale dependence). One may interpret this development as a response to the sudden drop in disturbance connected to the earlier management of the field. In the tropics, however, species richness usually increases steadily towards undisturbed mature forest.

## 11.5 Stability

### 11.5.1 Ecological stability

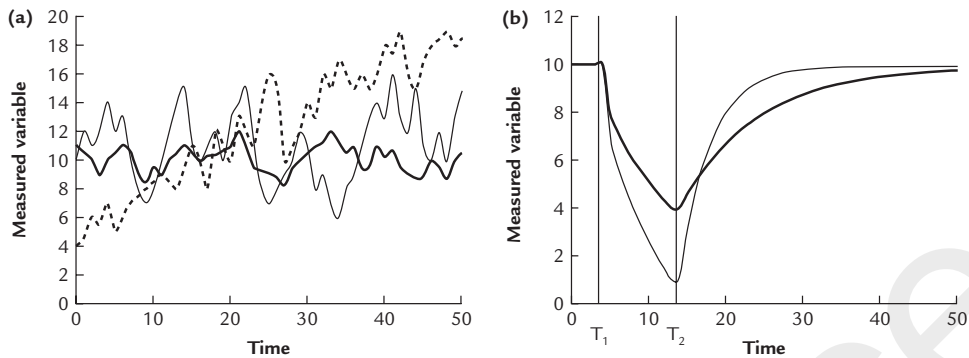
Ecologists have long believed that diversity begets stability (e.g. MacArthur 1955). On the other hand, May (1973) demonstrated that mathematical models predict a negative relationship between stability and complexity (including

diversity). However, the results were based on unrealistic models: contrary to the model assumptions, ecological communities are far from random assemblages of species, and by analysing a linearized model close to system equilibrium one does not learn much about the many-sided behaviour of ecological systems. May's model demonstrated that the probability of the stability of an equilibrium of a randomly generated community matrix (in terms of Liapunov stability) decreases with the size of the matrix, i.e. with the number of species in the model community. Also, Liapunov stability as used in mathematics – and in models of theoretical ecology – is not an ideal reflection of what ecologists consider to be ecological stability (see Section 11.5.2). A positive effect of May's book was that ecologists realized that it is necessary to define clearly what ecological stability is and how we should measure it in real ecological systems, and also that the positive relationship between diversity and stability is not a necessity – should it be predicted by a model, then it depends on the model assumptions. In mathematical models, we have various analytical tools that enable the analysis of system equilibrium (equilibria), and its (their) stability. The only way to assess ecological stability in nature is to follow a real system trajectory in a 'state space' defined by selected measured variables such as total biomass, population sizes and rates of ecosystem processes. The evaluation of stability is then dependent on the variables selected for measurement, and on the length of the period and the frequency of the measurements. Regarding plant communities, we are usually mostly interested in species composition, total biomass and nutrient retention. These characteristics may behave independently; the total community biomass may be fairly constant while the species composition fluctuates, or the other way around.

### 11.5.2 Characteristics of ecological stability vs. non-stability

Various aspects of ecological stability are distinguished (e.g. Harrison 1979; Pimm 1984; Fig. 11.5). The first two concepts are based on system behaviour under 'normal conditions':

- 1 *Directional changes in the system state.* A lack of directional changes is usually interpreted as 'stability' (the system is considered to be in a state of 'equilibrium'); systems undergoing directional changes are called transient or unstable. This concept corresponds more or less to the existence of a stable equilibrium in mathematics. It is linked to that of succession – successional communities are by definition unstable, i.e. not in an equilibrium – but climax communities and also some 'blocked' successional stages are stable. A system may also be subjected to cyclic succession, as described by Watt (1947; see Chapter 4). This aspect of stability can only become clear after long-term analysis. Slow and small directional changes might be masked by random variability. This is why we will always use quotation marks when speaking about 'equilibrium' in real communities. The concept is also scale-dependent. Depending on spatial and temporal scales, even climax communities undergo local successional and cyclic changes, and



**Fig. 11.5** Concepts of ecological stability. The measured variable is the choice of the researcher (e.g. community biomass, photosynthesis rate, or population size). (a) Community fluctuation in a constant environment. Broken line, unstable transient community; full lines, communities in some steady state; heavy line, the more constant (less variable) community. (b) Community stability when facing a perturbation (sometimes called a stress period), which starts at  $T_1$  and ends at  $T_2$ . Heavy line: the community which is more resistant, but less resilient than the community indicated by the light line. The time scale depends on the rate of ecosystem dynamics; for terrestrial plants, it is usually measured in years. (Adapted from various sources.)

in sufficiently long-term perspective, the communities adapt to climate changes.

- 2 *Temporal variation* (also indicated as variability) or, its opposite, *constancy*, determines how much the system fluctuates under ‘normal conditions’. Standard measures of variability are used (e.g. standard deviation, SD, in a temporal sequence), usually standardized by the mean. For example, for total biomass, the coefficient of variation ( $CV = SD/\text{mean}$ ) or the SD of log-transformed data would be appropriate measures of temporal variability. When the data are counts rather than a continuous variable, use of Lloyd’s index of patchiness:  $L = 1 + (SD/\text{mean} - 1)/\text{mean}$ , will lead to a reasonable standardization by mean. When we are interested in species composition, the measured variable is multivariate; for the evaluation of such data, we should apply methods of multivariate analysis. For example, we can follow the community trajectory in ordination space, or measure the average (dis) similarity between subsequent measurements, or use multivariate analogs of variance, standardized by corresponding means.

Ecological stability is often defined as the ability to remain in a state (‘equilibrium’) when facing some perturbation, and to return to the original state after the perturbation ceases. The next two characteristics are concerned with a response to external perturbation.

- 3 *Resistance*, the ability to resist a perturbation, and
- 4 *Resilience*, the ability to return to a pre-perturbation state. In both cases some period of ‘normal conditions’, i.e. some sort of equilibrium, is involved,

followed by a short period of limited perturbation. Each community exists in a variable environment, so that which variability is still 'normal' and which already means perturbation is quite arbitrary. Also, resistance and resilience should always be related to the perturbation under study.

Resistance is measured by the proximity to its original state of a system displaced by perturbation, i.e. by the similarity between the pre-perturbation and post-perturbation state. For example, during an extreme drought in 1976, young fallow decreased its standing crop by 64% in comparison with the 'normal' year 1975, but the old fallow only by 37% (Lepš *et al.* 1982, Fig. 11.6). So the old fallow was considered more resistant. When species composition of a community is concerned, we can use various (dis)similarity measures between the original and the perturbation state.

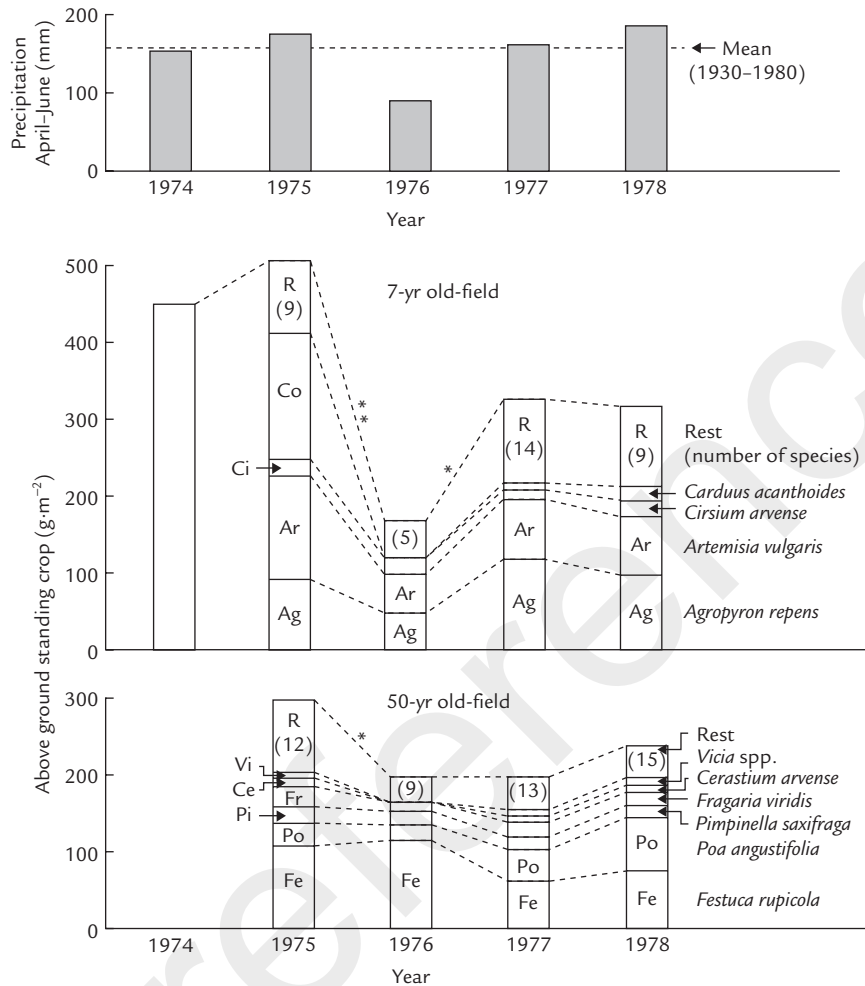
Resilience means the ability of a system to return to its original state after perturbation. It can, for instance, be measured as time, when the displacement caused by the perturbation has decreased to 50%. In many cases a return is neither smooth nor monotonous. Then, *ad hoc* measures of resilience have to be used, for example reduction of the displacement after a fixed period of time. The concepts of resistance and resilience can be applied to communities which are stable according to the first definition, i.e. being in 'equilibrium', a state towards which the system returns after perturbation. However, the concepts can also be applied to a successional community, provided that the rate of succession is much slower than the response to perturbation.

- 5 *Persistence*. In addition to these four frequently used aspects of stability there is *persistence*, defined as 'the ability of a system to maintain its population levels within acceptable ranges in spite of uncertainty of the environment' (Harrison 1979). Often the community is considered persistent when no species are lost during the observed time period.

After large or long-lasting perturbations, ecological systems may be too much damaged to recover, because species have become locally extinct, or the soil profile has been destroyed. These are examples of irreversible change. Thus, an important characteristic of stability is the range or/and the intensity of a perturbation from which the system is able to return to its original state.

For all aspects of variation, resistance and resilience, the temporal scale is very important. In comparative studies it might be more realistic to relate recovery time to the generation time of the constituent species.

Temporal variation, resistance and resilience reflect the community response to environmental fluctuation. An important part of the response by individual species is found in the physiological tolerance of their populations. In order to construct a realistic model, one would need to quantify the response of populations to environmental fluctuations (Yachi & Loreau 1999). Also, there is a physiological trade-off between growth rate and resistance to extreme events (MacGillivray *et al.* 1995); consequently the species that are highly resistant are usually not highly resilient. Similarly, communities composed of highly resistant species will not be highly resilient.



**Fig. 11.6** Comparison of resistance and resilience of a 7-year old-field and a 50-year old-field. (a) Course of the spring precipitation in 1974–1978 suggesting that 1976 was an extreme year and can be considered as a ‘perturbation period’. The decrease in the total productivity from 1975 to 1976 was considerably higher (and also more significant) in the younger field (so the younger field has a lower resistance). However, the younger field started earlier to return to the ‘normal’ state – so it has a higher resilience. Note that the characteristics were used for the successional stages; we expected that the successional development would be much slower than the response to drought. However, in the younger field, there is some decrease of productivity that should be taken into account – the standing crop never returned to the 1974 value in this plot. Differences between subsequent years were tested using the *t*-test (\* =  $P < 0.05$ , \*\* =  $P < 0.01$ ). The number of species constituting the rest (in parentheses) has indicative meaning only. (From Lepš *et al.* 1982.)

## 11.6 On the causal relationship between diversity and ecosystem functioning

### 11.6.1 On correlations and causes

Not only does diversity change in a more or less predictable way along ecological gradients, this will also be the case for functional characteristics, such as primary productivity, nutrient retention or stability. Consequently, diversity and function will often be correlated. However, this does not necessarily imply a causal relationship. Both diversity and function can be dependent on the same set of environmental constraints. Also, diversity might be the consequence rather than the cause of stability, particularly on an evolutionary time scale.

### 11.6.2 Biodiversity experiments

Experiments have been carried out where community diversity, considered as an independent variable, is manipulated and the functional response, considered as a dependent variable, is measured. A significant statistical relationship is strong evidence for a causal relationship. This approach has a weak point: changing the diversity implies changing the species composition. However, as demonstrated (e.g. Lepš *et al.* 1982; MacGillivray *et al.* 1995; Rusch & Oesterheld 1997; Grime *et al.* 2000), the identity of the constituent species, and hence the plant functional types they belong to, is the basic determinant of ecosystem functioning. Whether it is possible to separate diversity and identity in such experiments, is a difficult and still debated question; maybe carefully designed experiments can provide some insight (Hooper *et al.* 2005).

Some of these biodiversity experiments comprise very extensive field experiments. One example is the 'Jena experiment', located near the German city Jena, jointly supervised by German and Swiss institutions, including ecologists from Jena. It includes 16 replicates of species richness 1, 2, 4 or 8 species, then 14 replicates of richness 16, and four replicates of a mixture of 60 species; each replicate comprises a 20 × 20 m plot, while there are also many additional 3.5 × 3.5 m plots, including monocultures of all constituent species. See Plates 11.1, 11.2 and Roscher *et al.* (2005). Other examples are Cedar Creek (Tilman *et al.* 1996), and multi-site European projects BIODDEPTH (Hector *et al.* 1999), CLUE (van der Putten *et al.* 2000) and the experiments by the pan-European consortium (Kirwan *et al.* 2007).

How should such experiments be arranged? What are suitable methods for their analysis? And what are the lessons from their results for the functioning of real communities and ecosystems? Several analytical approaches are available, and they have various requirements on the experimental design. Consequently, the experimental design of a biodiversity experiment should ideally take the subsequent analytical tools into consideration. Further, irrespective of the analytical methods used, the species should as far as possible be represented equally at all richness levels, and individual richness levels should have replications differing in species composition.

A simple example may illustrate some of the problems. Three species, A, B and C are involved in an experiment on the effect of species richness ( $S$ ) in mixtures on the final biomass yield ( $Y$ ), which is often considered a parameter of 'ecosystem function'. When plants are grown from seed, biomass is a reasonable measure of productivity, and many of the functional characteristics (e.g. nutrient retention or  $\text{CO}_2$  assimilation), are usually correlated with biomass and/or productivity. In that case, most of the reasoning presented below for biomass can be applied to some other ecosystem functions. By choosing productivity we can also rely on the large number of earlier experiments, both ecological and agronomical (e.g. Trenbath 1974; Austin & Austin 1980; Vandermeer 1989). But, we should be aware that most of the studies of 'effects of biodiversity' are based on simple measurements of the above-ground biomass, and it seems that these effects are too easily interpreted as effects on 'ecosystem functioning'. As noted by Srivastava & Vellend (2005), high productivity is not always a desirable property of an ecosystem, and so higher community above-ground biomass does not necessarily mean 'better ecosystem functioning' from the nature conservation point of view.

In our three species example, if all replications at  $S = 1$  would be composed of species A, at  $S = 2$  of mixtures of A and B, and at  $S = 3$ , of mixtures of A, B and C, the specific effect of species B would be indistinguishable from the increase of  $S$  from 1 to 2, and of species C from the increase of  $S$  from 2 to 3. This type of design, where the species composition is constant in all replications at a given species richness level, which form a subset of the composition at higher  $S$ -levels, was used in the pioneering Ecotron experiment (Naeem *et al.* 1994). The results were then heavily criticized (Huston 1997). In a much better design, the replications at  $S = 1$ , are monocultures of all three species A, B and C, which are equally replicated; at  $S = 2$ , all three possible pairs (i.e. AB, AC and BC) are equally replicated, so that we have three mixtures of two species; at  $S = 3$  the (replicated) mixtures of all three species are included. In most experiments, a substitution design is used, leading to the replacement series of de Wit (1960), i.e. the total number of sown seeds is kept constant, and divided among the constituent species, which occur most often in equal proportions.

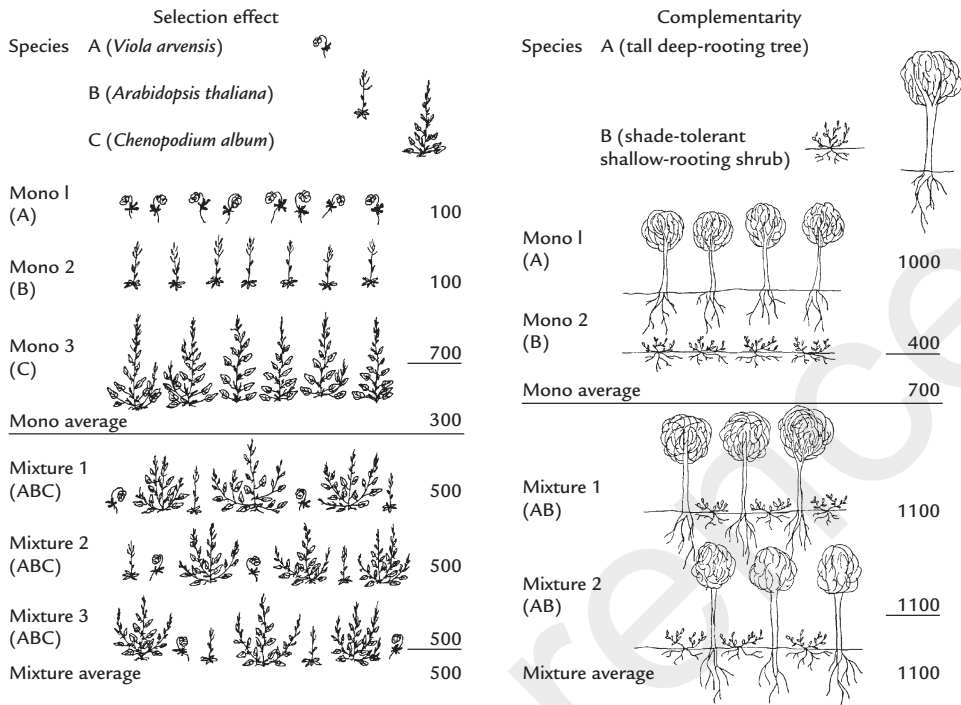
It is practical to have all the species combinations for mixtures up to say five species; however, we are usually not interested in the effects of diversity in five-species communities, but in considerably richer communities. Here, we will never have enough resources to include all possible species combinations for higher numbers of species; for  $S = 10$  we would already have 45 possible two-species combinations, 120 three-species combinations, 210 four-species combinations, and so on. Usually, we are not even able to cover all possible richness values, so we select just some of them, and for each of them, select some species combinations (and here we need to care about equal representation of species in various richness levels). For practical reasons, the number of experimental units which we are able to handle is more limited if we require that not only the total 'ecosystem function', but also the contributions of individual species are determined.

In most similar studies, the final yield of the community is positively correlated with species richness (see the meta-analysis of Cardinale *et al.* 2007). Two

main mechanisms are supposed to generate this relationship: the effect of the selection, sometimes called sampling or chance effect (Huston 1997; Aarssen 1997) and the effect of complementarity (which in some calculations also includes possible facilitation). We will use the simple three-species example from above to illustrate the selection effect (Fig. 11.7). Suppose A and B are small annual weeds (e.g. *Viola arvensis* and *Arabidopsis thaliana*) and C is a highly productive species (e.g. *Chenopodium album*). We expect that *Chenopodium* will dominate all mixtures where it is present, and consequently these communities will have a much higher biomass than the other ones. We also expect that – if the sowing density is not very low – *Chenopodium* will achieve a biomass in the mixtures which is close to its biomass in a monoculture, whereas the biomass of the other two monocultures, and the mixture of *Viola arvensis* and *Arabidopsis thaliana* will be very low. As the highly productive species (i.e. *Chenopodium*) is present in one third of the monocultures, in two thirds of the two-species mixtures and in all of the three-species mixtures, the average biomass will increase with species richness. Thus, we can expect a positive, highly significant regression of  $Y$  on  $S$  (the sampling or chance effect): by simply increasing the number of species we increase the chance that a productive species will be present. There was much controversy about this effect in the recent biodiversity debate. Loreau (2000) suggested that this is called the (positive) selection effect, to stress the fact that the most productive species has to prevail in the mixture to produce this effect, and this term is now often used. The average biomass increases as a consequence of the positive selection effect, but the selection effect itself is not sufficient for the biomass of the mixture to exceed the biomass of the most productive monoculture. When the mixture exceeds the biomass of its most productive constituent species monoculture, we speak of overyielding (Trenbath 1974). However, the term is also used in a much wider sense: for example Tilman (1999b) used the term for the situation where the productivity of a species in a mixture is higher than its yield in a monoculture divided by the number of species in a community. To avoid confusion, the term transgressive overyielding is used for the situation where the mixture is more productive than the most productive monoculture. Transgressive overyielding is strong evidence that there is more than a selection effect playing a role.

Mechanisms that potentially can (but need not) lead to transgressive overyielding, are complementarity and facilitation. Complementarity means that various species are limited by different resources, or differ in the mode of use of a resource. Typical examples are the different rooting depths of species (Fig. 11.7), or the separation in time of species (e.g. spring vs. summer species). Complementarity is equivalent to niche differentiation – which, in equilibrium theory, is considered a necessary condition for species co-existence – and is probably very common in nature. A typical example of facilitation is the increase of soil nitrogen as a consequence of the presence of legumes, leading to the increased productivity of other species. Usually, on the basis of the final outcome, complementarity cannot be distinguished from facilitation; here we need knowledge of the biology of the constituent species and supplementary experiments focused directly on the mechanisms of interactions. Of the three mechanisms mentioned, only facilitation potentially can (but need not) lead to a





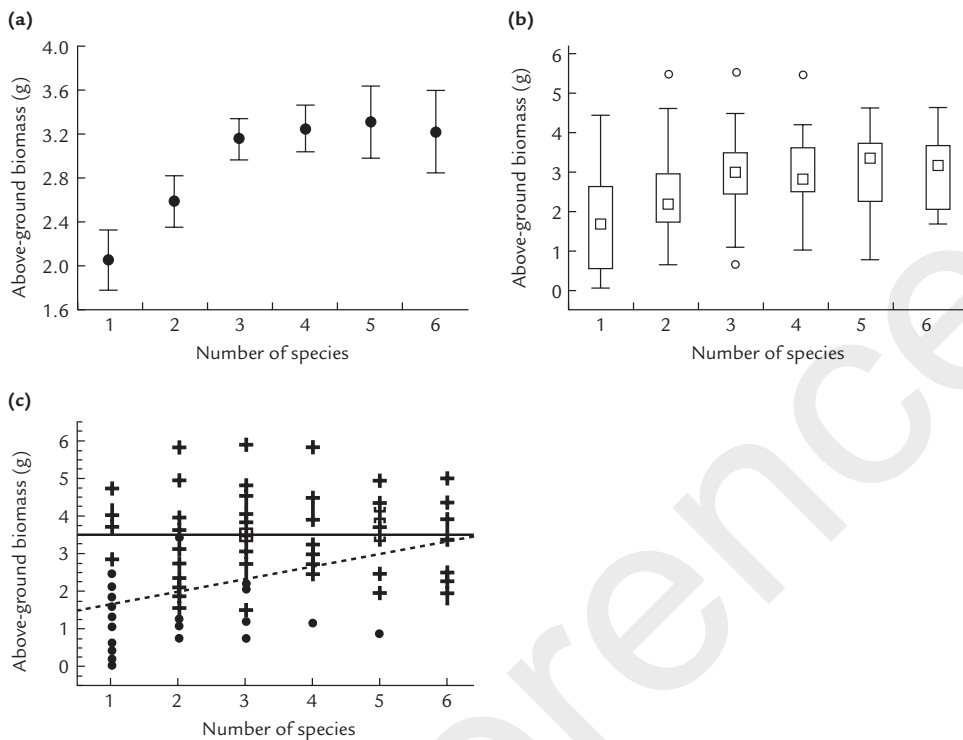
**Fig. 11.7** Selection (sampling, chance) effect and complementarity affecting the final yield in biodiversity experiments. Comparison of three monocultures (Mono1, Mono2, . . .) with mixture of the three species is shown for selection effect, of two monocultures and their mixture, for complementarity. Mixture 1, Mixture 2, are replications of the mixture. Final biomass (in arbitrary units) is taken as the response variable. In the selection effect, the most productive species (such as *Chenopodium album*) prevails in the mixtures, and suppresses the less productive species. When sown in sufficient density, the mixture biomass approaches the biomass of the most productive species, but does not surpass it. In the complementarity effect, the species use resources in a different way, and consequently, the biomass of the mixture might (but need not) exceed that of the most productive monoculture. (Figure drawn by Eva Chaloupecká.)

situation, where a population in the mixture has a higher biomass than in the monoculture.

To evaluate the results of biodiversity experiments, various indices of biodiversity effects were suggested. The most common are the ratio of the mixture biomass to the biomass of its most productive species, characterizing the transgressive overyielding and the additive partitioning of the net effect to selection and complementarity effects suggested by Loreau & Hector (2001). This method is based on the idea of relative yield total (RYT, de Wit 1960); the net effect is the difference between the actual yield of the mixture and the average of monoculture yields of its constituent species (corrected for sowing proportions if the

species are not sown in equal proportions). This value is partitioned into selection and complementarity effect on the basis of contributions of the individual species – selection effect is characterized by high covariance between a species monoculture yield and its deviation between realized and expected mixture yield (in other words, the selection effect is high if species with high monoculture yield prevail disproportionately in the mixture at the expense of species with low monoculture yield). Although highly intuitively appealing, the method of additive partitioning does not directly measure the mechanisms; these are just inferred from the productivity of individual species in mixtures. For example, the positive complementarity effect can be generated not only by real complementary use of resources, but also by facilitation (typically by the presence of a legume in the mixture), or by the fact that herbivores spread more easily (and so decrease the biomass more) in monocultures than in polycultures (see discussion in Trenbath 1974 or Vandermeer 1989). Simulations by Fibich & Lepš (2011) demonstrated that various shapes of dependence of final yield on sowing density in combination with the substitutive design used in these experiments can also generate non-zero values of these parameters in the absence of complementarity or facilitation. We should be aware that most of the recent conclusions about the mechanisms of biodiversity effects (e.g. in the meta-analysis of Cardinale *et al.* 2007 that the complementarity increases with duration of the experiment), are not based on direct measurement of mechanisms, but just on this additive partitioning of the net effect. Fox (2005) suggested a tripartite partitioning which is an extension of the method of Loreau & Hector (2001); it further divides the selection effect into two terms – dominance effect and trait-dependent complementarity. Other methods imply a direct application of classical statistical methods (general linear models, see Kirwan *et al.* 2007, 2009), where species identity in a mixture and species richness are used as sets of predictors of mixture performance (usually yield). In this way, the method should be able to separate the effect of species identity from the effect of species richness. A comprehensive review of the methods for the analysis of biodiversity experiments was recently published by Hector *et al.* (2009).

The meta-analysis of Cardinale *et al.* (2007) showed that mixtures were more productive than monocultures in 79% of the experiments. Similarly, species-rich communities are on average more efficient, for example in nutrient uptake (Tilman *et al.* 1996), or in overall catabolic activity of soil bacteria (Stephan *et al.* 2000). There is little doubt that this is a prevailing pattern; nevertheless, some studies found no effect of diversity on productivity (e.g. Kenkel *et al.* 2000). When the additive partitioning is used, the complementarity effect increases with the duration of the experiment (Cardinale *et al.* 2007). It also seems that this effect is saturating, i.e. it is most pronounced at low richness, but reaching an upper asymptote rather soon (Fig. 11.8). However, evidence that species-rich communities are more productive than the most productive monocultures or species-poor communities is mostly lacking (Cardinale *et al.* 2007 found transgressive overyielding in only 12% of experiments). This leaves room for contradictory interpretations (Garnier *et al.* 1997 vs. Loreau & Hector 2001). Fig. 11.8 gives an example of how different graphical presentations based on the same data might lead to different interpretations.



**Fig. 11.8** The perception of the results of a biodiversity experiment can be affected by the way of statistical analysis and graphing (data from the low sowing density in the pot experiment of Špačková & Lepš (2001)). (a) mean and standard error of mean showing that mean biomass increases with species richness. (b) Median values shown by squares, interquartile ranges by boxes, non-outlier extremes by whiskers, outliers by circles; outliers are more than 1.5× the interquartile range from the quartiles. Median values increase, minimum values increase as well, but the maximum is more or less independent of species richness. (c) Biomass value for each pot is shown separately. Data set divided into pots containing the most productive species, *Holcus lanatus*, (+, regression shown by full line) and those without this species (•, broken line). When the most productive species is absent, the average biomass is lower and increases with the number of species, as the probability that the second most productive species will be present increases.

Species richness is the directly manipulated variable in most biodiversity experiments. However, what should really matter for ecosystem functioning is the diversity of functional traits in a community (Loreau 2000); species richness is just a surrogate characteristic reflecting functional diversity. Indeed, some analyses show that functional or phylogenetic diversities are often better predictors of ecosystem function than the number of species (e.g. Lanta & Lepš 2006, Cadotte *et al.* 2008, 2009). Also, in the majority of experiments, the species are sown in equal proportions, and so attention is only paid to species richness.

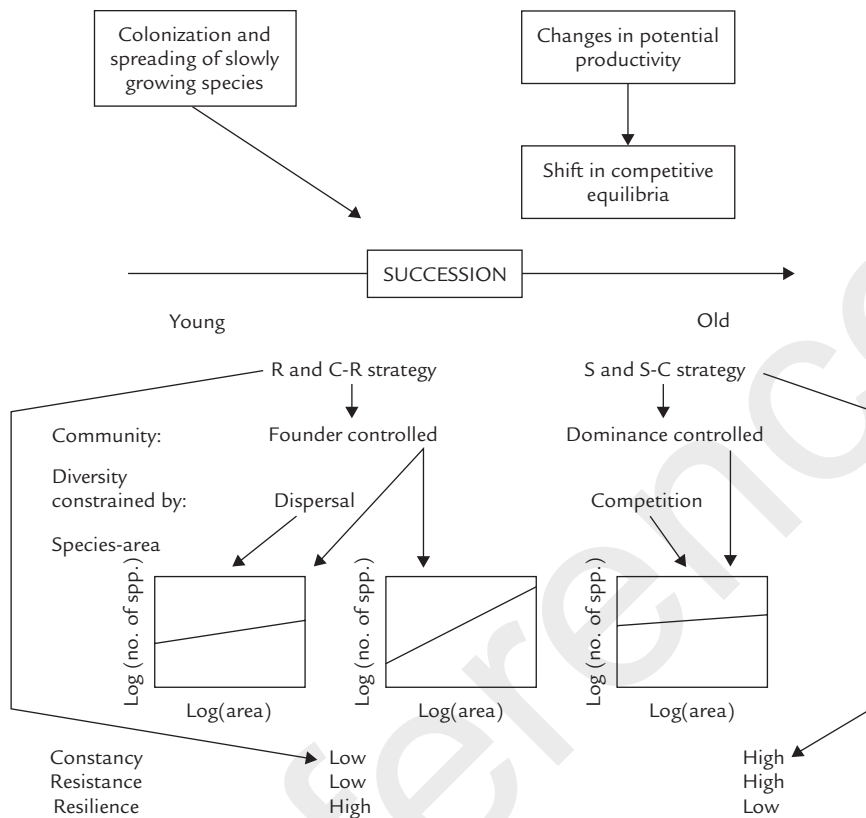
Nevertheless, as shown by Kirwan *et al.* (2007), evenness can be the driving force of biodiversity effects.

The problem of biodiversity experiments is that in nature, species richness is basically a 'dependent variable', i.e. the result of ecological forces. Plant communities can be species-poor for three basic reasons: (i) lack of species in the species pool, i.e. of species able to reach the site, (ii) an extremely harsh environment (low productivity or high disturbance), and (iii) a highly productive environment, where competitive exclusion is fast. We can expect that ecological functioning of these three types of species-poor communities will be very different. The low diversity treatments in biodiversity experiments are achieved by the low number of species sown (often together with weeding), which corresponds to a lack of species in the species pool (Lepš 2004a). The experimental gradient in species richness is created by limiting the number of species allowed to enter the experimental plot, which might correspond to plant communities limited by the size of the species pool, but very probably not to communities where a highly productive environment leads to fast rates of competitive exclusion. The simulation study of Stachová & Lepš (2010) demonstrated that a pronounced increase in productivity with an increasing number of species in the community is expected only when the underlying richness gradient is caused by limitation of the species pool, i.e. limitation of number of species available at the site. This can explain why many patterns observed in biodiversity experiments are not confirmed in nature (e.g. the predicted positive correlation between species richness and productivity). Also, an important difference may exist between synthetic communities in biodiversity experiments and mature natural communities. Grace *et al.* (2007), on the basis of a structural equation modelling approach controlling for possible environmental effects, suggested that the influence of small-scale diversity on productivity in mature natural systems is weak.

### 11.6.3 Does diversity beget stability?

Like ecosystem functioning, ecological stability is mostly determined by the life histories of the prevailing species (Fig. 11.9). A community of cacti will be highly drought resistant, regardless of its species richness. However, when damaged, the recovery, depending on the resilience, will be slow, regardless of the species richness. Since the species (and life history) composition is determined by habitat characteristics, the latter are expected to be the main determinants of both species richness and stability.

Ecosystem functioning (energy flow and matter cycling) is dependent on a limited number of dominant species. The subordinate species will not be very important for the actual functioning of the community, but they might play an important role when the conditions change (Grime 1998). As far as the environment is variable, species richness might help to cope with these changes. MacArthur (1955), when proposing the Shannon index as an index of stability, suggested that the functional redundancy amongst species may increase the possibility that when a species fails to fulfil its role in the community, its function can be taken over by another species (risk spreading). Since then,



**Fig. 11.9** Mechanisms behind changes in the species–area curve and stability characteristics during secondary succession. (Based on an old-field succession in Central Europe: Lepš *et al.* 1982; Lepš & Štursa 1989; Osbornová *et al.* 1990.).

several mechanisms have been proposed, some with rather complicated mathematical models; however, these are mostly variations on the original idea of MacArthur.

Doak *et al.* (1998) suggested that aggregate community characteristics such as total biomass should be less variable as an effect of statistical averaging. It follows from basic probability laws that the coefficient of variation (CV; see section 11.5.2) of the sum of *independent* random variables should generally decrease with the number of variables included (Doak *et al.* 1998). According to Tilman (1999b), this decrease will depend on (i) the way the variance is scaled with the mean, and (ii) the independence of the variables. The stabilizing effect would weaken when the more abundant species are less variable, i.e. have a lower CV than the less abundant species, which is often the case (Lepš 2004b). In that study, the CV of the dominant species (*Molinia caerulea*) was, in an unfertilized semi-natural meadow, smaller than the CV of the whole community, including *Molinia*. This suggests that the ability to attain dominance might be

dependent on similar traits as is the ability to maintain a constant biomass over time. However, the negative correlation between average biomass and CV is usually not strong enough to fully compensate for the averaging effect. The assumed independence of the variables may be even more important: biomass variation over time will not be damped by diversity when the different species involved respond to environmental variation in a concordant way. However, only a perfect positive correlation could counteract the averaging effect, but this is rather unlikely. Species are different to the extent that they will respond in different ways to environmental variation (which corresponds to MacArthur's idea that when one species fails, it can be replaced by another species). Moreover, due to the effect of interspecific competition in the community, decline of one species can enable an increase of its competitor, leading to negative correlation. However, in a grassland community study where environmental variation was restricted to weather fluctuations, species responded concordantly and thus were positively correlated (Lepš 2004b).

Yachi & Loreau (1999) used a different mathematical model to describe risk spreading (called 'insurance hypothesis' by them), which is based on the differences in species responses to environmental variation. However, the more different species responses are, the lower will be the correlation of species abundances in a variable environment (as in Doak *et al.* 1998). Community resistance will thus be higher in species-rich communities. We can also expect a higher resilience, because there is a greater possibility that a fast regenerating species forms part of the community which can compensate for the decline of other species. Consequently, under conditions of natural environmental fluctuations, community biomass will be less variable in species-rich communities. However, the species composition will change; consequently, species richness does not support compositional stability (Tilman 1999b). Data on the variability in the BIODEPH experiment support this pattern – the total community biomass CV decreased, but the population biomass CV increased with species richness of a community (Hector *et al.* 2010). Should a relative constancy of ecosystem function be achieved by the internal substitution of species, then the substituting species should have a similar effect on ecosystem functioning (as suggested by MacArthur 1955), but differ in response to the environmental variation. Lavorel & Garnier (2002) argued that the insurance effect will be dependent on a decoupling between 'response traits', i.e. traits that determine the species response to environmental variation, and 'effect traits', i.e. traits that determine the species effects on ecosystem function.

In comparisons between habitats in nature, much depends on how the richness differences originated. Species richness may vary along environmental or successional gradients. Community stability (relative constancy in biomass) seems to be determined by the impact of species life history rather than species richness as such. For an old-field succession (Lepš *et al.* 1982; Figs 11.6, 11.9) community productivity decreased, while strategy types according to Grime 2001 shifted from R-strategy via C-R strategy to S-strategy. This change was related to a change in the species–area curve. The S-strategists which grow in number are able to co-exist on small areas; in the stage dominated by C-R strategists, a mosaic of diverse species-poor patches are found which at larger spatial scales

are richer in species (Lepš & Štursa 1989; Osbornová *et al.* 1990). The C-R dominated stage is more productive, less resistant and more resilient than the S-strategist stage.

Resistance to invasion of alien species can be seen as a special case of stability. Species-rich communities were traditionally considered more resistant to invasions of exotic species (Elton 1958). This statement was partly based on a comparison between species-rich tropical forests and species-poorer extra-tropical communities (comparison subject to the effects of confounding factors). A theoretical explanation here is that in a species-rich community there are less 'empty niches' available for possible newcomers. Indeed, when species richness was manipulated, species-poor communities were shown to be more susceptible to invasions (Naeem *et al.* 2000). However, empirical support from observational data is not unequivocal (Rejmánek 1996). Undisturbed tropical forests are both extremely rich in species and highly resistant to invasions; on the other hand, some extra-tropical centres of diversity such as the South African Cape Floral Region are very vulnerable to plant invasions. Some of the factors promoting species co-existence (e.g. repeated disturbance in African fynbos) can also promote invasions. Consequently, rather than species richness *per se*, the factors determining species richness are also important for invasibility.

It seems that there is a difference between communities that are species-poor because of the harsh environment or strong competition on one hand and communities where low diversity is a consequence of limited size of the species pool (e.g. as on islands) on the other hand. Only the latter type is more vulnerable to invasions, as predicted by biodiversity experiments. This corresponds well to the larger invasibility of island ecosystems (Rejmánek 1996; see Chapter 13).

#### 11.6.4 Biodiversity experiments, real consequences of species losses and conservation consequences

Some biodiversity experiments and the biodiversity debate were encouraged by the reality of the global decline of diversity. Will the loss of species impair the functioning of ecosystems? Will biodiversity experiments help predict changes in ecosystems? And do they provide directions for conservation efforts?

In biodiversity experiments, the set of sown species (in fact, the species pool) is manipulated; hence it is considered as an independent variable (predictor of ecosystem functioning). Not all the species usually survive to form the actual community, but data on the resulting species richness are seldom reported. If the actual pool in individual experimental units is a random subset of some larger species pool of the whole experiment (e.g. a random selection of species used in experiments or simulations), the realized richness is positively correlated with the size of the species pool (Stachová & Lepš 2010). If new species are added to an existing species pool, and the new species differ in their traits from those in the original species pool, the actual result need not always be an increase in realized species richness, similarly the experimental removal of a species from a community (and so a factual reduction of the species pool available there) can result in an increase of actual species richness in a community. In a long-term multisite study (Lepš *et al.* 2007), high and low richness meadow species

mixtures were sown in a newly abandoned field (thus enhancing the species pool), the plots were not weeded and were left to colonize naturally. The sown meadow species were different from the pool of natural colonizers (mostly competitively weak species). After 10 years, the productivity generally decreased (as expected from biodiversity experiments) in the order: high richness mixture > low richness mixture > unsown control plots. Nevertheless, the unsown (low productive) control exhibited the highest actual number of species, because in the sown plots the competitive exclusion of naturally colonizing species was faster. As a result, the productivity was positively related to the number of sown species, but not to the realized species richness.

We should be aware that there are important differences between the gradient of species richness created by biodiversity experiments and a sequence created by the loss of species in nature. The equal representation of species on all the diversity levels, important for disentangling the effects of species diversity from the effect of species composition, corresponds to the situation when species are lost from the community at random, irrespective of their traits. In nature, however, the species that are lost from the communities are not a random subset of their species (Lepš 2004a, Srivastava & Vellend 2005). If we want to construct a realistic scenario of species loss, we need to identify the expected sequence of species to be lost, probably according to their traits. In this case, however, we will not get the effect of species richness *per se*, but the expected effect of the loss of particular species (i.e. those that we consider candidates for extinction). For example, in Central Europe, the most endangered species are those of nutrient-poor habitats (which are usually less productive), while the non-endangered species are more productive (Lepš 2004a). In Central European grasslands, species loss is mostly the result of agricultural intensification leading to increased productivity.

In natural communities, species are usually not lost at random (Lepš 2004a; Srivastava & Vellend 2005), but as a result of many specific factors, some of them being species-specific, and some not. Species-specific factors are usually direct and negative in their effect; a typical example is the introduction of a new pathogen or a specialized herbivore. Also, human exploitation is often species-specific, for example selective logging or the collection of plants for pharmaceutical use. The species affected by species-specific negative effects are often selected independently of their function in a community and independently of their effect traits, which also means independently of their competitive strength. Dutch elm disease (*Ceratocystis ulmi*) eliminated *Ulmus* from part of the European forest; species of the genus *Ulmus*, but no other functionally similar species were affected; similarly the decline of *Gentiana pannonica* in the Bohemian forest in the first half of the 20th century was caused by selective digging of its roots for a local liqueur – their functionally analogous species were not affected. Both cases are examples of the decoupling of the response and effect traits (Lavorel & Garnier 2002); the species lost can be functionally replaced by other species from the community that were not affected and the chance that an ‘appropriate’ species will be present increases with diversity. In those cases, the lessons from the biodiversity experiments are relevant. Indeed, in the case of elimination of elms from part of European forests, their functional role was taken over by other



tree species in mixed forests, and the general functioning of the respective ecosystems did not change considerably. In contrast, elimination of *Picea abies* in Central European mountain forests, where the species was a single dominant tree with no functional analogues, led to tremendous changes in the whole ecosystem, regardless of whether the spruce was planted or indigenous, and regardless of whether the spruce dieback was caused by emissions (acid rain) or by a bark beetle outbreak.

When environmental conditions (e.g. productivity or disturbance regime) are changed, many if not all species are affected simultaneously. Typical examples are land-use changes, changes in nature management, large-scale pollution (e.g. nitrogen deposition) or climate change. Under such circumstances, some species are eliminated or at least negatively affected, while other species may benefit, or invade the community undergoing change. Regardless of the final net change in species richness, the most pronounced effect is the change in life history spectra, which will probably overrule any possible diversity effect (Srivastava & Vellend 2005). Functionally similar species will be affected in similar ways, and so there is only a small chance that lost species will be replaced by functionally analogous species. The species will be outcompeted. The change in the productivity or in the disturbance regime will affect species according to the traits that are important for competitive strength, which are usually also important for primary productivity and other ecosystem functions; there is no or slight decoupling of response and effect traits and species richness has a small stabilizing effect. Although changes in environmental conditions can lead to both increase and decline of species richness, most of the recent changes result in a net decline of species richness. Typical examples are: the recent loss of species due to eutrophication; where few productive species prevail in a community; excluding less competitive species; and loss of species due to the abandonment of previously extensively managed grasslands (Bakker 1989) – cessation of regular mowing or grazing leads to extinction of many species, usually less productive, weak competitors. The serious loss of biodiversity in European meadows is partially caused by the increasing nutrient load, which leads to an increased productivity. Conservationists in several European countries have tried to persuade farmers to keep productivity of species-rich grasslands low in order to keep diversity high. Under those circumstances, the use of the argument based on biodiversity experiments that keeping diversity high might be economical because of increased productivity (as suggested by Tilman 1999a) is counter-productive.

Whatever the impact of the loss of species on community functioning, the identity of lost species is probably more important than their number (Aarssen 2001). The loss of any species means that the functional properties of a community is impaired to some extent. As Stampfli & Zeiter (1999) showed for an abandoned formerly managed meadow, the loss of species cannot easily be reversed by the re-introduction of mowing, because the species lost would not return to the earlier state, because the propagules are no longer available. Stampfli & Zeiter (2010) also found that the productivity of these less species-rich meadows is lower than that of the meadow in its original state. The ability of a community to respond to environmental change could be a function of the

richness of the species pool rather than the number of species already present in the community. With the exception of species with a permanent seed bank, and species with long-distance dispersal mechanisms, the species pool is determined by species growing in nearby communities in the landscape (Cantero *et al.* 1999). From this point of view, the simultaneous loss of species in the landscape (which we recently observed in various types of previously species-rich grasslands in Europe) would have serious consequences, not envisaged by small-scale biodiversity experiments.

Both species gains and species losses are considered negatively by conservationists. Gaining a new species by an alien invasion or by expansion of the original area of distribution is in fact an increase of a community species pool, which can, however, have detrimental effects on the native biota (Wardle *et al.* 2011; Chapter 13). As noted by Wardle *et al.* (2011), research on the effects of species gains and species losses has developed largely independently from each other; however, they have a common basis: for the functioning of the new community, it is important which traits are gained/lost in the process (in comparison with the traits of the other species in a community). Thus, for the community to function, trait composition is much more important than the number of species.

The relationship between biodiversity and ecosystem functioning is not only of academic interest, but also has important consequences for environmental policy. Research efforts on this topic resulted in several books providing new syntheses (e.g. Kinzig *et al.* 2001; Naeem *et al.* 2009), and also attempts to reconcile contrasting interpretations (Loreau *et al.* 2002; Loreau 2010). This chapter has concentrated on the study of vascular plant communities (where we expect the competition to be the main interspecific interaction). However, vascular plants (and their diversity) are not the only ecosystem component determining ecosystem functioning; particularly the linkage to below-ground components is also of basic importance (Wardle 2002; see Chapter 9).

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