Biodiversity, Ecosystem Functioning, and Human Wellbeing

An Ecological and Economic Perspective

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CHAPTER 7

The analysis of biodiversity experiments: from pattern toward mechanism

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7.1 Introduction

This chapter reviews the methods developed to investigate the mechanisms that generate relationships between diversity and functioning in biodiversity experiments. What do we mean by mechanism? An important recent advance in ecology and evolution has been the championing of mechanistic statistical models (Mangel and Hilbourn 1997). These statistical models are mechanistic in the sense that their parameters refer to biological processes that can be quantified, rather than to unmeasureable abstract concepts that often prove useful in purely theoretical models of ideas. Similarly, non-linear regression analysis is often described as 'semi-mechanistic' when parameters can be at least loosely related to biological processes (Pinheiro and Bates 2000). In many areas of science there are often multiple layers of mechanism underlying the phenomena of interest. As we will explain below, some of the models reviewed in this chapter could be termed fully mechanistic in that they can be built to include parameters that refer directly to ecological processes (e.g. predation rates), whereas some of the other methods could be termed semi-mechanistic in the sense that they can indicate the presence of ecological processes (e.g. 'complementarity effects') even if, as explained above, they cannot quantify the exact biological process that underlies these effects. To understand the motivation for the development of these methods we first review the debate over the mechanisms responsible for relationships between biodiversity and ecosystem functioning.

7.1.1 Background

Following a landmark conference in 1992, the study of the relationship between biodiversity and ecosystem functioning became a focused area of research. In the edited book that arose from that meeting (McNaughton 1993, Schulze and Mooney 1993) quoted the following from Chapter 4 of *On The Origin of Species*: 'It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised'. The quote concisely makes a prediction – that more diverse plant communities should be more productive – and indicates the underlying mechanism. Darwin contrasts one species with several distinct genera, implying that it is the ecological niche differences between species that underlie this effect. More extensive text from Darwin's *Natural Selection* (Stauffer 1975) clarifies that Darwin really was relating biodiversity to ecosystem functioning via what he termed the 'ecological division of labour' (Hector and Hooper 2002) when he wrote that, 'A greater absolute amount of life can be supported . . . when life is developed under many and widely different forms . . . the fairest measure of the amount of life being probably the amount of chemical composition and decomposition within a given period.' Following McNaughton many researchers have reproduced this quote and its popularity reflects the tendency of ecologists at this time to focus on these ecological niche differentiation mechanisms and the species 'complementarity' (as introduced by Woodhead 1906) that results from these differences. However, there is a second class of potential mechanisms that was under-represented in the early literature. The sampling effect hypothesis (Aarssen 1997, Huston 1997, Loreau 1998a, Tilman *et al.* 1997c) proposes that in biodiversity experiments randomly assembled diverse communities have a higher probability of containing and being dominated by the species which is most productive when grown alone. The selection effect (Loreau and Hector 2001) and dominance effect (Fox 2005b) are similar but more general effects that relate the relative abundance of species in mixtures to their performance when grown alone (see below).

Species complementarity is sometimes used with reference only to resource partitioning. However, both conceptually and in practice, it is often difficult to separate resource partitioning from facilitation and other ecological processes such as diversity-dependent differences in natural enemy impacts (Connell 1978, Janzen 1970, Root 1973, Zhu *et al.* 2000). This set of 'complementarity effects' and the alternative set of 'sampling', 'selection' or 'dominance effects' are not mutually exclusive (they often can and do occur together) and can produce very similar patterns. This means that when analyzing biodiversity experiments, process cannot be inferred from pattern alone. Distinguishing the contributions of these alternative classes of mechanism has become an important goal in the analysis of biodiversity experiments, since they can indicate what sorts of ecological processes have generated the observed pattern and are important considerations in interpreting the results of these experiments.

7.1.2 Limitations and needs

Some of the methods available to investigate mechanism in biodiversity experiments have limitations that mean they cannot be applied to many existing datasets. Two of the main limitations of these methods are that they require measurements of how species affect ecosystem functioning when grown alone (that is all species must be grown in monoculture) and the contributions of individual species to the ecosystem functioning of mixtures (e.g. the total productivity of a mixed community must be broken down into the contributions of individual species). For certain organisms and for particular functions, these requirements are often difficult or impossible to meet. Hence there is the need for a varied toolbox of methods for the analysis of mechanism in biodiversity experiments that can encompass all organisms and all ecosystem processes. We think that this suite of tools now exists and the aim of this chapter is to provide a comparative review and users guide to these methods. Given the number of methods and limited space, and the fact that all of the methods have already been described in the literature, we restrict the main text to general descriptions only (with detailed supplementary material provided by the authors of each method). The literature has mainly focused on productivity as an ecosystem function and our discussion does the same even though some of these methods can be applied to other ecosystem process.

7.2 Analysis of mechanism in biodiversity experiments

7.2.1 Transgressive overyielding

One of the simplest analyses that can be performed is a comparison of the functioning of mixtures relative to the best-performing single-species community (monoculture). Mixtures that perform significantly better than the best monoculture are said to transgressively overyield and transgressive overyielding has often been seen as the acid test for positive effects of biodiversity (Cardinale *et al.* 2006a, Cardinale *et al.* 2007, Hector *et al.* 2002b, Kirwan *et al.* 2007).

7.2.2 Overyielding: relative yields

A second approach is to look for overyielding more generally by comparison to the single-species performances of all of the species present in a mixed community. The concept of 'relative yields' (RYs) has been used for this purpose in plant ecology and agriculture since the mid-twentieth century (De Wit and Van den Bergh 1965, Harper 1977, Vandermeer 1989). The relative yield of a plant species is simply its biomass in mixture expressed as a proportion of its biomass in monoculture. Summing the relative yields for all species in a mixture provides a relative yield total (RYT). Relative Yield Total values greater than one show that increases in the abundance of some species in mixture have not been exactly compensated by decreases in others (as would be the case in a zero-sum game (Hubbell 2001)). Overyielding (as distinct from transgressive overyielding) is often taken to indicate resource partitioning but can also occur through facilitation and other mechanisms, such as the reduction of natural enemy impacts in mixtures (as described above). Loreau (1998b) devised a more general scheme of deviations from expected values that are closely related to the earlier relative yield-based measures. Overyielding-based methods usually assume a substitutive experimental design in which total density is held constant, independent of diversity, although the method can be adapted for additive designs too (where additive means that the total density is the summed total of the densities of all of the component species).

7.2.3 Additive partitioning methods

7.2.3.1 Two-way additive partitioning of biodiversity effects

The additive partitioning method (Loreau and Hector 2001) extends the relative yield approach described above to define an overall net biodiversity effect and to partition this into two additive components: a complementarity effect and a selection effect (see supplementary material). In a substitutive experiment, the net biodiversity effect (for a community formed from species started at equal densities) is simply the difference between the observed yield of the mixture and the average of the monoculture yields. The net biodiversity effect equals zero when individual plants grow equally well in monoculture and mixture. The complementarity effect is based on changes in relative yields (or rather, differences in observed relative yields versus their null expectation values) and is linearly related to RYT (but scaled to a null value of zero rather than 1). Complementarity effect values > 0 indicate positive effects of biodiversity on overyielding while values < 0 indicate interference competition. The other half of the partition is a covariance term that was inspired by the Price equation from evolutionary genetics (although as we explain below the additive partitioning method and Price equation are different). The selection effect measures the covariance between a species trait (e.g. monoculture biomass) and its performance in mixture. Positive selection effect values indicate that species with greater than average monoculture biomass perform better than expected in mixture, while negative values indicate the converse. While the Loreau–Hector additive partitioning method does not examine biological processes directly, it has allowed major advances in the debate over the mechanisms underlying the patterns found in biodiversity experiments (e.g. Loreau and Hector 2001, Cardinale *et al.* 2007).

7.2.3.2 Tripartite additive partitioning of biodiversity effects

One limitation of the additive partition is that it assumes, as do relative yields, that complementarity is distributed equally across species. This means that it may over- or underestimate total complementarity, some of which falls under the selection effect (Petchey 2004). The tripartite partition (Fox 2005b) is a modification of the additive partition of Loreau and Hector (2001) described above. The two versions share the same goal of identifying whether, and for what reasons, the functioning of a given mixture of species deviates from that expected under a simple null hypothesis (see supplement). However, the tripartite version partitions the difference between observed and expected function into three additive components: the dominance effect (DE), trait-independent complementarity effect (TICE), and trait-dependent complementarity effect (TDCE). The two versions are related as follows. The complementarity effect from the two-way additive partition corresponds exactly to the trait-independent complementarity effect from the tripartite version. However, the tripartite partition can be thought of as taking the original two-way split into complementarity and selection effects from Loreau and Hector (2001) and performing a further split by dividing the selection effect into the dominance effect and a trait-dependent complementarity effect (SE = DE + TDCE). Species with particular traits (monoculture yields) can do better than expected in mixtures either at the expense of other species (pure competitive replacement as quantified by the dominance effect), or not at the expense of other species (trait-dependent complementarity effect).

7.2.4 Applying the Price equation to biodiversity experiments

Relative yield-based approaches, and the related additive partitioning approaches, have primarily been used to aid the interpretation of substitutive experiments with plants or similar organisms. In such experiments, interest centres on whether the functioning of a diverse mixture of species deviates from that expected under the null model that intra- and interspecific interactions are identical. However, in many circumstances, interest centres on comparing the functioning of different sites directly with one another, rather than on comparing each to a null model. This may be because no appropriate null model exists, because information to parametrize a null model is lacking, or simply because the investigator wishes to consider all processes that cause ecosystem function to vary among sites rather than factoring out the effects of some processes by comparison to a null model. For instance, an investigator might be interested in how the functioning of a site has changed since a historical extinction event, or in explaining variation in function along a natural diversity gradient. The Price equation partition (Fox 2006, Fox and Harpole 2008) was designed for such cases.

The Price equation partition classifies the mechanisms that cause two sites (a 'pre-loss' site of higher species richness, and a 'post-loss' site of lower species richness) to differ in ecosystem function (see supplement). The Price equation partition assumes that the species at the post-loss site comprise a nested subset of the species at the pre-loss site, and that total ecosystem function comprises the sum of the separate contributions of individual species (Fox 2006). The assumption of a 'summed' ecosystem function covers primary productivity and many other functions, but does not cover many others (see Fox and Harpole 2008). The Price equation partition divides the difference in total function between two sites, ΔT, into three additive components. The species richness effect (SRE) is that part of ΔT attributable to random loss of species richness, independent of which species were lost. The species composition effect (SCE) is that part of ΔT attributable to non-random loss of species making higher- or lower-than-average contributions to total ecosystem function. The context dependence effect (CDE) is that part of ΔT attributable to between-site differences in the functional contributions of the species present at both sites (i.e. the functional contributions of these species are not constant, but rather are context-dependent).

The Price equation partition takes (and extends) the original Price equation developed in evolutionary biology to classify and partition the causes of evolutionary change in mean phenotype (Frank 1995, 1997, Price 1970, 1995) and applies it to the effects of changes in biodiversity on ecosystem processes. In evolution, the mean phenotype of an offspring population can differ from that of a parental population for two reasons: natural selection (covariation between parental fitness and parental phenotype), and imperfect transmission (factors, such as environmental change, that cause the phenotypes of offspring to deviate on average from those of their parents). In mathematical terms, natural selection is analogous to the Species Composition Effect. For instance, non-random death of (selection against) large-bodied individuals will reduce mean body size in the next generation, assuming body size is heritable and all else being equal. Analogously, non-random extinction of high-functioning species will reduce mean function per species, and thus total function, all else being equal. Imperfect transmission is precisely analogous to the Context Dependence Effect. For instance, if all offspring to have larger body sizes than their parents then, all else being equal, mean offspring body size will exceed mean parental body size. Analogously, if all species remaining at the post-loss site function at a higher level than they did at the pre-loss site, mean function per species, and thus total function loss, all else being equal, will be higher at the post-loss site (while functioning is usually thought of as declining with species loss it could also increase).

7.2.5 Classical statistical analysis of mechanisms

7.2.5.1 Random partitions design and analysis

Bell *et al.* (2005b) introduced a direct approach to the analysis that avoids calculating derived values (e.g. complementarity effects) which must then be statistically analyzed in a second stage. Their approach is a direct analysis of the primary data using normal least squares and general linear models. The Bell *et al.* approach includes several notable features of both the design and analysis.

The design takes a full species pool, N, and forms a diversity gradient by dividing by integer factors of N. For example, Bell *et al.* selected a pool of 72 study species (from 103 available species) so that their diversity gradient comprised the series 72 (72/1), 36 (72/2), 24 (72/3), 18 (72/4), 12 (72/6), 9 (72/8), 8 (72/9), 6 (72/12), 4 (72/18), 3 (72/24), 2 (72/36), 1 (72/72). In other words, the species pool was randomly divided in half, randomly divided into thirds and so on. The resulting communities were termed a 'partition' of the selected species pool (to avoid confusion note the use the word in a difference sense to the additive partitioning equations described above). This approach was then repeated using different random selections to produce different replicate partitions, that is replicate diversity gradients that divide up the species pool in different ways (for example, two replicate gradients would divide the species pool into two different half-pools rather than using the same selection of species). This approach ensures that, within each replicate partition, each species is present once at every level of diversity (a species is present in one monoculture, in one two-species community and so on).

The method fits a least-squares model to the data that includes terms for the species richness, the presence/absence (identity) of each species, and the composition of the community. The level of ecosystem functioning, y, is modelled as:

$$y = \beta_0 + \beta_{LR}x_{LR} + \beta_{NLR}x_{NLR} + \left(\sum_{i}^{s} \beta_i x_i\right) + \beta_Q x_Q + \beta_M x_M + e$$

where β_0 is the intercept, β_{LR} is the coefficient associated with linear richness (richness treated as a continuous variable), β_{NLR} is the coefficient associated with species richness treated as a categorical variable, the $\beta_i{}'\ s$ are the coefficients associated with the presence/absence of each species, β_Q is the coefficient associated with each partitioned species pool, β_M is the coefficient associated with each composition, and e is a normally distributed random variable. One important feature of this method of analysis is that, when it is used along with the experiment design described above, the non-linear richness and species identity terms are orthogonal (do not share sums-of-squares). Consequently, it is possible to parse some of the explained variation into either variation due to species identity or to variation due to non-linear richness. Another unique feature of the design is that the collective effects of species interactions can be captured by the non-linear richness term (β_{NLR}). This 'deviation from linearity' term provides an ensemble test for all species interactions combined.

7.2.5.2 The diversity–interactions statistical modelling approach

The diversity–interactions approach (Kirwan *et al.* 2007) is also a more direct application of classical statistical methods that has several similarities to the analysis conducted by Bell *et al.* (2005b) (see http://www.diversity-model.com/). The approach is based on a framework of statistical models whose coefficients reflect the effects of species identity and species interactions. The initial community compositions are described by the abundance of each species as a proportion of total initial abundance (M). The species proportions (P_i) are either planned experimental proportions or the relative abundances of species measured early in the experiment. The regression equations describe the ecosystem process response variable (y) as follows:

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \sum_{i,j=1,\, i<j}^{s} \delta_{ij} P_i P_j + \varepsilon$$

Here, β_i (the identity effect of the ith species) is the expected monoculture performance of the ith species, α is the effect of overall initial abundance, δ_{ij} is a measure of the strength of interaction between species i and j, and ε is the residual term. The model is fitted using standard regression techniques. The sign of an interaction coefficient δ_{ij} indicates whether the interaction between species i and j has a synergistic or antagonistic effect on ecosystem function. The total contribution to ecosystem function of the interaction is $\delta_{ij} P_i P_j$ and also depends on the initial relative abundances of the two species. The response in a mixed community expected solely from monoculture performance is $y = \sum_{i=1}^{s} \beta_i P_i$. The net biodiversity effect in model (7.1) is $\sum_{i,j=1,\, i<j}^{s} \delta_{ij} P_i P_j$, the sum of all pairwise interactions among species. This diversity effect generalizes to a rich class of alternative models based on alternative assumptions about the strength of pairwise species interactions. For example, the strength of pairwise interactions may all be the same (identical values of δ_{ij}) leading to a diversity effect $\delta \sum_{i,j=1,\, i<j}^{s} P_i P_j$ that is related to evenness (Kirwan *et al.* 2007). Alternatively, there may be clear patterns among the δ_{ij} that reflect the traits of the species in the mixture (e.g. a functional group model that has a common interaction coefficient for all pairwise interactions between species from different functional groups). Interactions may also involve more than two species or more complex functions. Many of these alternative models are hierarchical to model (7.1) or to the model with a single interaction coefficient, which leads to straightforward comparisons of models to identify the most appropriate. For example, a pair of nested models with and without species interactions can be compared to test whether the ecosystem process response is determined only by species identity effects or by identity effects and species interactions. The complexity to which we can describe patterns of interaction, and the sensitivity to discriminate between alternative patterns, depend on the range and patterns of relative abundances that were selected in the experimental design. Many diversity–function experiments use communities with varying species richness, but equal relative abundances. Diversity–interaction models can be fitted to data from such a design. However, by including experimental communities that provide good coverage of the design space, such as communities dominated by one or a subset of species, we can test for more complex patterns of species interaction (Kirwan *et al.* 2007). Also, prediction of the diversity effect may be reliable over a wider range of communities in which all component species are not equally represented.

7.3 Discussion

7.3.1 Pattern

Meta-analysis of the results from the first decade of research in this area clearly shows a positive relationship between biodiversity and ecosystem functioning; a pattern which is consistent across trophic groups (producers, herbivores, detrivores, and predators) and present in both terrestrial and marine ecosystems (Balvanera *et al.* 2006, Cardinale *et al.* 2006a, Worm *et al.* 2006). However, in terrestrial ecosystems the relationship between biodiversity and ecosystem functioning is generally quickly saturating with increasing diversity (Cardinale *et al.* 2006a) suggesting that the effect of random biodiversity loss on ecosystem functioning will be initially weak but accelerating (Hector *et al.* 1999).

7.3.2 Transgressive overyielding

The low frequency of transgressive overyielding in the meta-analysis performed by Cardinale *et al.* (2006a) led them to suggest that the general positive relationship between biodiversity and productivity in their analysis was most likely due to sampling effects. The logic is that if complementarity is present it should increase the performance of the mixed community above that of even the best single species. However, as we show below, there can be widespread complementarity without transgressive overyielding. In other words, lack of transgressive overyielding does not mean lack of complementarity. On the contrary, it has been shown using the classical Lotka–Volterra competition model that stable coexistence can occur in mixed communities via niche complementarity without transgressive overyielding (Beckage and

Gross 2006, Loreau 2004). This can be simply illustrated as follows. Consider two species that differ in their productivities when grown alone so that the first is more productive than the second. Assume that these two species can stably coexist together through some form of resource partitioning (or equivalent form of niche differentiation). Complementary resource use will act to increase the productivity of the two-species mixtures above the level that would be expected if the two species were not complementary, that is if resource competition were a zero-sum game. However, this effect will be countered by the reduction in productivity caused simply by the replacement in the mixture of some of the more productive species by individuals from the less productive species. Transgressive overyielding will only occur when the increase in productivity due to complementarity is stronger than the reduction in productivity caused simply by the 'dilution' of the most productive species by the introduction into the mixture of individuals of less productive species.

The comparison of the yields of a variety of polycultures with particular monocultures selected *post hoc* also raises several statistical issues that complicate the test (Schmid *et al.* 2008). Furthermore, it is not clear how to best define transgressive overyielding in biodiversity experiments. The situation in an agricultural setting is clearer: for a farmer the question is whether a mixture can overyield the most productive monoculture (although even the agricultural reckoning is complicated by issues of monoculture and mixture production and price stability of components over time with varying climates and biotic challenges). However, outside of agriculture the choice is less clear because, in principle, every monoculture provides a potential benchmark for comparison (Hector *et al.* 2002a). The traditional agricultural test for overyielding is arguably the most natural test when the species with the highest monoculture yield dominates the depauperate communities. However, it is easy to imagine cases where traditional agricultural overyielding is not the only natural choice. One example occurs when the species that is highest yielding in monoculture is not highly abundant in the mixtures. Abundance is often taken as inversely related to extinction risk (small populations are often at greater risk of extinction) so that a species which is not highly abundant in the original full community may be one of the species which is lost as diversity declines. In this example, it is not clear that the species with the highest-yielding monoculture should be the benchmark for comparison since it may not even be present in the later depauperate community, let alone the dominant species (Hector *et al.* 2002a). As we discuss below (see: negative selection effects), in biodiversity experiments it is often the case that the species that dominate communities are not those that are most productive when grown alone (indeed they often have lower-than-average monoculture yields). In these situations the case for taking the species with the most productive monocultures as the benchmark for comparison is not clear. An alternative approach would be to take the monoculture value of the species that dominates mixtures instead since, for example, this is the species that would be expected to go extinct last based on population size arguments (Hector *et al.* 2002a).

7.3.3 Overyielding and the additive partitioning methods

Additive partitioning methods allowed the first attempts at identifying the relative importance of the different classes of mechanism underlying the patterns reviewed above (see also Schmid *et al.* this volume). Meta-analysis of plant biodiversity experiments reveals that almost all studies are driven by a combination of complementarity and selection effects but that overall complementarity effects are nearly twice as strong as selection effects (Cardinale *et al.* 2007). However, even though complementarity effects have a greater effect than selection effects they are not strong enough to cause mixtures to do significantly better than the best monocultures in most cases, as discussed above.

Another feature revealed by the additive partitioning method is the unexpected frequency of negative selection effects (e.g. counter to the predictions of the original sampling effect hypothesis). In the meta-analysis of additive partitioning results from experiments with plants 44% of studies showed negative selection effects. In other words, in nearly half of all experiments communities were

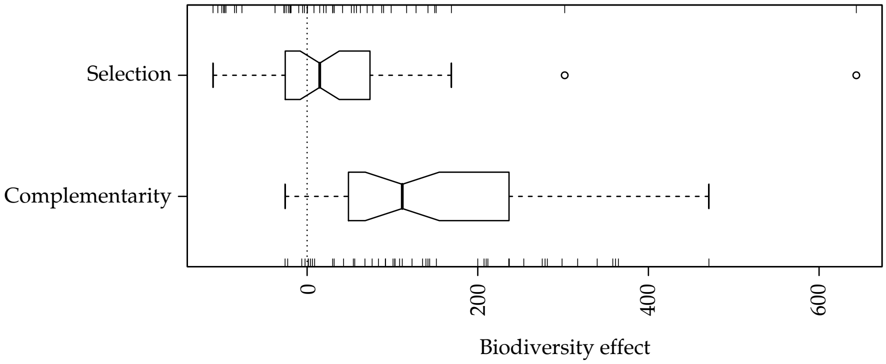

Figure 7.1 Box-and-whisker plot summary of the 44 studies with additive partitioning data reviewed in Cardinale *et al.* (2007). The box and whiskers show quartiles of the distributions of the selection (above) and complementarity (below) effects. The heavy central bar is the median and the notches on the boxes indicate an approximate $P = 0.05$ test for the median values versus zero. Points show two positive outliers for the selection effect values.

not dominated by highly productive species but by species with a lower-than-average monoculture biomass (Fig. 7.1). By looking only at the outcome of competition in mixtures plant ecologists have too often equated high productivity with competitive dominance. While this is often the case, there are many situations where less productive species are able to become dominant. The mechanisms by which they achieve this remain poorly understood and could be addressed by future research.

The key innovation of the tripartite additive partitioning method was the identification of the trait-dependent complementarity effect. Ecologically, a non-zero trait-independent complementarity effect occurs when the ecological mechanisms that mediate the strength of interspecific interactions relative to intraspecific interactions differentially affect high-yielding species, so that monoculture biomass covaries with traits that allow species to overyield in mixture (Petchey 2004). Fox (2005b) suggests that such covariation might reflect ‘nested niches’ (also called ‘included niches’). In this view, species with ‘larger’ niches benefit from being planted in mixture, because their niches contain those of species with ‘small’ niches with ‘room to spare’. However, species with ‘small’ niches experience equal niche overlap whether planted in monoculture or mixture. Therefore, species with larger niches grow better in mixture than in monoculture, but not at the expense of species with small niches. This leads to a positive or negative trait-dependent complementarity effect, depending on whether species with ‘larger’ niches have high or low monoculture biomasses.

The hypothesis that trait-dependent complementarity effects arise from ‘nested niches’, while trait-independent complementarity effects arise from non-overlapping niches, could be tested experimentally by manipulating the scope for niche differentiation. For instance, Dimitrakopoulos and Schmid (2004) planted monocultures and mixtures of plants in various depths of soil, and found an increasing selection effect with increasing soil depth. The complementarity effect (equivalent to the trait-independent complementarity effect from Fox 2006) increased with soil depth so it is possible that the increase in the selection effect was due, at least in part, to an increasingly strong trait-dependent complementarity effect in deeper soil. Increasing soil depth might be expected to increase the trait-dependent complementarity effect if some species with low monoculture biomass can produce only shallow roots, while species with high monoculture biomass can produce shallow and deep roots. Deep soil would allow species with high monoculture biomass to access a resource pool unavailable to shallow-rooted species, allowing deep-rooted species to attain high biomass in mixture, but not at the expense of shallow-rooted species.

To date, there have been few formal comparisons of the bi- and tripartite versions of the additive partitioning method. In other words, there have been few formal assessments of the contribution made by the trait-dependent complementarity effect. Our published (Fox 2005b) and unpublished results to date suggest that trait-dependent complementarity often makes a relatively minor contribution. One interpretation of the typically small magnitude of the trait-dependent complementarity effect is that niches are not usually 'nested'. That is, the ecological mechanisms that mediate the strength of interspecific interactions relative to intraspecific interactions typically do not differentially affect high-yielding species. This hypothesis could be tested by manipulating factors thought to mediate the ecological differentiation of species. It would also be interesting to look for the trait-dependent complementarity effect in circumstances in which it might be expected to be large (e.g. to examine the functioning of mixtures of generalist and specialist consumers).

As a general procedure we recommend analysts compare these related overyielding and partitioning approaches and, all else being equal, select the simplest one that describes the data well. For example, presenting the tripartite method will be essential when trait-dependent complementarity plays an appreciable role but presenting the selection and complementarity effect may otherwise suffice (in the limit, when trait-dependent complementarity effects are zero the dominance and selection effects are mathematically equivalent). In other cases, near equal monoculture biomasses make the selection effect covariance term trivial and relative yield totals or deviations from expected values (Loreau 1998b) provide a simpler alternative to additive partitioning (e.g. Vojtech *et al.* 2008).

7.3.4 The Price equation

The Price equation partition is a natural approach when interest centres on the effects of species loss from an initially diverse community, and the ecosystem function of interest comprises the summed contributions of individual species. The other major approach for comparing observed ecosystem function among sites is classical statistics (see Section 7.2.5). The Price equation partition and classical statistics can be viewed as trading off retention of information *vs* general applicability. The Price equation partition requires knowledge of the functional contributions of individual species, and retains the information about which species were lost. Indeed, the reason for assuming that the less diverse site comprises a strict subset of the species in the more diverse site is so that information about which species were lost can be retained in a useful fashion (see Appendix B in Fox and Harpole (2008) and our supplementary material). By retaining this information, the Price equation partition defines terms (SRE, SCE, and CDE) that have a straightforward mechanistic interpretation independent of the details of study design. In situations where either the Price equation partition or classical statistical approaches can be applied, the investigator should carefully consider the question of interest in order to select the most useful approach.

7.3.5 The diversity–interaction statistical modelling approaches

One advantage of the application of these classical statistical methods to biodiversity experiments is that they avoid calculation of derived values (complementarity effects and so on) that must then be analyzed in a second stage. Furthermore, the methods do not require monocultures (as with additive partitioning), nor a full mixture (as in the Price equation), nor individual species contributions to the functioning of mixtures. Ideally a simplex design assures that species are grown in different combinations and at different relative abundances but species may be simply present (100 per cent) or absent (0 per cent). When species are simply present or absent the analysis of Bell *et al.* (2005b) can be seen as a special case of the approach of Kirwan *et al.* (2007). So, while the additive partitioning and Price equation approaches have mainly been applied to aboveground biomass production in plants these classical statistical approaches should be applicable to any ecosystem function (e.g. Sheehan *et al.* 2006). One advantage of classical statistical approaches is that they do not require knowledge of the functional contributions of individual species, and some classical statistical approaches also omit information about which species are absent from which sites. By omitting this information, classical statistics gains

Table 7.1 Overview of when the methods reviewed in this chapter can be applied depending on the information collected (whether or not individual species contributions to ecosystem processes can or has been measured) and type of experimental design (whether the relative abundance of species in communities is known or simply their initial presence or absence; and whether species mixtures and monocultures are all nested subsets of a single high-diversity community.

Information/Design	Transgressive overyielding	Random partitions	Diversity interactions	Relative yields and additive partitioning	Price equation partition
No individual species contributions Species presence/absence	√	√			
No individual species contributions Species relative abundance	√	√	√		
Individual species contributions	√	√	√	√	
Individual species contributions Nested communities	√	√	√	√	√

more general applicability, for instance to ecosystem functions that do not comprise the summed contributions of individual species, and to sites that do not comprise nested subsets of species. The general applicability of classical statistics allows a greater range of cross-study comparisons (Balvanera *et al.* 2006), although this generality comes with the risk of allowing statistically valid comparisons whose scientific interpretation is obscure (Fox and Harpole 2008). One cost of omitting information is that the interpretation of the terms of a fitted statistical model will necessarily depend on the details of the model and the study design. For instance, effects of species richness found by studies with different designs will have differing interpretations because of the other terms included in the respective statistical models. A final limitation of the classical statistical approach is that it cannot identify biological mechanism directly, but its ability to identify strong patterns among species interactions should direct the focus of more detailed explanatory research.

7.4 Conclusions and recommendations

Our main conclusion is that the range of techniques developed for the analysis of mechanisms in biodiversity experiments is now broad enough that we judge that some investigation of mechanisms should be possible for all studies published to date that examine effects of diversity within a single trophic level (plant biodiversity experiments for example; Table 7.1). This should enable a move from purely phenomenological studies to those that also address the underlying mechanisms. Wider application of the methods described here should help resolve the debate over mechanism that has continued largely due to the failure of many studies to address the underlying biological processes in an informative way (Cardinale 2006a, 2007). We finish with some words of warning and suggestions for future work.

Few, if any, of the methods reviewed here have been comprehensively explored. By that, we mean their behaviour has not been investigated with extensive simulation studies. This is a clear need for future work. Furthermore, most studies to date have tended to select one method and apply it in isolation. On the one hand, it is good that analyses should focus on the most appropriate method at the design stage. On the other hand, we are at a stage where it would also be interesting to run the different methods on the same dataset and to compare and contrast the results. In this way we can see where the different methods agree or disagree and demonstrate the advantages of one method over another in terms of what they reveal about the underlying biology. These approaches also need to be extended, or alternatives invented, that can deal with mechanism in multitrophic biodiversity experiments.

Finally, while our review emphasizes the ways in which analytical methods have tried to move closer to biological mechanisms, none of the methods described here measures the processes involved. Ideally the analyses described here will be supplemented by experimental approaches that directly quantify the processes involved in species interactions and which are not applied *post hoc* but are specified at the experimental design stage. These could include direct measures of natural enemy attack in monocultures and mixtures for example, or the use of isotope methods that can identify stocks and flows of resources. Only then will we be able to ask how well derived measures, like the biodiversity effects from the additive partitioning analyses and the statistical interactions from classical approaches, map onto biological interactions in diverse communities.