

Measuring the functional value of biodiversity in plant communities

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Evidence across a wide range of organisms suggests a positive relationship between diversity and ecosystem function. The methods used to analyse biodiversity experiments have largely relied on ANOVA or graphical representation. We propose a framework based on biologically meaningful coefficients that quantify the separate contribution of each species and various interactions among species to the functional response. Recent work (Kirwan et al, 2007, *Journal of Ecology* 95:530-539) and preliminary analysis with data from a 9-species experiment suggest that diversity-function (DF) relationships can largely be described in terms of the identity of species and low order species interactions.

The following provides a starting point for modelling a functional response (y) in a community of t species selected from a pool of s species. P_i is the initial proportion of the i th species in the community ($0 \leq P_i \leq 1$).

$$y = \beta_{av} + \sum_{i=1}^s (\beta_i - \beta_{av})P_i + \delta_{av} \sum_{i < j} P_i P_j + \sum_{i < j} (\delta_{ij} - \delta_{av})P_i P_j + \varepsilon \quad [1]$$

β_{av} is the average response of monocultures, β_i is the monoculture performance of the i th species, δ_{ij} is the strength of the interaction between the i th and j th species. The diversity effect is the excess(reduction) of response above(below) what would be predicted based on a proportional mix of the monoculture responses. The contribution of the two species to the diversity effect is $\delta_{ij}P_iP_j$ which depends on the interaction strength between the species and their relative abundance in the community. δ_{av} is the average value of δ_{ij} . The residual ε is assumed normally distributed with constant variance σ^2 .

We propose a range of models based on [1] to provide a description of the functional response. To discriminate between our models we used data of 206 experimental plots and 100 different plant assemblages of grassland species that varied in species richness (1, 2, 3, 4, 6 and 9 species, Roscher et al, 2004, *Basic and Applied Ecology* 5, 107, data supplied courtesy of Dr Christiane Roscher, Max-Planck-Institute for Biogeochemistry in Jena, Germany).

For large species pools (large s) the number of parameters can be very great, more than the number of data points. We propose a variant of [1] in which β_i and δ_{ij} are random with means β_{av} and δ_{av} and with variances σ_β^2 and σ_δ^2 , respectively. This version of the model gave parameter estimates (all estimates in $g\ m^{-2}$): $\hat{\beta}_{av}$ (312), $\hat{\sigma}_\beta$ (212), $\hat{\delta}_{av}$ (926), $\hat{\sigma}_\delta$ (385) and $\hat{\sigma}$ (123). The model describes the data as well as the 99 degrees of freedom between all assemblages.

The model can be used to address a wide range of theoretical questions about diversity-function relationships including:

- Does the diversity effect saturate with increasing richness and is there a simple characterisation/explanation of this effect?
- What is the relative importance of the average diversity effect, the sampling and selection effects in contributing to the DF relationship?
- What is the relative importance of the identity and diversity effects?
- Is there evidence for transgressive overyielding (do mixtures perform better than the best monoculture)?

In addition, the model is flexible enough to explore changes in DF relations through time and the effect of species clusters and species traits