

MINI REVIEW

The Plant Ecology of Nature-Based Solutions

Design principles for multi-species productive grasslands: Quantifying effects of diversity beyond richness

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Abstract

1. Productive grasslands in temperate regions have relied strongly on low plant diversity with high management intensity and fertiliser inputs. Increasing plant diversity can provide high yields of digestible forage for livestock production with lower environmental impacts, and thus represents a diversity-dependent nature-based solution that can deliver multiple ecosystem functions.
2. Sharing lessons from the design of managed, productive grassland communities, we address the following questions: how can we identify combinations of plant species that best deliver a selected function or multiple functions? and; when is community composition more important than species richness?
3. We describe approaches that separate plant diversity into its underlying components: species richness, composition and relative abundance. Disentangling these three components facilitates a more nuanced understanding of how diversity can contribute to the design of diversity-dependent nature-based solutions.

KEYWORDS

agronomy, community composition, complementarity, Diversity-Interactions models, ecosystem function and services, mixtures, species interactions

1 | PLANT DIVERSITY FOR MORE ENVIRONMENTALLY SUSTAINABLE FORAGE PRODUCTION

Grasslands are a globally important biome that provides multiple ecosystem functions and services. In temperate areas, productive grasslands are characterised by low species richness (often monocultures in arable crop rotations) and intensive management that includes regular re-sowing of agronomic cultivars of forage species and the application of inorganic nitrogen fertiliser to

maximise the yield of digestible forage. They differ considerably from semi-natural grasslands, which typically have much higher species richness, do not apply nitrogen fertiliser and have lower yields (see references below). Increasing plant diversity in productive grasslands is being widely investigated as a nature-based solution to mitigate environmental impacts and increase resilience while maintaining biomass yield (e.g. Grange et al., 2021; Komainda et al., 2020; Lüscher et al., 2022; Nyfeler et al., 2009). A redesign of more environmentally sustainable and productive grasslands would ideally lead to: higher yields with less nitrogen

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fertiliser, lower greenhouse gas emissions, higher resilience to environmental disturbance and improved soil health. The identity and number of plant species is a fundamental design feature of sown grasslands, and recommending changes to these properties must be strongly evidence-based.

To date, numerous studies have shown that increasing plant diversity in productive grasslands under high management intensity provides desired ecosystem functions, including high forage yield and quality (Finn et al., 2013; Suter et al., 2015), higher nutrient use efficiency (Suter et al., 2021), yield stability (Haughey et al., 2018), weed suppression (Connolly et al., 2018; Suter et al., 2017), and resistance to and recovery from extreme weather events (Grange et al., 2021; Hofer et al., 2016). One prominent nature-based solution associated with designed multi-species mixtures is the displacement of inorganic nitrogen fertiliser by symbiotic N_2 fixation (e.g. Baker et al., 2023; Nyfeler et al., 2009) and its associated environmental impacts (Cummins et al., 2021), in addition to benefits on soil fertility (Fox et al., 2020) and soil biodiversity (Ikoyi et al., 2023). These studies demonstrate the benefit of moderate levels of plant diversity for improved delivery of multiple ecosystem functions in productive grasslands and represent diversity-dependent nature-based solutions.

Here, we outline advances in developing a design and analytical framework to better quantify how diversity affects ecosystem functions and services, and specifically: how do species richness, community composition, and relative abundance jointly and individually contribute to ecosystem functions? How does such knowledge assist in identifying best-performing communities? We review the role of plant diversity in maintaining yield and other ecosystem services in the face of environmental disturbance. We present recent evidence and advances in the analysis of multifunctionality. Finally, we discuss why lessons from semi-natural grasslands do not necessarily translate to productive grasslands and provide a roadmap for future research to enhance the ecosystem functioning of productive grasslands.

2 | BETTER QUANTIFYING AND PREDICTING THE EFFECT OF DIVERSITY ON ECOSYSTEM SERVICES

2.1 | How to disentangle composition, richness and relative abundance?

Field-scale grassland diversity experiments typically manipulate plant species number (richness), identities (community composition) and relative abundances (evenness) of species across plots to generate a gradient of diversity, and measure a plot-level ecosystem function. However, when assessing the biodiversity and ecosystem function (BEF) relationship, species diversity is frequently equated to species richness alone (Figure 1a). Analysis based on only species richness effectively assumes that variation due to composition and relative abundance is part of the model residual error variation;

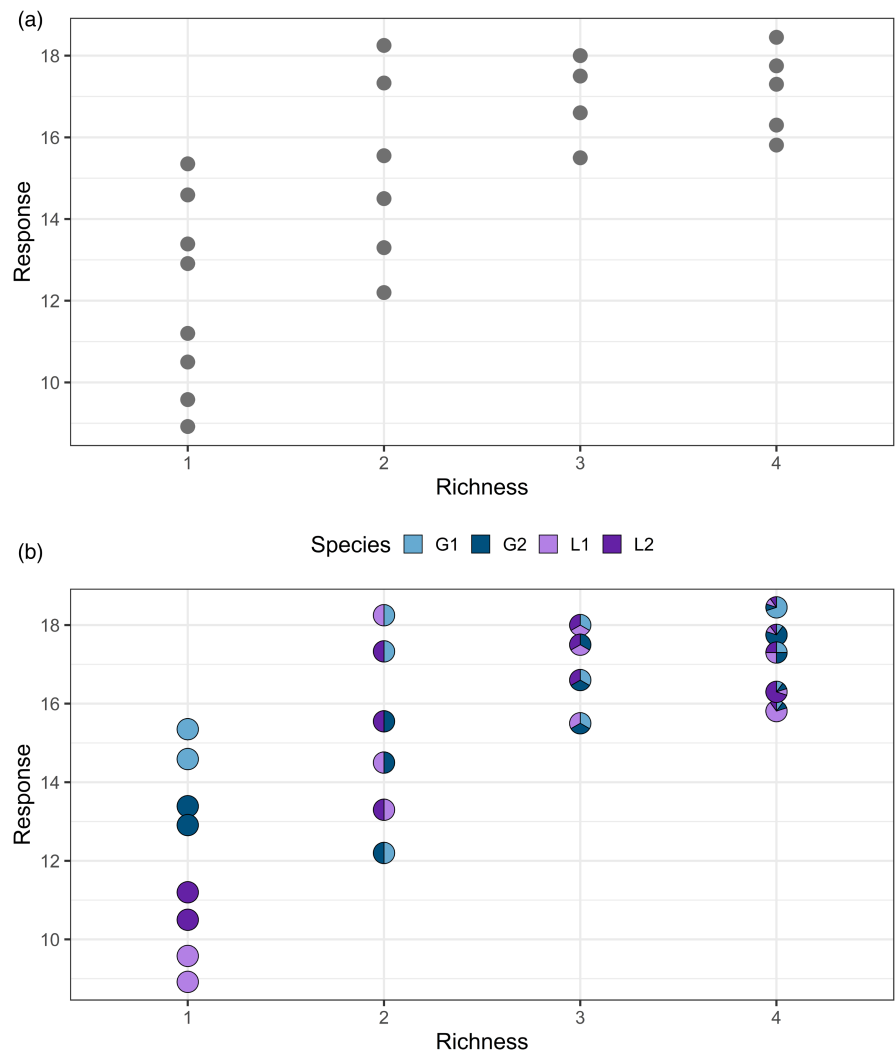
however, methods for modelling the BEF relationship should jointly capture the effects of richness, composition and relative abundance that are inherent in this type of data (Figure 1b).

Diversity-Interactions models (Kirwan et al., 2009) use a multiple regression modelling framework to separately quantify the effects of species' identities, species' proportions and interspecific interactions on an ecosystem function (see Appendix S1 for the principles involved). The statistical approach is supported by the `DIModels` R package (Moral et al., 2023).

To disentangle the contributions of richness, composition and relative abundance on ecosystem function from a Diversity-Interactions model fitted to experimental data, one can predict from the model across the species diversity gradient. Figure 2 illustrates predictions from three Diversity-Interactions models (model details in Appendix S2):

- In Figure 2a, there are species-specific identity effects, but neither antagonistic nor synergistic pairwise interactions. On average, the predicted response is not related to richness and predictions deviate from the average depending on species identity (composition) and relative abundance of species in a community. The predicted response is the weighted average of the species identity effects. A mixture strongly dominated by a single species will be similar to that dominant species' performance in monoculture, highlighting how influential relative abundance can be in mixtures (e.g. at each level of richness, the predicted response for a community dominated by G1 is similar to the G1 monoculture).
- In Figure 2c, there are species-specific identity effects, the interaction between any pair of species is the same, and the exponent on pairwise interactions, θ , equals 0.5 (Connolly et al., 2013; Vishwakarma, Byrne, et al., 2023). On average for equi-proportional communities, this model leads to a linear increase with increasing richness (Moral et al., 2023). In this scenario, richness, composition and relative abundance jointly affect the predicted response. For equi-proportional communities, higher richness leads to better performance on average, but composition and species proportions can be highly influential. For example, the six-species mixture dominated by H2 has a considerably lower predicted response than the equi-proportional six-species mixture, despite both having richness=6.
- In Figure 2e, there are species-specific identity effects, and species interactions are dictated by functional group membership. There is one within functional group interaction term for each of the two grasses, the two legumes and the two herbs, and there are three between functional group interactions (grass–legume, grass–herb, legume–herb, see Table S2). Here, the predicted response increases but saturates with increasing richness. In this scenario, the response is determined by a combination of richness, composition (species and functional group identity) and relative abundance. The most species-rich communities are not necessarily the best-performing communities, for example, the equi-proportional three-species mixture with G1, G2 and L2 outperforms many four-, five- and six-species mixtures.

FIGURE 1 Illustration of simulated data typically arising from a grassland BEF study. The design consists of four species: two grasses (G1 and G2) and two legumes (L1 and L2). Both panels (a) and (b) show the same data, with a positive and saturating relationship between the observed ecosystem function and sown species richness. Panel (b) jointly illustrates how richness (x-axis), composition (species identities via the pie-glyphs) and species' relative abundances (pie-glyphs) are components of species diversity and can jointly affect the response. Panel (b) was produced using the *PieGlyph* package (Vishwakarma, Brophy, & Hurley, 2023).



A general feature of multiple regression and response surface modelling is the ability to interpolate across all combinations of species proportions (the design space; Moral et al., 2023; but the usual caveats apply, see Appendix S5). A major additional advantage of the Diversity-Interactions approach in BEF methodology is that predictions and inference can be made across all possible combinations of species' relative abundances, not just on average across richness, and not just for communities that were in the experimental design (Moral et al., 2023). This is an important tool to identify optimally-performing communities and facilitates the design of optimal communities for nature-based solutions. For multi-species mixtures in productive grasslands, Figure 2b,d,f shows the predictions for the models corresponding to Figure 2a,c,e as shown in a ternary diagram in which each point predicts for a specific combination of relative abundances of grass, legume and herb (see also Figures S2 and S3).

The Diversity-Interactions modelling approach and associated experimental designs have been used to model the BEF relationship across different ecosystems and responses including earthworm community structure (Sheehan et al., 2007), dung decomposition (O'Hea et al., 2010) and bacterial respiration rates (Connolly

et al., 2013). Additional methodological challenges being addressed, including multifunctionality (Dooley et al., 2015; Suter et al., 2021), repeated measures and multiple sites (Finn et al., 2013), and large numbers of species (Brophy et al., 2017; McDonnell et al., 2023; these studies model 72- and 16-species systems respectively).

3 | THE ROLE OF DIVERSITY IN DELIVERING ECOSYSTEM SERVICES IN THE FACE OF HIGHER ENVIRONMENTAL VARIATION

Maintaining forage yield and the delivery of multiple other ecosystem functions across environmental variation is an essential design consideration in productive grasslands. Productive grasslands encounter a range of variation in space (e.g. soil type and fertility) and time (e.g. climate and management factors). Climate change is causing grasslands to encounter a greater degree of variation in biotic and abiotic conditions (e.g. extreme weather events, pests, diseases and invasive species). Higher plant diversity reduces the impact of environmental disturbance on forage yield. Yield stability was higher

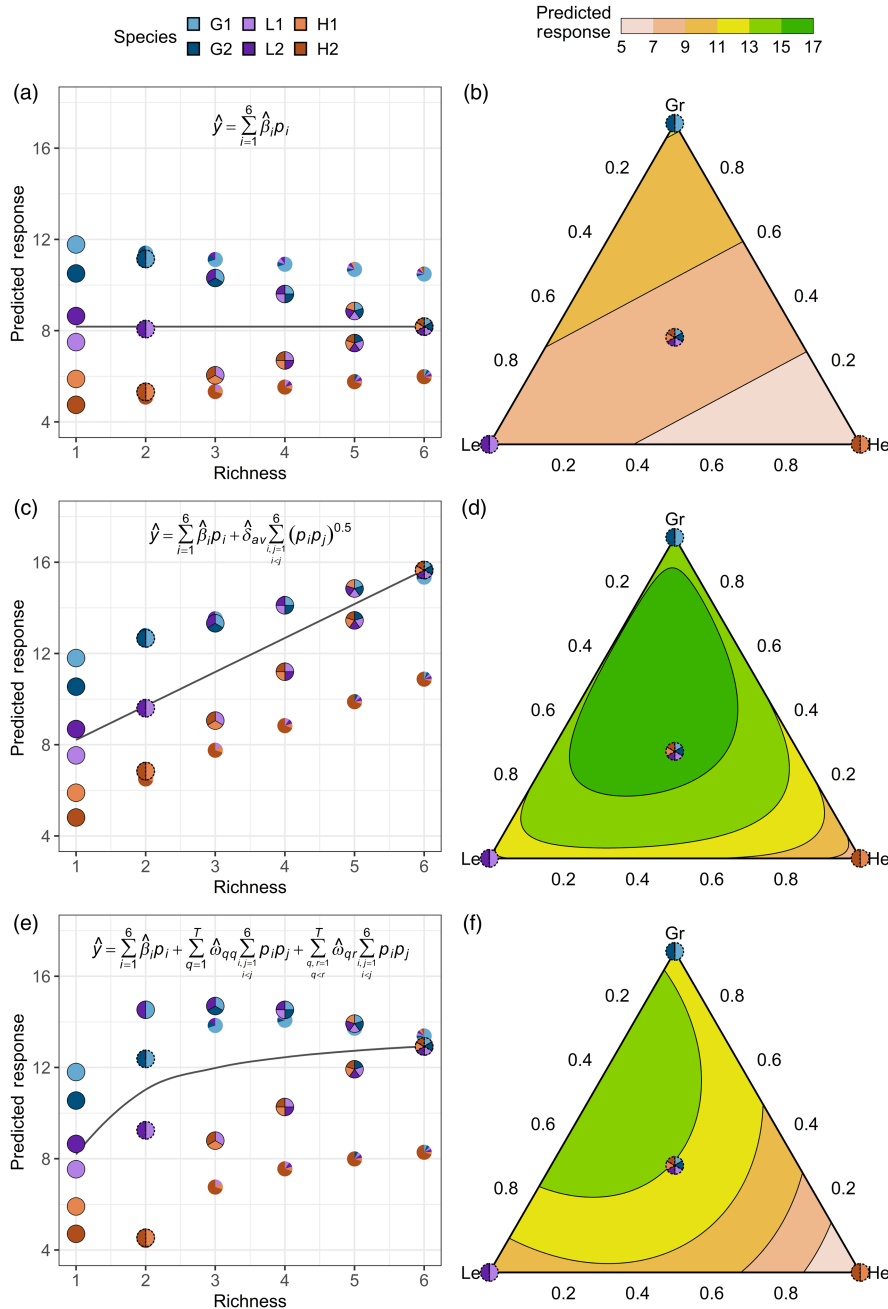


FIGURE 2 Predicted ecosystem function (response) from three different Diversity-Interactions models for a six-species system comprising two grasses (G1, G2), legumes (L1, L2) and herbs (H1, H2); see Appendix S3 for additional interpretation. Identity effects of the six species (richness = 1) are similar across the three panels and differences in BEF relationships across the panels are due to different types of interspecific interactions: (a) and (b), model based on species-specific identity effects, but no interactions; (c) and (d), species-specific identity effects and all pairs of species interact in the same way; and (e) and (f), species-specific identity effects, with interactions dictated by functional group membership. The solid black line (a, c, e) shows the underlying BEF relationship on average (for equi-proportional communities only) with richness. Predicted responses are shown for the highest- and lowest-performing equi-proportional mixtures (larger pie-glyphs with solid black border) at each richness level; these predictions highlight the potential influence of community composition. Further predictions are shown for mixture communities dominated by the highest- and lowest-performing monocultures (smaller pie-glyphs without borders) at each level of richness; these predictions highlight the potential influence of community evenness on the BEF relationship. Additionally, the 50:50 mixtures of the two grasses, legumes and herbs along with the six-species equi-proportional mixture (pie-glyphs with dotted borders) are also shown for comparison of community performance between the two panels for each DI model. The equations in each example include species-specific identity effects (β coefficients) and interactions (δ and ω coefficients); see Table S2 for parameter estimates for each model. Each point in the ternary diagrams represents a relative abundance of grass, legume and herb in the given community. The two species within each functional group are split 50:50, hence the vertices consist of the 50:50 grass (Gr), legume (Le) and herb (He) mixtures, the edges comprise four-species mixtures, while points inside the ternary comprise six-species mixtures (see Figure S2 for deviations from this). Diversity-Interactions modelling supports interpolation (b, d, f) and inference (see Figure S3 in Appendix S4).

in four-species mixtures than in monocultures (Ergon et al., 2016; Haughey et al., 2018; Suter et al., 2021); moreover, strong synergistic interactions that drive mixture effects were evident in productive mixtures subjected to experimental drought (Grange et al., 2021), and mixtures under drought could equal or out-yield monocultures under rainfed conditions (Grange et al., 2021; Haughey et al., 2018; Hofer et al., 2016). Plant community composition, rather than species richness per se, can underlie higher yields in response to experimental drought (Grange et al., 2021; Hofer et al., 2016; Komanda et al., 2020) or flooding (Oram et al., 2020).

The impact of plant community composition on yield stability could be attributed in part to increasing functional diversity. In productive grasslands, functionally diverse communities stabilise yield over time due to compensatory effects between plant species with different functional traits and strategies, as well as asynchrony among species (Lüscher et al., 2022). More functionally diverse communities are typically more robust in the face of higher environmental variation and are better able to maintain yields compared with functionally similar communities (Lüscher et al., 2022). This was also shown in semi-natural grassland communities (Hallett et al., 2017; Isbell et al., 2015). Disentangling the effects of species richness, functional diversity and species (or functional) identity effects is thus crucial to designing productive grasslands that maintain yield stability with increasing climatic variation.

4 | EXTENDING THE MULTIVARIATE MODELLING FRAMEWORK TO MULTIFUNCTIONALITY

Evaluating multiple ecosystem functions (multifunctionality) in agroecosystems aims to best quantify the nature and extent of trade-offs among the multiple functions and services that productive grasslands deliver (see Neyret et al., 2023). In productive grasslands, sown mixtures with four complementary species simultaneously improved selected (agronomic) functions without any trade-off (Suter et al., 2021); in contrast, trade-offs among agronomic functions were found in Grange et al. (accepted) and in a study of agronomic and biodiversity-related functions (Argens et al., 2023). The Diversity-Interactions modelling framework can be extended to assess multiple functions via multivariate regression (Dooley et al., 2015; Suter et al., 2021); this approach provides the usual DI model estimates for each assessed function and variance-covariance parameters that quantify the associations between functions. From the estimated multivariate regression model, a combined estimate of overall multifunctionality (MF value) can be calculated by a linear, weighted mean from these estimates. Standard errors for the overall MF value and comparisons of interest can be calculated from the estimated variance-covariance parameters within the multivariate model; crucially, this accounts for covariances between functions in the calculation of any inference measure of overall multifunctionality. This method differs from the averaging method (which averages the raw data of multiple ecosystem function responses and to which modelling

approaches are then applied); the effect of correlated functions on the interpretation and the inference of multifunctionality is generally neglected by analyses based on averaging and threshold approaches (e.g. Byrnes et al., 2014; Maestre et al., 2012; see Dooley et al., 2015 for an extended discussion).

The outcome of a multifunctionality analysis (applied to the same data underlying the analysis in Figure 2) using the multivariate Diversity-Interactions modelling framework is illustrated across the grass-legume-herb design space in Figure 3. The MF value is calculated as a weighted average of the predicted values of three individual functions, and the community with optimal multifunctionality depends on how the individual functions are weighted (Figure 3, cf. MF values A and B). A key benefit of the multivariate modelling framework is that a statistical inference can be made for MF values, and over-performance (i.e. mixture performance is better than the weighted average of monocultures) or transgressive over-performance (i.e. mixture performance is significantly higher than the best-performing monoculture) can be validly tested and visualised (Figure 3). Preferences for certain functions over others can be quantitatively incorporated by adjusting the weighting of single functions (cf. Figure 3a,b).

5 | LESSONS FOR DIVERSITY-DEPENDENT NATURE-BASED SOLUTIONS FROM THE INVESTIGATION OF PRODUCTIVE GRASSLAND MIXTURES

Experimental manipulations of plant diversity have been frequently reported in BEF research, especially in semi-natural grasslands under low to medium management intensity, and such studies have contributed considerable empirical evidence and theoretical development. Several factors, however, caution against directly applying lessons from semi-natural grasslands to productive, intensively management grasslands (e.g. see Klaus et al., 2020). Most experiments with species from semi-natural grasslands: rarely apply and manipulate nitrogen fertiliser or other agricultural management factors, often have considerably lower yields than those in productive grasslands, have infrequent harvesting, do not analyse forage quality, have high species richness, focus on species richness as an explanatory variable, have a wide range of performance (e.g. yield) among species, have a random selection of species for experimental assembly of communities, implement the equi-proportional mixtures within richness levels and usually ignore experimental manipulation of relative abundance. In semi-natural grasslands with >10 species m^{-2} , richness per se may not be a major driver of community biomass and ecosystem functioning (Freitag et al., 2023; Lisner et al., 2023; van der Plas, 2019), indicating no clear functional response (including yield) to species richness at higher richness levels. Thus, research on BEF within species-rich grassland communities that have experimentally investigated the richness effect of random species loss (usually) at plot scale may not be the most appropriate for the purpose of identifying the best combinations of species to maximise or

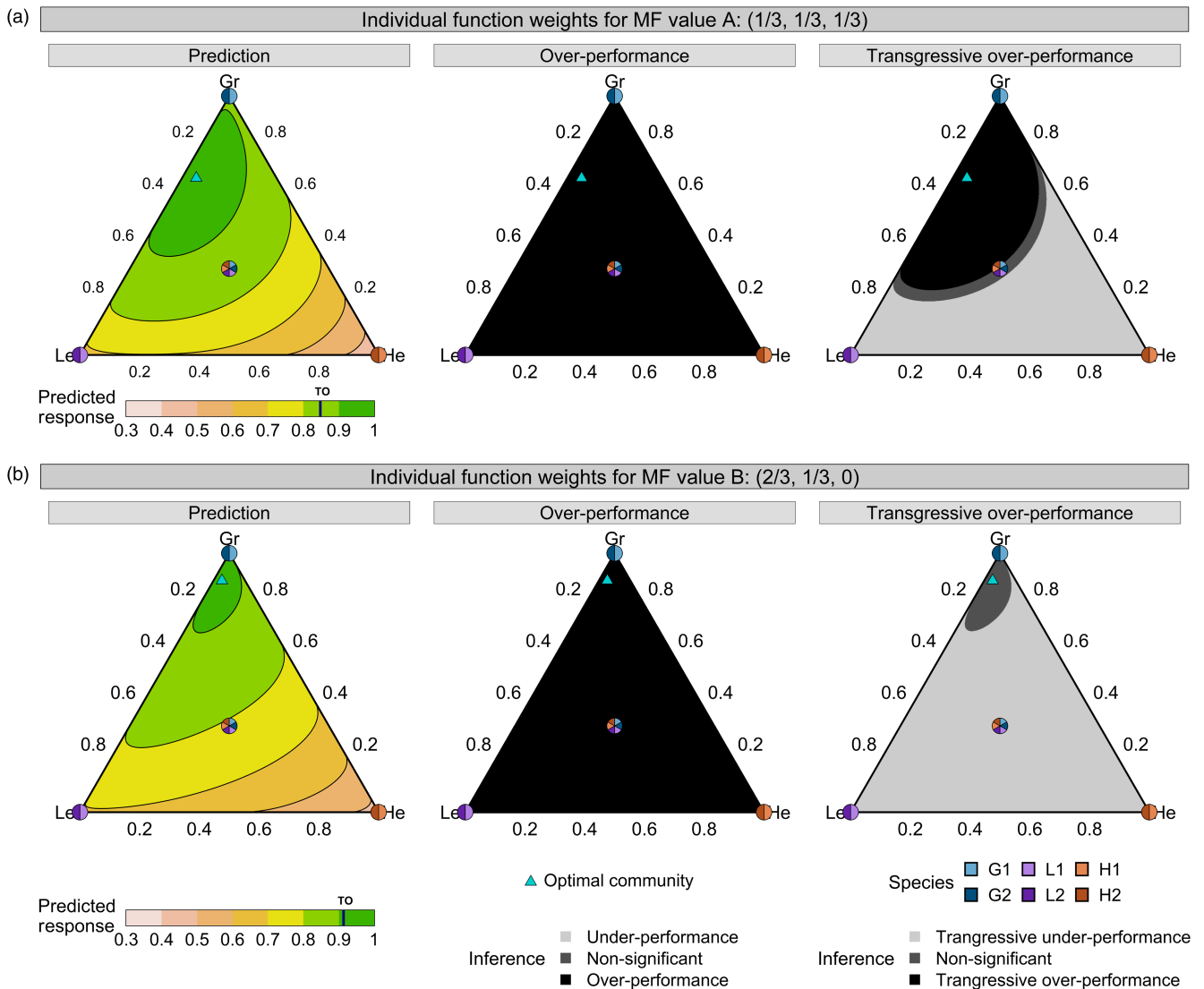


FIGURE 3 Prediction and inference of multifunctionality (MF value) using the multivariate Diversity-Interactions modelling framework. Using the same simulated dataset underlying the analysis shown in Figure 2 (details in Appendix S2), each ecosystem function was scaled from 0 to 1, and a multivariate DI model was estimated. We predicted the (weighted average) MF value using the weights (a) $[\frac{1}{3}, \frac{1}{3}, \frac{1}{3}]$ and (b) $[\frac{2}{3}, \frac{1}{3}, 0]$ for functions 1, 2 and 3, respectively. For both weights, we show the predicted MF value (left-hand ternaries) across all possible grass–legume–herb (Gr–Le–He) proportions (with the two species within each functional group equal to 50:50). Regions with significant over-performance (middle ternaries; mixtures better than the weighted average of monocultures) and significant transgressive over-performance (right-hand ternaries; mixtures better than the best-performing monoculture) are also shown. The inference for the MF value utilises the estimated variance–covariance parameters of the multivariate DI model. The best-performing monoculture for each weighting is shown on the predicted response legend (marked TO for transgressive overyielding cut-off). The cyan triangle represents the community with the highest MF value.

optimise the performance of single or multiple ecosystem functions, because these represent quite different objectives.

Despite the rich empirical data and theory derived from BEF research on semi-natural grasslands, a lot of those lessons are not directly translatable and design principles have been developed that are specific to productive grasslands. Compared with grass monocultures that rely on high nitrogen input, modest increases in species diversity with lower nitrogen input have high potential as a nature-based solution for productive grasslands and we identify a number of related design principles (adapted from Lüscher et al., 2022). First, across several semi-natural grassland

experiments, the performance of single functions often saturates at about 10–15 species (Isbell et al., 2017; Tilman et al., 2014), and under certain conditions saturation at low species numbers also holds true for overall multifunctionality (Gamfeldt & Roger, 2017; Slade et al., 2019). Much of this saturation can be explained by the selection effect associated with the random allocation to communities of varying richness of species that have very different performance potential (Tilman et al., 2014). For productive grasslands, their agronomic objectives lead to the selection of species that satisfy agronomic performance criteria, for example, high-yielding (for the relevant agro-climatic conditions that also apply

a strong environmental filter on the relevant species pool), highly digestible, tolerant of frequent defoliation, and strong ability to acquire and use plant-available nitrogen. Thus, investigations of mixture combinations should use the best-performing species (usually evaluated in monocultures, i.e. not randomly selected), which ensures high performance with a lower number of species. Given this principle, designed productive grassland mixtures typically saturate at relatively low species richness of about six to eight species (Lüscher et al., 2022) because adding species with lower performance potential to mixtures that already include the species with the highest potential does not further improve the overall performance (unless there are beneficial species interactions that are sufficiently strong to compensate for lower identity effects). Second, productive multi-species mixtures often exhibit transgressive over-performance (e.g. Connolly et al., 2018; Finn et al., 2013; Grange et al., 2021; Nyfeler et al., 2009), which is attributed to strong synergistic grass–legume interactions (Nyfeler et al., 2011), as well as synergistic effects with herbs (Grange et al., 2021). Thus, productive mixtures should target species that maximise complementarity for desired functions, which enhances performance without the need for many species. Empirical evidence from productive and semi-natural grasslands indicates that high functional diversity within the selected species can promote synergistic effects on a range of agronomically relevant functions (e.g. Mason et al., 2020; Nyfeler et al., 2009; Suter et al., 2021; Tilman et al., 2014). Third, select species that maintain a stable community composition over time and over variable environmental conditions, and/or that respond to adaptive management to ensure this. The relative abundance of a species is important to ensure it is represented sufficiently to contribute via its identity and interaction effects. No matter how well a plant can perform, it cannot contribute much with 1% relative abundance.

6 | SYNTHESIS

Nature-based solutions that are related to species diversity are likely to require methods that can identify specific communities that: provide the best performances (or perform above a desired high level); are robust to moderate variation in community structure (i.e. are somewhat insensitive to changes in relative abundance, see above); and perform consistently over a range of environmental variation (e.g. tested with multi-site experiments or with environmental levels as a treatment).

The Diversity-Interactions modelling framework for disentangling richness, composition and evenness underpins investigation of such objectives for diversity-dependent nature-based solutions. Higher species richness per se does not necessarily improve ecosystem function beyond a relatively small set of species that best deliver the function/service of interest (e.g. Figure 2e), and the effects of changing composition and/or relative abundance may be much greater. The richness levels to achieve high/saturating functioning are well within the reach of productive grassland management. The more specific the objective (e.g. a single ecosystem function), and

the fewer species likely to be needed (e.g. three to eight), then the greater the need to be able to quantify the effect of changing these different aspects of diversity.

Much of the research on multi-species mixtures has focused on the plot scale, and farm- or systems-scale investigations are a priority. This includes investigation of the agronomic and economic effects of increased functional diversity as a risk-reduction action during exposure to extreme weather events, and potential trade-offs in yield and forage quality during periods of average climatic conditions. A key research need is to elucidate the relationship between plant diversity in productive grasslands and the impact of single and multiple (combined) disturbances, on ecosystem functions.

Future research should target how the components of plant diversity—species richness, composition and evenness—affect multifunctionality to determine the number and identity of plant species that optimise nature-based solutions in productive grasslands. It is likely that more species are needed to sustain multiple services over longer time scales and under more variable environmental conditions, and this needs more explicit investigation. Given the different relative values assigned to different services, multifunctionality analyses should include the focus and preferences of stakeholders (Neyret et al., 2023) and economic assessments (e.g. see Finger & Buchmann, 2015; Schaub et al., 2020).

The Diversity-Interactions modelling framework can help address these knowledge gaps by integrating abiotic and biotic factors as fully factorial combinations (e.g. food supply and earthworm community biomass, Sheehan et al., 2007; drought, Hofer et al., 2016). In addition, to better assess the magnitude of benefits or trade-offs, there is a need to include reference communities that represent either a high level of performance and/or conventional practice (e.g. grass monocultures with high nitrogen application; Nyfeler et al., 2009; Grange et al., 2021). By better quantifying the contributions of multiple facets of diversity to yield stability under increasing environmental variation over time and space, one can better design productive grasslands that safeguard ecosystem functioning in a changing environment (Lüscher et al., 2022).

AUTHOR CONTRIBUTIONS

All authors contributed to the conception, design and writing. All authors contributed critically to the drafts and gave final approval for the publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Code to reproduce the model and figures is available at: <https://zenodo.org/doi/10.5281/zenodo.10953302> (Vishwakarma, 2024).

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SUPPORTING INFORMATION

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

Appendix S1. Principles underpinning Diversity-Interactions model.

Figure S1. The effect of species richness, composition, and evenness on an ecosystem function (response) in a two-species grass-legume system, as predicted by a fitted Diversity-Interactions model.

Appendix S2. Explanation of the underlying data and the models illustrated in Figures 2 and 3.

Table S1. Coefficients and variance-covariance matrix used to simulate data for fitting the three individual models in Figure 2 and the multivariate model in Figure 3.

Table S2. Estimated coefficients for the three univariate Diversity-Interaction models fitted to our simulated dataset.

Appendix S3. Interpreting ternary diagrams that show predictions for functional group proportions.

Table S3. Selected examples of different relative abundances of the two species within each functional group of Legume, Grass and Herb.

Figure S2. Effect of changing species composition of the functional groups on interpolation using Diversity-Interactions models.

Appendix S4. Inference from a Diversity-Interactions model, illustrated in ternary diagrams.

Figure S3. Interpolation and inference using Diversity-Interactions models.

Appendix S5. Experimental design and interpolation.

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