







APPLICATION

Going beyond richness: Modelling the BEF relationship using species identity, evenness, richness and species interactions via the DImodels R package

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Abstract

1. Biodiversity and ecosystem function (BEF) studies aim to understand how ecosystems respond to a gradient of species diversity. Generalised Diversity-Interactions (DI) models are suitable for analysing the BEF relationship. These models relate an ecosystem function response of a community to the identity of the species in the community, their evenness (proportions) and interactions. The number of species in the community (richness) is included implicitly in a DI model.
2. It is common in BEF studies to model an ecosystem function as a function of richness; while this can uncover trends in the BEF relationship, by definition, species diversity is broader than richness alone, and important patterns in the BEF relationship may remain hidden. Here, we introduce the DImodels R package for implementing DI models. We show how richness is mathematically equivalent to a simplified DI model under certain conditions, and illustrate how using the DI multidimensional definition of species diversity can provide deeper insight to the BEF relationship compared to traditional approaches.
3. Using DI models can lead to considerably improved model fit over other methods; it does this by incorporating variation due to the multiple facets of species diversity. Predicting from a DI model is not limited to the study design points, the model can interpolate or extrapolate to predict for any species composition and proportions (assuming there is sufficient coverage of this space in the study design).
4. Expressing the BEF relationship as a function of richness alone can be useful to capture overall trends. However, collapsing the multiple dimensions of species diversity to a single dimension (such as richness) can result in valuable ecological information being lost. DI modelling provides a framework to test the multiple components of species diversity in the BEF relationship. It facilitates uncovering a deeper ecological understanding of the BEF relationship and can lead to enhanced

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inference. The open-source DImodels R package provides a user-friendly way to implement this modelling approach.

KEYWORDS

biodiversity and ecosystem function relationship, community composition, Diversity-Interactions models, species interactions

1 | INTRODUCTION

In biodiversity and ecosystem function (BEF) studies, there is usually a range of communities that may vary in the number, identities and/or proportions of species, and in overall density. One or more ecosystem function responses are recorded for each community a period after species diversity is manipulated (an experiment) or observed (an observational study). Since communities in BEF studies are characterised by the initial richness, composition (species identities) and evenness (species proportions) of their species, statistical analyses should ideally jointly assess how ecosystem function (community-level responses) is affected by these three variables. Diversity-Interactions (DI) modelling, introduced by Kirwan et al. (2009) and Connolly et al. (2013), jointly assesses the effects of species identity, richness, evenness, community composition and interspecific species interactions on an ecosystem function in a regression modelling framework. The DImodels package (Moral et al., 2022) for R software (R Core Team, 2023) implements this approach.

DI models typically include three components in the linear predictor:

$$y = \text{Identities} + \text{Interactions} + \text{Structures} + \varepsilon, \quad (1)$$

where y is a community-level response (e.g. biomass for a plant community); *Identities* are the effects of species identities and enter the

model as initial individual species proportions; *Interactions* are the pairwise effects of interspecific interactions between the initial species proportions; while *Structures* include other experimental structures, such as blocks, treatments or environmental gradients. A possible DI model (excluding structures) is:

$$y = \sum_{i=1}^s \beta_i p_i + \sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} (p_i p_j)^\theta + \varepsilon, \quad (2)$$

where p_i is the initial proportion of species i , β_i is the identity effect of species i , δ_{ij} is the interaction parameter for species i and j and ε is a normally distributed random error term, with constant variance. The non-linear exponent parameter θ on each $p_i p_j$ in the *Interactions* component, determines the shape of the BEF relationship by allowing the importance and impact of interaction terms to be directly modelled (Connolly et al., 2013). Imposing different constraints in the *Interactions* term can make DI models more biologically informative and estimable (Table 1).

A major strength of the DI modelling framework is its ability to decompose the various elements of species diversity, including species identity (composition), species richness and evenness (Kirwan et al., 2007). While 'richness' does not appear explicitly in Equation (2), richness is implicitly included (see appendix S1 in

TABLE 1 The *Identities'* and *Interactions* components for a range of DI models; there are s species in the pool that are categorised by T functional groups (FGs), and p_i is the initial proportion of species i .

Model name	Identities	Interactions	Model tag ^a
Species identity (no interactions)	$\sum_{i=1}^s \beta_i p_i$	–	ID
Average pairwise (all interactions equal)	$\sum_{i=1}^s \beta_i p_i$	$\delta \sum_{\substack{i,j=1 \\ i < j}}^s (p_i p_j)^\theta$	AV
Functional groups (interactions dictated by functional group membership)	$\sum_{i=1}^s \beta_i p_i$	$\sum_{q=1}^T \omega_{qq} \sum_{\substack{i,j \in FG_q \\ i < j}} (p_i p_j)^\theta + \sum_{\substack{q,r=1 \\ q < r}}^T \omega_{qr} \sum_{i \in FG_q, j \in FG_r} (p_i p_j)^\theta$	FG
Additive species (species-specific contribution)	$\sum_{i=1}^s \beta_i p_i$	$\sum_{\substack{i,j=1 \\ i < j}}^s (\lambda_i + \lambda_j) (p_i p_j)^\theta$	ADD
Full pairwise (all interactions unique)	$\sum_{i=1}^s \beta_i p_i$	$\sum_{\substack{i,j=1 \\ i < j}}^s \delta_{ij} (p_i p_j)^\theta$	FULL

^aEach model can be implemented in the DImodels package and the DImodel argument within the DI() function is referred to as the 'model tag' (see Section 2).

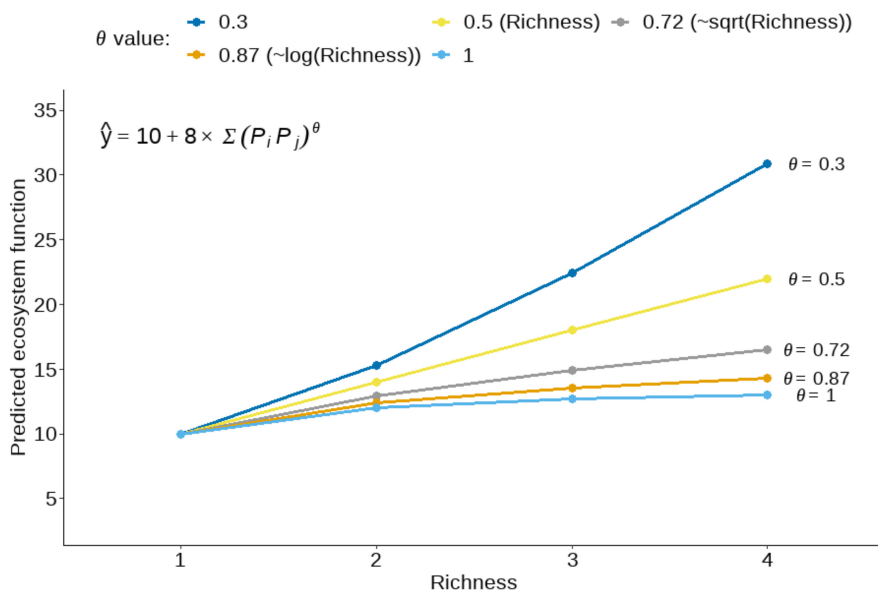
Connolly et al., 2013): when modelling data with monocultures and/or mixtures that have an equal proportion of their nonzero species (equi-proportional mixtures), the average pairwise DI model (see Table 1) with $\theta = 0.5$ and all Identity effects set equal is equivalent to the richness model (Figure 1a). A mathematical proof and illustration of this equivalency are in S11. Under the same conditions, a $\theta = 0.72$ approximates the BEF model with predictor the square root of richness, and $\theta = 0.87$ approximates the log(richness) model (Figure 1a). Through DI models, we can go beyond richness as the main explanatory driver of the BEF relationship and additionally test for: (1) deviations from a linear richness BEF relationship (the shape of the BEF relationship changes with θ : Figure 1a); (2) species-specific effects (different identity effects (β_i), Figure 1b); (3) departures from equi-proportional communities (the richness model is not sensitive to changes in species proportions at a given richness);

and (4) varying interaction structures (the richness model assumes any pair of species interacts with the same strength). These benefits of DI models are illustrated in S11 and Section 3.

The DI model framework can be used to analyse community-level responses without the need to have the response broken down into the various species contributions (a requirement of partitioning models, see Loreau & Hector, 2001). This is particularly relevant for community-level responses that *cannot* be partitioned (e.g. greenhouse gas measurements; see Cummins et al., 2021), and for community-level responses that are labour intensive to partition into species contributions. DI models relate a 'total' ecosystem function to initial (e.g. sown proportions in a grassland biodiversity experiment) or previous species diversity.

Here, we present the DImodels R package for fitting DI models and showcase its functionality. We also compare DI modelling to other commonly used BEF modelling approaches.

(a) Changing θ alters the shape of the BEF relationship



(b) Predictions from a DI model can be on average at each level of richness (black points) and for specific communities with varying combinations of species (pie-glyphs)

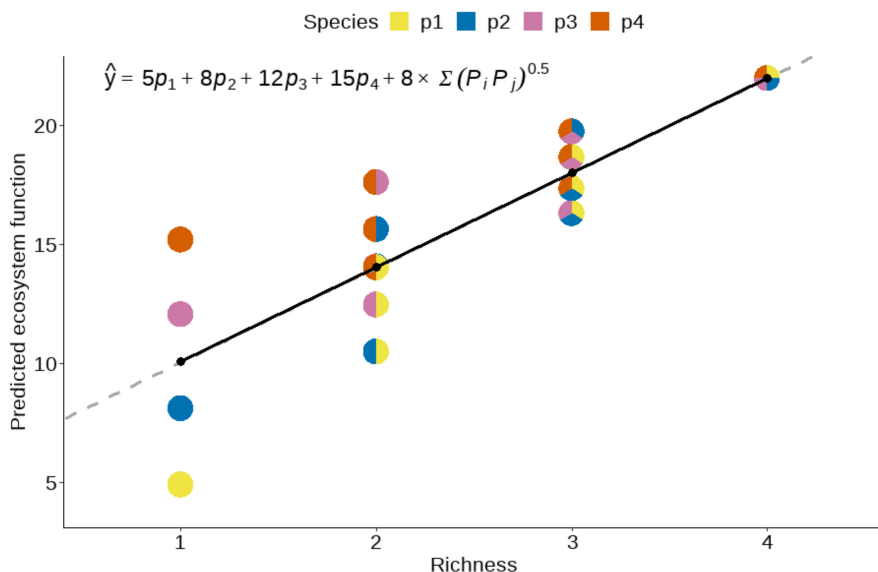


FIGURE 1 Conceptual diagram to illustrate how richness is implicitly included in a DI model. It is assumed the underlying data come from a balanced design with only equi-proportional communities from a pool of four species. Predicted ecosystem function versus richness for: (a) a range of DI models where all species interact in the same way (AV model in Table 1), with identity effects equal, and with θ varying, and (b) a DI model with unique identity effects for each species and an average interaction term with $\theta = 0.5$; predictions are shown for select individual communities (the pie glyphs show the initial community proportions) and on average for each richness level (black dots; computed as $\hat{y} = \frac{5+8+12+15}{4} + 8 \sum (p_i p_j)^{0.5}$). The dotted grey line is the fitted richness model, it coincides with the average DI model predictions.

2 | THE DImodels R PACKAGE

The DImodels package provides users with the flexibility to fit and compare different types of DI models. A typical workflow consists of (1) loading and exploring the dataset; (2) performing automatic model selection using the `autoDI()` function; and (3) refitting and/or extending the `autoDI()` selected model using the `DI()` and (sometimes) the `DI_data()` functions (Figure 2). A dataset suitable for use with the package will contain a response variable and columns indicating the initial species proportions; it may also include block, treatment, density and/or community explanatory variables. The package contains simulated and real example datasets for illustration.

2.1 | Automatic model selection

The `autoDI()` function provides an automatic model selection procedure to fit a limited range of DI models. The user may choose between different criteria for model selection, such as F-tests and likelihood-based information criteria. Using `autoDI()`, a four-step selection process identifies the best DI model from those fitted (Box 1). While `autoDI()` is an excellent starting point, it fits a limited number of DI models; it is strongly recommended to assess the diagnostics of

the selected model and to explore additional models as appropriate via the `DI()` function. For instance, `autoDI()` does not test for interactions of a treatment with other variables in the model.

The package provides the `richness_vs_DI()` function, a second automated model selection procedure. This function compares the richness model to a small subset of DI models (SI1).

2.2 | Fitting individual DI models

The syntax for the `DI()` function is:

```
DI(y, prop, DImodel, data, block, density, treat, FG, extra_formula,
  custom_formula, estimate_theta, theta)
```

The `data` argument specifies the dataset for analysis. The arguments `y`, `prop`, `block`, `density` and `treat` specify the corresponding column name (or number) in the dataset. The arguments `block`, `density` and `treat` constitute the *Structures* component of the DI model. The argument `DImodel` takes specific model tags (Table 1) and defines the corresponding *Identities* and *Interactions* components. When fitting a functional groups model (FG tag in Table 1), the argument `FG` is used to declare the functional group names. Additional terms may be added by specifying a formula in the argument `extra_formula`, for

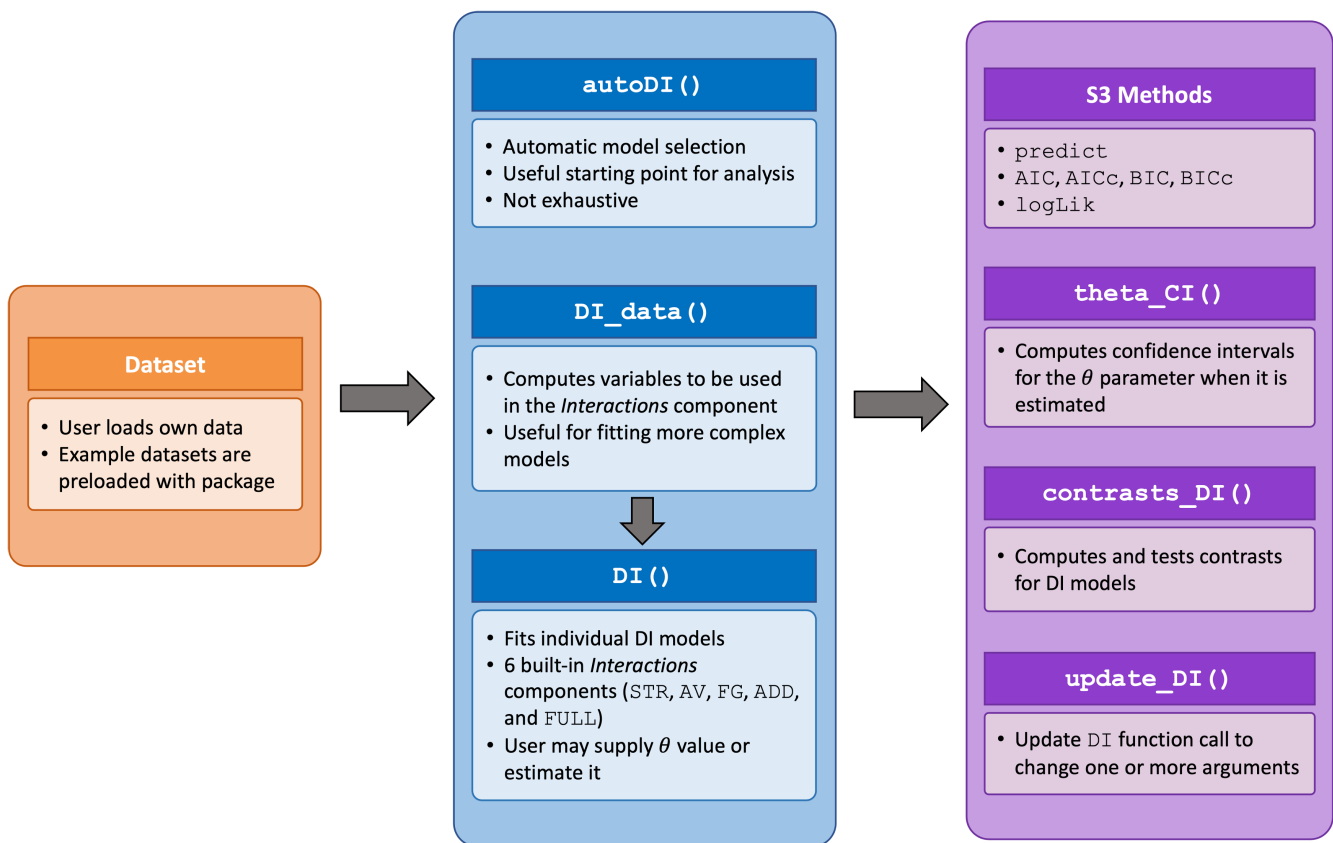


FIGURE 2 Schematic diagram representing a typical workflow and the conceptual map of the DImodels package. A dataset (orange column) is passed through the core package functions (blue column) and the resulting model objects can be passed through additional functions (purple column).

BOX 1 Overview of autoDI()

The autoDI() function implements a four-step model selection procedure, plus an optional initial step (Figure 3). 'Step 0' (optional) investigates the significance of Structures by comparing the intercept-only model with models including the Structures terms. In 'Step 1', θ is estimated for the average interactions (AV) model and is tested for a difference from 1. In 'Step 2', the Interactions term is investigated using forward selection with five different Interactions structures, including the estimate of θ from 'Step 1', if it was significantly different from 1, or assuming $\theta = 1$ otherwise. In 'Step 3', the treatment (if present) is tested for inclusion in the model selected in 'Step 2'. Finally, in 'Step 4' (also optional, but conducted by default), autoDI() carries out a lack-of-fit test by comparing the model selected in 'Step 3' with the reference (community) model, which includes a factor variable representing each unique combination of species proportions, as the linear predictor.

example, interactions between species proportions and treatment effects. By default, a DI model fitted using DI() will assume $\theta = 1$, however, it can be set to a numeric value with the theta argument or can be estimated using estimate_theta = TRUE.

Ordinary least squares estimation is used when $\theta = 1$. The main challenge lies in generating the interaction terms of the model matrix. The DImodels package uses the species proportions input to internally prepare the appropriate model matrices depending on the specifications of the Identities and Interactions components. When θ is estimated, we optimise the log-likelihood $L(\theta)$ of the model using Brent's (1973) method.

2.3 | Working with fitted DI models

Both autoDI() and DI() return objects of class DI, for which different S3 methods are available to calculate predictions and associated standard errors, information criteria and log-likelihood values, and compare nested models using F-tests (Figure 2). Specific contrasts and their standard errors are provided by contrasts_DI() (see example in SI2.9). Updated calls to the DI() function are obtained via update_DI(). Confidence intervals for the θ parameter can be computed via the theta_CI() function (see example in SI4.5). We obtain $100(1 - \alpha)\%$ confidence intervals for θ by profiling $L(\theta)$ over a pre-defined grid and obtaining the values of θ that correspond to the solutions of the equation $L(\theta) - L(\hat{\theta}) = \frac{1}{2} \chi^2_{1,\alpha}$, where $L(\hat{\theta})$ is the log-likelihood evaluated at the maximum likelihood estimate $\hat{\theta}$ and $\chi^2_{1,\alpha}$ is the $100\alpha\%$ percentile of the chi-squared distribution with 1 degree of freedom.

Data manipulation steps are carried out automatically within the autoDI() and DI() functions. However, the user can compute and

store interaction variables using the DI_data() function and, for instance, may wish to use them in the extra_formula argument within the DI() function (see SI4 for an example), or moving beyond the DImodels package to other types of extended modelling approaches (e.g. Bayesian inference via MCMC samplers, or inclusion of random block effects). Moreover, users may extract the full model matrix of a fitted DI model using the model.matrix() S3 method for glm objects, or by using the extract() S3 method for DI objects, which extracts specific parts of the model matrix.

3 | CASE STUDIES

We present two case studies to highlight the benefits of DI models and the features of our package. SI2 (simulated data) and SI3 (Bell dataset on a bacterial experiment) reproduce the analyses in the case studies. SI4 presents an additional case study on data from a grassland biodiversity experiment. All three datasets are available in the DImodels package.

3.1 | Simulated data case study

We simulated a BEF dataset, assuming a pool of three species, with 16 unique communities each characterised by the proportions of species 1, 2 and 3 respectively: p_1 , p_2 , and p_3 . The design (Figure 4b and SI2.2) consisted of:

- monocultures of each species (e.g., 1:0:0),
- binary communities: equi-proportional (e.g., 0.5:0.5:0) and unbalanced (e.g., 0.8:0.2:0), and
- three-species communities: equi-proportional (0.333:0.333:0.333) and unbalanced (e.g., 0.6:0.2:0.2).

A response (ecosystem function) was simulated for four replicates of each community, giving 64 experimental units (this 'sim0' dataset is available in the DImodels package). The responses were simulated from:

$$y = \sum_{i=1}^3 \beta_i p_i + \sum_{\substack{i,j=1 \\ i < j}}^3 \delta_{ij} p_i p_j + \epsilon, \quad (3)$$

with values: $\beta_1 = 25$, $\beta_2 = 20$, $\beta_3 = 15$, $\delta_{12} = 30$, $\delta_{13} = 20$ and $\delta_{23} = 40$, with $\epsilon \sim N(0, \sigma^2 = 4)$. A positive interaction means that combining the interacting species will result in a higher expected mean than the weighted average expected identity effects; for example, in the absence of any interaction between species 1 and 2, the expected response for a 40:60 initial two-species mix of species 1 and 2 would be $(25)(0.4) + (20)(0.6) = 22$, however, given the positive interaction term, the expected response from Equation (3) is $(25)(0.4) + (20)(0.6) + (30)(0.4)(0.6) = 29.2$.

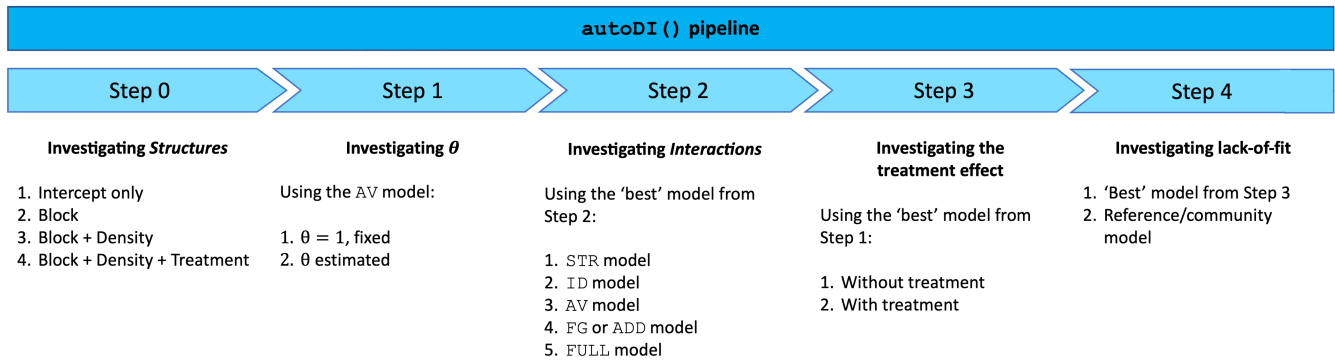
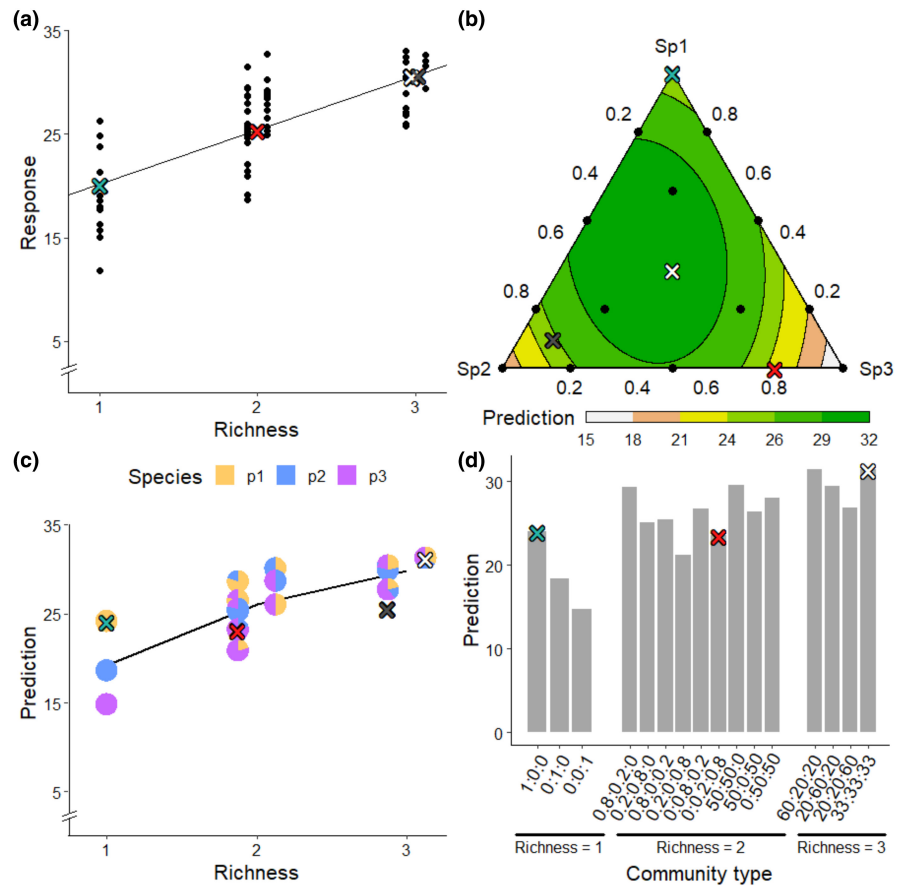


FIGURE 3 A schematic representation of the autoDI() pipeline.

FIGURE 4 (a) the fitted richness model with raw data; (b) the predicted response values across the three-dimensional simplex space, predicted from fitting a DI model (with design points marked with a dot or X, the grey coloured X highlights a prediction that is not a design point); (c) the predicted response for each design point from fitting a DI model, with the pie-glyphs (jittered) illustrating the initial proportions and trendline connecting the average prediction at each level of richness; (d) predicted response for each community from a one-way ANOVA model. The coloured X's in each panel highlight select predictions for each analysis: turquoise for a monoculture of species 1, red for 20% of species 2 and 80% of species 3, white for an equi-proportional three-species mixture and grey for 10% of species 1 and 3 and 80% of species 2.



We analysed the simulated data by fitting: (1) the richness model, (2) a full pairwise DI model and (3) a one-way ANOVA model (a factor with a level for each of the 16 unique communities). We found:

The richness model: As richness increased, the response also increased (Figure 4a, $p < 0.001$). All variation around the line is assumed to be residual error variation ($MSE = 11.24$, 62 residual df). At each level of richness, some variation is likely due to changing composition and/or changes in the proportions of species.

The full pairwise Diversity-Interactions model: Species identities and interactions strongly influenced the response, as evidenced by

the 'dome' shape in the ternary diagram (Figure 4b; $MSE = 3.54$, 58 residual df). The DI model can predict for any combination of species proportions around the three-dimensional simplex space (Figure 4b). Figure 4c also illustrates DI model predictions and highlights the increasing trend in predictions as richness increases; variation in predictions due to species composition and proportions is additionally represented by the pie-glyphs (Vishwakarma et al., 2023).

The one-way ANOVA model: There was a strong effect of changing species diversity (Figure 4d, $p < 0.001$; $MSE = 3.75$, 48 residual df). Comparisons can be made between any two communities in the design space but there are limitations to generalise patterns

across species diversity. The main strength in the ANOVA model is its ability to act as a reference or a test for lack of fit.

To illustrate the varying inferential ability of the three approaches, we highlight the predictions from each model for select communities; see the coloured X's in Figure 4. The ANOVA and DI models give a tailored prediction for the three communities in the design space (turquoise, red and white X's). The richness model only gives an average prediction at any given level of richness. Only the DI model can predict uniquely for any set of species proportions. Thus, DI models can predict across levels of richness (as with the richness model), predict for any community in the design (as with the ANOVA model) and predict for any combination of p_1 , p_2 , and p_3 by interpolating and extrapolating around the simplex space, assuming there is reasonable coverage of the design space.

The MSE was highest for the richness model (11.24; AIC=340.45), while the DI model (3.54; AIC=270.26) and ANOVA model (3.75, AIC=281.76) had similar MSE values. This supports that the lower numbers of parameters in the DI model explained as much variation as the ANOVA (reference) model and was an improvement over the richness model.

3.2 | The Bell dataset case study

This case study comes from a 72-species bacterial biodiversity experiment (Bell et al., 2005). The bacterial ecosystems used were from semipermanent rain pool depressions near the base of European beech trees *Fagus sylvatica*. Microcosms were inoculated with combinations of bacterial species isolated from these ecosystems. A total of 1374 microcosms were constructed at richness levels of 1, 2, 3, 4, 6, 8, 9, 12, 18, 24, 36 and 72 species. The daily respiration rate of the bacteria in each microcosm averaged over three time intervals (days 0–7, 7–14 and 14–28) was analysed.

With 72 species, the Bell dataset presents some challenges for DI models: a full pairwise interactions model would have 72 identity and 2556 interaction effects. Fitting this model is neither possible (there being only 1374 experimental units) nor desirable since estimating so many interaction terms is unlikely to provide valuable biological information. We fitted the three models in Table 2. The average pairwise

DI model with θ set to 1 gives a higher AIC than the richness model, however, when θ was estimated, the AIC was much lower (Table 2; $\hat{\theta} = 0.79 < 1$, more importance is given to interactions when proportions are lower). Raw data and the predictions from each model are shown in Figure 5; four θ values are shown to illustrate the flexibility of the DI modelling framework in modelling the shape of the BEF relationship. Of the three models fitted, the third model (AV + θ estimated) is the best according to AIC (Table 2; Connolly et al., 2013), although the model with all identity effects assumed equal (but keeping AV + θ estimated) gives a comparable AIC value (S13.2). It is clear that for these data, assuming a BEF relationship to be linear with richness would be inappropriate, as would assuming $\theta = 1$.

4 | FINAL REMARKS

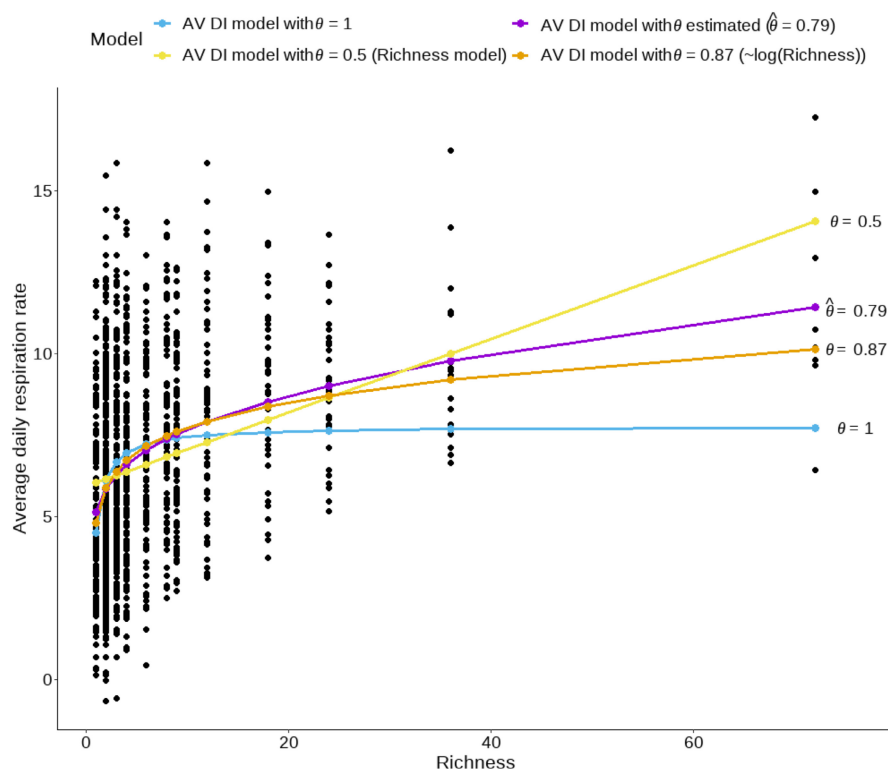
This DIModels package provides a user-friendly means to fit a range of models. The autoDI() function provides an automated preliminary analysis of a BEF dataset and is particularly beneficial to users new to the modelling approach. Only a subset of possible models that can be fitted to a given dataset are tested in autoDI(), and users should supplement the autoDI() analysis with further analysis using the DI() function.

Use of the full pairwise interactions DI model is typically constrained to datasets with a smaller number of species than (e.g.) the Bell data as it can have limited biological value (too many parameters) or may not be estimable (e.g. in studies where a pair of species do not occur together). However, alternatives involving the DI modelling framework are available to deal with datasets where communities are species rich. One solution is to use random pairwise interactions (Brophy et al., 2017; McDonnell et al., 2023); in this approach the pairwise interactions are assumed to be latent realisations of normal random variables, and it is only necessary to estimate their mean and variance rather than all possible combinations. Another solution is to specify *Interactions* components that utilise fewer degrees of freedom, such as the average pairwise interaction structure (Table 1). Indeed, even the average pairwise interaction model alone can have considerable value by allowing estimation of the shape of the BEF relationship rather than imposing a linear richness relationship, for example. Moreover, in studies where a specific pair of species is not observed in the same observational/experimental unit, their

TABLE 2 Models fitted to the Bell dataset, with their AIC values.

Model description	Equation(s)	AIC
Average interactions model, identity effects equal, θ set to 0.5 (equivalent to the richness model, see S11)	$y = \alpha + \delta \sum_{\substack{i,j=1 \\ i < j}}^{72} (p_i p_j)^{0.5} + \epsilon$	6789.95
Average interactions model, θ set to 1	$y = \sum_{i=1}^{72} \beta_i p_i + \delta \sum_{\substack{i,j=1 \\ i < j}}^{72} p_i p_j + \epsilon$	6814.61
Average interactions model, θ estimated	$y = \sum_{i=1}^{72} \beta_i p_i + \delta \sum_{\substack{i,j=1 \\ i < j}}^{72} (p_i p_j)^{\theta} + \epsilon$	6751.12

FIGURE 5 Average daily respiration rate versus richness for the raw data (black dots) and the fitted predictions from the average interactions models with $\theta = 1$ (blue line), $\theta = 0.5$ (yellow line), $\theta = 0.87$ (orange line) and with θ estimated ($\hat{\theta} = 0.79$; purple line). Predictions for each model are computed as the average of all design communities (black dots) at each level of richness, with a smoothed line imposed across richness levels. The model with $\theta = 0.5$ depicts the BEF relationship with a linear richness shape, while the model with $\theta = 0.87$ approximates the BEF relationship with a log(richness) shape.



pairwise interaction coefficient cannot be estimated by a full pairwise DI model, and hence the alternative strategies outlined above can be useful.

When designing an experiment suitable for analysis using DI modelling, replicates of each community are not required. This is because DI modelling is analogous to a response surface analysis and replication is across the continuous simplex space. Of course, it may be beneficial to have replicates in some parts of the simplex design space to provide additional power; in particular, it is recommended (but not required) to have replication at the extremities of the design at the monoculture points. DI modelling is applicable to BEF data where species identities and proportions have been manipulated across an evenness and richness gradient (e.g. the Switzerland Case Study, see S14), and also applicable for BEF data where only equi-proportional mixtures are available (provided that a range of richness levels is included in the design, e.g., the Bell Case Study). DI models can jointly assess the effects of species identity, richness, evenness and species interactions on ecosystem function responses in a wide range of BEF studies.

Estimating θ in a DI model allows the data to identify the best shape of the BEF relationship (rather than the user imposing, e.g., a log or linear richness relationship). Frequently richness alone will not capture all variation due to species diversity and DI modelling provides a versatile framework to model the multiple dimensions of species diversity effects in the BEF relationship.

AUTHOR CONTRIBUTIONS

Rafael de Andrade Moral, Caroline Brophy and John Connolly developed the DImodels R package, Rishabh Vishwakarma

contributed to the package and case study materials. Rishabh Vishwakarma and Catherine Hurley developed the novel visualisation approaches. Rafael de Andrade Moral, Caroline Brophy and John Connolly wrote the initial draft of the paper. Rishabh Vishwakarma, Laura Byrne, Catherine Hurley and John Finn each contributed to various conceptual developments and to writing the paper.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/2041-210X.14158>.

DATA AVAILABILITY STATEMENT

All datasets used in this paper are available in the DImodels R package (<https://cran.r-project.org/web/packages/DImodels/index.html>), and indexed by Zenodo (<https://zenodo.org/record/7963535>; Moral et al., 2023). All code is made available as supplementary material. The DImodels R package is open-source and free, and while the stable version is available on CRAN, the development version is available at <https://github.com/rafamoral/DImodels>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1: Richness is implicitly included a DI model.

Data S2: Vignette: The analysis of the sim0 dataset.

Data S3: Vignette: The analysis from the Bell Case Study.

Data S4: Vignette: Analysis of the Switzerland dataset.

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