Biodiversity, Ecosystem Functioning, and Human Wellbeing
An Ecological and Economic Perspective

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CHAPTER 2

Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments

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2.1 Introduction

2.1.1 Two meta-analyses of biodiversity studies published in 2006

The study of patterns in the distribution and abundance of species in relation to environmental variables in nature (e.g. Whittaker 1975), and to species interactions (Krebs 1972), has had a long tradition in ecology. With increasing concern about the consequences of environmental change for species extinctions, researchers started to assess the potential of a reversed causation: does a change in species diversity affect environmental factors and species interactions, such as soil fertility or species invasion? Manipulative experiments that explicitly tested the new paradigm started in the early 1990s and since then the number of such studies has been increasing exponentially (Balvanera et al. 2006, Chapter 3).

In 2006, two meta-analysis papers were published which together provided the most comprehensive quantitative assessment of the overall trends observed in manipulative biodiversity experiments to date. Both studies showed that, on average, random reductions in diversity resulted in reductions of ecosystem functions, but differed in the covariates examined. First, Balvanera et al. (2006) analyzed studies published from 1974–2004. This meta-analysis showed that biodiversity effects, measured as correlation coefficients between some measure of biodiversity (usually species richness) and a representative response at the ecosystem, community, or population level, were significantly influenced by several factors; the specifics of experimental designs, the type of system studied, and the category of response measured. For example, biodiversity effects were particularly strong when the experimental designs included high-diversity mixtures (>20 species) and in well-controlled systems (i.e. laboratory mesocosm facilities).

A second meta-analysis was conducted by Cardinale et al. (2006a) which focused on experiments, published from 1985–2005, where species richness was manipulated at a focal trophic level and either standing stock (abundance or biomass) at that same trophic level, or resource depletion (nutrients or biomass) at the level ‘below’ the focal level was measured. Cardinale et al. (2006a) used log ratios of responses to characterize biodiversity effects. Their analyses showed that species-rich communities achieved higher stocks and depleted resources more fully than species-poor communities, but that diverse communities did not necessarily capture more resources or achieve more biomass than the most productive species in monoculture. Cardinale et al. (2006a) also fitted data from experiments to a variety of functional relationships, and found that experiments were usually best approximated by a saturating function. The results from both meta-analyses were remarkably consistent across different trophic levels and between terrestrial and aquatic ecosystems. In this
chapter we present further analyses of the two meta-data sets, in parallel, and attempt a joint interpretation.

2.1.2 The two meta-data sets used in this chapter

The two meta-data sets assembled by Balvanera et al. (2006) and Cardinale et al. (2006a) are hereafter referred to as B and C, respectively. Together, the two databases contain more than 900 published effects of biodiversity on ecosystem functioning (Schmid et al. 2009, Cardinale et al. 2009). In B, these effects were extracted directly from the publications and therefore rely on the analysis (assumed to be correctly executed) carried out by the original authors. In more than half of the cases, the extracted biodiversity effects were correlation coefficients (Balvanera et al. 2006). For these, and for additional cases, significance, direction, and shape of the relationship between biodiversity and each response variable could be extracted. In C, the mean values of response variables were available for each level of species richness. This allowed the authors to decide whether a linear, log-linear, or saturating curve (Michaelis–Menten) was the best fitting relationship (see Cardinale et al. 2006a). For ease of comparison with B, the correlation coefficients obtained using the log-linear fit in C are used for this chapter. These were very closely correlated with the correlation coefficients on the Michaelis–Menten scale ($r = 0.99$, $n = 105$). The significance was not assessed in C because the relationships were calculated from means.

If the same response variable was measured repeatedly in an experiment, it was only entered once in each of the two meta-databases: B focused on the first date on which measurements were taken in a study (excluding establishment phases of experiments) while C selected the last date of published measurements. Although about half of the measurements contained in C are also in B, the two data sets were kept separate for our new analyses because of the different ways in which biodiversity effects were initially extracted or calculated.

We speak of a ‘biodiversity effect’ if a function varies among different levels of biodiversity. Because different levels of biodiversity can be ordered from low to high, in most cases a biodiversity effect can be more specifically defined as a positive or negative relationship between variations in biodiversity as the explanatory variable and a function as response variable. Thus, a positive diversity effect occurs when a relationship is positive and a negative biodiversity effect occurs when a relationship is negative.

2.1.3 Hypotheses

The goal of meta-analyses of biodiversity–ecosystem functioning experiments is to assess to what extent biodiversity effects reported in single studies can be generalized across different design variables, system types, and response categories. Ideally, hypotheses about variation between studies should be derived, a priori, from underlying mathematical theory about mechanisms responsible for biodiversity effects. In practice, however, it is often only possible to look for patterns in variation of biodiversity effects and then develop explanatory hypotheses in retrospect. This is primarily due to the fact that the majority of biodiversity experiments included in our meta-databases focused on demonstrating biodiversity effects rather than attempting to test specific mechanistic hypotheses (for an exception, see e.g. Dimitrakopoulos and Schmid 2004). The hypotheses presented in this chapter are derived from patterns found in the previous meta-analyses of B and C. To avoid repetition of results reported in Balvanera et al. (2006), we omit hypotheses relating to the influence of specific experimental designs. Instead, we consider several new hypotheses (see below). We also consider the shape of the relationship between biodiversity and specific response variables.

Our first hypothesis is that biodiversity effects differ among ecosystem types (Hooper et al. 2005). Differences in biodiversity effects among ecosystems could arise, for example, from variation in the ratios of producer/consumer stocks, or the size, generation times, or growth rates of dominant organisms. For example, Giller et al. (2004) suggested that biodiversity–ecosystem functioning relationships differ between aquatic and terrestrial ecosystems because of more rapid turnover of material and individuals in aquatic systems. However, despite the often expressed concern that
extrapolation from one ecosystem type to another is unwarranted (Hooper et al. 2005, Balvanera et al. 2006), we were unable to find specific predictions about the direction of differences in biodiversity effects between ecosystem types.

We distinguish between population-level functions, recorded for individual target species, such as density, cover or biomass; community-level functions, recorded for multi-species assemblages, such as density, biomass, consumption, diversity; and ecosystem-level functions, which could not be assigned to population- or community-level and included abiotic components such as nutrients, water or CO$_2$/O$_2$. Our second hypothesis then is that species richness enhances community (and ecosystem) responses but affects population responses negatively (Balvanera et al. 2006). This follows from basic Lotka–Volterra dynamics (see e.g. Kokkoris et al. 1999, Loreau 2004), and the assumption of a maximum community response given by the total availability of resources in the environment. Consider for example a system with $s$ species, where the population growth rate ($r_i$) of species $i$, with carrying capacity $K_i$ in monoculture, will be reduced by its own population size ($N_i$) as well as the populations of $s$–1 competing species ($N_1 \ldots N_j$):

$$r_i = r_{i,\text{max}} \cdot (K_i - N_i - x_{i,1}N_1 - x_{i,2}N_2 - \ldots - x_{i,j}N_j)/K_i$$

Every addition to a community with species $i$ of a species $j$ with an inter-specific competition coefficient $x_{i,j} > 0$ will reduce the growth rate $r_i$ and thus negatively affect the population size of species $i$. However, if $x_{i,j} < 1 > x_{i,p}$, the sum of the two species $i$ and $j$ can produce a larger community size $N_i + N_j$ than each species by itself. That is, if inter-specific competition coefficients are generally smaller than 1, the community size can increase with increasing species richness according to Lotka–Volterra dynamics. Hypothetically, with increasing species richness, total community responses can be summed over more populations, but individual populations will each be under increasing pressure (McGrady-Steed and Morin 2000, Brown et al. 2001, Bunker et al. 2005).

Our third hypothesis predicts that standing stocks should respond differently to species richness manipulations than rates (or depletion of resources). However, as with differences between ecosystem types, it is difficult to predict the direction of the differences. Using the argument made above that, for example, community size (as a measure of standing stock) may have upper limits due to the total availability of resources in the environment, whereas rates of change in community size should not be restricted in this way, it follows that rates should be affected more strongly than stocks. This argument is used by researchers who claim that plant species richness may well increase plant productivity but not carbon storage (see e.g. Körner 2004). On the other hand, the theory developed by Michel Loreau (personal communication) predicts that stocks should be more responsive than rates.

Whereas the above hypotheses can already be applied to biodiversity studies focusing on a single trophic level, our fourth hypothesis specifically concerns biodiversity effects observed in multi-trophic studies. We consider the effect of changing biodiversity at one trophic level on functions carried out by a different (mostly adjacent) trophic level. If the latter is above the manipulated level, we speak of bottom-up biodiversity effects; if it is below the manipulated level, we speak of top-down biodiversity effects. Despite some similarities between systems with one versus two trophic levels (Ives et al. 2005), biodiversity effects may be more difficult to generalize and predict in multi-trophic systems because of the many possibilities for positive and negative feedback (see e.g. Petermann et al. 2008), as well as differences between generalist and specialist interactions (Petchey et al. 2004a, Thébault and Loreau 2006, Petchey et al. 2008). Theory and some empirical results suggest that bottom-up effects of biodiversity should usually be negative because higher diversity increases resistance to disease and predation (Koricheva et al. 2000, Loreau 2001, Fox 2004a, Petchey et al. 2004a, Keesing et al. 2006, Duffy et al. 2007). However, some empirical results suggest opposite trends (e.g. Koricheva et al. 2000, Pfisterer et al. 2003, Gamfeldt et al. 2005). Top-down biodiversity effects should also be negative because a more diverse community at trophic level $t$ should be able to deplete the community at trophic level $t - 1$ more completely, thus reducing functions such as...
standing stock at the this lower trophic level (Fox 2004b, Petchey et al. 2004a, Fox 2005a, Duffy et al. 2007). This leaves positive effects of biodiversity for within-trophic level (a large number of studies surveyed in the two meta-analyses) and for symbiont relationships. However, these patterns may differ between green (living plant-based) and brown (detrital-based) food webs. A recent meta-analysis of top-down and bottom-up effects in detrital food webs (Srivastava et al., 2009) showed that detrital processing (top-down effects) was increased by high detritivore diversity, but showed variable responses to detrital diversity (bottom-up effects).

Finally, positive effects may also be expected if the trophic distance between the level at which biodiversity is varied and the level at which the response is measured is two or a multiple of two (e.g. top-down from secondary consumers at level $t$ to primary producers at level $t - 2$, or, conversely, from trophic levels $t$ to $t + 2$), because two negative interactions can together lead to a positive one. Such effects are implicit in the Hairston–Smith–Slobodkin (1960) hypothesis and can be seen in some of the output from simulation models (Petchey et al. 2004a). In the previous meta-analysis of Balvanera et al. (2006), however, we observed that biodiversity effects tend to get weaker the greater the trophic distance is between the level at which diversity is manipulated and the level at which a function is measured.

Our fifth and final hypothesis considers the premise that if increasing species richness of a community increases total resource and space use, then less of the resource or space should be available to potential invaders unless they are competitive dominants that displace the existing native species. That is, if the number of species that can fit in the community depends on the ‘niche dimensionality’ of the environment (Harpole and Tilman 2007), then the more species that are already there in a community, the more difficult it will be for further species to successfully colonize (Fargione et al. 2003, Mwangi et al. 2007).

### 2.1.4 Shape of the biodiversity–ecosystem functioning relationship

In the expected shape of the relationship between biodiversity and response functions. Using a survey, Schläpfer et al. (1999) canvassed expert opinions as to whether the relationship was either constant (i.e. no relationship), idiosyncratic, linear, non-linear (logistic, optimum), log-linear, or asymptotic.

The simplest hypothesis about the shape of biodiversity–ecosystem functioning relationships is that of a constant response for all species richness levels, either including or excluding a species richness level of zero. However, including zero species provides a stricter hypothesis that has almost never been tested empirically (in most experiments the zero-richness level was not included) and will therefore not be discussed further. A problem with the hypothesis of constant response is that it cannot be tested for statistical significance.

The experts in Schläpfer et al. (1999) predicted log-linear or saturating shapes for relationships between biodiversity and primary production, nutrient cycling, or water cycling. Such shapes are also predicted by niche theory, which assumes complementarity in resource use among species, but increasing niche overlap with increasing species richness (Tilman 1997, Loreau 1998a, Schmid et al. 2002b). Linear, logistic, or even exponential relationships may be expected between biodiversity and bioregulation (e.g. biocontrol or resistance to the spread of disease), if interactions among species are highly specialized (Stephan et al. 2000, cf. gene-for-gene interactions in host–parasite systems). Indeed, about half of the experts in the survey of Schläpfer et al. (1999) predicted an exponential or logistic shape for relationships between biodiversity and bioregulation.

In the last part of our analyses, we ask, if a function asymptotes at high diversity, how many species are required for a 50 per cent of the maximum function. If the biodiversity–function relationship is log-linear, we ask how much a 50 per cent or 75 per cent reduction in species richness changes the function.

### 2.1.5 Methods of analysis

Our new analyses of the influence of explanatory terms on both the variation and shape of biodiversity effects were based on the data descriptions
and methods presented in B and C. For B, we added data on the significance, direction, and shape of biodiversity effects to the correlation coefficients used in the original analysis. We distinguished the following shapes of biodiversity effects in B: negative, negative linear, negative log-linear, no relationship, positive, positive linear, positive log-linear, positive but not linear, and none of these conditions. For C, we calculated correlation coefficients after fitting log-linear relationships, excluding studies with only two species richness levels (where correlation coefficients can only be 1 or -1). Furthermore, we used log-linear fits because these were often also used in the original papers. To assess the shape of biodiversity effects in C, we fitted linear, log-linear, and saturating (Michaelis–Menten) curves.

In B, we used three different measures of the relationship between biodiversity and response to analyze differences in biodiversity effects: (1) correlation coefficients \( r \) standardized to \( Zr \) values, (2) significances (0 for relationships with \( P \geq 0.05 \), 1 for relationships with \( P < 0.05 \)), and (3) signs (-/+, only significant relationships). In C, we used only correlation coefficients standardized to \( Zr \) values in the analysis. Correlation coefficients were converted into \( Zr \) values to improve normality (correlation coefficients are bound between -1 and 1 and thus not normally distributed). The formula for the conversion is (Rosenberg et al. 2000):

\[
Zr = 0.5 \ln \left( \frac{1 + r}{1 - r} \right).
\]

The number of plots, \( N \), used for the determination of each single biodiversity effect in the original publications, corrected by the degree of freedom, was used as weighting variable in B (note that \( n \), as opposed to \( N \), will be used later to refer to the number of effects rather than the number of plots used to calculate a single effect). Because the correlation coefficients in C were calculated from the means at each level of species richness, \( Zr \) values were weighted by the number of species richness levels used in fitting the relationship. In both B and C, analyses with unweighted \( Zr \) values yielded similar results and are therefore not presented.

We used linear mixed-model analyses to test the influence of explanatory terms on the \( Zr \) values. Study site and publication were used as random terms. Latitude and longitude were tested against site as an error term. Explanatory terms which varied within sites (but not within publications) were tested against site as an error term (as in B and C). To avoid problems of confounding and correlated responses, all explanatory terms were fitted both individually and in a combined analysis. Only if a fixed term was significant in both cases (comparing the likelihood of a model with and without the term) was it retained for further analysis. With these stringent rules, we tried to ensure that hypothesis tests were robust across an entire data set and not due to influences of correlated variation in other factors. Interactions between explanatory terms were also tested, but were seldom retained in the model under the stringent rules mentioned above.

Logistic mixed models were used to analyze differences in significances (probability of observing significant biodiversity effects) and signs (probability of observing a significant positive biodiversity effect among the significant effects) in relationships between biodiversity and response in B. Significance corresponds to the finding that a standardized correlation coefficient is significantly different from zero. Even if information about the correlation coefficient was not available, the direction of the effect could be extracted from the original publications, and therefore positive versus negative significance could be distinguished. To avoid overrating studies with small sample sizes in the logistic models, the number of experimental units per study divided by the mean number of experimental units across all studies was used as a weighting variable for each data point. To test the five hypotheses, we used ratios of mean deviances as approximate \( F \)-values (McCullagh and Nelder 1989). This allowed us to use publication as the appropriate error term for corresponding fixed terms that did not vary within publications.

All presented means of \( Zr \) values, percentages of significant biodiversity effects or percentages of positive directions among significant biodiversity effects, are weighted means using the weighting variables mentioned above. Values and significance levels that are not presented in figures or tables are given in the text.
2.2 Hypotheses to explain variation in biodiversity effects

Before the detailed presentation of the results, an overview of the analyses, including all the explanatory terms discussed below, is provided (Table 2.1). This table first lists the fixed terms in the different models (generally in descending order of $F$-values) followed by the random terms. In the analysis of meta-data set C, which contained more homogeneous data and thus fewer candidate explanatory terms than the larger meta-data set B, only one fixed term was retained in the model. In B, terms for finer categories of responses were fitted to reduce the amount of unexplained variance (residual).

2.2.1 Distribution of studies

The reported biodiversity effects came from more than 100 independent experiments, mainly carried out in North America and Europe (Fig. 2.1).

Table 2.1 Multivariate mixed-model analyses for (a) data in B (cf. Balvanera et al. 2006) and (b) data in C (cf. Cardinale et al. 2006a).

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Degree of freedom</th>
<th>% var. explained</th>
<th>$F$-ratio</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Proportion of significant effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Responses of communities $\neq$ ecosystems $\neq$ populations (see 2.2.3)</td>
<td>2</td>
<td>5.4</td>
<td>31.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses vary among ecosystem types (see 2.2.2)</td>
<td>7</td>
<td>8.5</td>
<td>6.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses of residents $&gt;$ invaders (see 2.2.6)</td>
<td>1</td>
<td>0.5</td>
<td>6.0</td>
<td>0.015</td>
</tr>
<tr>
<td>Responses vary among response groups</td>
<td>27</td>
<td>4.7</td>
<td>2.0</td>
<td>0.002</td>
</tr>
<tr>
<td>Responses vary among study sites (random term)</td>
<td>92</td>
<td>22.4</td>
<td>1.3</td>
<td>0.189</td>
</tr>
<tr>
<td>Responses vary among publications (random term)</td>
<td>41</td>
<td>7.4</td>
<td>2.2</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>595</td>
<td>51.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Proportion of positive within significant effects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Responses of residents $&gt;$ invaders (see 2.2.6)</td>
<td>1</td>
<td>11.0</td>
<td>145.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses of stocks $\neq$ rates (see 2.2.4)</td>
<td>1</td>
<td>5.3</td>
<td>70.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses of communities $\neq$ ecosystems $\neq$ populations (see 2.2.3)</td>
<td>2</td>
<td>5.9</td>
<td>39.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Top-down and bottom-up responses $\neq$ others (see 2.2.5)</td>
<td>5</td>
<td>4.7</td>
<td>12.3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses vary among ecosystem types (see 2.2.2)</td>
<td>7</td>
<td>12.1</td>
<td>5.3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses vary among response groups</td>
<td>24</td>
<td>8.5</td>
<td>4.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses vary among study sites (random term)</td>
<td>81</td>
<td>17.7</td>
<td>0.7</td>
<td>0.936</td>
</tr>
<tr>
<td>Responses vary among publications (random term)</td>
<td>40</td>
<td>12.9</td>
<td>4.3</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>291</td>
<td>21.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Z-values</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Responses of communities $\neq$ ecosystems $\neq$ populations (see 2.2.3)</td>
<td>2</td>
<td>18.6</td>
<td>88.9</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses of residents $&gt;$ invaders (see 2.2.6)</td>
<td>1</td>
<td>4.2</td>
<td>40.4</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses decrease with cos(latitude)</td>
<td>1</td>
<td>2.5</td>
<td>11.6</td>
<td>0.001</td>
</tr>
<tr>
<td>Responses of stocks $\neq$ rates (see 2.2.4)</td>
<td>2</td>
<td>3.3</td>
<td>15.8</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Responses vary among ecosystem types (see 2.2.2)</td>
<td>7</td>
<td>12.9</td>
<td>6.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Top-down and bottom-up responses $\neq$ others (see 2.2.5)</td>
<td>5</td>
<td>1.2</td>
<td>2.3</td>
<td>0.042</td>
</tr>
<tr>
<td>Responses vary among response groups</td>
<td>24</td>
<td>4.1</td>
<td>1.7</td>
<td>0.031</td>
</tr>
<tr>
<td>Responses vary among study sites (random term)</td>
<td>63</td>
<td>13.3</td>
<td>0.8</td>
<td>0.834</td>
</tr>
<tr>
<td>Responses vary among publications (random term)</td>
<td>30</td>
<td>8.4</td>
<td>2.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>302</td>
<td>31.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(b) Z-values</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Responses of stocks $\neq$ resource depletion (see 2.2.4)</td>
<td>1</td>
<td>4.2</td>
<td>9.5</td>
<td>0.003</td>
</tr>
<tr>
<td>Responses vary among publications (random term)</td>
<td>43</td>
<td>67.8</td>
<td>3.6</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>63</td>
<td>28.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Interestingly, Zr values declined significantly with increasing cosine of latitude in the larger data set B (Table 2.1(a)). However, this trend was largely explained by higher values in Europe (n = 187, mean Zr = 0.26) relative to those from North America (n = 234, mean Zr = –0.6), with the latter representing lower latitudes (higher cosines). Biodiversity effects did not vary across altitudes of study sites, but most of these were located < 500 m above sea level. The geographical distribution of studies indicates a strong bias towards locations where the major funding is, rather than where the science is most warranted (see Chapter 3). Experiments undertaken in the tropics (e.g. Potvin and Gotelli 2008) and at high latitudes are urgently needed to further test biodiversity effects under more contrasting conditions. To what extent the difference in Zr values between European and North American studies may be confounded by researcher preferences remains unknown.

A larger number of biodiversity effects are documented for terrestrial studies than are documented for aquatic studies (Table 2.2(a)). Of the terrestrial fraction, a large number of the biodiversity effects reported are from studies carried out in grassland ecosystems (60 per cent in B and 45 per cent in C). It is therefore not surprising that a large number of biodiversity effects are reported from studies manipulating plant diversity, with detritivores plus mycorrhizae coming second, herbivores third, and carnivores fourth (Table 2.2(a)). In B, 154 of all biodiversity effects could be classified as an ecosystem
response, 434 as a community response and 183 as a population response. Ecosystem service groups covered in B included 251 biodiversity effects on primary production (including abundance and standing biomass), 254 on bioregulation, 195 on soil fertility, 46 on nutrient and water cycling, and 10 on climate regulation.

The majority of biodiversity effects concerned responses of standing stock, but a considerable number was also related to rates (in B) or resource depletion (in C; Table 2.2(b)). Resource depletion in C was measured as (1) instantaneous rate ($n = 5$) or as a reduction in resource compared with (2) control without species ($n = 44$, or $n = 28$ for experiments that lasted less than one generation time) or (3) the beginning of the experiment ($n = 21$, or $n = 13$ for experiments that lasted less than one generation time); one value was not classified. In B, relationships between the trophic level at which species richness was manipulated and the one at which a response was measured (above, below, ecosystem, same, symbiont, within [multitrophic diversity manipulations]) were distributed more or less regularly across both stocks ($n = 99, 11, 66, 321, 40, 14$, respectively) and rates ($n = 86, 6, 30, 83, 5, 8$, respectively). However, there were only a few relations that could be classified as top-down biodiversity effects (category ‘below’, $n = 17$). Among the bottom-up biodiversity effects (category ‘above’, $n = 185$), about a third were cases where detrital diversity of primary producers was manipulated and decomposer functions were measured ($n = 65$).

### Table 2.2

(a) Number of studies in which different trophic groups have been manipulated in aquatic and terrestrial ecosystems and (b) number of studies in which different trophic groups have been manipulated and stocks or rates/depletion of resources have been measured.

<table>
<thead>
<tr>
<th></th>
<th>Consumers</th>
<th>Detritivores or mycorrhizae</th>
<th>Herbivores</th>
<th>Plants</th>
<th>Multitrophic manipulations</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Database B</strong> (cf. Balvanera et al. 2006)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aquatic</td>
<td>3</td>
<td>12</td>
<td>41</td>
<td>54</td>
<td>40</td>
<td>150</td>
</tr>
<tr>
<td>Terrestrial</td>
<td>4</td>
<td>87</td>
<td>5</td>
<td>510</td>
<td>15</td>
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<td><strong>Database C</strong> (cf. Cardinale et al. 2006)</td>
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</tr>
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<td>24</td>
<td>64</td>
<td></td>
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</tr>
</tbody>
</table>

(b) Database B (cf. Balvanera et al. 2006)

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<tr>
<th></th>
<th>Consumers</th>
<th>Detritivores or mycorrhizae</th>
<th>Herbivores</th>
<th>Plants</th>
<th>Multitrophic manipulations</th>
<th>Total</th>
</tr>
</thead>
<tbody>
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<td>0</td>
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<td>2</td>
<td>0</td>
<td>2</td>
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<tr>
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<td>99</td>
<td>46</td>
<td>564</td>
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<td>771</td>
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Database C (cf. Cardinale et al. 2006)

<table>
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<tr>
<th></th>
<th>Consumers</th>
<th>Detritivores or mycorrhizae</th>
<th>Herbivores</th>
<th>Plants</th>
<th>Multitrophic manipulations</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
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<td>34</td>
<td>24</td>
<td>64</td>
<td></td>
<td>147</td>
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</tbody>
</table>

2.2.2 Biodiversity effects vary among ecosystem types (hypothesis 1, Table 2.3)

In both B and C biodiversity effects came mainly from four broadly defined ecosystem types: grassland, fresh-water, marine, and forest. Note that the breadth of definition is narrower for those ecosystem types in which a larger number of studies have been carried out (grassland) than in those with fewer studies (aquatic marine). The remaining biodiversity effects were represented by approximately the same number of other ecosystem types (bacterial microcosm, crop/
successional, ruderal/salt marsh, soil community). Zr values varied significantly between ecosystem types in B, but not in C (Table 2.3). When tested, the significance remained when ecosystem service groups (refer to previous paragraph) or finer categories of responses (see Table 2.1(a)) were fit before ecosystem type in the analyses. However, because the significant variation in B was, at least partly, due to stronger biodiversity effects in the ecosystem types with lower values of n (see B), it is too early to draw any general conclusions. More importantly, there was no overall tendency in any of the analyses for biodiversity effects to be more (or less) frequently positive (or more or less often significant) in terrestrial systems than it was for aquatic ecosystems. This supports the view that similar mechanistic processes underpin the biodiversity–ecosystem functioning relationship under terrestrial and aquatic conditions.

2.2.3 Biodiversity effects differ among ecosystem, community, and population levels (hypothesis 2, Table 2.3)

Our results strongly suggest that while increasing species richness often enhances the performance of entire communities, it also often reduces the average contributions of individual species. Biodiversity effects on ecosystem-level (abiotic) responses also tend to be positive, but not as much and not as often as the biodiversity effects on community-level responses (Fig. 2.2(a)). This suggests a more direct mechanistic link in the latter case. In the meta-analysis of B, the difference among ecosystem-, community-, and population-level responses was identified as the strongest explanatory factor for variation in biodiversity effects. In the new analysis presented here, this is true for both Zr values and significances (Table 2.3, Fig. 2.2(a)). The result remained highly significant ($F_{2,209} = 82.5, P < 0.001$; mixed model with site and publication as random terms) even if only significant Zr values were analyzed ($n = 307$).

2.2.4 Biodiversity effects differ between stocks and rates (or depletion of resources) (hypothesis 3, Table 2.3)

In B, biodiversity effects on stocks and rates were distinguished: stocks referred to levels of an ecosystem property (e.g. standing biomass) whilst rates referred to changes in such levels over time. In C, biodiversity effects on stocks and depletion of resources were distinguished: stocks referred to levels of an ecosystem property only at a focal trophic group (see Table 2.2(b)) whilst depletion referred to direct rates of resource depletion, or to differences between the consumed and unconsumed resource levels at a trophic group below the focal one (see Section 2.2.1). In the following test of our third hypothesis, we treat resource depletion as equivalent to rates.

<table>
<thead>
<tr>
<th>Number</th>
<th>Hypothesis</th>
<th>Cardinale</th>
<th>Balvanera</th>
<th>Balvanera</th>
<th>Balvanera</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Zr ($n = 108$)</td>
<td>Zr ($n = 449$)</td>
<td>P (sign.)($n \leq 766$)</td>
<td>P (pos. sign.)($n \leq 766$)</td>
</tr>
<tr>
<td>1</td>
<td>Biodiversity effects vary among ecosystem types</td>
<td>no ($P &gt; 0.1$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
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<td>2</td>
<td>Biodiversity effects differ between ecosystem, community and population level</td>
<td>–</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
</tr>
<tr>
<td>3</td>
<td>Biodiversity effects differ between stocks and rates or depletion of resources</td>
<td>yes ($P = 0.003$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
</tr>
<tr>
<td>4</td>
<td>Biodiversity effects depend on trophic relationships</td>
<td>– (confounded with above)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P = 0.035$)</td>
</tr>
<tr>
<td>5</td>
<td>Biodiversity affects residents and invaders differently</td>
<td>–</td>
<td>yes ($P &lt; 0.001$)</td>
<td>yes ($P = 0.004$)</td>
<td>yes ($P &lt; 0.001$)</td>
</tr>
</tbody>
</table>

Table 2.3 Tests of hypotheses about variation in biodiversity effects (see Sections 2.1.3 and 2.1.5). ‘Cardinale’ and ‘Balvanera’ refer to data in C (cf. Cardinale et al. 2006a) and in B (cf. Balvanera et al. 2006), respectively.
In B, we found more significant and more positive effects of species richness on stocks than we did on rates (Table 2.3, Fig. 2.2(b)). Overall, 55 percent of the significant biodiversity effects on rates were negative, as were the average Zr values for those rates. For example, resource extraction from primary producers (disease severity, consumed biomass) usually declined with increasing plant species richness. These results were robust to changes in fitting sequence of other hypotheses.

A similar result was found in C, where Zr values for stocks (mean Zr = 1.53) were significantly ($F_{1,63} = 9.52, P < 0.01$; mixed model with publication as random term) larger than Zr values for depletion of resources (mean Zr = 1.01). If those depletion measures which were taken after a time interval of a generation or more were excluded (see Section 2.2.1), then the difference between Zr values for stocks and depletion of resources (mean Zr = 0.82) became even larger ($F_{1,49} = 13.48, P < 0.001$; mixed
model with publication as random term). The Zr values were higher in C than in B. This was probably due to two differences between the analyses: in B, Zr values were averaged over a more heterogeneous set of responses, whilst in C, Zr values were calculated from means at each species richness level, thereby excluding variation around means. When compared to stocks, the significantly lower Zr values for depletion of resources in C may in part be due to a difference in trophic distance: stocks in C were measured at the trophic level where diversity was manipulated and there was depletion of resources at the trophic level below (see hypothesis 4).

2.2.6 Biodiversity affects residents and invaders differently (hypothesis 5, Table 2.3)

In B, 93 of the 771 biodiversity effects concerned the response of invaders to the species richness of the residents in a community. Of these, 76 per cent were significant biodiversity effects. The vast majority (89 per cent) of the significant biodiversity effects were negative, as were the average Zr values. That is, invader functions were reduced at higher biodiversity of residents, corresponding to an increased invasion resistance of more diverse resident communities. This contrasts with 59 per cent significant biodiversity effects on responses of residents, of which only 31 per cent were negative (Fig. 2d). These results demonstrate that one of the most general effects of high biodiversity is increased invasion resistance (Knops et al. 1999, Hector et al. 2001, van Ruijven et al. 2003, Fargione and Tilman 2005, Spehn et al. 2005, Mwangi et al. 2007), thereby corroborating our fifth hypothesis.
shape for biodiversity effects, the linear function actually did fit best in 34 out of 108 cases (32 per cent) in C; and it was observed in 164 out of 771 cases (21 per cent) in B (Table 2.4). Where the highest species richness was < 10, linear relationships were observed in 27 per cent and 40 per cent of the studies in B and C, respectively. Among studies in which the highest species richness was ≥ 10, 19 per cent in B and 28 per cent in C were linear. The majority of biodiversity effects that were assigned a shape, however, were not linear, reflecting the predictions of the majority (78 per cent) of experts and consistent with theoretical expectations (Section 2.1.4; see also Chapter 8). Experts and authors of the publications used in B did not distinguish between non-linear curves that do (Michaelis–Menten) or do not saturate (log-linear). In C, however, this distinction could be made and showed that the average $R^2$ value was 0.690 and 0.682 for the saturating Michaelis–Menten and log-linear relationship, respectively. Furthermore, if the linear relationship was included in the comparison, the log-linear was the best fitting in only 25 studies, whereas the saturating curve was the best fitting in 49 studies (Table 2.4). However, the log-linear was the worst-fitting relationship in only seven cases, compared with 66 for the linear and 35 for the saturating relationship. Thus the log-linear relationship has an intermediate position: it crudely fits a large number of biodiversity effects. This may reflect a mixture of operating mechanisms, including complementarity and selection effects (Schmid et al. 2002b). Nevertheless, most theoretical models (see e.g. Tilman et al. 1997c, Loreau 1998a, Cardinale et al. 2004) show that biodiversity effects should saturate, at least at high levels of species richness, which are seldom ascertained in experimental studies. It should be noted that $R^2$ values and vote counting are very crude measures for distinguishing between functions of different shape.

### 2.3.2 Shapes of biodiversity effects differ between major response categories

Whilst the previous section focused on the general shape of all analyzed biodiversity effects, the
following section will investigate differences in the shapes of biodiversity effects between studies. In particular, we want to test the hypothesis that biodiversity effects on primary production and nutrient and water cycling are log-linear (or saturating), whereas those on bioregulation are more often linear or logistic. The data in B and C provide some support for these hypotheses (6–8 in Table 2.4). A large number of observed effects of plant diversity on primary production, or responses related to it, including all types of abundance measures, were log-linear or saturating, whereas the few examples for responses related to nutrient and water cycling did not reveal any clear pattern (Table 2.4). Responses related to bioregulation in B showed the lowest proportion of log-linear relationships and the highest proportion of linear ones. This is broadly consistent with the hypothesis and the expectation of the experts (Schläpher et al. 1999), who predicted the smallest amount of log-linear biodiversity effects or, in other words, redundancy for these responses. Despite the large body of literature on biocontrol there is, to our knowledge, no general theory about how the diversity of hosts should be related to diversity of enemies. This is the case even though empirical work on quantitative interaction webs across varying diversity levels has been done (e.g. Albrecht et al. 2007) and the importance of distinguishing between interactions with generalists versus specialists has been demonstrated in models of multitrophic diversity manipulations (Petchey et al. 2004a, Thébault and Loreau 2005).

2.3.3 Consequences of observed shapes of biodiversity effects

Under the assumption of a positive, saturating relationship, the experts in Schläpher et al. (1999) greatly overestimated the number of species required to reach 50 per cent of the maximum response. The average estimate was between 5–6 species (Schläpher et al. 1999), whereas analysis of the data in C suggested that an average of only 1.2 species are needed (Table 2.4). This result suggests that the presence of a single species results in almost half of the response. However, one limitation of fitting Michaelis–Menten curves is that they assume a zero response for the species richness level of zero, which is not always appropriate, as for example in the case of evapotranspiration of an ecosystem. We think a more interesting question is how many species does one need relative to a one-species monoculture to obtain some percentage of maximal function.

When experts were asked to predict the consequences of a 50 per cent species loss from 16 to 8 species, they overestimated the reduction in the response by a factor of three under the assumption of a positive, log-linear relationship (Table 2.4). The empirical log-linear results from C suggest that, with each halving of species richness, the response would be reduced by about 11 per cent of the 16-species richness level. Reduction in the number of species from 16 to 1 species would involve four halving events, corresponding to a reduction by about 44 per cent. Similarly, if we assume a saturating Michaelis–Menten relationship the average reduction in C from 16 to 8 species would be 5.2 per cent and from 16 to 1 species would be 38.8 per cent. Comparing the expert predictions for the reduction from 16 to 8 (30 per cent) and from 16 to 4 (40 per cent; see Schläpher et al. 1999) suggests that the experts assumed a linear relationship between species richness and response, even though they selected a weaker relationship more often (see Section 2.3.1).

2.4 What have we learned from biodiversity manipulation experiments?

The joint interpretation of results from of the new analyses of the two meta-data sets of B and C demonstrates that, despite the large heterogeneity of data, biodiversity effects are a general feature of most biological systems. Recent discussions have focused on the details of experimental design and analyses, as well as the mechanisms underpinning biodiversity effects (see e.g. Cardinale et al. 2007). It is gratifying to see that these issues could not mask the influence and importance of major biological factors in explaining the variation in biodiversity effects.

2.4.1 Hypotheses to explain variation in biodiversity effects

The major biological factors used in the analyses presented in Table 2.1 involve multilevel factors
such as different ecosystem types or types of response variables (i.e. response groups), where we could only state the existence of significant variation, and factors, with few well-interpretable levels and contrasts between these levels. We tested five hypotheses regarding the influence of these biological factors on the strength and direction of biodiversity effects (see Table 2.3). The first hypothesis that biodiversity effects vary between ecosystem types and therefore restrict the potential for generalizations from one ecosystem to another, was confirmed (Section 2.2.2). However, the surprising (cf. Giller et al. 2004) similarity of responses between terrestrial and aquatic ecosystems (and among the ecosystem types studied most often) shows that there are very likely to be common processes and patterns operating among different ecosystems.

The second hypothesis, that an increasing diversity of species positively affects responses at the community (and ecosystem) level and negatively affects responses at the population level, was also confirmed (Section 2.2.3). This supports predictions from basic Lotka–Volterra theory and arguments about density compensation (McGrady-Steed and Morin 2000). If total resource or energy inputs from the environment fix the response at community or ecosystem level (see e.g. Bunker et al. 2005), and if these inputs are distributed among several species, the average response of species at population level must go down as diversity goes up. The evidence for this effect in the current analysis was very strong and robust across the large range of biodiversity effects in the meta-dataset of B. It would be interesting to explore whether a theoretical relationship can be found between positive/negative effects of biodiversity on community/population-level responses, as found here, and the better-known positive/negative effects of biodiversity on temporal variation in community/population-level responses (May 1974, Tilman 1996, Flynn et al. 2008). The comparatively weak influence of biodiversity on ecosystem-level responses may reflect an indirect relationship between biotic components, whose biodiversity was manipulated, and abiotic components of which functional responses were measured.

Our third hypothesis was that biodiversity effects on stocks might differ from biodiversity effects on rates, but we could not predict the direction of the difference (Section 2.2.4). Nevertheless, we clearly showed that there were differences between stocks and rates and that, in fact, biodiversity influenced stocks more strongly and more positively than rates (or depletions of resources). This result was consistent in both analyses of the B and C meta-data sets, despite some differences between the two. In C, stocks were measured directly in the diversity-manipulated group, whereas depletions of resources were measured at the trophic level below. In B, stocks and rates were measured at the same or at different trophic levels above or below the one manipulated. Our results are still difficult to understand, but we can at least conclude that the assumption that rates or depletion of resources should be more responsive to biodiversity than stocks is wrong. This becomes relevant, for example, in the context of rates and stocks in ecosystem carbon cycling (Körner 2003, Körner 2004). According to our results, there is no longer a reason to believe that high biodiversity will simply increase turnover rates rather than storage.

The fourth hypothesis predicted that increased biodiversity at one trophic level reduces functions at other trophic levels (negative bottom-up and top-down biodiversity effects), whereas it increases functions at the same trophic level or for symbionts (Section 2.2.5). Indeed, these predictions were met, with the exception that bottom-up biodiversity effects (mainly detrital diversity of primary producers) on detritivore functions were mostly positive. In a new meta-analysis using a larger number of such studies, Srivastava et al. (2009) found equal numbers of positive and negative effects of detrital diversity on detritivore functions. Although other bottom-up biodiversity effects and top-down biodiversity effects were mostly negative in the present analysis, this was not the case when two trophic levels separated the manipulated and the measured groups. This indicates that two negative biodiversity effects between adjacent trophic levels can multiply to a positive effect between more distant levels. It is gratifying to see that even for multi-trophic
biodiversity studies predictions made on theoretical grounds (e.g. Loreau 2001, Fox 2004a, Fox 2004b, Fox 2005a, Petchey et al. 2004a, Keesing et al. 2006, Duffy et al. 2007) are broadly supported by data, although it is still too early to derive further generalizations.

Our fifth hypothesis, that increasing biodiversity should affect the responses of residents positively and the responses of invaders negatively, was strongly supported by the data in B and was highly robust across the span of measurements and ecosystems (Section 2.2.6). Nevertheless, there has been some debate whether this is a general trend or a specific feature of experiments (Levine and D’Antonio 1999, Fridley et al. 2007). The problem here is that in non-experimental situations it is hard to distinguish invaders from residents unless the invasion process is directly observed; also, conditions that favour diversity in general cannot be dissected from those that promote invaders in particular (Espinosa-García et al. 2004). Nevertheless, niche theory predicts a lowered availability of free niche space with increased species richness (Fargione et al. 2003, Harpole and Tilman 2007, Mwangi et al. 2007), as well as the results from the experiments presented here, both of which are consistent with positive biodiversity effects on invasion resistance.

2.4.2 Alternative shapes of biodiversity effects

Although a large number of biodiversity effects have the shape of a log-linear or a saturating curve, these shapes are by no means the only ones (e.g. Chapter 1) – especially if responses related to bioregulation are considered (both beneficial and detrimental interactions between species whose diversity was manipulated and those species whose responses were measured). For the latter, biodiversity effects often did not diminish or saturate over the range of species richness levels tested. In contrast, responses related to primary production and nutrient or water cycling did show evidence of deceleration or reaching saturation (Section 2.3.2). This difference between biodiversity effects on bioregulation and biodiversity effects on water or element cycling was expected on theoretical grounds as well as being predicted by experts (Schläpfer et al. 1999). Saturating relationships for resource uptake and conversion are consistent with increasing overlap of resource niches that are expected with increasing diversity (Tilman 1997, Loreau 1998a). Such limitations may not affect relationships between biodiversity and bioregulation. However, it should be noted that studies of bioregulation tend to manipulate just a few species across minimal levels of species richness and this may provide an alternative explanation for the differences.

With the detailed metadata contained in C, it is possible to calculate how severe reductions of species richness might be in comparison to estimates provided by the experts 10 years ago. When doing so, we were surprised to find that experts assumed that a much larger number of species (5–6) would be needed to maintain responses at half-saturation level than the empirical investigations estimate. The empirical estimates suggest that the average monoculture should already reach the half-saturation level. Similarly, in comparison to empirical findings, experts overestimated the consequences of halving species richness by a factor of three. This suggests that experts often do not think about the difference between systems with no species and a system with a single species, perhaps because experts do not consider it meaningful to measure ecosystem properties at a species richness level of zero.

At this juncture, one fundamentally important caveat should be considered. As Hector and Bagchi (2007) have shown, it is likely that more than one species will be needed to maintain multiple responses at half-level. Thus it could well turn out that as the number of responses considered are increased, the number of species needed to maintain multi-response half-levels is also likely to increase to (or above) an expert-estimated saturation of around 5–6 species.

2.4.3 Recommendations for the next-generation biodiversity experiments

It was only possible to review biodiversity effects reported until summer 2005. In the meantime, the number of studies has increased further and new meta-analyses could be started. We hope that some of the new and future studies will look
more specifically at mechanisms generating biodiversity effects. If so, future meta-analyses can go beyond the testing of rather phenomenological hypotheses and begin to understand mechanistic processes.

We suggest that the old and new data should be combined in an open-access data table that would allow continuous monitoring of overall trends and further analysis. Comparing the variables used in the two existing databases showed that a similar reduced set was independently derived by the two groups of authors from a multitude of candidate variables (Table 2.5). Values for this set of variables should be reported, if possible, by every new study on biodiversity–ecosystem functioning relationships. The latter will require a change in ethos and a willingness to share data both nationally and internationally (a trend which is increasing across many disciplines, such as molecular biology), but would significantly bolster crosscutting analyses aimed at identifying the generalities of biodiversity effects.

Acknowledgements

We thank Michel Loreau, Peter Morin, Shahid Naeem, and an anonymous reviewer for very useful comments on the manuscript of this chapter. We thank the Swiss Agency for the Environment, Forests and Landscape (SAEFL) for financial support.

Table 2.5 Some variables that should be included in publications and meta-data bases of biodiversity experiments.

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<td>Experiment/study identification</td>
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<td>Level of control (enclosed, field)</td>
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<td>6</td>
<td>Cause of diversity gradient</td>
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<td>The species diversity measure used</td>
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<td>Highest species richness</td>
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<td>Total number of different species compositions</td>
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<td>Mean response</td>
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<tr>
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<td>Shape of functional response to biodiversity</td>
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References


References


REFERENCES


References


REFERENCES 313


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REFERENCES

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