Multi-species mixtures - new perspectives on models and mechanisms

Connolly J.[1], Bell T.[2], Brophy C.[3], Carnus T.[1,4]., Finn J.[4], Kirwan L.[5], Luscher A.[6], Sebastia M.T.[7] and Weigelt A.[8]

[1]*School of Mathematical Sciences, UCD, Ireland, [2]Dept of Zoology, University of Oxford, UK, [3]Dept of Mathematics, NUIM, Ireland, [4]Johnstown Castle, Teagasc, Wexford, Ireland, [5]Dept of Mathematics WIT, Waterford, Ireland, [6]Agroscope ART, Zurich, Switzerland, [7]CTFC, Solsona, Spain, [8]Institute of Biology, University of Leipzig, Germany*
Corresponding author: john.connolly@ucd.ie

Abstract

The delivery of essential ecosystem functions (primary productivity, maintenance of soil fertility, resistance to weed invasion etc.) may be compromised by global declines in biodiversity. There is still controversy about the description of, and mechanisms behind, Biodiversity-Ecosystem Function (BEF) relationships. The Diversity-Interactions model quantified BEF relationships in terms of all the pairwise interactions between the species in a community. The model gives the contribution of two species (i and j) to the functional response in a community as $\delta_{ij}P_iP_j$, where δ_{ij} reflects the potential of the two species to contribute to the response and its actual contribution depends also on P_i and P_j, the initial relative abundance of the two species in the community. This model and variants fitted well to a wide range of functional responses (biomass production, respiration) from several, but not all, experiments that examined a wide range of organisms (plants, microorganisms) and levels of species richness (1 to 72 species). A modified version introduces a more complex effect of pairwise interaction. The properties of this more flexible model and its implications for BEF relationships are discussed, particularly in the context of grass-clover contributions to sward functions.

Keywords: Diversity-Interactions model, BEF relationship, species richness.

Introduction

Increasing biodiversity can positively influence ecosystem functioning in natural grassland systems (e.g. Hooper *et al*., 2005, Cardinale *et al.,* 2007). Explanations for this positive biodiversity-ecosystem function (BEF) relationship centre on complementary species interactions due to niche partitioning and facilitation (e.g. Hector *et al*., 1999; Tilman, 1999) and selection effects (Loreau and Hector, 2001). Recently, models of BEF have been proposed (Kirwan *et al.,* 2007; Kirwan *et al.,* 2009) that characterise the functional response for a community as due largely to an identity effect (the expectation of response based on the monoculture performance of species in a community) and a diversity effect (DE), which is the sum of the effects of all the pairwise interactions between species in a community. The contribution of each pair of species depends on their relative abundances and their propensity to interact. This approach has been used in understanding the BEF relationship in a 33-site study of mixtures of four agronomic species (Kirwan *et al.,* 2007; Lüscher *et al.,* 2008) and in a analysis of effects within two of these sites (Frankow-Lindberg *et al.,* 2009; Nyfeler *et al.,* 2009). BEF modelling seeks 1: to provide a simple summary that captures most of the structure of the data, 2: to provide insight into the mechanisms driving the diversity effect.

Materials and methods

Diversity-Function model based on two-species interactions: Suppose that the species pool contains *s* species from which communities of various levels of richness may be constructed. If the average and particular diversity effects depend only on pairwise species interactions, the following provides a simple description of the functional response (*y*) in a *t*-species community (t ≤ s). P_i and P_j are the sown proportions of the *i*th and *j*th species in the community (= 0 if the species is not in the community) and M is the overall initial abundance.

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

In several cases examined, this model fitted well but did not explain all the variation among community responses other than that due to variation between replicate communities. An alternative was examined in which the term $(P_i P_j)$ was replaced by $(P_i P_j)^{\theta}$ where θ was estimated by profile likelihood (Pawitan, 2001).

Datasets: Two data sets were used. (1) Total stand biomass from a Jena dataset**:** Standardised protocols were used to establish experimental assemblages of grassland species (grasses and forbs) that varied in species richness from 1, 2, 3, 4, 6 to 9 (Roscher *et al.*, 2004). Plots were established in summer 2002. Aboveground plant biomass production was measured for each plot. In total, the experiment comprised 206 plots and 100 different plant assemblages (9 monocultures and 36, 24, 18, 12 and 1 mixtures with 2, 3, 4, 6 and 9 species, respectively, replicated at least twice). For each assemblage, all species present were equally represented at sowing. (2) A field experiment was established in autumn 2006 at Johnstown Castle research centre, Ireland. Plant species were two grasses (G1: *Lolium perenne* and G2: *Phleum pratense*) and two legumes (L1: *Trifolium pratense* and L2: *Trifolium repens*). The design consisted of 4 monocultures, all 6 binary mixtures and various four-species mixtures; dominated in turn by each species (88:4:4:4); dominated in turn by each species at a lower percentage of the dominant, (70:10:10:10); six mixtures co-dominated by each pair of species (40:40:10:10) and four mixture with species equally represented (25:25:25:25). The design was repeated at two levels of overall initial abundance (low being 60% of high). All plots received a baseline 45 kg ha^{-1} yr^{-1} N in two applications and were harvested 3 times in 2007. Total aboveground biomass for 2007 was analysed. Model 1 and the alternative were fitted to aboveground biomass for the two datasets. In addition, a null model was fitted that included assemblage as a factor (1 degree of freedom for each assemblage) in addition to overall abundance for dataset (2). The total number of plots was 56. There was no replication and residual error was variation around the fitted model.

Results

For the Jena data, model [1] with 48 coefficients (9 identity, 36 pairwise and 3 block) gave a residual Mean Square (RMS) lower than that of the null model (102 coefficients, 100 for assemblages and 3 for block) and so fitted better than it (Table 1). Adding the coefficient θ (estimate 0.95) further reduced the RMS but not significantly ($P = 0.213$). For Johnstown Castle data model [1] with 11 coefficients (4 identity, 6 pairwise and 1 total abundance) gave a higher RMS than the null model (NS) with 25 coefficients (24 for communities and 1 for overall abundance). Adding θ (estimate 0.43) reduced the RMS ($P = 0.038$) and gave the lowest RMS of the three models.

Table 1: Details of model fitting for two datasets.

Model	Model	Resid df	Resid ss	Resid ms	Comparison of models	P value
Jena						
1	Null Model	103	1618167	15710		
2	Model [1]	158	2408032	15241	2 vs 1	0.638
3	Model [1] Theta 0.95	157	2383403	15085	3 vs 2	0.213
Johnstown Castle						
1	Null Model	30	105.44	3.515		
2	Model [1]	45	168.28	3.739	2 vs 1	0.306
3	Model [1] Theta 0.43	45	151.8	3.373	3 vs 2	0.038

Discussion and conclusion

The extra coefficient improved model fit only for the Johnstown Castle data. This coefficient is related to the way in which pairs of species interact, has implications for the rate at which the BEF relationship increases with increasing richness and provides a unifying description that includes many of the empirical BEF relationships that have been proposed. More experience with this model is required.

References

Cardinale B.J., Wright J.P., Cadotte M.W., Carroll I.T., Hector A., Srivastava D.S., Loreau M. and Weis J.J. (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences of the United States of America* 104, 18123-18128.

Frankow-Lindberg B.E., Brophy C., Collins R.P. and Connolly J. (2009) Biodiversity effects on yield and unsown species invasion in a temperate forage ecosystem. *Annals of Botany* 103, 913-921.

Hector A., Schmid B., Beierkuhnlein C., Caldeira M.C. *et al.* (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123-1127.

Hooper D.U., Chapin F.S., Ewel J.J., Hector A., Inchausti P., Lavorel S., Lawton J.H. *et al.* (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75, 3-35.

Kirwan L., Lüscher A., Sebastia M.T., Finn J.A. and Collins R.P. *et al.* (2007) Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. *Journal of Ecology* 95, 530-539.

Loreau M. and Hector A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72-76.

Lüscher A, Finn J.A., Connolly J., Sebastia M.T., Collins R.P., Fothergill M., Porqueddu C., Brophy C., Huguenin-Elie O., Kirwan L., Nyfeler D., Helgadottir A. (2008) (2008) Benefits of sward diversity for agricultural grasslands. *Biodiversity* 9, 29-32.

Nyfeler D., Huguenin-Elie O., Suter M., Frossard E., Connolly J. and Lüscher A (2009) (2009) Strong mixture effects among four species in fertilized agricultural grassland led to persistent and consistent transgressive overyielding. *Journal of Applied Ecology* 46, 683-691.

Pawitan Y. (2001) *In all Likelihood: Statistical Modelling and Inference Using Likelihood.* Clarendon Press, Oxford.

Roscher C., Schumacher J., Baade J., Wilcke W. Gleixner G., Weisser W.W., Schmid B and Schulze E.D. (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology* 5, 107-121.

Tilman D. (1999) The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80, 1455-1474.