



Analysis of biodiversity experiments: A comparison of traditional and linear-model-based methods



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ABSTRACT

The relationship between diversity and ecosystem functioning is often studied by biodiversity experiments. Traditionally, the mechanisms behind biodiversity effects observed in these experiments have been evaluated by relative yield,overyielding and Loreau and Hector's additive partitioning of net biodiversity effect, and more recently by linear-model-based methods such as Kirwan's diversity—interaction model and Bell's random partition model. We compared data required and results given by these traditional and linear-model-based methods using three data sets: a simulated data set and two pot biodiversity experiments. For the simulated data, we also compared expected outputs based on defined ecological species traits with actual outcomes of the methods. BEF experiments were designed to answer five fundamental questions: Q1) How does sown species richness change ecosystem functioning? Q2) What ecological mechanisms cause this change? Q3) How does the importance of ecological mechanisms change with sown species richness? Q4) Which species are responsible for given ecological mechanisms? Q5) How do other experimental treatments change answers to all questions above?

We show that all methods were capable of answering Q1 and to some extent also Q5 although different methods use different procedures to reach the answer. Concerning Q2–Q4, we found that traditional methods provide more detailed insight into the ecological mechanisms than the linear-model-based methods which leave us just with brief information. A direct comparison between traditional biodiversity effects and effects from linear-model-based methods showed that species interactions from the diversity—interaction model were significantly positively correlated with the net effect, while species identity effects from diversity—interaction model were related to the species relative yield. The selection of an appropriate method for BEF experiment analysis thus depends on the questions we ask which in turn also affect the design of the BEF experiment.

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1. Introduction

Increasing species loss due to human impact and related concerns about deterioration of ecosystem services for humanity triggered the development of biodiversity—ecosystem functioning (BEF) experiments as a new branch of ecological research (Diaz et al., 2006; Dickson and Wilsey, 2009; Hector, 1998; Hector et al., 2009; Mora et al., 2011; Yesson et al., 2007). Their main purpose is to evaluate the relationship between species richness and various “ecosystem functions”. In these experiments, the species richness is manipulated and subsequently treated as an

independent variable and the measure of functioning (in plant ecology usually aboveground biomass) is considered as a response variable. The traditional belief that higher species richness enhances ecosystem functioning is supported by the majority of plant ecology BEF experiments which use aboveground biomass as a measure of functioning (e.g., Cardinale et al., 2006; Hooper et al., 2005; Sheehan et al., 2006).

Two mechanisms have been proposed to explain the positive diversity—functioning relationship: the selection effect and the complementarity effect (Loreau and Hector, 2001). The selection effect corresponds to situation where with increasing number of species, the chance that highly productive species will be included increases, and results in situation where dominant species (e.g. having the highest yield in mixtures) are those with high monoculture yield. The complementarity effect is driven by ecological

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mechanisms: niche differences among species, such as interspecific differences in resource use, enable more efficient acquisition and utilization of resources which in turn increase functioning (and chance for differentiation increases with species richness).

However, comparing the performance of communities of differing species diversity and of mixtures and monocultures is not a trivial task and has been discussed from the early days of biodiversity experiments (Aarssen, 1997; Garnier et al., 1997). In fact, various methods of analysis were used much earlier in the intercropping research (Trenbath, 1974). The most frequently used is the additive partitioning of the net effect into selection and complementarity effect (Loreau and Hector, 2001), together with a simple comparison of the mixture function with the function of the best monoculture: the measure of transgressive overyielding (Garnier et al., 1997). We will call these methods “traditional” in further text. More recently, methods based on linear models have been suggested (Bell et al., 2009; Connolly et al., 2013; Kirwan et al., 2009), we will refer to them as “linear-model-based” methods.

In BEF research, experiments were designed to answer five fundamental questions: Q1) How does sown species richness change ecosystem functioning? Q2) What ecological mechanisms cause this change? Q3) How does the importance of ecological mechanisms change with sown species richness? Q4) Which species are responsible for given ecological mechanisms? Q5) How do other experimental treatments change answers to all questions above?

Our aim is to compare traditional and linear-model-based methods for biodiversity experiments analysis: their specific data and experimental design requirements and their ability to answer the above questions, i.e. ecological interpretation of their results. To illustrate the differences among the methods and compare their results, we analyze data from three BEF experiments. The first data set is a simulated biodiversity experiment (SE in further text) using four species with defined traits providing expected outcomes. The second data set originates from a glasshouse biodiversity experiment in which one to four species were planted in mixtures ranging from low to high initial sown density (GE1). The last data set is a seasonal glasshouse pot experiment using six plant species grown in all species combinations (GE2).

As the individual methods present their results in a rather different way, we aim mainly to compare the ecological interpretations of the numerical results. In addition, we match the outputs of different methods directly to seek for correlations. We present the species level interpretation as it is the species level information that primarily enters all the analyses. In our opinion this provides the best insight into how the different methods work and deal with the challenge of evaluating which ecological mechanisms operate in a community. To our knowledge, there has been no such comparison of methods for biodiversity experiment evaluation (based on real and simulated data, using both traditional and linear-model-based methods) done to date.

2. Methods

We will first mention some general points concerning the data requirements and procedures applied in all methods. We will also present their outputs and provide details on each method. Finally, we briefly describe the datasets studied. In the following text, we use the terms biomass and yield, as they are used in “classical” BEF experiments in plant ecology, nevertheless, there might be also different measures of “ecosystem functioning”.

2.1. Data required

Various types of data are required by various methods for BEF experiment analysis (Table 1). In particular, additive partitioning (Loreau and Hector, 2001) requires two information components which are often complicated and laborious to gain: monoculture yield of all constituent species and yield of each species in all mixtures. Practically, this means sorting all the harvested biomass into individual species, which is laborious, but still feasible. However, if some emergent property (e.g. nutrient leaching or gaseous emissions) is considered to be a response, determination of individual species contributions is even more problematic. Both these pieces of information are very useful for subsequent biological interpretation; however, they considerably restrict the experimental setup, limit the number and size of experimental/sampling units and the length of species richness gradient. Linear-model-based methods require neither of these: this allows for larger species pool size or treatment/replicate range.

2.2. General differences among procedures and outcomes

One of the most important differences among the methods for evaluation of biodiversity experiments lies in the procedures we apply. Traditional methods, such as overyielding and additive partitioning (Garnier et al., 1997; Loreau, 1998; Loreau and Hector, 2001) use a two-step procedure: first, the biodiversity effects are calculated separately for each mixture (with the use of information on corresponding monocultures) and second, these values are then used to analyze the effects of all possible predictors (i.e. species richness, number of functional groups, sowing density etc.) Statistically, the biodiversity effect values for single replications are not independent data points: they are all based on a limited number of monoculture yields. This may inflate the significance of statistical tests. In spite of these facts, a majority of studies neglect this problem and continue to use standard statistical methods, and we are not aware of any statistical method to correct for this partial dependence.

Linear-model-based methods, such as the diversity–interactions model (Kirwan et al., 2009) or analysis of random partition design (Bell et al., 2009) apply classical statistical methods. The diversity effects are included in a single statistical model for the whole experiment, not taking into account

Table 1
Requirements of the common biodiversity methods denote if monocultures (single species performance), final species contributions (how much each species contributed to the final mixture performance) or initial species proportions are necessary for the methods.

Data required	Traditional methods			Linear-model-based methods	
	Overyielding	Relative yield	Loreau & Hector method ^a	Bell's method ^b	Kirwan's method ^c
Monocultures	Yes	Yes	Yes	No	No
Final species contributions	No	Yes	Yes	No	No
Initial species proportions	No	Yes	Yes	No	Yes

^a Additive partitioning (Loreau and Hector, 2001).

^b The method of random partition design (Bell et al., 2009).

^c The diversity–interaction model (Kirwan et al., 2009).

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