

# An improved model to predict the effects of changing biodiversity levels on ecosystem function

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## Summary

1. The development of models of the relationship between biodiversity and ecosystem function (BEF) has advanced rapidly over the last 20 years, incorporating insights gained through extensive experimental work. We propose Generalised Diversity-Interactions models that include many of the features of existing models and have several novel features. Generalised Diversity-Interactions models characterise the contribution of two species to ecosystem function as being proportional to the product of their relative abundances raised to the power of a coefficient  $\theta$ .
2. A value of  $\theta < 1$  corresponds to a stronger than expected contribution of species' pairs to ecosystem functioning, particularly at low relative abundance of species.
3. Varying the value of  $\theta$  has profound consequences for community-level properties of BEF relationships, including: (i) saturation properties of the BEF relationship; (ii) the stability of ecosystem function across communities; (iii) the likelihood of transgressive overyielding.
4. For low values of  $\theta$ , loss of species can have a much greater impact on ecosystem functioning than loss of community evenness.
5. Generalised Diversity-Interactions models serve to unify the modelling of BEF relationships as they include several other current models as special cases.
6. Generalised Diversity-Interactions models were applied to seven data sets and three functions: total biomass (five grassland experiments), community respiration (one bacterial experiment) and nitrate leaching (one earthworm experiment). They described all the nonrandom structure in the data in six experiments, and most of it in the seventh experiment and so fit as well or better than competing BEF models for these data. They were significantly better than Diversity-Interactions models in five experiments.
7. *Synthesis.* We show that Generalized Diversity-Interactions models quantitatively integrate several methods that separately address effects of species richness, evenness and composition on ecosystem function. They describe empirical data at least as well as alternative models and improve the ability to quantitatively test among several theoretical and practical hypotheses about the effects of

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biodiversity levels on ecosystem function. They improve our understanding of important aspects of the relationship between biodiversity (evenness and richness) and ecosystem function (BEF), which include saturation, effects of species loss, the stability of ecosystem function and the incidence of transgressive overyielding.

**Key-words:** biodiversity, complementarity, diversity manipulations, ecosystem function, ecosystem services, evenness and richness, Generalised Diversity-Interactions models, saturation, species loss and extinctions, stability, transgressive overyielding

## Introduction

In the face of global changes to biodiversity, there has been increased attention on the consequences of changed biodiversity on ecosystem functions and services (Schulze & Mooney 1994). Quantifying the relationship between different biodiversity levels and ecosystem functioning (BEF) is an essential challenge facing ecology in the 21st century (Hooper *et al.* 2005; Cardinale *et al.* 2011; Isbell *et al.* 2011). Loss of biodiversity can influence ecosystem functioning in natural and experimental systems, and across habitats and trophic levels (Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2009; Hooper *et al.* 2012; Reich *et al.* 2012).

Interest in quantifying the relationship between biodiversity and ecosystem function (BEF) has driven two decades of experimentation and statistical modelling (Hector *et al.* 1999; Schmid *et al.* 2002; Bell *et al.* 2005; Kirwan *et al.* 2007; Cardinale *et al.* 2009; Isbell *et al.* 2011). Most of the existing modelling approaches relate ecosystem function to richness as the sole measure of diversity, ignoring community evenness and species' relative abundances (Chapin *et al.* 2000; Wilsey & Polley 2002; Kirwan *et al.* 2007; Hillebrand, Bennett & Cadotte 2008). Recently, there has been an increase in the number of experiments and analyses investigating the importance to ecosystem functioning of community characteristics other than species richness. These include: species identity (Wardle *et al.* 1998); functional group richness (Petchey *et al.* 2004; Roscher *et al.* 2005; Kirwan *et al.* 2007; Weigelt *et al.* 2008); community evenness (Wilsey & Potvin 2000; Polley, Wilsey & Derner 2003; Wilsey & Polley 2004; Kirwan *et al.* 2007; Hillebrand, Bennett & Cadotte 2008; Isbell *et al.* 2008; Isbell, Polley & Wilsey 2009; Wittebolle *et al.* 2009); species' and functional group interactions (Kirwan *et al.* 2007, 2009) and phylogenetic and functional trait diversity (Petchey *et al.* 2004; Cadotte *et al.* 2009; Connolly *et al.* 2011; Flynn *et al.* 2011).

In addition to describing BEF relationships in detail, linking coefficients of BEF models to underlying mechanisms and process should be one of the aims of modelling. Complementary species interactions based on niche partitioning and facilitation have been advanced as mechanisms leading to a diversity effect in biodiversity–ecosystem–function (BEF) relationships (Hector *et al.* 1999; Tilman 1999; Cardinale, Palmer & Collins 2002; Hooper *et al.* 2005; Isbell, Polley & Wilsey 2009; Marquard *et al.* 2009; van Ruijven & Berendse 2009; Cardinale *et al.* 2011). In communities of resource competitors, partial niche overlap predicts increasing function-

ing with increasing richness, but with a BEF relationship that decelerates and perhaps saturates with increasing richness (Tilman, Lehman & Thomson 1997; Cardinale *et al.* 2009; Schmid, Pfisterer & Balvanera 2009). Diversity effects have also been partially attributed to selection, arising from the dominance of communities by a few species irrespective of initial species relative abundances (Loreau & Hector 2001; Adler, HilleRisLambers & Levine 2007). Despite the accepted importance of interspecific interaction, analytical methods have rarely been capable of identifying the contribution of particular interactions as opposed to measuring the net effect of all interactions (Kirwan *et al.* 2007; Hector *et al.* 2009).

Models of the BEF relationships are becoming increasingly descriptive, integrative and insightful, aiming to allow discrimination between different theories based on the relationship between diversity and ecosystem functioning. Ideally, a model of ecosystem functional response would provide clear evidence on mechanism, but we accept that this is not possible in respect of the class of BEF and competition models based only on information on the value of ecosystem function and the relative abundances and densities of species of which the model proposed below is one (Connolly, Wayne & Bazzaz 2001; Bell *et al.* 2009). Despite that major constraint, there are differences between descriptive models. We would like a model of BEF to be:

**1** Descriptive: It should allow hypotheses about the effects on ecosystem functioning of varying species' richness, species' identities, their relative abundances, density and biotic and abiotic environmental factors to be addressed. It should allow generalisation or qualification of results across spatial and temporal gradients in experiments. It should be parsimonious without reducing explanatory power. The model should fit experimental data well and be generally superior in range and explanatory power to competing models.

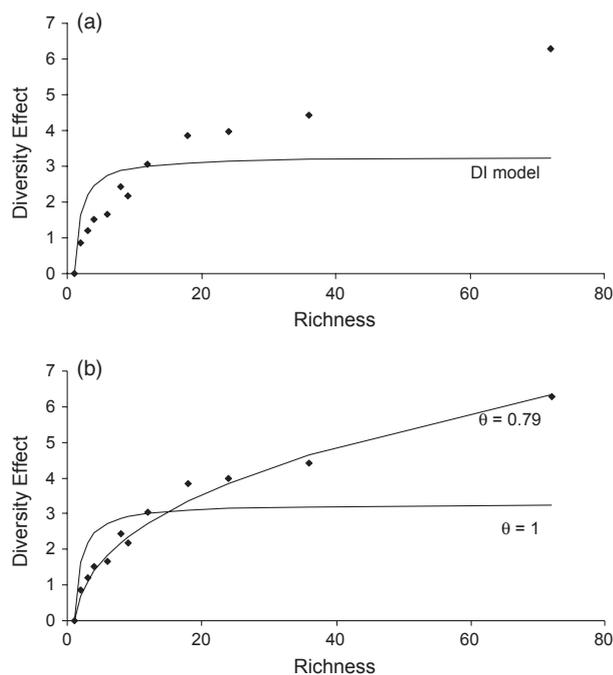
**2** Integrative: It should facilitate the exploration of hypotheses about ecosystem functioning based on patterns in species biology through a few focused coefficients. For example, does functional grouping of species affect their contribution to functioning? Can the different mathematical forms used to describe the relationship between ecosystem function and richness be incorporated as different values of a single coefficient? The model should be flexible in incorporating additional explanatory variables (e.g. based on species traits) to give more generalised descriptions of ecosystem functioning.

**3** Insightful: It should be based on a small number of underlying biologically motivated ideas. If so, then it should lead

to hypotheses about processes and mechanisms of ecosystem functioning based on those ideas. For example, does it suggest mechanisms of how species interactions affect ecosystem functioning that can be experimentally tested or predict the effects on ecosystem functioning of diversity loss through changing evenness compared with reducing richness?

Diversity-Interactions models (Kirwan *et al.* 2007, 2009) address many of the issues above within a single framework. They have been used in understanding the BEF relationship in a number of plant and invertebrate assemblages (Sheehan *et al.* 2006; Kirwan *et al.* 2007; Connolly *et al.* 2009, 2011; Frankow-Lindberg *et al.* 2009; Nyfeler *et al.* 2009; O’Hea, Kirwan & Finn 2010; Brophy *et al.* 2011). However, they do not fit all data adequately (Fig. 1a). In Diversity-Interactions models, the BEF relationship saturates at a rate determined by the number of species in the experiment irrespective of the ecosystem being studied and thus may not provide a universally acceptable representation of the effects of diversity.

Here, we show that modifying the formulation of the contribution of pairwise interaction to functioning in Diversity-Interactions models leads to Generalised Diversity-Interactions models that provide a far more flexible framework within which to explore issues such as effects of diversity loss, functional stability, saturation, and how species combine to affect functioning. Generalised Diversity-Interactions models include Diversity-Interactions models and other BEF models as special cases. We test the proposed Generalised Diversity-Interactions models using data from seven biodiversity



**Fig. 1.** Estimates of the average diversity effect (diamonds) calculated from the raw data of Exp1 (Bell *et al.* 2005) plotted against community richness. Also shown are (a) predictions of the diversity effect from a Diversity-Interactions model (Kirwan *et al.* 2007) and (b) predictions of the diversity effect from Generalised Diversity-Interactions model 3a ( $\theta = 1$  and hence this is the DI model) and 3b ( $\theta = 0.79$ ).

experiments based on a range of ecosystems (five grassland, one microbial and one based on worm assemblages) and several ecosystem functions (above-ground biomass production for the grassland systems, community respiration and  $\text{NO}_3\text{-N}$  in soil for the microbial and worm ecosystems, respectively).

The aims of this study are to: propose Generalised Diversity-Interactions models of the BEF relationship and to assess whether they satisfy the criteria outlined above. In particular, we discuss how a basic assumption about the contribution of pairwise species interaction to functioning has major consequences for the community-level provision of ecosystem services and generates testable hypotheses about the mechanism of species interaction in complex communities. We also discuss how the Generalised Diversity-Interactions framework provides novel insights into the effects of diversity loss, provides a unifying framework for modelling the saturation properties of the BEF relationship and provides an insight into functional stability across communities and transgressive overyielding.

## Generalised Diversity-Interactions models

### THE MODELS

Suppose that the species pool contains  $s$  species from which communities of various levels of richness ( $r$ , where  $r \leq s$ ) may be constructed. Diversity-Interactions models propose the following description of the functional response ( $y$ ) in an  $r$  species community. The functional response for a community in the absence of any diversity effect is given by

$$y = \sum_{i=1}^s \beta_i P_i + \alpha A + \varepsilon. \quad \text{eqn 1}$$

Here,  $P_i$  is the proportion of the  $i$ th species in the community ( $=0$  if the species is in the species pool but not in the community), and  $A$  includes all density and blocking/treatment effects, and so  $\alpha$  may be a vector including several coefficients. Here,  $\beta_i$  is the contribution to ecosystem function of the  $i$ th species in monoculture ( $P_i = 1$ ) at mean levels of terms in  $A$ . The residual term  $\varepsilon$  is assumed to be normally distributed with constant variance  $\sigma^2$ .

Additional diversity effects arise from interactions among species. The Diversity-Interactions model where these arise from pairwise interactions among the species in a community is (See Table 2 for full description of all models used)

$$y = \sum_{i=1}^s \beta_i P_i + \alpha A + \sum_{i < j}^s \delta_{ij} P_i P_j + \varepsilon. \quad \text{eqn 2a}$$

Here,  $\delta_{ij}$  reflects the potential of species  $i$  and  $j$  to interact. The contribution of the interaction to the functional response is  $\delta_{ij} P_i P_j$ . The contribution to ecosystem function from all the pairwise interactions in the community is called the diversity effect and is  $\sum_{i < j}^s \delta_{ij} P_i P_j$ . Following Kirwan *et al.* (2009) this model can be extended in several ways. For example, the

diversity effect may consist of an average interaction term or interaction terms for between and within functional groups of species. It may include more complex interactions among species and the effects of time and environmental factors.

Model 2a is based on a very simple conception of how a pairwise species interaction contributes to function, that is, a coefficient representing the propensity of two species to interact, scaled by the product of their relative abundance in the community. This specification leads to a simple, saturating shape for the BEF with increasing richness (Kirwan *et al.* 2007). We propose Generalised Diversity-Interactions models by assuming a more general form for the contribution of the pairwise interaction of species  $i$  and  $j$  as  $\delta_{ij}(P_i P_j)^\theta$ .

The basic Generalised Diversity-Interactions model is

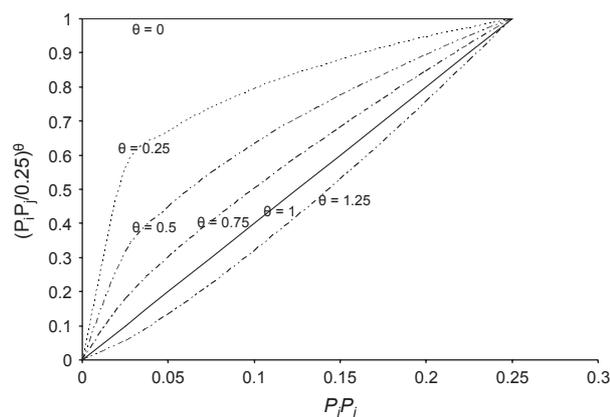
$$y = \sum_{i=1}^s \beta_i P_i + \alpha A + \sum_{i < j} \delta_{ij} (P_i P_j)^\theta + \varepsilon. \quad \text{eqn 2b}$$

If all interactions have the same interaction potential, that is,  $\delta_{ij} = \delta_{av}$  for all pairs of species, this becomes

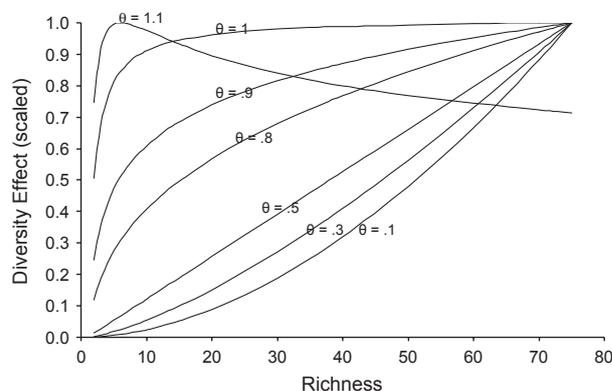
$$y = \sum_{i=1}^s \beta_i P_i + \alpha A + \delta_{av} \sum_{i < j} (P_i P_j)^\theta + \varepsilon. \quad \text{eqn 3b}$$

Adding the extra coefficient,  $\theta$  allows a very wide range of forms for the contribution of species pairwise interactions to ecosystem response and leads to a wide range of forms for the BEF relationship. The contribution of a pairwise interaction (Fig. 2) and the overall diversity effect (Fig. 3) change very much with varying  $\theta$ . For example, for values of  $\theta < 1$ , the contribution curve has an increasingly higher ‘shoulder’ at lower values of  $\theta$  (Fig. 2) and each pair of species contributes more to ecosystem functioning than might be expected from their joint relative abundance (Hurlbert 1971; Kirwan *et al.* 2007).

We distinguish between the statistical interactions in the above model and the underlying biological interactions among species in the community. Statistical interactions simply reflect the impact on ecosystem function of the presence of various species in different relative abundances. Species interactions important for the survival and abundance of



**Fig. 2.** Illustration of the contribution of pairwise interaction to function for a two species component: Form of  $(P_i P_j)^\theta$  as a function of  $P_i P_j$  for various values of  $\theta$ . The values in all series are scaled by  $1/0.25^\theta$ , its maximum value.



**Fig. 3.** The Diversity Effect  $(r(r-1)/(2r^{2\theta}))$  in model 3b for various values of  $\theta$  and community richness ( $r$ ) where  $r \leq 75$ . Here, it is assumed that each species present in a community is equally represented. For comparison purposes, the values of the diversity effect are scaled to have a maximum of 1 for each value of  $\theta$ .

species would not emerge as interactions in our statistical approach unless they also drove an aggregate measure of ecosystem function. The underlying biological mechanisms and processes cannot be directly inferred from the statistical interactions, although the size of interactions and patterns among them may suggest the strength and perhaps the type of biological interaction (e.g. complementarity, facilitation or selection) operating in the community.

#### SOME IMPORTANT PROPERTIES OF GENERALISED DIVERSITY-INTERACTIONS MODELS

Generalised Diversity-Interactions models provide a coherent, simple structure within which to investigate the properties of BEF relationships, based on identity effects, pairwise interactions and a coefficient that modifies the contribution of pairwise interactions to ecosystem function. Interaction coefficients may be positive, negative or zero.

- 1  $\theta$  and the evaluation of interaction:** Pairwise species interactions can have a relatively high effect on ecosystem function ( $0 < \theta < 1$ ) even at low levels of relative abundance, with the effect being greater for smaller  $\theta$  (Fig. 2). Compared to the product of their relative abundance, at low levels of joint relative abundance, species joint contribution may be higher than might be expected leading to a greater joint contribution to functioning. As joint relative abundance increases to its maximum of 0.25, this effect declines.
- 2  $\theta$  and the BEF relationship:**

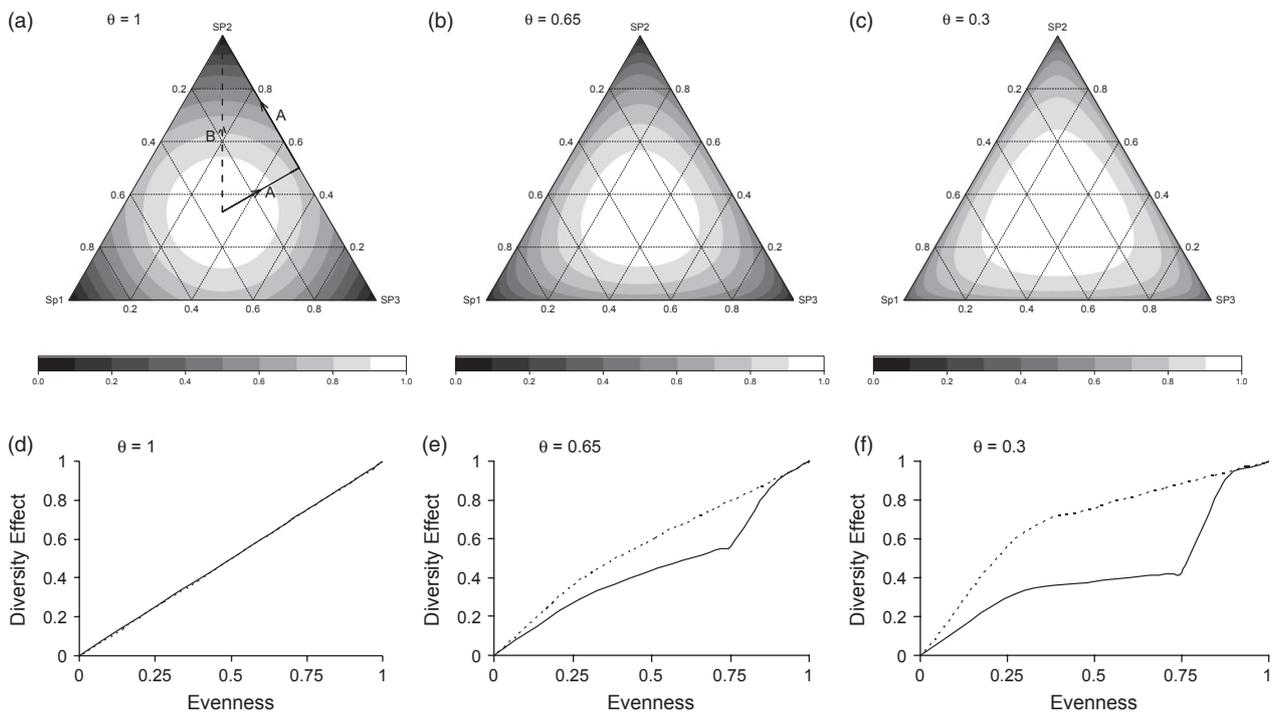
**A The shape of the BEF relationship is described by  $\theta$ :** The effect of  $\theta$  on the BEF relationship is captured through its contribution to the diversity effect. In a community of  $r$  species, the number of pairwise interactions is  $r(r-1)/2$ . In model 3b, if all species in a community have equal relative abundance  $1/r$ , each pairwise interaction contributes  $\delta_{av}/r^{2\theta}$ , and so, their aggregate contribution is the diversity effect  $= \delta_{av}r(r-1)/2r^{2\theta}$  (Fig. 3). The diversity effect changes with species richness and  $\theta$ . For  $\theta > 1$ , the diversity effect peaks with increasing richness and subsequently

declines. When  $\theta = 1$ , the relationship saturates; for  $0.5 < \theta < 1$ , the diversity effect increases with richness at a decreasing rate but does not saturate; when  $\theta = 0.5$  it increases linearly; and when  $0 \leq \theta < 0.5$  it increases at an increasing rate.

**B** Many of the BEF relationships proposed in the literature are special cases of Generalised Diversity-Interactions models (See Appendix S1 in Supporting Information for a fuller discussion). Values of 0 and 1 for  $\theta$  give the contribution of pairwise interactions as in Bell *et al.* (2005) and Diversity-Interactions models (Kirwan *et al.* 2007), respectively. Other previous models propose a linear relationship between functional response and some function of species richness ( $r$ ), and these can be approximated by Generalised Diversity-Interactions models with specific values of  $\theta$ . These functions include  $\log(r)$  ( $\theta = 0.87$ ; Bell *et al.* 2005; Cardinale *et al.* 2009; Schmid, Pfisterer & Balvanera 2009; Cardinale 2011), a linear relationship with  $r$  ( $\theta = 0.5$ ; Cardinale 2011; Isbell *et al.* 2011). Generalised Diversity-Interactions models can also be approximately related to power ( $br^a$ ) and hyperbolic ( $ar/(r + K)$ ) relationships with richness (Cardinale *et al.* 2009; Cardinale 2011).

**3  $\theta$  and the relationship with evenness:** Generalised Diversity-Interactions models predict ecosystem function for all patterns of species' relative abundance and so can address questions about the change of function with changing evenness, species composition and the joint effect of changing evenness and richness. [Here, evenness is defined as  $E = \frac{2s}{s-1} \sum_{i < j} P_i P_j$  as in Kirwan *et al.* (2007)]. For example, for model 3b as  $\theta$  decreases from one towards zero, the contribution of diversity to the functional response is stable across a wider range of evenness (see Fig. 4 for a 3-species illustration). For low values of  $\theta$ , the diversity effect is close to its maximum (white zone > 90% of maximum) over a much wider range of relative abundances than for high  $\theta$  and declines much more slowly as evenness reduces, remaining quite high for mixtures close to the monocultures.

**4** The range of parsimonious models proposed in Kirwan *et al.* (2009) to identify pattern in the interaction coefficients are available in Generalised Diversity-Interactions models but involve some modification in how they are fitted. These include models where all coefficients are equal to give a single average interaction effect, where coefficients are averaged



**Fig. 4.** The effect of species richness and species relative abundance on the diversity effect (scaled to have a maximum of 1) in a 3-species community for 3 values of  $\theta$  (1, 0.65 and 0.3) and for model 3b in which the coefficient of pairwise interaction is the same for all pairs of species. Contour plots of the diversity effect, scaled to have a maximum of 1, are shown for three values of  $\theta$  in (a–c). For low values of  $\theta$ , the diversity effect is more stable (white zone indicates communities that provide >90% of maximum diversity effect) over a much wider range of relative abundances than for high  $\theta$  and declines much more slowly as evenness reduces, remaining quite high for mixtures close to the monoculture. Also shown (a) are two trajectories across communities simulating diversity loss. Trajectory A, *richness loss* (solid line). This trajectory starts with a community with three species of equal relative abundance. It then traces communities in which the relative abundance of species 1 declines to zero (loss). In this part of the trajectory, the other two species are equally abundant, with their relative abundance rising to a final value of 50% for each species. The trajectory then traces through two species communities in which species 2 is increasingly dominant and ends with a monoculture of species 2. Trajectory B, *reducing evenness* (hatched line). This trajectory traces through communities in which species 2 is increasingly dominant with the relative abundance of the two other species declining at an equal rate. (d–f) The corresponding value of the diversity effect calculated for three values of  $\theta$  for each community in both trajectories (trajectory A represented by the solid line, trajectory B represented by the hatched line). For trajectory A, species loss occurs at evenness = 0.75 (3 to 2 species) and at evenness = 0 (2 to 1 species).

by functional groups or across individual species. Generalised Diversity-Interactions models can be extended to include the effects of abiotic environment, higher order interactions as in Kirwan *et al.* (2009) or the effects of covariates based on species traits as in Connolly *et al.* (2011).

## Materials and methods

We used the Generalised Diversity-Interactions framework to better understand results from seven experiments (Table 1 and see Appendix S2), from bacterial (Exp1), grassland (Exp2 to Exp6) ecosystems and earthworm assemblages in soil (Exp7). Across the data sets, the maximum community richness varied from 3 to 72, and the number of different communities (different in species composition or species initial relative abundances) ranged from 13 to 683. The number of experimental units ranged from 50 to 1374 and replication per community was two or more in data sets Exp1, Exp2, Exp5 and Exp6. At Exp3, Exp4 and Exp7, there was no replication, but the distinct communities were sown at two levels of density (Exp3, Exp4) or at four levels of an applied treatment (Exp7). There were up to four functional groups of species at Exp2 to Exp7 with functional groups generally being represented by more than one species except at Exp7. The functional responses analysed were total CO<sub>2</sub> transpired from each community (Exp1), above-ground biomass for a harvest (Exp2) or a year of the experiment (Exp3 to Exp6) and NO<sub>3</sub>-N nitrate in soil (Exp7).

## DATA ANALYSIS

We fitted a series of up to eight models (depending on the data set) with which we tested hypotheses about the importance of interactions in BEF experiments (Table 2 and See Appendices S2 and S3). Model 1 included coefficients for species identity, density and blocking/treatment effects (A). Models 2a and 2b add all pairwise interactions to model 1, with  $\theta = 1$  and  $\theta$  as a coefficient to be estimated, respectively. The effect of adding separate pairwise interaction effects is tested by comparing models 2a and 2b with previous models. Models 3a and 3b add an average interaction term between the relative

abundances ( $P_i$ ) of all pairs of species in the community to model 1, with  $\theta = 1$  and  $\theta$  as a coefficient to be estimated, respectively. Models 4a and 4b are based on 3a and 3b, respectively. Comparison of models 4a vs. 3a and 4b vs. 3b test whether adding functional group interaction effects further improves the model. Whether Generalised Diversity-Interactions models fit better than Diversity-Interactions models was determined by testing whether  $\theta$  differs from 1.

Our analysis not only tests the improvement in Generalised Diversity-Interactions models relative to the Diversity-Interactions framework, but also allows indirect comparison with all competing BEF models. Model 0 is a reference model that includes a coefficient for each distinct community and blocking structure or treatments. The residual variation [residual mean square (RMS)] from this model is a measure of true error variation, and hence, this model explains structure in the data introduced through community composition or blocking or treatments. Thus, the RMS from model 0 is a target for any BEF model; ideally, the best BEF model should explain as much structure as the reference model and thus have a similar level of residual variation. Hence, if Generalised Diversity-Interactions models fit as well as the reference model then they can broadly be taken as fitting as well as, or better than, any competing BEF model.

Models 0, 1, 2a, 3a and 4a were fitted by ordinary multiple regression and models 2b, 3b and 4b used nonlinear methods to estimate  $\theta$  (See Appendices S3, S5 and S6). The best fitting Generalised Diversity-Interactions model was selected using  $F$  and chi-squared tests. Comparisons between hierarchical models not involving  $\theta$  were made using  $F$  tests. Tests of the null hypothesis that  $\theta = 1$  were based on comparing the log likelihoods of models with  $\theta = 1$  and  $\theta$  as an estimated coefficient (Pawitan 2001). The  $F$  test was used to compare the best fitting model with the reference model.

Models were fitted using SAS/STAT<sup>®</sup> procedures. Code for SAS and R is shown in Appendices S5 and S6 respectively.

## Results

Here, the primary purpose of the data analysis is to establish the credibility of Generalised Diversity-Interactions models as

**Table 1.** Summary of characteristics of data from seven experiments. Listed are the name of the experiment, the organism or ecosystem/species assemblage studied, the number of distinct community compositions, the maximum number of species per community, the number of experimental units, the level of replication (Reps), the functional groups among the species and the function examined in each experiment

Expt	Name*	Organism/ ecosystem	No. of communities	Max no. species	Exp. units	Reps	Functional groups	Function
Exp1	Bacterial	Bacteria	683	72	1374	≥ 2	None	CO <sub>2</sub> respired
Exp2	Jena	Grassland	100	9	206	≥ 2	3: Grass (5), Herb (2), Legume (2)	Above-ground biomass
Exp3	Swiss	Grassland	25	4	50	2†	4: Grass (2), Legume (2)	Above-ground biomass
Exp4	Teagasc	Grassland	25	4	56	2†	4: Grass (2), Legume (2)	Above-ground biomass
Exp5	Bidepth (IE)	Grassland	31	8	66	≥ 2	3: Grass (4), Herb (4), Legume (2)	Above-ground biomass
Exp6	Iowa	Grassland	51	8	102	2	4: Grass (4)§, Herb (1), Legume (3)	Above-ground biomass
Exp7	Earthworm	Earthworms	13	3	52	2‡	3: Epigees, endogeas, aneic	NO <sub>3</sub> -N ppm in soil

\*Data are from Exp1: Bell *et al.* (2005), Exp2: Roscher *et al.* (2005), Exp3: Nyfeler *et al.* (2009), Exp4: Carnus, PhD Thesis, Exp5: Hector *et al.* (1999), Exp6: Picasso *et al.* (2008) and Exp7: Sheehan *et al.* (2006). Evenness was manipulated in the design in experiments Exp3, Exp4 and Exp7, in all other experiments all species in a community were equally represented at sowing.

†There was no replication but density was included as a factor at two levels.

‡There was no replication but there were thirteen distinct communities at two levels of density and two levels of food.

§There were two grass functional groups cool-season (2) and warm season (2).

**Table 2.** Generalised Diversity-Interactions (GDI) and Diversity-Interactions (DI) models fitted to data from seven experiments. These form the basis of tests of hypotheses about pairwise interactions between species and whether the Generalised framework improves the Diversity-Interactions formulation. Here, FG means functional group

Model	Description	Fitted in Experiments
0	Mixture + Block: Each community type, Blocking and other structure fitted	All
1	Block + ID: Identity and blocking and other structure fitted $y = \sum_{i=1}^s \beta_i P_i + \alpha A + \varepsilon$	All
2a	Model 1 + all pairwise: DI all pairwise interactions: $y = \sum_{i=1}^s \beta_i P_i + \alpha A + \sum_{i<j}^s \delta_{ij} P_i P_j + \varepsilon$	All except Exp1
2b	Model 1 + all pairwise: GDI all pairwise interactions: $y = \sum_{i=1}^s \beta_i P_i + \alpha A + \sum_{i<j}^s \delta_{ij} (P_i P_j)^\theta + \varepsilon$	All except Exp1, Exp5
3a	Model 1 + $\delta_{av}$ : DI average interaction model ( $\theta = 1$ ): $y = \sum_{i=1}^s \beta_i P_i + \alpha A + \delta_{av} \sum_{i<j}^s P_i P_j + \varepsilon$	All
3b	Model 1 + $\delta_{av} + \theta$ : GDI average interaction model: $y = \sum_{i=1}^s \beta_i P_i + \alpha A + \delta_{av} \sum_{i<j}^s (P_i P_j)^\theta + \varepsilon$	All
4a	Model 1 + FG: Functional group interactions ( $\theta = 1$ ):	All except Exp1, Exp7
4b	Model 1 + FG + $\theta$ : Functional group interactions ( $\theta \neq 1$ ):	All except Exp1, Exp7

a framework for analysing data from experiments on BEF by examining its fit to a fairly wide range of data sets. It is not the purpose of this study to focus on the detailed analysis of any particular data set but to establish the range of values of  $\theta$  that can occur in real data and also to establish that the model generally fits well with only a few coefficients needed to describe the diversity effect. To fit well, Generalised Diversity-Interactions models have to fit as well or better than Diversity-Interactions models. They also have generally to fit as well or better than competing BEF models.

Generalised Diversity-Interactions models fitted better than Diversity-Interactions models for five of the seven experiments ( $\theta$  significantly different from 1; Table 3). In those cases, the greater flexibility provided by Generalised Diversity-Interactions models was necessary to describe the data. For Exp1, the superior fit of the Generalised Diversity-Interactions model ( $\theta = 0.79$ ) over the corresponding Diversity-Interactions model ( $\theta = 1$ ) is illustrated in Fig. 1b. Across experiments, the value of  $\theta$  ranged from 0.44 to 1.3; it was significantly  $< 1$  for Exp1, Exp3, Exp4 and Exp6 and significantly  $> 1$  for Exp5. The best Generalised Diversity-Interactions model performed as well as the reference model

for all experiments except Exp3 (Table 3) and thus can be broadly considered as fitting as well or better than any competing BEF model for these data.

The diversity effect was associated with patterns among interaction coefficients that could be described with only a few degrees of freedom in five experiments. The model that only included the average interaction coefficient ( $\delta_{av}$ ) provided the best fit for Exp1, Exp4 and Exp7, indicating that a very simple description based on only  $\delta_{av}$  and  $\theta$  was sufficient to describe the diversity effect across all evenness and richness possibilities. For Exp3 and Exp5 coefficients based on grouping of interaction coefficients by functional type and  $\theta$  were required to describe the diversity effect. The number of coefficients associated with the diversity effect was low for five of the experiments, providing a simple framework for interpretation.

## Discussion

The Generalised Diversity-Interactions models system provides a flexible methodology for predicting community response to species identities, richness, relative abundance,

**Table 3.** Summary of analyses for seven experiments. Shown for each experiment are details of the reference model [residual mean square (RMS) and number of model coefficients], the best-fitting model (model name, RMS, total number of coefficients, number of diversity coefficients, and  $P$ -value for a test vs. the reference model) and the theta analysis (estimate of  $\theta$  and test of  $H_0: \theta = 1$ )

Experiment	Name	Reference model		Best model				Theta analysis		
		RMS	Coeffs	Name	RMS	Coeffs		Test vs. ref. ( $P$ )	Estimate of $\theta$	$P$ $H_0: \theta = 1$
Total	Diversity									
Exp1	Bacterial	7.46	683	3b	7.55	74	2	0.372	0.79	$< 0.001$
Exp2	Jena	15710	103	2a	15241	48	36	0.638	0.95	0.145
Exp3	Swiss	1.366	26	4b	2.27	9	4	0.019	0.77	0.034
Exp4	Teagasc	3.515	26	3b	3.168	7	2	0.791	0.44	0.011
Exp5	Biodepth (IE)	21904	32	4b	22887	19	7	0.407	1.25	0.001
Exp6	Iowa	19523	52	2b	20824	32	23	0.269	0.68	0.018
Exp7	Earthworm	3.296	16	3a	3.406	7	1	0.345	1.3	0.575

species composition, and the effects of environment for the range of plant, animal and microbial systems and functions examined. Although it does not speak directly to elucidating underlying mechanisms, we believe that it is currently the best available option for analysing BEF experiments where only community-wide measures of functioning and measures of species relative abundances and community density are available. Based on species identity effects and the contributions of all pairwise interactions between species in the community, it includes Diversity-Interactions models as a special case ( $\theta = 1$ ) and incorporates all the strengths of that approach (Kirwan *et al.* 2007, 2009; Connolly *et al.* 2011; criterion a). The addition of a single extra coefficient ( $\theta$ ) provides the basis for establishing hypotheses as to how pairs of species combine to contribute to functioning and how this leads to important community-level effects (criterion c). It enables a comprehensive quantification of the effects of various trajectories of diversity loss (through pathways of decreasing evenness and richness), saturation properties of ecosystems, the role of functional groups and the importance of additional variables. It includes a range of options for describing the change in BEF relationships with increasing diversity that mimic those already proposed in the literature (criterion b). When tested across a range of different functional responses from seven microbial, grassland or soil ecosystems or species assemblages. Generalised Diversity-Interactions models usually fitted the data as well as could be expected for any BEF model, explaining all the variation among experimental communities (except that arising from replication). In most cases, the best models had relatively few diversity coefficients and did not use more than two species interactions. Generalised Diversity-Interactions models performed better than Diversity-Interactions models in five of seven cases and as well in the other two. We mainly confine our discussion to the extra capacities introduced in the Generalised Diversity-Interactions models system. For brevity, we will mainly highlight important features assuming model 3b, where the diversity effect is based on an average interaction coefficient and assume that the coefficient is positive.

#### INTERPRETATION OF $\theta$

The diversity effect reflects two types of process: (i) Niche differences or complementarity (Adler, HilleRisLambers & Levine 2007) or (ii) selection effects, compositional changes from the initial relative abundance that favour species which have higher (or lower) functioning in monoculture (Loreau & Hector 2001). Thus, the contribution of a pair of species can be affected by the competitive dominance of a higher functioning species and/or by strong niche separation. A value of  $\theta \neq 1$  is a measure of the degree to which the strength of these two effects is not simply driven by the product of the competitors' relative abundance. The increase in the diversity effect with richness that occurs for  $\theta < 1$  is based on the nature of the contribution of pairwise interactions between species (whose aggregate effect is the diversity effect for a community). If niche differentiation underlay this effect, it

might operate as follows. At very low relative abundance, niche separation creates non-overlapping resource zones for the species where realized competition between them may be very low. In the extreme, each species can satisfy most of its requirements with little interference from the other, leading to a joint contribution to function more proportional to the sum than the product of their relative abundances. Here, intraspecific competition is likely to dominate the competitive relationships between plants. With higher relative abundances, resource demand in the niche overlap zone becomes greater and so the joint contribution of species, while enhanced by their greater relative abundance, is dampened by stronger interspecific competition, leading to a joint contribution to functioning that is more related to the product of their relative abundances. The magnitude of this effect is related to the size of the 'shoulder' in Fig. 2. In comparing communities of different levels of species richness, first, the more species rich community has smaller average relative abundances  $P_i$ , and hence, pairs of species benefit more from the rarity effect just discussed than in the less rich community. Second, each pairwise interaction may contribute less due to their lower joint relative abundance, but third, there are more pairwise interactions. The aggregate effect of the tradeoffs between these three factors is that the richer community, with more, and more enhanced, interaction effects, will have a greater diversity effect than the less rich one, leading to a value of  $\theta < 1$ . A similar argument based on the relative strengths of intraspecific and interspecific competition was used in Hillebrand, Bennett & Cadotte (2008).

One consequence of this argument is that an observed value of  $\theta < 1$  might be expected if complementarity is the explanation of a diversity effect. It also suggests that in an environment with a high niche dimensionality, niche overlap between pairs of species could be less than in a poorer environment, broadening the range of relative abundance over which interspecific competition was low, leading to a smaller value of  $\theta$ . This may partly explain the results of Cardinale (2011) who found an approximately linear BEF relationship ( $\theta = 0.5$ ) in a relatively heterogeneous environment and a very rapidly saturating hyperbolic relationship ( $\theta$  close to 1) in a relatively homogeneous environment.

A relationship between  $\theta$  and environmental heterogeneity is also suggested by the work of Nyfeler *et al.* (2011). They showed that grass and clover species mutually stimulated each other's growth when either was at low relative abundance, in a way that led to an expansion of the niche of the other species. This would result in a greater than expected contribution to yield where the product of relative abundances of the two species was low. This is consistent with a value of  $\theta < 1$  (0.77 in Exp3) and the above mechanism may also apply in Exp4 ( $\theta = 0.44$ ), a similar model system.

Of course,  $\theta$  could also be influenced by the selection effect and may not exclusively map onto the complementarity effect. Community-level measures such as  $\theta$ , while suggesting possible mechanisms, summarize many population- and individual-level processes and always require more detailed experimentation to discriminate among the processes.

## UNIFICATION OF BEF MODELS

Generalised Diversity-Interactions models provide a uniform framework for modelling BEF relationships that can be a considerable improvement on the Diversity-Interactions approach (e.g. Fig. 1b). Current models of the shape of the BEF relationship are usually based on empirical transformations of richness (Schmid, Pfisterer & Balvanera 2009; Cardinale 2011; Reich *et al.* 2012). The unification of several such relationships within a single model (see Appendix S1) is a significant outcome of this work. The  $\theta$  coefficient describes the shape of the BEF relationship, including the extent to which it decelerates or saturates, and thus provides a convenient way quantitatively to compare competing hypotheses regarding the consequences of changing biodiversity and changing environment. It avoids the necessity to invoke several mathematical forms of the BEF relationship in addressing these questions (Cardinale 2011; Reich *et al.* 2012).

The BEF relationship might be expected to eventually saturate as more species are added (Tilman, Lehman & Thomson 1997; Hooper *et al.* 2005) but Generalised Diversity-Interactions models do not do so for  $\theta < 1$ . However, if the relationship only saturates at an unrealistically high number of species, then it may be appropriate to model it with a non-saturating function over the richness range of interest. The decelerating rate of change of the diversity effect with increasing richness (and also of ecosystem function) for  $0.5 < \theta < 1$  is exemplified in Fig. 1b for  $\theta = 0.79$ , where the BEF shows no sign of saturation but appears to increase at a decelerating rate. Values of  $\theta \leq 0.5$  imply a linear ( $\theta = 0.5$ ) or accelerating change in BEF with richness. Models that imply values of  $\theta$  in this latter range (e.g. the presence-absence model (Hector & Bagchi 2007; Isbell *et al.* 2011) should be treated with caution and should be strongly supported by the data.

## EFFECTS OF SPECIES LOSS ON FUNCTIONAL RESPONSE

Recent reviews confirm the positive relationship between species richness and several important ecosystem functions (Hooper *et al.* 2005, 2012; Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2009; Reich *et al.* 2012). The separate impacts of richness and evenness on ecosystem functioning have been stressed (Chapin *et al.* 2000; Hillebrand, Bennett & Cadotte 2008). Anthropogenic change can modify evenness long before species are lost, and the effects of changing evenness can have important consequences for ecosystems before species extinction. With Generalised Diversity-Interactions models, we can predict functioning at any combination of species relative abundances in a community and so can explore the impact of species loss and changing evenness (or relative abundances) on functioning far more effectively than heretofore.

There are many possible trajectories by which diversity may be lost from a community, differing in how the relative abundances of species change and whether (and which) species are lost. Each trajectory of loss is associated with a

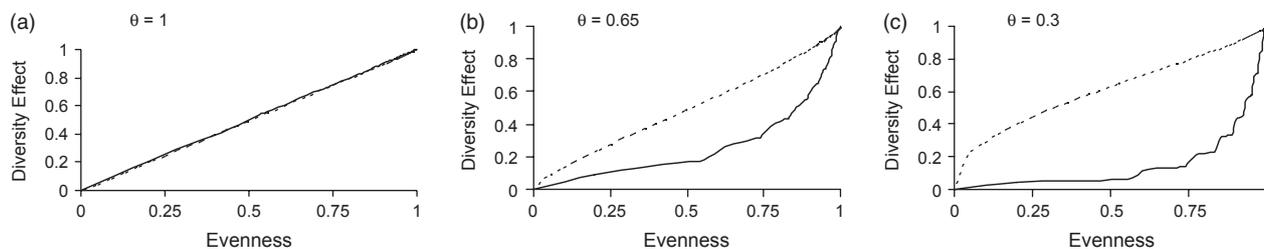
particular pattern of change in ecosystem functioning, with consequences for the identity effect (ID) and the diversity effect. We use a 3-species example to illustrate the effect of diversity loss on the diversity effect. Figure 4 shows the diversity effect (scaled to have a maximum of 1) from a model of type 3b for all possible communities from a pool with three species, and for 3 values of  $\theta$ . For  $\theta = 1$  (Fig. 4a), the diversity effect is linearly related to evenness (as defined above) for model 3b and the concentric shaded areas correspond to isoclines of both the diversity effect and evenness. For lower values of  $\theta$ , evenness (not shown) remains as in Fig. 4a, but diversity effect isoclines show a surface that is flatter at higher evenness levels. Consider two trajectories of diversity loss: (A) *loss of species* (Fig. 4a, solid line A): declining richness from  $s$  to  $s-1$  occurs through the gradual decline of the proportion of one of the three species to zero and the equal dominance of all remaining species. The next stage of loss repeats that pattern until only one species remains. Thus, starting from equal relative abundance of all species, one possible trajectory is  $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3}) \rightarrow (0, \frac{1}{2}, \frac{1}{2}) \rightarrow (0, 1, 0)$ . (B) *Loss of evenness only* (Fig. 4a, hatched line B): declining richness from  $s$  to 1 occurs through the gradual increase in the dominance of one species with the other  $s-1$  species having equal but declining relative abundances.

For  $\theta = 1$ , both evenness and the diversity effect (scaled to have maximum of 1) decline linearly along either trajectory A or B (Fig. 4a,d). When  $\theta < 1$  loss of species has a greater effect on the diversity effect than loss of evenness and this is accentuated for smaller  $\theta$  (Fig. 4b,c,e,f). Declining evenness (trajectory B) has less impact on the diversity effect with lower compared with intermediate  $\theta$ ; the contrary holds with loss of richness (trajectory A). These effects are not just artefacts of low species numbers as they are also very marked with 10 species (Fig. 5a-c).

While this simple example shows the importance of the trajectory of diversity loss, other considerations may also apply. Here, we have explored only the effects of loss of species and evenness on the diversity effect for the simple system of model 3b in which all interaction coefficients  $\delta_{ij}$  are equal. If identity effects differ, then ecosystem function will also be affected by the identity of the species lost in trajectory A and the identities of the dominant species in trajectory B.

## FUNCTIONAL STABILITY ACROSS COMMUNITIES AND TRANSGRESSIVE OVERYIELDING

The patterns in Fig. 4 show how ecosystem function may be affected by  $\theta$ . In our example, the diversity effect exceeds 90% of maximum for a much wider range of community evenness at low compared with high values of  $\theta$ . The ecosystem is more robust to changes in evenness at higher evenness levels for lower values of  $\theta$ . If the identity effects (not dependent on  $\theta$ ) do not vary much across species, then overall, where  $\theta$  is low, functioning will also tend to vary less across mixtures containing the same species but at different levels of relative abundance. These two factors, relatively low variation in yield across monocultures and the lower value of  $\theta$  may



**Fig. 5.** (a–c) The diversity effect (scaled to have a maximum of 1) for two trajectories of diversity loss in a 10-species system for three values of  $\theta$  and Model 3b. Trajectory A, *richness loss* (solid line). This trajectory starts with a community of 10 species of equal relative abundance. The trajectory traces communities with richness declining to a single species. Along this trajectory, the relative abundance of one species declines until it reaches zero, and the remaining species are equally abundant. Another species then declines until its relative abundance reaches zero, while the remaining species are again equally abundant and so on until the trajectory ends with a monoculture of one of the species. Trajectory B, *reducing evenness* (hatched line). This trajectory traces communities in which one species becomes increasingly dominant until it finally ends with a monoculture, with all other species declining at an equal rate. (a–c) The value of the diversity effect calculated for each community in both trajectories for three values of  $\theta$  (trajectory A represented by the solid line, trajectory B represented by the hatched line). For values of  $\theta < 1$ , the effect of species loss (trajectory A) is more severe than reducing evenness (trajectory B), and the difference between trajectories becomes more accentuated with declining  $\theta$ .

explain the relatively unchanged ecosystem response across a wide range of relative abundance of grass and legume species in Nyfeler *et al.* (2009). Where there is large variation in the identity effects of species, the outcome is not so clear, because of the separate effects of changing evenness on the identity and diversity components of functioning. Functional stability for more complex models can be explored by predicting functioning along several trajectories of interest as above.

Transgressive overyielding occurs when a mixed community has greater functioning than the best monoculture. The potential for transgressive overyielding can be related to values of  $\theta$ . Along a trajectory of type B ending with the species whose monoculture yield is highest, a mixed community with a high relative abundance of the best species will have an ID effect close to the highest monoculture yield. The additional diversity effect for this community increases as  $\theta$  decreases (compare hatched lines in Fig. 4d–f), while its ID effect is unaffected by  $\theta$ , thereby increasing the likelihood of transgressive overyielding. The range of communities delivering transgressive overyielding will be related to the size of the diversity effect and how it varies with evenness.

In agronomic systems, increased stability of function across a wide range of evenness and the severe impact of species loss on functioning identified for low values of  $\theta$  have particular relevance. Managing relative abundance within tight limits for a multispecies community would be less critical. Also, our findings on species loss suggest that the impact of species absence from the system may be considerable, leaving the possibility to select compatible species to add to the mix to increase ecosystem function. Thus, an addition of species even at low levels of relative abundance to increase functioning may often be a practical option in both agronomic and managed natural systems.

The Generalised Diversity-Interactions framework proposed here provides a flexible, unifying structure to describe BEF relationships that allows us to address sophisticated theoretical and practical questions on specific functions and ecosystems.

We have shown that functional responses from microbial, grassland and soil ecosystems can be well described using Generalised Diversity-Interactions models. The simple specification of the contribution of pairwise interaction can have profound consequences for community characteristics that include saturation of BEF with increasing richness, trajectories of species loss, functional stability across communities and transgressive overyielding. It also provokes hypotheses about how species interact in complex communities in various environments.

We leave some other important issues for another occasion. The symmetry of specification of the pairwise interaction and the omission of higher order interactions could both be modified in an extended Generalised Diversity-Interactions models system, although the data sets analysed here did not suggest the necessity for such modifications. The consequences of changing species relative abundances over time for model fit and model relevance (Kirwan *et al.* 2007, 2009) will not be discussed here.

Generalised Diversity-Interactions models provide a useful addition to other models of BEF. However, we believe that they are just a stage in our increasing understanding of processes and mechanisms underlying the effects of diversity. We should aim to improve BEF models by including information based on increased understanding of fundamental constraints on interactions (as suggested by e.g. metabolic theory, ecological stoichiometry) or, for example of the genetic/evolutionary underpinning of differences between species (e.g. Connolly *et al.* 2011). This should lead to improved prediction of empirical outcome increasingly based on mechanism and process.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Generalised Diversity-Interactions models compared with other BEF functions in communities in which all species present have the same relative abundance and where richness is up to 75 species.

**Table S1.** Relationship between the diversity effects in the Generalised Diversity-Interactions models and other models of BEF.

**Table S2.** Details of various models fitted to datasets from Exp1 to Exp7 and tests between the models.

**Appendix S1.** Various forms of the relationship between biodiversity and ecosystem function (BEF) are approximated by Generalised Diversity-Interactions models with specific values of  $\theta$ .

**Appendix S2.** Brief description of experiment and modelling results for seven datasets.

**Appendix S3.** Details of Generalised Diversity-Interactions models, their analysis and interpretation.

**Appendix S4.** Data for example of analysis of Generalised Diversity-Interactions models.

**Appendix S5.** Code for the analysis of Generalised Diversity-Interactions models using SAS/STAT®.

**Appendix S6.** Code for the analysis of Generalised Diversity-Interactions models using R.