Diversity–interaction modeling: estimating contributions of species identities and interactions to ecosystem function

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Abstract. We develop a modeling framework that estimates the effects of species identity and diversity on ecosystem function and permits prediction of the diversity–function relationship across different types of community composition. Rather than just measure an overall effect of diversity, we separately estimate the contributions of different species interactions. This is especially important when both positive and negative interactions occur or where there are patterns in the interactions. Based on different biological assumptions, we can test for different patterns of interaction that correspond to the roles of evenness, functional groups, and functional redundancy. These more parsimonious descriptions can be especially useful in identifying general diversity–function relationships in communities with large numbers of species. We provide an example of the application of the modeling framework. These models describe community-level performance and thus do not require separate measurement of the performance of individual species. This flexible modeling approach can be tailored to test many hypotheses in biodiversity research and can suggest the interaction mechanisms that may be acting.

Key words: biodiversity–ecosystem function; diversity effect; diversity–interaction models; functional groups; functional redundancy; species identity; species interactions.

Introduction

Ecosystem function is strongly affected by biodiversity. However, controversy has surrounded the statistical design and analysis of diversity–function experiments and the extent to which mechanistic explanations of relationships can be inferred from their results (Hooper et al. 2005). Early diversity–function experiments used analysis of variance (ANOVA) techniques to separate effects of species composition and species richness (Schmid et al. 2002). However, these methods provide no information on how different species contributed to an ecosystem function and confound the effects of species identity and diversity. This was overcome by defining a diversity effect (DE) as the excess of mixture performance over that expected from component species' monoculture performances, the species identity (ID) effect (Loreau 1998). Such benefits of diversity can derive from interspecific interactions (e.g., niche partitioning and facilitation) among species in a community.

The additive partitioning methods (Loreau and Hector 2001, Fox 2005) estimate an overall diversity effect of species interactions on ecosystem function (the "complementarity effect"), but contain limitations. For example, to use the equations, it is necessary to measure the contribution of each species in a mixture to the ecosystem performance. This can be difficult, expensive and sometimes impossible (e.g., measuring the contribution of each species in a mixture to nutrient leaching or gaseous emissions). The complementarity measure also does not indicate how different interspecific interactions contribute to the diversity effect. Complementary and facilitative interactions among species can result in positive effects on an ecosystem function; however, antagonistic interactions may also occur, and some species may not interact at all.

For a particular community composition, we view the observed overall diversity effect as the combined effect of multiple interspecific interactions that may each differ in direction and magnitude. The contribution of this paper to the interpretation of diversity–function relationships is to quantify the direction and magnitude of separate interspecific interactions, and combine them to calculate the net effect of diversity in a mixture (Sheehan et al. 2006, Kirwan et al. 2007). Our modeling framework (1) explicitly quantifies the effects of species identity, (2)

quantifies the contributions of individual interspecific interactions to the diversity effect, and (3) proposes a range of models with simple patterns among the interspecific interactions. These models can explain most of the diversity effect using a low number of coefficients, which is of particular importance in species-rich systems with many possible interactions. By testing between the alternative descriptions of interaction pattern, we can test biologically meaningful hypotheses about how species interactions contribute to diversity effects. In addition, the approach only requires the measurement of the ecosystem performance for the whole community and not for each contributing species, and can be applied to a variety of ecosystem functions and organisms.

We present the models by starting with the simplest description of the relationship between diversity and function, the null hypothesis of no effect of diversity. We then introduce species identity effects and alternative patterns of species interactions. Many of the models are generalizations of more simple models and form a hierarchy in the complexity of the patterns described. This hierarchy of models is discussed in the context of the biological hypotheses that are investigated by testing between alternatives. The formulation of the models is based on response surface models developed for mixture experiments (Cornell 2002) in a diversity–function setting (Kirwan et al. 2007). The models proposed can be fitted by standard regression methods or using generalized linear models. Random components can also be incorporated to describe, e.g., site-to-site or year-to-year variation (Kirwan et al. 2007). Further technical discussion, a worked example, and SAS code are provided in the Supplement and the Appendix.

DIVERSITY–INTERACTION MODELS

The general formulation of the linear model is $y = \text{ID} + \text{DE} + \text{residual}$. The response ($y$) is a community-level ecosystem function (e.g., total annual biomass, nutrients leached, and so on). Species identity effects (ID) and diversity effects (DE) are incorporated in the models through functions of the initial proportions of species in the community (denoted P_i for the ith species) and total overall initial abundance (M) of the community (it is assumed that M is centered to average to zero, so that all other terms in a model are interpreted at average initial overall abundance). For communities formed with species drawn from a pool of s species, community composition is denoted ($P_1, P_2, \ldots P_s$). The initial species proportions and overall initial community abundance are usually determined by the experimental design using some measure of "functional density," e.g., biomass or leaf area measured early in the experiment (Connolly et al. 2001). For a study over several periods, the initial values may be the relative abundances or total abundances in the previous period or at the start of the period. The inclusion of a range of initial overall abundance levels in addition to relative proportions is

to avoid issues arising from replacement series design (Connolly et al. 2001).

The null model

The null hypothesis in diversity–function studies is that a change in diversity has no effect on ecosystem function. Model 1 is the null model:

$$y = \beta + \alpha M + \varepsilon.$$

The coefficient α reflects the effect of changing initial overall abundance on ecosystem function; β is the level of ecosystem functioning (at average M) and does not vary with species richness or species' relative abundances. Species identity effects are all equal (ID $= \beta + \alpha M$) and there is no diversity effect (DE $= 0$). In this scenario, species perform identically and do not interact with each other. Ecosystem function will remain constant with addition or loss of species (Fig. 1a).

Species identity model: function depends only on the abundances of species

When monoculture performances of individual species differ, the addition or loss of a species from a multispecies community will have an impact on ecosystem function (Fig. 1b). In the absence of species interactions, the performance of a mixture can be determined by the identities and relative abundance of the species present and initial overall community abundance. Model 2 includes identity effects:

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \varepsilon.$$

Here, and subsequently, α is as defined in Model 1. The coefficient β_i is the estimated performance of species i in monoculture (its identity effect). For a monoculture of species i, $P_i = 1$, all other $P_j = 0$ and the predicted ecosystem function is β_i. Ecosystem function in mixture is an average of the identity effects of the component species, weighted by their initial proportions in mixture

$$\text{ID} = \sum_{i=1}^{s} \beta_i P_i + \alpha M.$$

Model 2 assumes that species do not interact in their impact on ecosystem function (DE $= 0$). Under such an assumption, the response of a mixture of species can be predicted directly from monoculture responses. This is not equivalent to the hypothesis that diversity has no effect on ecosystem function. Even without species interactions, ecosystem function can change with species richness if species have different identity effects. When species identity effects differ, but species do not interact, the community with the optimal ecosystem function will be the best performing monoculture. Variants of this and subsequent models can occur if identity and interaction effects change with M or if the response to initial overall abundance is not linear.
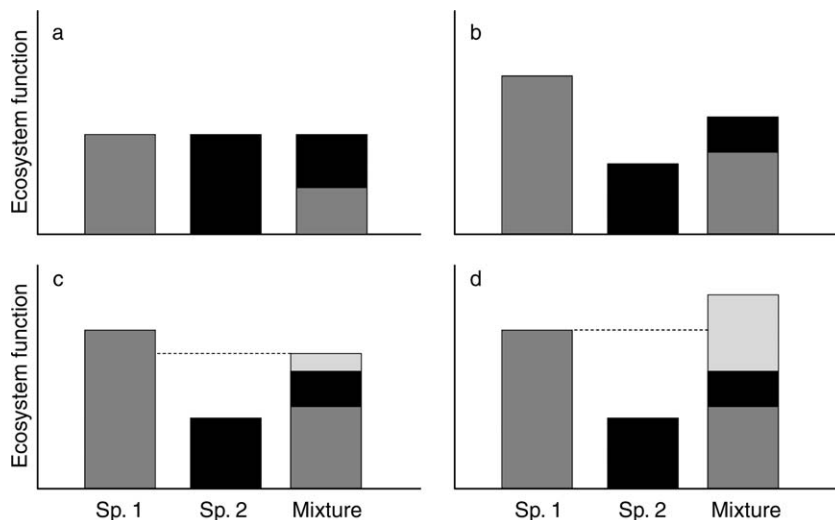
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Fɪɢ. 1. The effect on ecosystem function of combining two species in a 50:50 mixture where (a) species 1 and 2 perform identically; they do not interact, and the mixture performance is equal to the common identity effect; (b) species 1 has a greater identity effect than species 2; they do not interact, and mixture performance is equal to an average of the two identity effects; (c, d) species 1 has a greater identity effect than species 2. The mixture performance exceeds the average of the two identity effects. This additional performance (light gray area) is due to species interactions. In panel (c), despite there being a benefit from mixing, the performance of the mixture does not exceed the identity effect of species 1 (non-transgressive overyielding). In panel (d), the mixture performance exceeds the identity effects of both species and transgressive overyielding occurs.

Species interactions

When species interactions occur, the performance of a mixed community can differ from that expected from a combination of the individual species performances. This difference between the actual performance of a mixture and the performance expected from the monoculture performances is the diversity effect, DE (Fig. 1c, d) (Loreau 1998). Interactions among species can be synergistic or antagonistic in their effect on ecosystem function. Diversity–function research predicts that the net effect of species interactions on the ecosystem performance will be positive (Hooper et al. 2005). Diversity benefits are thought to be the result of differences in resource use among species (niche partitioning), and facilitation. Through niche partitioning, a more diverse community should be able to use resources more completely. Facilitation occurs when certain species help or allow other species to grow by modifying the environment in a way that favors a co-occurring species (Cardinale et al. 2002). Species may also combine antagonistically to have a negative impact on ecosystem function and a number of different positive and negative interactions may operate simultaneously. The diversity effect is the net result of all of these. The positive and negative contributions may counteract each other, and in some instances even lead to a net diversity effect of zero.

The degree of expression of an interaction between two species may depend on the relative abundances of the species involved. Species may have the ability to interact, but if they are not present in large enough abundance, the expression of this interaction will generally not be strong enough to detect. Model 3 (separate pairwise interactions) includes interactions between pairs of species:

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

The δ_{ij} term measures the strength of interspecific interaction between species i and j, and the sign of the coefficient indicates whether the relationship is synergistic or antagonistic. In this model, the contribution of the interaction between species i and j to the ecosystem function is $\delta_{ij} P_i P_j$, the strength of interaction times a term that reflects the relative abundance of the two species. The contribution of a particular interaction is zero if only one, or neither, species are present and increases as their relative abundances become more equal. The net diversity effect is

$$DE = \sum_{\substack{i,j=1 \\ i<j}}^{s} \delta_{ij} P_i P_j$$

and may be positive, negative, or zero. As the ecosystem performance is related to both identity and interaction effects, the community with the optimal performance will depend on the relative values of these two effects. If there are strong species identity effects and/or a weak positive diversity effect, maximum performance may occur in communities dominated by the best-performing monoculture (Fig. 1c). This scenario is termed non-

transgressive overyielding (Loreau 1998). If the diversity effects are strong enough, such that the performance of a mixture exceeds that of the best performing monoculture (Nyfeler et al. 2009), then the mixture exhibits transgressive overyielding (Fig. 1d). Of course, the inverse argument applies where a reduction in the level of ecosystem function is preferable, e.g., nutrient leaching.

Species interactions may be more complex and multispecies interactions may contribute to the diversity effect. For example, the presence of a third species may alter the pairwise interaction between two species. We can test for a three-way interaction between species i, j, and k by including a $\delta_{ijk}P_iP_jP_k$ term in the model. The contribution of species i and j to the diversity effect is then $P_iP_j(\delta_{ij} + \delta_{ijk}P_k)$, i.e., it is modified by the relative abundance of species k. Models similar to Model 3 can be developed to allow for higher order interactions but are not discussed here.

SPECIES INTERACTION PATTERNS

The number of model coefficients rapidly increases as the number of species in an experiment increases. Including the effects of identity, all possible multispecies interactions and overall abundance effects in a model requires the estimation of 2^s coefficients. Even when only pairwise interactions are included (Model 3), the number of coefficients can quickly become sizeable (Table 1). Patterns in the interspecific interactions may reflect characteristics of the species such as functional types or species traits. We show how incorporating patterns in our models can greatly reduce the number of coefficients needed to describe the diversity function relationship.

Average interaction effect (evenness model)

The strengths of interspecific interaction may be the same for all pairwise species combinations. If so, Model 3 may be rewritten to have a single interaction coefficient (δ_{AV}), producing Model 4, the evenness model:

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

The sum

$$\sum_{i<j}^{s} P_i P_j$$

is a measure of the distribution of the relative abundances of the species in the community (evenness; Kirwan et al. 2007) and is maximum when species are all equally represented. In this model, the DE is linearly related to the evenness of the community and the DE is maximum at maximum evenness. However, since the ecosystem function is related to both identity and diversity effects, the overall optimal performance may not occur at maximum evenness. The relationship between evenness and ecosystem function may not be linear; and may require quadratic and higher order evenness terms (Kirwan et al. 2007).

Additive species-specific contributions to interactions

Model 4 above describes a diversity effect that is derived when all pairwise interaction strengths are the same. Another alternative is when the potential contribution that a species makes (in its pairwise interactions) is the same, regardless of the species with which it is interacting. As a simple example, a legume species might transfer a similar level of fixed nitrogen to each of several grass species in mixture, and grass yield for each species benefits equally. However, different species may differ in their potential to interact with others (e.g., different legume species transfer different total amounts of fixed nitrogen). Model 5 (additive species-specific contributions) postulates a fixed contribution for each species to its pairwise interactions (λ_i):

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i<j}}^{s} (\lambda_i + \lambda_j) P_i P_j + \varepsilon.$$

The coefficient λ_i is the contribution that species i makes to its interaction with any other species. The interaction between species i and j is then the sum of the interaction strengths for the two species ($\delta_{ij} = \lambda_i + \lambda_j$). Note that this model can be estimated simply by using the identity

$$\sum_{\substack{i,j=1 \\ i<j}}^{s} (\lambda_i + \lambda_j) P_i P_j = \sum_{i=1}^{s} \lambda_i P_i (1 - P_i)$$

and fitting the $P_i(1 - P_i)$ as covariates.

Functional group effects

Species can play different functional roles with respect to ecosystem function and species with similar roles can form functional groups (e.g., legumes, grasses). Interactions among species from different functional groups may be stronger than among species within a group (Lavorel and Garnier 2002, Hooper and Dukes 2004). Model 6, the functional group model, is a diversity model for a community of s species, with t species of functional group a, and $s - t$ species of functional group b. Here, the proportion of the community made up of functional group a is the sum of all species proportions within a and is denoted P_a:

$$y = \sum_{i=1}^{s} \beta_i P_i + \alpha M + \delta_{aa} \sum_{\substack{i,j=1 \\ i<j}}^{s} P_i P_j + \delta_{bb} \sum_{\substack{i,j=t+1 \\ i<j}}^{s} P_i P_j$$

$$+ \delta_{ab} P_a P_b + \varepsilon.$$

The coefficient δ_{ab} measures the interaction between species from different functional groups. Species within functional groups may also interact and produce

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TABLE 1. Number of coefficients in Models 2–6 as the number of species (s) increases.

s	2) ID only	3) Pairwise interactions	4) Evenness	5) Additive contributions	6) Two functional groups	All possible interactions (2^s)
3	4	7	5	7	6	8
4	5	11	6	9	8	16
5	6	16	7	11	9	32
10	11	56	12	21	14	1024
16	17	137	18	33	20	65 536
25	26	326	27	51	29	33 554 432

diversity effects. The coefficients δ_{aa} and δ_{bb} measure the interaction between species of the same functional group. In this model all interactions between species of different functional groups have the same strength (δ_{ab}) and similarly for the within functional group interactions. Hypotheses about the relative strengths of between- and within-functional-group interactions can be tested if this model fits well. The functional group formulation in Model 6 can be extended to include more than two functional groupings with coefficients representing between- and within-functional-group interactions.

Functional redundancy

Some species may be redundant with respect to an ecosystem function (Lawton and Brown 1993). Functional redundancy requires that different species perform the same functional role in ecosystems, so that partial or total replacement of a redundant species by such other species does not affect ecosystem function. For either of two species to be substitutable, monocultures of either species and any mixtures of the two must all perform identically in their contributions to function and their interactions with other species.

For a strict test of functional redundancy among a number of species there are three conditions that must be satisfied. The species must (1) perform in the same way in monoculture (have the same identity effect), (2) interact in the same way with all the other species (pairwise and higher order), and (3) not interact with each other in a pairwise or higher order interaction. In short, we should be able to combine the species proportions and include them as a single component species in the model. For example, in a three-species system, Model 3 (the model of separate pairwise interaction) will reduce to Model 7, the functional redundancy model, if species 1 and 2 are functionally redundant:

$$y = \beta'(P_1 + P_2) + \beta_3 P_3 + \delta'(P_1 + P_2)P_3 + \varepsilon.$$

Here, P_1 and P_2 are combined and included as a single species. They can be substituted for each other without compromising the ecosystem function and so testing between Models 3 and 7 is a test of functional redundancy. In this model, species 1 and 2 have the same identity effect ($\beta_1 = \beta_2 = \beta'$), they interact in the same way with species 3 ($\delta_{13} = \delta_{23} = \delta'$) and they do not

interact with each other ($\delta_{12} = 0$). Although this method can test whether species are substitutable with respect to a particular ecosystem function, ecosystems perform many functions and the species may not be redundant when other ecosystem functions are considered.

Effect of environment or other covariate on diversity–function relationships

An environmental factor (experimental treatment or measured covariate) may affect the species performances differentially. It may affect the species identity effects, species interactions, or both. The effect of an environmental factor or covariate (T) can be included by crossing it with all model terms, to create Model 8, the effect of environment:

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

$$+ \alpha_1 M \times T + \sum_{\substack{i,j=1 \\ i<j}}^{s} \gamma_{ij} P_i P_j \times T + \varepsilon.$$

The coefficients γ_i, α_1, and γ_{ij} measure the impact of the environment on the identity effect of species i, the effect of M and the interaction between species i and j, respectively.

Testing biological hypotheses

The models described above form a hierarchy of complexity in the description of species identity and interaction effects (Fig. 2). By comparing the goodness of fit of models in this hierarchy, we can test among biological hypotheses about how species identity and interaction effects contribute to ecosystem function. Hypotheses A–G can be tested within this framework (see Fig. 2):

A) Do species differ in their individual monoculture performances?

B) On average, is there a diversity effect?

C) Do separate pairwise interactions differ, or is a single interaction coefficient sufficient to describe the diversity effect?

D) Do species contribute the same amount to interaction, irrespective of the identity of the species with which they interact?
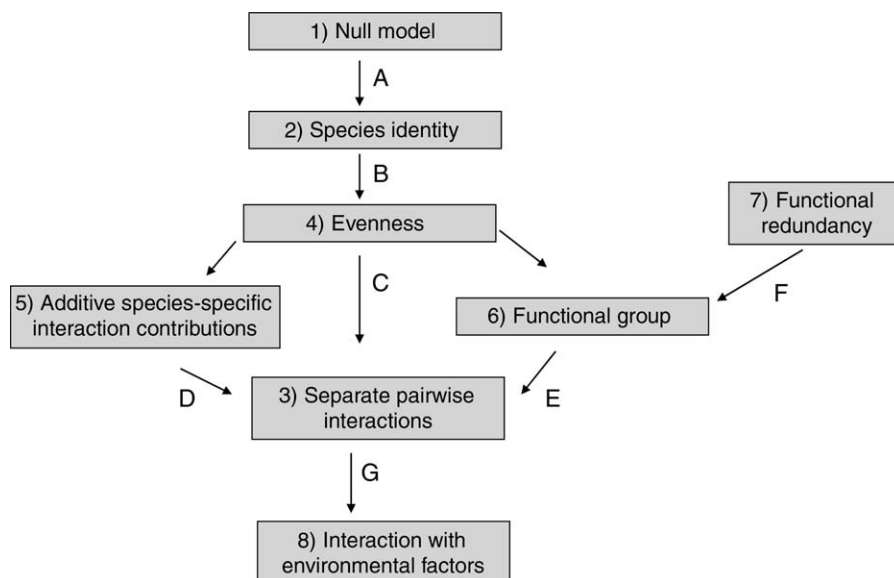
Fig. 2. Hierarchy of diversity–interaction models, starting with the simplest relationship between diversity and ecosystem function, and progressing through more complex patterns. The arrows indicate where a model is hierarchical to the one below. The letters denote alternative biological hypotheses A–G that represent different assumptions about the relationship between diversity and ecosystem function. By comparing the goodness of fit of the linked models, the way in which species identity and interaction effects affect ecosystem function can be investigated.

E) Can patterns in pairwise interactions be described by functional groups?

F) Are species within functional groups redundant?

G) Are species identity and interaction effects altered by an environmental factor?

This is not an exhaustive discussion of the hypotheses that can be tested within this framework. For example, interactions may occur among three or more species.

Discussion

The modeling approach proposed here can estimate the effects of species identity, can reveal patterns in how different species interactions contribute to the overall diversity effect and predict the diversity–function relationship for a pool of species. The benefit of estimating the contributions of separate interactions to the overall diversity effect is especially important when both positive and negative interactions are occurring, as the net effect could be zero. When the interactions differ, the diversity effect will change depending on the relative abundance distribution of the community. Using these models we can estimate the diversity effect for any mixture and relative abundance distribution of the species. It is a strength of this modeling approach that the species identity effects are implicitly estimated rather than just being discounted for. The species interaction effects must be assessed relative to the sizes of the identity effects. If there is a species that performs particularly well, a monoculture of that species may outperform the mixtures, irrespective of the presence of positive interactions.

The species interaction effects detected by the models may themselves be the net effect of a number of biological processes and so care is required when directly attributing an observed interaction to a biological mechanism. No analysis at the level of the community can measure the effect of any one process or mechanism (Petchey 2003). Only by experimentally manipulating the factors that influence processes such as resource use differentiation, facilitation or competition, can we estimate their individual importance for ecosystem function. A major value of the models proposed here is not to provide definitive evidence for particular mechanisms but, by observing patterns in species interactions, to suggest what species mechanisms may be occurring.

These models can be applied to data from traditional diversity–function studies, although the experimental design will impact on the level of complexity to which the models can be generalized. As the species richness in a community increases, so too does the number of possible interactions. For the proposed modeling approach to be applied to experiments where the levels of species richness are high, model reduction techniques are crucial. The evenness, species-specific and functional group models suggested here provide a method for reducing the number of interaction coefficients that require estimation (Table 1). However, these different interaction patterns do not just serve as a model reduction technique. One of the major contributions of the modeling approach is the ability to test among alternative hypotheses of how species interactions contribute to the diversity effect. Additionally, although we have only

dealt with interaction patterns here, there may also be patterns in the identity effects that relate to the functional groupings or species traits, etc.

These models do not require separation of the ecosystem function into contributions from individual species. This is highly relevant for investigation of community level ecosystem functions such as decomposition rate, gas fluxes or nutrient fluxes. This flexible approach can be applied to the data from diversity–function studies that manipulate the diversity of a variety of organisms and that measure any ecosystem function.

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APPENDIX

The diversity–interaction modeling approach: a worked example (*Ecological Archives* E090-140-A1).

SUPPLEMENT

The diversity–interaction modeling approach: SAS code required to run the worked example (*Ecological Archives* E090-140-S1).