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RESEARCH ARTICLE

Low-cost management interventions and their impact on multilevel trade-offs in agricultural grasslands

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Abstract

1. Cost-effective strategies to increase biodiversity are a fundamental requirement to reconcile conservation and food production in agricultural landscapes. Key for the implementation of such strategies is an accurate quantification of both their benefits and potential associated trade-offs.
2. We therefore assessed, in a commercially managed grassland, biodiversity responses to two low-cost management interventions and their mediating effects on ecosystem services.
3. In a 6-year experiment, we showed that a one-time seed bank activation treatment had strong initial impacts on biodiversity, increasing plant richness in year 1 by 61%. Long-term effects, which were also driven by the second management intervention, the propagation of the keystone species yellow rattle, were weaker but nonetheless substantial. These positive biodiversity responses improved ecosystem multifunctionality through additive positive effects of richness, evenness and phylogenetic distinctiveness on nectar production and structural habitat complexity.
4. In contrast, hay biomass production was negatively affected by both management interventions, resulting in a multilevel trade-off between biomass production competing with biodiversity conservation and the provisioning of other ecosystem services.
5. *Synthesis and applications*. In this study, we demonstrate that the maximisation of either biodiversity or biomass production requires largely different land management practices. The evaluation of this trade-off, however, is strongly dependent on its social, economic and ecological context and requires clearly defined land management priorities for both food production and biodiversity conservation.

KEYWORDS
agroecology, biodiversity, ecosystem services, long-term experiment, multifunctionality, nectar production

1 | INTRODUCTION

Human population growth and increasing per-capita consumption rates are driving a continuous rise in global food requirements (Tilman et al., 2011; Willett et al., 2019). Already high levels of demand are predicted to further increase by 50% within the next 30 years (Keating et al., 2014). Although crop production has been successfully augmented this century (25% increased per-capita production from 2000 to 2015; Pretty, 2018), changes in agricultural management have come at a steep environmental cost as a consequence of agricultural intensification and land expansion (Kremen, 2015). Increases in food production have led to frequent overexploitation and habitat degradation (Beckmann et al., 2019; Ray et al., 2012), both key drivers of global biodiversity loss (IPBES, 2019; Tilman et al., 2017; Willett et al., 2019). This very same loss in biodiversity endangers the long-term sustainability of agricultural productivity. Biodiversity in agricultural landscapes supports pivotal ecosystem services of large economic importance such as pollination and natural pest control (Chaplin-Kramer et al., 2011; Potts et al., 2016). The loss or degradation of these services is, in itself, a threat to global food production, and therefore, the transition to more sustainable agricultural systems is a key requirement for improving future food security (Amelung et al., 2020; Mason-D'Croz et al., 2019).

The linkages between biodiversity, agricultural ecosystem services and land management can be concisely summarised in a triangular relationship (Figure 1). This triangular relationship is a centrepiece of current land management debates (Seppelt et al., 2020) and encompasses direct impacts of land management on agricultural production and biodiversity as well as indirect feedbacks of biodiversity changes on production. An inherent characteristic of this triangular relationship is its multidimensionality at several process levels. Firstly, agricultural systems are not merely production-focused but multifunctional systems, supporting a broad range of ecosystem services (Manning et al., 2018). Likewise, biodiversity comprises multiple independent components such as richness, evenness and phylogenetic diversity, which jointly contribute to an ecosystem's conservation value (Winter et al., 2013). Individual ecosystem services and different components of biodiversity show nuanced and sometimes even contrasting responses to changes in agricultural management practices. The resulting complexity can lead to the emergence of management trade-offs at multiple levels (Figure 1) with important management implications.

First, there are potential conservation trade-offs between independent, individual components of biodiversity. For example, a particular management practice may increase species richness but favour the abundance of few species (loss in evenness) or trigger the local extinction of phylogenetically distinct linages (loss in phylogenetic diversity). Second, there are trade-offs among ecosystem services that result from differential responses of individual services to management actions (Howe et al., 2014; Linders et al., 2021), and which are an important focus of ecosystem multifunctionality research (Manning et al., 2018; Maskell et al., 2013). Finally, there may arise biodiversity–ecosystem service trade-offs (Figure 1). These trade-offs, in themselves, can be multifacetted as (i) the same biodiversity component can show opposing relationships with individual ecosystem services (Zavaleta et al., 2010) and (ii) individual ecosystem services might show different responses to different biodiversity components (e.g. positive richness–production as in Cardinale et al., 2012 vs. negative evenness–production relationships; Binder et al., 2018; Filstrup et al., 2019).

The consideration of these multilevel trade-offs is a prerequisite for integrative land management. Past studies on ecosystem multifunctionality have demonstrated that the evaluation of trade-offs differs among stakeholder groups (Linders et al., 2021) and that decision-making processes require a reconciliation approach. Both stakeholder reconciliation and the design of optimal land-use strategies rely on an accurate quantification of the impacts of potential management practices. Hence, the quantification of synergies as well as trade-off associated opportunity costs (i.e. the loss in biodiversity and non-target ecosystem services per unit gain of the target ecosystem service) will be an essential requirement for effective land management.

Agricultural grasslands, including rangelands and hay meadows, constitute a major agricultural production system that accounts for over two-thirds of agricultural land-use world-wide (O'Mara, 2012). Both biodiversity–ecosystem service relationships and ecosystem multifunctionality are well studied in grasslands, which have long served as model systems for ecological research (Cardinale et al., 2007; Tilman et al., 1997). Many of these past research initiatives have used grasslands as field laboratories for conceptual ecology (e.g. requiring annual weeding to maintain diversity differences), but applied questions such as the economic costs of interventions to increase biodiversity are rarely considered (Binder et al., 2018). Nonetheless, economic effectiveness of management interventions is an important requirement to capitalise on previous knowledge and facilitate the integration of biodiversity into land use management.

In this study, we implemented two low-cost management interventions to enhance biodiversity in a highly replicated 6-year grassland experiment in the United Kingdom. Chosen interventions were the activation of soil seed banks through scarification of the topsoil, and the propagation of yellow rattle (*Rhinantus minor* L.), a keystone plant species which reduces grass dominance (Hartley et al., 2015; Pywell et al., 2004). Our main aim was to examine multilevel management trade-offs and synergies among- and between-individual biodiversity components and ecosystem services. We therefore focused our assessment on three measures of plant alpha diversity (richness, evenness, phylogenetic diversity) and on the three key ecosystem services; nectar provision, structural habitat complexity and hay biomass production. We selected these three ecosystem services as they affect farm income directly (biomass production) and indirectly by supporting pollination and natural pest control services for neighbouring fields (via nectar provision and structural complexity; Albrecht et al., 2020; Pywell et al., 2015). Using structural equation modelling and a subsequent scenario simulation approach, we quantified emerging trade-offs and evaluated how they affect the success of specific land management strategies.

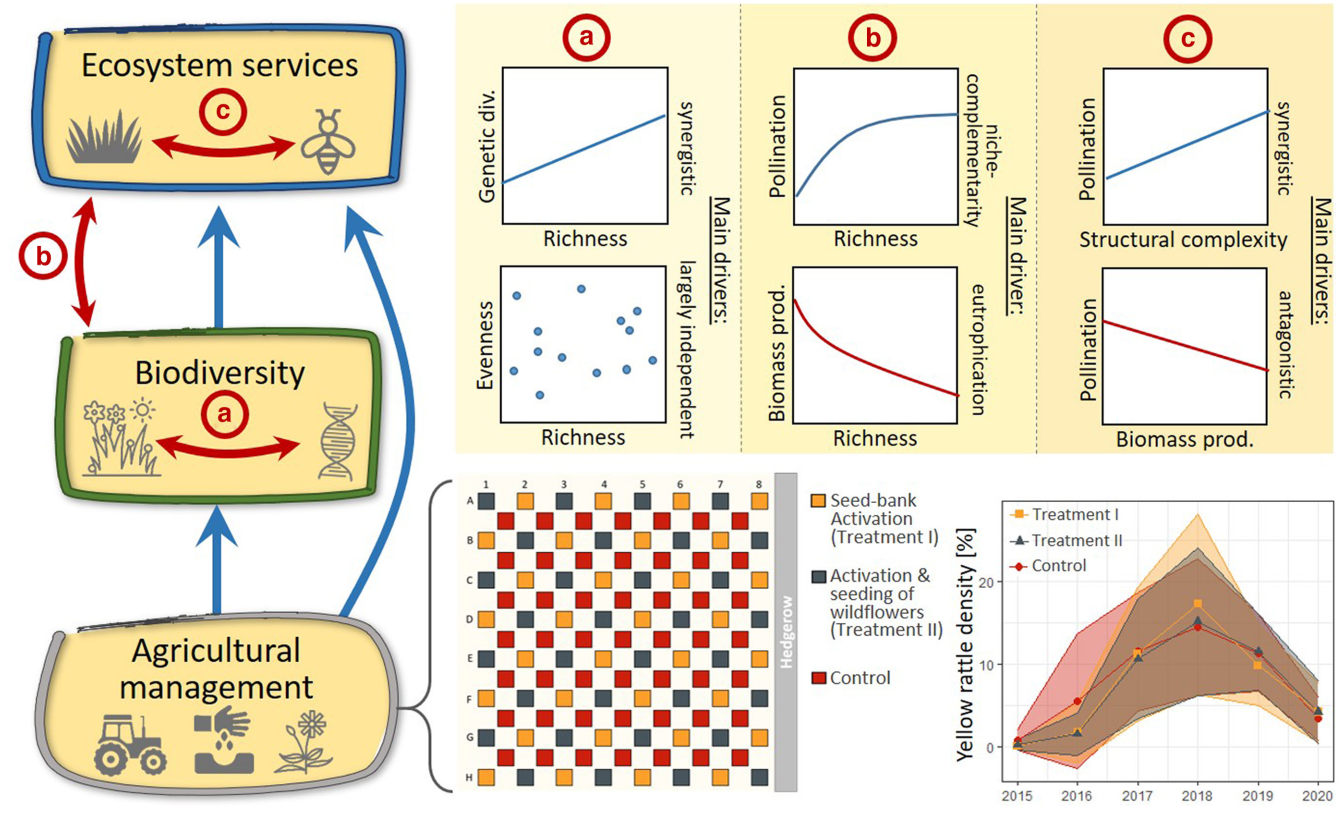

FIGURE 1 Conceptual overview of multilevel trade-offs in the management of grassland ecosystems. Agricultural management interventions directly influence biodiversity and ecosystem services (left). Additionally, management effects on biodiversity in agricultural landscapes can be indirectly transmitted to ecosystem services. Consequently, multilevel trade-offs may emerge from (a) differential responses of individual biodiversity components, (b) potential negative relationships between diversity and individual ecosystem services and (c) antagonistic effects on different ecosystem services. The relationships that determine multilevel trade-offs (top right; a–c) can vary across systems and depend on the identity of the considered biodiversity component and ecosystem services. In this study, management interventions to increase biodiversity (bottom right) included the propagation of the grassland keystone species yellow rattle (*Rhinanthus minor*) and the implementation of seed bank activation treatments (spatial arrangement is depicted for two treatment levels, the first one without the second one with additional wildflower seeding; in total 113 replicates). Yellow rattle was included in the wildflower seed mix as management intervention to increase biodiversity, and additionally spread from a neighbouring site where it was introduced in 2014 (see bottom right for display of temporal dynamics).

2 | MATERIALS AND METHODS

2.1 | Field experiments

Low-cost management interventions to enhance biodiversity were implemented in an agricultural grassland in Derbyshire (UK, 52°57′27″ N 1°34′00″ W; see Table S1 for soil elemental characteristics) in 2015 and subsequent plant community responses were monitored annually for 6 years in 113 3 × 3 m plots (Figure 1; 1.4 m minimum buffer zone around plots). Interventions included (a) the implementation of seed bank activation treatments and (b) the propagation of yellow rattle, a keystone species regulating biodiversity in grasslands (Hartley et al., 2015; Westbury, 2004).

Seed banks were activated in two management treatments based on one-time interventions in March 2015. The two treatments represented two levels of management intensity. Both included the activation of the seed bank by creating ~5 cm deep soil furrows (32 plots), following the cutting of the plant biomass, to stimulate the germination of dormant seeds in deeper soil layers (Klaus et al., 2018). The second treatment combined seed bank activation with sowing of a wildflower seed mix to provide additional seed input (32 plots; see Table S1 for seed composition; a total of 443 mg seeds m^{-2}). Soils in the 49 control plots remained undisturbed.

Our second intervention was the propagation of yellow rattle (*Rhinanthus minor* L.), a hemi-parasitic flowering plant that parasitises the root system of neighbouring plants (Westbury, 2004). Due to its preference for grass species hosts, yellow rattle can substantially alter plant community structures (Bardgett et al., 2006; Hartley et al., 2015) and is frequently used to enhance wildflower abundance and overall species richness in the United Kingdom (e.g. Pywell et al., 2004). Yellow rattle was propagated by including it in the wildflower seed mix for the second seed bank activation treatment (see above), and it additionally spread from a neighbouring site (~30 m distance), where it was sown in 2014. Yellow rattle propagation was not a treatment in a strictly experimental sense as its spread was after the initial seeding, and was not subsequently controlled. We decided, because of the strongly applied focus of our study, against introducing consistent disturbances through weeding in half of our plots to fix yellow rattle coverage and we instead carefully monitored its temporal dynamics (Figure 1) to include them as factor in our analyses (see below).

A further measure to increase the practical applicability of our results was to keep the study site under active management during the entire duration of the experiment. It was cut for hay production at the end of June/beginning of July and used as rangeland from July–October (cattle grazing in a paddocking system). Experimental plots were only marked out for field data collection from mid-June to early-July and applied management practices (e.g. grazing regimes) were consistent in the years before and after the start of the experiment, allowing us to link observed changes directly to the implementation of interventions. Part of this continuity was the application of manure on the fields every 7–8 years to compensate nutrient loss from plant biomass removal, which also prevented experimental result to be driven by de-eutrophication. Manure application took place in early spring of 2018 and resulted in the addition of ~750 kg nitrogen, 200 kg phosphorus and 50 kg potassium per ha. Fieldwork was implemented with the permission of the private land owner of the site, no licences for sampling were required.

2.2 | Biodiversity and ecosystem service assessments

Annual surveys were conducted to record the number of plant species and their relative spatial cover in each of the 113 quadrats (see Supporting Information [SI], Section S1 for details). These data allowed us establish the three key biodiversity components (i) plant species richness, (ii) Pielou's evenness and (iii) species' phylogenetic distinctiveness. Phylogenetic distinctiveness is a phylogenetic diversity measure related to the Faith index that is based on a bootstrap approach (see SI, Section S2) and is, by definition, independent of species richness (Tsirogiannis & Sandel, 2016). Hence, the investigated alpha diversity indices are methodologically independent of each other, and correlations indicate co-dependence on joint drivers (Figure 1).

Furthermore, we assessed three plant-derived ecosystem services: (i) structural complexity, (ii) plant biomass production and (iii) nectar production. Structural complexity was classified as a supporting ecosystem service as it is strongly connected to invertebrate food web structure (Brose, 2003) with potential positive knock-on effects in adjacent crop production areas (e.g. pollination, pest control; Altieri & Letourneau, 1982; Franzén & Nilsson, 2008). We computed structural complexity as the sum of the cover of individual plant species, a measure that frequently reached >200% due to multiple canopy layers in the study meadow. Plant biomass production per plot was recorded in 3 years (2018–2020). Plant material was cut in late June to approximately 3 cm height and collected in hessian bags for air-drying in a well-ventilated polytunnel. Biomass was measured (accuracy: ±10 g) after a 1-month drying period to evaluate plant biomass production in the first half of the season. Nectar production per plot was computed based on plant community structure and the annual nectar production of plant monocultures after Baude et al. (2016; see also SI, Section S4).

2.3 | Data analyses

First, we established univariate relationships between (i) management interventions (yellow rattle propagation, seed bank activation treatments) and biodiversity components, (ii) management interventions and ecosystem services and (iii) biodiversity components and ecosystem services. Linearisation of relationships was achieved by establishing models with un-, log- and exponentially transformed predictors and selecting the best fit based on the Bayesian information criterion (BIC). All variables were range-standardised to facilitate comparisons of effect sizes. Treatment implementation was coded as a two-level factor (treatment vs. control) because of large similarities between the two seed bank activation treatments (see Section 3). Furthermore, we used the control plots of year one as reference level to evaluate the effect size of management interventions as seeds propagated from treatment to control plots, leading to indirect effects such as positive spill-over of species richness over time (also see Section 3). Time was included in relationship tests by including it as random effect (both on intercepts and slopes) whenever it improved overall model fit. Care was taken to avoid aggregation effects (i.e. effects that only emerge from across group relationships; Simpson, 1951). Residuals were evaluated to assess the fulfilment of statistical requirements. The size of treatment effects was established by comparing measurement values against values in the control plots of year 1, and not to control plots in the same year.

A multivariate system analysis was implemented in a structural equation model (SEM) assessing direct and indirect impacts of management interventions on biodiversity and ecosystem services. The two main R-packages currently used for SEM ('lavaan' and 'piecewiseSEM') were not suitable for the specific characteristics of our dataset (see Section S5 for details), and hence, we followed the recommendations by Grace (2022) for a custom-built approach. We first established a path diagram containing all possible links between (i) management interventions and biodiversity components, (ii) management interventions and ecosystem services and (iii) biodiversity components and ecosystem services (Figure S1). Furthermore, we developed for each dependent variable in our path diagram multiple submodels and selected the most parsimonious submodel (more detailed description in Section S5) based on a BIC-based model comparisons. BIC was used because of the large sample size of our dataset (Brewer et al., 2016). Standardised path coefficients and r^2 were computed for submodels following Grace (2022).

In our SEM approach, we were interested in whether relationships changed systematically over time, as it was expected, for example, for the effect of the one-time soil activation treatments to decrease over time. Hence, we also considered models with time as a numeric fixed effect interacting with other predictor variables. This led to the consideration of four model sets: (i) models without time if there was not a risk of aggregation effects (see above), (ii) models with time as random effect to account for random changes across years (e.g. wet vs. dry growth season), (iii) models with time as a fixed effect to account for systematic changes of relationships over time (e.g. decrease of effect size of one-time treatments over time) and (iv) models with time included as both as a fixed and random effect. We ran, for each of the four model sets, a full-model comparison and selected the model with the lowest BIC value for the SEM.

In a last analysis, we applied a scenario approach to assess whether changes in management objectives would have an impact on the identity of optimal management practices. In three scenarios, we defined different management targets and then determined the management interventions that are best suited to fulfil these targets. The three scenarios, respectively, aimed to maximise (a) biomass production, (b) biodiversity (given equal valuation of all diversity components) and (c) ecosystem service provisioning (given equal valuation of all measured ecosystem services). Based on the response of biodiversity components and ecosystem services established in the SEM, we simulated all possible system responses to different implementation levels of management interventions. Thereby, implementation levels for yellow rattle propagation spanned from 0% to 100% of its range recorded during our field sampling. The implementation level for seed bank activation treatments included the non-implementation as well as treatment implementation in intervals ranging from 1 to 6 years. Hence, we established 707 simulations accounting for all combinations of the two management interventions (see SI, Section S5 for details). Our approach was based on the assumption that repeated treatment implementation does not have additive effects, but instead an annual treatment implementation resulted in maintaining initial effects, for example, species richness levels of year 1 in treatment plots. For a more detailed discussion of further assumptions, see Section S6 of the SI. All analyses were implemented using the software R, version 4.1 (R Development Core Team, 2021).

3 | RESULTS

3.1 | Management impact on biodiversity

The one-time implementation of the soil seed bank activation treatments in 2015 had a strong and lasting positive effect on plant species richness (Figure 2). In year 1, plant species richness increased by 61% in treatment compared to control plots (ANOVA; $F_{(2,110)} = 138$, $p < 0.001$). In year 2, some of these gains were lost (18% loss compared to year 1; *t*-test; $p < 0.001$), but richness nonetheless remained significantly greater in seed bank activated plots compared to control plots in each of the 6 years of the experiment (one ANOVA for each year; $F_{(1,111)} > 7$, $p < 0.01$). Moreover, we observed a significant increase in richness within control plots in year 2 (18%, *t*-test, $p < 0.001$), a pattern that continued throughout the study period

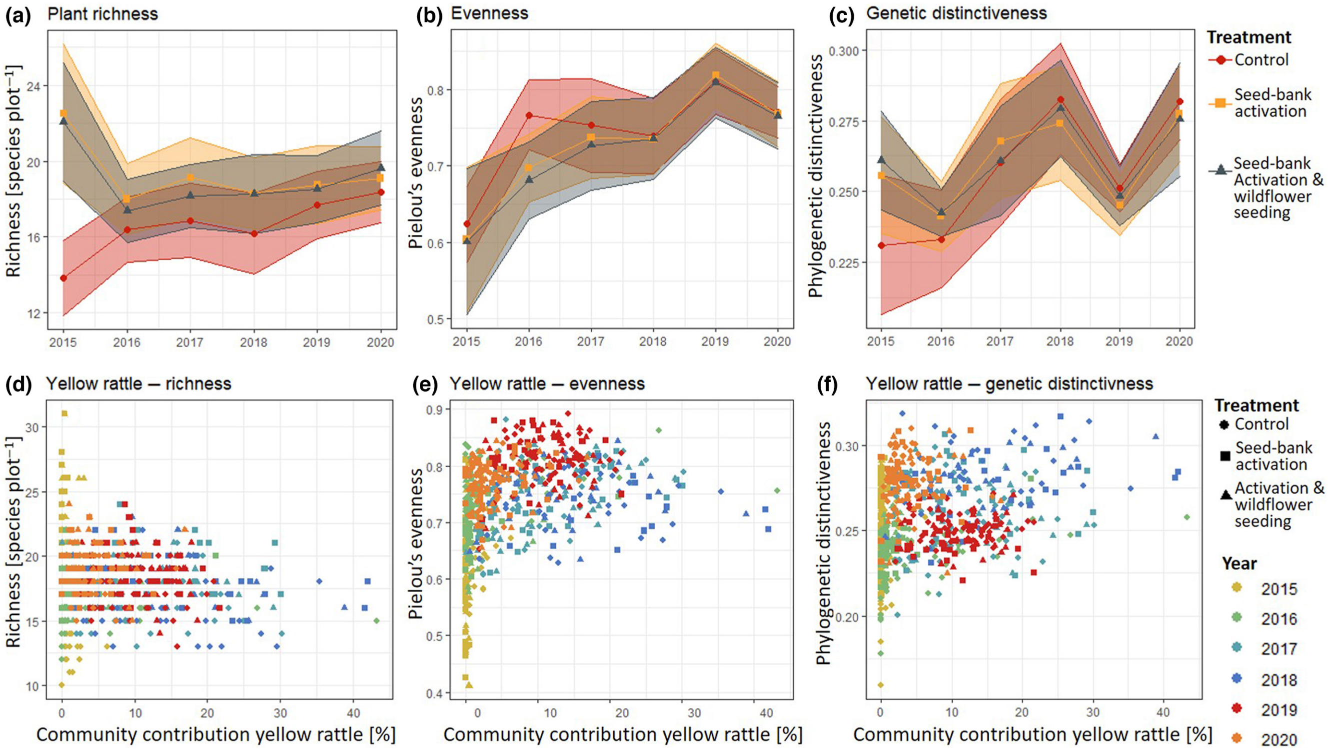

FIGURE 2 Changes in key components of alpha diversity after the implementation of seed bank activation treatments (a–c) and with increases in yellow rattle relative cover (d–f). The investigated diversity components were plant species richness (a, d), evenness (b, e) and phylogenetic distinctiveness, a richness-independent measure of genetic diversity (c, f). Seed bank activation incorporated two levels, without and with additional sowing of wildflower seeds. Points in (a)–(c) represent means, coloured bands ±1 standard deviations.

(Regression; $r^2 = 0.30$, $p < 0.001$). The two intensities of soil bank activation treatments (with and without wildflower sowing) showed highly similar responses in richness (Figure 2a) and most other response variables (Figures 2 and 3).

Seed bank activation also had a marked impact on evenness and the phylogenetic distinctiveness of plant communities (Figure 2b,c). However, the directionality of the response differed between the two diversity components with seed bank activation affecting phylogenetic distinctiveness positively and evenness negatively (both effects diminished over time; Figure 2b). Impacts of yellow rattle densities were less evident in univariate assessments (Figure 2d–f). There were positive, univariate relationships between yellow rattle density and evenness as well as phylogenetic distinctiveness (mixed-effect regressions; $p < 0.01$), but yellow rattle density explained only a relatively small amount of the total variation in response variables ($r^2 < 0.08$; Table S3). No significant impact of yellow rattle density on species richness was detected ($p = 0.09$).

3.2 | Management impact on ecosystem services

Our focal ecosystem services—biomass production, structural complexity and nectar production—were, to various degrees, influenced by seed bank activation treatments and changes in yellow rattle densities. While structural complexity showed only a minor positive response to seed bank activation treatments (mixed-effect regression; $r^2 = 0.03$, $p < 0.001$), annual nectar production was strongly influenced by treatment–time interactions (Table S3). Across treatments, nectar production increased more than fivefold from 1.03 to 5.19 $\mathrm{g\,m^{-2}}$ during our study period (Figure 3). Yellow rattle densities had no significant impacts on structural complexity or nectar production but negatively affected biomass production across years ($r^2 = 0.10$; p-value < 0.001), which also responded to seed bank activation (Table S3).

3.3 | Biodiversity and ecosystem relationships

In our assessment of biodiversity–ecosystem service relationships, we found both potential synergies and trade-offs (Figure 4). Out of the nine univariate relationships between individual biodiversity components and ecosystem relationships, six were significantly positive (Figure 4a; Figure S2; Table S4), highlighting the potential to capitalise on joint positive responses. These multiple positive relationships were not rooted in co-variation among different diversity components (Table S5). Rather, richness, evenness and phylogenetic distinctiveness were largely uncoupled from each other (Figure 4b), and structural complexity and nectar production seemed to show multiple positive responses to individual biodiversity components. An important exception to this pattern was biomass production, which was strongly negatively related to phylogenetic diversity (Figure 4a), indicating a potential trade-off among management targets.

3.4 | Trade-offs and synergies emerging in full system analyses

An SEM-based, multivariate assessment provided additional insights into potential trade-offs at two different levels (Figure 5a). First, we found a relatively minor trade-off in the impact of seed bank activation on biodiversity, reflected in positive effects on richness and phylogenetic diversity contrasting with negative effects on evenness. A second, more pronounced, trade-off emerged between biomass production on the one hand and plant biodiversity, nectar provision and structural complexity on the other hand (Figure 5a). This second trade-off was partly mediated by yellow rattle densities. Yellow rattle reduced biomass production directly as well as indirectly via its impact on phylogenetic diversity (Table S6). In contrast, yellow rattle density had a positive direct impact on all three measured biodiversity components, and consequently indirect positive effects on structural complexity and annual nectar production.

In a scenario analysis based on the SEM results, we evaluated whether observed trade-offs resulted in a dependency of optimal land use practices on specific management objectives. The highest biomass production (target of scenario no. 1) was attained without seed bank activation and in the absence of yellow rattle. However, this was linked to predictions of below average values of all other ecosystem services and all biodiversity components (Figure 5b). In contrast, biodiversity components were maximised (target of scenario no. 2) when yellow rattle densities were 70% of maximum values and seed banks were activated in a 6-year cycle. An equal valuation of all ecosystem services (target of scenario no. 3) resulted in a similar output (Figure 5b), which was reached by a 6-year seed bank activation cycle and intermediate yellow rattle densities. Hence, different land use objectives were best fulfilled with largely differing land management practices.

4 | DISCUSSION

Ecosystem services in agricultural landscapes are directly influenced by land management, as well as indirectly via management-driven changes in biodiversity and natural community composition (Kremen, 2015; Seppelt et al., 2020). Here, we showed that simple, low-cost management interventions in agricultural grasslands can effectively increase biodiversity and ecosystem multifunctionality. Key drivers of this outcome were additive positive responses of two ecosystem services (nectar provision and structural complexity) to plant species richness, evenness and phylogenetic distinctiveness. However, biomass production, the ecosystem service with the strongest direct link to food production and farm revenues, was negatively affected by the investigated management interventions. The consequence was a multi-level trade-off between biodiversity conservation and the provision of diverse ecosystem services on the one hand, and biomass production on

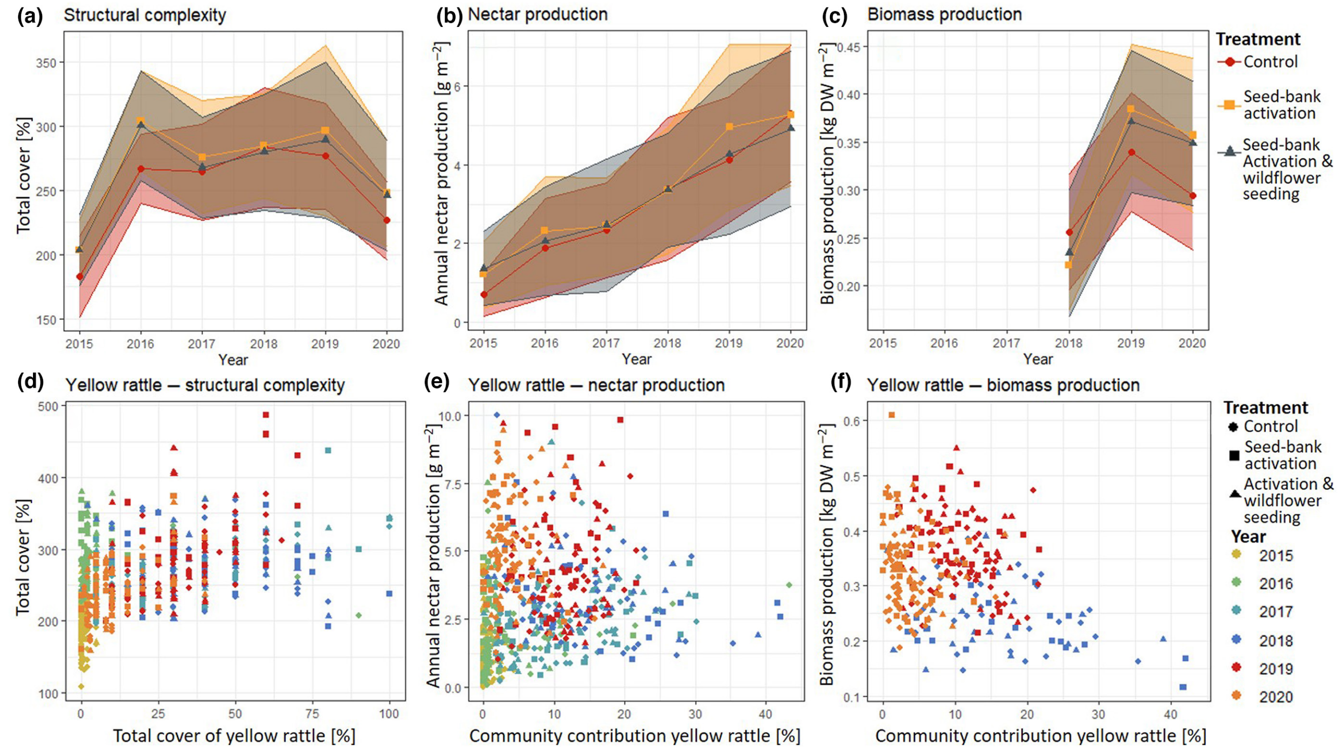

FIGURE 3 Changes in focal ecosystem services after the implementation of seed bank activation treatments (a–c) and with increases in yellow rattle relative cover (d–f). The investigated ecosystem services where structural complexity of plant species community (a, d), annual nectar production (b, e) and above-ground biomass production (c, f). Biomass was measured from 2018 onwards (3 years of data available). Seed bank activation incorporated two levels, without (Treatment I) and with (Treatment II) sowing of wildflower seeds. Points in (a)–(c) represent means, coloured bands range of standard deviations.

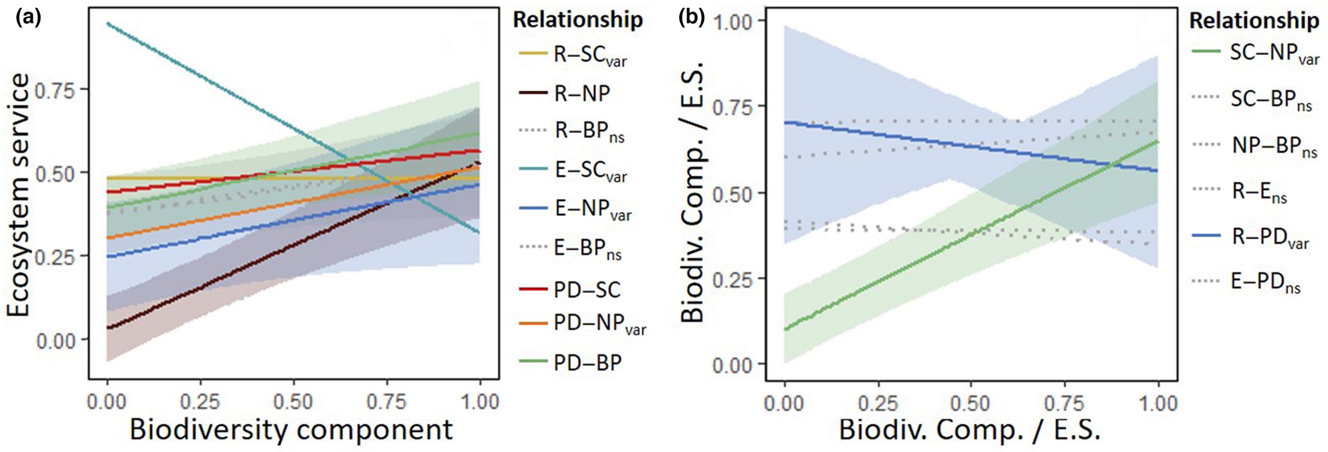

FIGURE 4 Overview of the relationships between key components of diversity and focal ecosystem services. Displayed are (a) the slopes of the relationships between biodiversity components and ecosystem services and (b) relationships among individual diversity components as well as among individual ecosystem services. Coloured lines represent significant, grey lines non-significant relationships. Relationships that were variable in time are indicated in the legend (with var) and the confidence intervals of slopes are depicted by shaded areas. Non-significant relationships are indicated by grey lines and the subscript ns in the legend. In B, the relationship between richness and phylogenetic distinctiveness showed a systematic change from significantly positive to negative relationships over time, which is reflected in the broad, blue-shaded area. BP, biomass production; E, evenness; NP, nectar production; PD, phylogenetic diversity; R, richness; SC, structural complexity.

the other hand. This trade-off resulted in a strong dependency of optimal management practices on land use objectives. Hence, effective land use planning will require clearly defined management targets and the accurate quantification of both trade-offs and synergies emerging from multiple biodiversity–ecosystem service relationships.

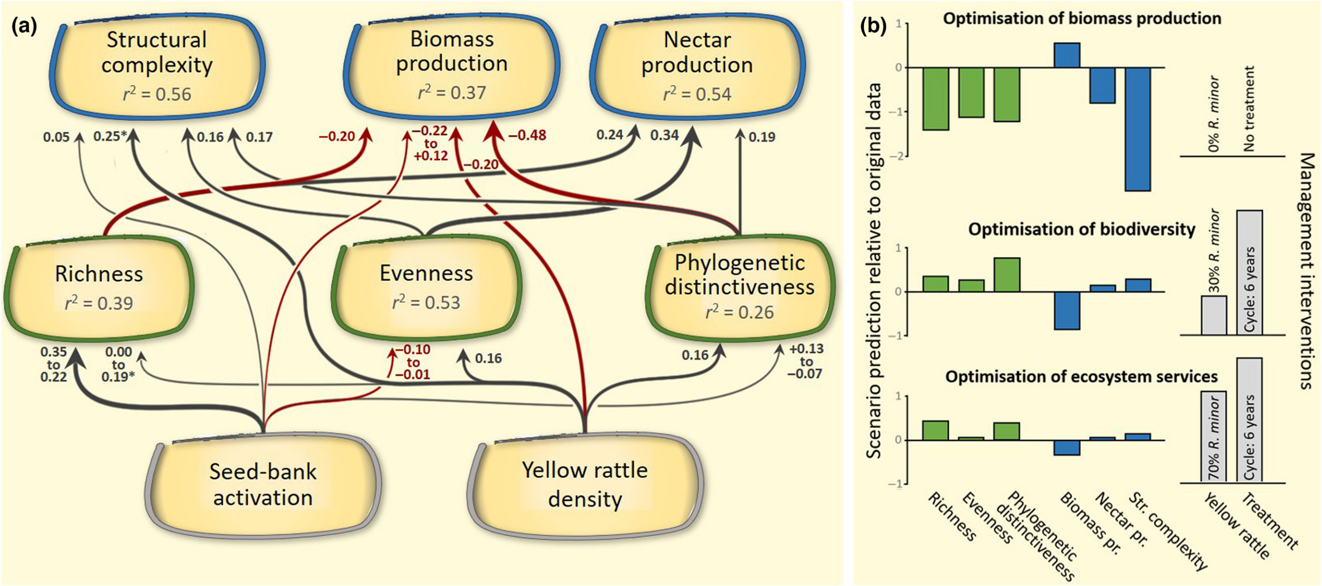

FIGURE 5 Analysis of the direct and indirect effects of low-cost management interventions on key diversity components and ecosystem services based on structural equation modelling. (a) Management interventions had positive (black arrows) and negative (red arrows) effects on biodiversity components and ecosystem service resulting in a multilevel management trade-off. The numbers next to the arrows depict standardised path coefficients, indicating the proportion of its range the response variable shifts when the predictor changes from its minimum to its maximum value. Data ranges next to an arrow indicated a systematic change of a predictor's impact over the 6-year study period. Stars indicate hump-shaped relationships. (b) Predictions of biodiversity components (green) and ecosystem services (blue) under different management scenarios (grey bars on the right). Displayed are three management scenarios that lead to the optimisation of biomass production (top), the sum of ecosystem services (middle) or the sum of biodiversity components (bottom). Predictions are displayed relative to z-standardised original data and yellow rattle densities are represented as percent of the maximum value encountered during the sampling period (see Section 2).

4.1 | Quantifying the impact of biodiversity interventions

Seeding of wild flowers, seed bank activation and the propagation of yellow rattle can be effective measures to increase biodiversity in meadow systems (Bullock et al., 2007; Kardol et al., 2008; Pywell et al., 2004; Westbury et al., 2006). In our study, seed bank activation had a substantial immediate effect on plant species richness. The positive impact of the one-time treatment decreased somewhat in the following year, but plant species richness in year 6 was still ~40% higher than in control plots at the time of treatment implementation. Likewise, evenness and nectar production also increased substantially over the course of the experiment (the latter by over 400%). The observed differences between treatment and control plots in year 6 were, however, much smaller, as control plots were equally exposed to yellow rattle propagation (Figure 1), due to the spatial spread of the species. Furthermore, control plots likely also profited from positive spill-over effects through seed dispersal from neighbouring treatment plots.

Hence, the most relevant benchmark for comparing the combined impact of the two management interventions is the control plots in the year of treatment implementation. This is corroborated by the fact that other management practices such as mowing and grazing regimes, as well as nutrient management during the experiment, were continuations of those implemented prior to the study. Furthermore, our study covered a period with very variable environmental conditions that encompassed both a very dry and a very wet growing season in 2018 and 2019, respectively. The trends in richness, evenness and nectar production were nevertheless largely consistent throughout the 6-year period, highlighting that the observed changes during our study period were most likely not environmentally triggered and rather the result of the implemented management interventions.

4.2 | Consistency of biodiversity–ecosystem service relationships?

Positive relationships between biodiversity and both ecosystem functioning and service provision are believed to belong to the few universal relationships that have been found in ecological research (Benkwitt et al., 2020). Although we recorded mostly positive relationships between individual biodiversity components and ecosystem services, biomass production was an important exception, being negatively related to plant richness and phylogenetic distinctiveness. Negative biodiversity–productivity relationships are not entirely uncommon (Grace et al., 2016) and have been reported in grasslands, for example after yellow rattle introductions (Hartley et al., 2015; Pywell et al., 2004) or as a consequence of eutrophication (Hautier et al., 2009).

In the case of yellow rattle, negative biodiversity–productivity relationships are likely rooted in species identity effects (e.g. shifts in mean trait values), which can confound the positive impact of biodiversity gains (Grime, 1997). Yellow rattle is a hemi-parasitic plant with a wide host range, but with a preference for targeting grass species (Jiang et al., 2010; Westbury, 2004). This selective, negative impact on grasses can help to break their dominance, which can promote plant species diversity, as was the case in our study. However, grasses commonly produce a greater above-ground biomass per area than forbs (Jiang et al., 2010). Hence, the presence of yellow rattle often triggers a shift in mean trait values, leading to the observed negative correlation between biodiversity and production (Hartley et al., 2015; Pywell et al., 2004). Similar effects may be caused by fertiliser applications when higher nutrient availability increases productivity and reduces the number of limiting resources. The resulting reduction in the number of constraining niche dimensions can decrease the number of coexisting species in conceptual and applied assessments (Harpole et al., 2016; Hautier et al., 2009). In both cases, positive biodiversity–ecosystem productivity relationships might still persist (Isbell et al., 2015), but are cancelled out by shifts in community structure, resulting in biodiversity–productivity trade-offs.

4.3 | Additive effects of multiple biodiversity components

An important driver of synergies in our study was complementary positive effects of different biodiversity components on nectar provisioning and structural complexity (Figure 5). Past research investigating diversity–ecosystem service relationships has traditionally focused on species richness (Díaz & Cabido, 2001), which is positively associated with niche complementarity, the main driver of biodiversity–ecosystem service relationships (Barry et al., 2019). More recently, it has been suggested to replace richness with phylogenetic diversity (commonly assessed using Faith's index; Faith, 1992) because of its better correspondence with niche complementarity (Flynn et al., 2011; Gravel et al., 2011; Srivastava et al., 2012). However, richness and Faith's phylogenetic diversity are not independent of each other, and therefore, both measures have been considered as alternatives rather than as complementary drivers (Cadotte, 2015; Venail et al., 2015).

In our study, we relied on phylogenetic distinctiveness, a measure of phylogenetic diversity that is independent of species richness (Schweiger et al., 2008; Tsirogiannis & Sandel, 2016). This independence enabled the integration of multiple biodiversity components into our assessments, resulting in the case of nectar provision for example, in additive, positive effects of richness, evenness and phylogenetic diversity (Figure 5a). An important reason for the additivity of these effects is likely to be that niche complementarity is neither fully characterised by species richness nor phylogenetic diversity (Cadotte, 2015). Accordingly, a focus on richness or phylogenetic diversity alone would have reduced predictive power and caused an underestimation of the strength of biodiversity–ecosystem service relationships. Hence, we want to encourage the consideration of potentially complementary biodiversity components in both ecological research and applied management approaches.

4.4 | Multilevel trade-offs and their management implications

We found that different biodiversity components and ecosystem services showed synergies but also trade-offs in their responses to management interventions. A relatively minor trade-off was the contrasting effect of treatment implementation on richness and evenness, which had little consequence for ecosystem service provisioning. Furthermore, there could be a trade-off between fodder quantity and quality, which can be attained by a higher diversity of forbs (Grace et al., 2019; Kearns et al., 2022). However, a central factor in our study was a multilevel trade-off that was rooted in the negative response of plant biomass production to management interventions. This negative impact of biodiversity interventions on biomass production, which was also recorded in earlier studies (Hellström et al., 2011; Pywell et al., 2004), caused a strong dependency of optimal management practices on land use targets in our simulations. Hence, the decision to implement the investigated management interventions hinges on the relative valuation of hay production versus other ecosystem services and the conservation of biodiversity.

An important element in the evaluation of different management scenarios (Figure 5b) is their overall impact on farm revenues. In our study, we selected two low-cost management interventions (seed bank activation and yellow rattle propagation), which currently would have implemented together a one-time implementation cost of approximately £300 ha^{-1} (see SI, Section S6 for more detailed cost estimation). Furthermore, the reduction in hay harvest would result in a loss of about £430 $\mathrm{ha}^{-1}\,\mathrm{year}^{-1}$, assuming a hay price of £148 t^{-1} and accounting for the fact that our study only quantified the biomass production during half of the growing season. Increased biodiversity in grasslands can result in substantial financial benefits for crop production on neighbouring fields (Martin et al., 2019). These benefits can be driven by yield increases through promoting pollinators (Garibaldi et al., 2016; Kremen & Chaplin-Kramer, 2007) through the provision of nectar resources when crops are not flowering (Pywell et al., 2015), or by lowering pesticide costs due to natural pest control (Zou et al., 2020). However, advantages of improved pollination and natural pest control are highly context specific. They depend on a variety of factors including the levels of crop pollination dependency (Klein et al., 2007), landscape structure (Martin et al., 2019) and the level of services already provided by natural landscapes in the area (Goldenberg et al., 2022). Furthermore, the benefits for farm revenues will also be subject to the land ownership configuration of neighbouring fields, complicating general cost–benefit assessments. This strong context specificity certainly poses a central challenge for the design of land management policies and compensatory payments. Nonetheless, our study highlights that strategies to increase biodiversity and ecosystem multifunctionality can be linked to low implementation costs and still be highly effective in increasing multiple components of biodiversity.

5 | CONCLUSIONS

The assessment and quantification of potential trade-offs between biomass production, biodiversity and other ecosystem services is a key requirement for the reconciliation of food production and biodiversity in agricultural landscapes. We implemented two different low-cost management interventions in an agriculturally managed grassland system and recorded biodiversity components and three different key ecosystem services over a 6-year period. Our results demonstrate that one-time management interventions had strong, positive, long-term effects on biodiversity components and nectar provision but decreased plant biomass production. The synergies between biodiversity and non-production ecosystem services were thereby supported by complementary effects of multiple biodiversity components such as species richness and phylogenetic diversity. The trade-offs of hay production with biodiversity and non-production ecosystem services, however, resulted in a strong dependency of 'optimal' land management practice on the specific land use targets of a location. Hence, while the implementation of low-cost management interventions can be relatively straightforward, the outcomes are complex, interdependent and context-specific, requiring an evidence-based consideration of land use targets in advance of implementation.

AUTHOR CONTRIBUTIONS

Mark Bulling designed and implemented together with Godfrey Meynell the experimental field site; Alan Willmot, Mark Bulling, Debbie Alston, Alfred Burian, Briony A. Norton, Sarah Reynolds and Godfrey Meynell conducted the fieldwork; Alfred Burian, Briony A. Norton and Paul Lynch supported laboratory analyses; Alfred Burian and Mark Bulling analysed the data; and all co-authors contributed to the manuscript compilation and revision.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.44j0zpckg (Burian & Bulling, 2023).

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REFERENCES

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., & Entling, M. H. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*, 1488–1498.

Altieri, M. A., & Letourneau, D. K. (1982). Vegetation management and biological control in agroecosystems. *Crop Protection*, *1*, 405–430.

Amelung, W., Bossio, D., de Vries, W., Kögel-Knabner, I., Lehmann, J., Amundson, R., Bol, R., Collins, C., Lal, R., & Leifeld, J. (2020). Towards a global-scale soil climate mitigation strategy. *Nature Communications*, *11*, 5427.

Bardgett, R. D., Smith, R. S., Shiel, R. S., Peacock, S., Simkin, J. M., Quirk, H., & Hobbs, P. J. (2006). Parasitic plants indirectly regulate below-ground properties in grassland ecosystems. *Nature*, *439*, 969–972.

Barry, K. E., Mommer, L., van Ruijven, J., Wirth, C., Wright, A. J., Bai, Y., Connolly, J., De Deyn, G. B., de Kroon, H., & Isbell, F. (2019). The future of complementarity: Disentangling causes from consequences. *Trends in Ecology & Evolution*, *34*, 167–180. https://doi.org/10.1016/j.tree.2018.10.013

Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A., Morton, R. D., Smart, S. M., & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, *530*, 85–88. https://doi.org/10.1038/nature16532

Beckmann, M., Gerstner, K., Akin-Fajiye, M., Ceaușu, S., Kambach, S., Kinlock, N. L., Phillips, H. R., Verhagen, W., Gurevitch, J., & Klotz, S. (2019). Conventional land-use intensification reduces species richness and increases production: A global meta-analysis. *Global Change Biology*, *25*, 1941–1956. https://doi.org/10.1111/gcb.14606

Benkwitt, C. E., Wilson, S. K., & Graham, N. A. (2020). Biodiversity increases ecosystem functions despite multiple stressors on coral reefs. *Nature Ecology & Evolution*, *4*, 919–926. https://doi.org/10.1038/s41559-020-1203-9

Binder, S., Isbell, F., Polasky, S., Catford, J. A., & Tilman, D. (2018). Grassland biodiversity can pay. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 3876–3881.

Brewer, M. J., Butler, A., & Cooksley, S. L. (2016). The relative performance of AIC, AICC and BIC in the presence of unobserved heterogeneity. *Methods in Ecology and Evolution*, *7*, 679–692.

Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia*, *135*, 407–413.

Bullock, J. M., Pywell, R. F., & Walker, K. J. (2007). Long-term enhancement of agricultural production by restoration of biodiversity. *Journal of Applied Ecology*, *44*, 6–12.

Burian, A., & Bulling, M. (2023). Data from: Low-cost management interventions and their impact on multi-level trade-offs in agricultural grasslands. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.44j0zpckg

Cadotte, M. W. (2015). Phylogenetic diversity and productivity: Gauging interpretations from experiments that do not manipulate phylogenetic diversity. *Functional Ecology*, *29*, 1603–1606.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., & Wardle, D. A. (2012). Biodiversity loss and its impact on humanity. *Nature*, *486*, 59–67. https://doi.org/10.1038/nature11148

Cardinale, B. J., Wright, J. P., Cadotte, M. W., Carroll, I. T., Hector, A., Srivastava, D. S., Loreau, M., & 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.

Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J., & Kremen, C. (2011). A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecology Letters*, *14*, 922–932.

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*, 646–655.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*, 1–10.

Filstrup, C. T., King, K. B., & McCullough, I. M. (2019). Evenness effects mask richness effects on ecosystem functioning at macro-scales in lakes. *Ecology Letters*, *22*, 2120–2129. https://doi.org/10.1111/ele.13407

Flynn, D. F., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology*, *92*, 1573–1581.

Franzén, M., & Nilsson, S. G. (2008). How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography*, *31*, 698–708.

Garibaldi, L. A., Carvalheiro, L. G., Vaissière, B. E., Gemmill-Herren, B., Hipólito, J., Freitas, B. M., Ngo, H. T., Azzu, N., Sáez, A., & Åström, J. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science*, *351*, 388–391. https://doi.org/10.1126/science.aac7287

Goldenberg, M. G., Burian, A., Seppelt, R., Ossa, F. A. S., Bagnato, C. E., Satorre, E. H., Martini, G. D., & Garibaldi, L. A. (2022). Effects of natural habitat composition and configuration, environment and agricultural input on soybean and maize yields in Argentina. *Agriculture, Ecosystems & Environment*, *339*, 108133.

Grace, C., Lynch, M., Sheridan, H., Lott, S., Fritch, R., & Boland, T. (2019). Grazing multispecies swards improves ewe and lamb performance. *Animal*, *13*, 1721–1729.

Grace, J. (2022). General guidance for custom-built structural equation models. *One Ecosystem*, *7*, e72780.

Grace, J. B., Anderson, T. M., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hautier, Y., Hillebrand, H., Lind, E. M., Partel, M., Bakker, J. D., Buckley, Y. M., Crawley, M. J., Damschen, E. I., Davies, K. F., Fay, P. A., Firn, J., Gruner, D. S., Hector, A., … Smith, M. D. (2016). Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, *529*, 390–393. https://doi.org/10.1038/nature16524

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., & Mouquet, N. (2011). Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature*, *469*, 89–92.

Grime, J. P. (1997). Biodiversity and ecosystem function: The debate deepens. *Science*, *277*, 1260–1261.

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., & Hillebrand, H. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, *537*, 93–96. https://doi.org/10.1038/nature19324

Hartley, S. E., Green, J. P., Massey, F. P., Press, M. C., Stewart, A. J., & John, E. (2015). Hemiparasitic plant impacts animal and plant communities across four trophic levels. *Ecology*, *96*, 2408–2416.

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*, 636–638.

Hellström, K., Bullock, J. M., & Pywell, R. F. (2011). Testing the generality of hemiparasitic plant effects on mesotrophic grasslands: A multi-site experiment. *Basic and Applied Ecology*, *12*, 235–243.

Howe, C., Suich, H., Vira, B., & Mace, G. M. (2014). Creating win-wins from trade-offs? Ecosystem services for human well-being: A meta-analysis of ecosystem service trade-offs and synergies in the real world. *Global Environmental Change*, *28*, 263–275.

IPBES. (2019). *Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. S. M. Díaz, J. Settele, E. Brondízio, & H. Ngo (Eds.). IPBES Secretariat.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T. M., Bonin, C., Bruelheide, H., & De Luca, E. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Jiang, F., Jeschke, W. D., Hartung, W., & Cameron, D. D. (2010). Interactions between Rhinanthus minor and its hosts: A review of water, mineral nutrient and hormone flows and exchanges in the hemiparasitic association. *Folia Geobotanica*, *45*, 369–385.

Kardol, P., Van der Wal, A., Bezemer, T. M., de Boer, W., Duyts, H., Holtkamp, R., & Van der Putten, W. H. (2008). Restoration of species-rich grasslands on ex-arable land: Seed addition outweighs soil fertility reduction. *Biological Conservation*, *141*, 2208–2217.

Kearns, M., Ponnampalam, E. N., Jacquier, J.-C., Grasso, S., Boland, T. M., Sheridan, H., & Monahan, F. J. (2022). Can botanically-diverse pastures positively impact the nutritional and antioxidant composition of ruminant meat?—Invited review. *Meat Science*, *197*, 109055. https://doi.org/10.1016/j.meatsci.2022.109055

Keating, B. A., Herrero, M., Carberry, P. S., Gardner, J., & Cole, M. B. (2014). Food wedges: Framing the global food demand and supply challenge towards 2050. *Global Food Security*, *3*, 125–132.

Klaus, V. H., Hoever, C. J., Fischer, M., Hamer, U., Kleinebecker, T., Mertens, D., Schäfer, D., Prati, D., & Hölzel, N. (2018). Contribution of the soil seed bank to the restoration of temperate grasslands by mechanical sward disturbance. *Restoration Ecology*, *26*, S114–S122.

Klein, A.-M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 303–313.

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences*, *1355*, 52–76.

Kremen, C., & Chaplin-Kramer, R. (2007). Insects as providers of ecosystem services: crop pollination and pest control. In *Insect conservation biology: proceedings of the royal entomological society's 23rd symposium* (pp. 349–382). CABI Publishing.

Linders, T. E., Schaffner, U., Alamirew, T., Allan, E., Choge, S. K., Eschen, R., Shiferaw, H., & Manning, P. (2021). Stakeholder priorities determine the impact of an alien tree invasion on ecosystem multifunctionality. *People and Nature*, *3*, 658–672.

Manning, P., van der Plas, F., Soliveres, S., Allan, E., Maestre, F. T., Mace, G., Whittingham, M. J., & Fischer, M. (2018). Redefining ecosystem multifunctionality. *Nature Ecology & Evolution*, *2*, 427–436.

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P., Holzschuh, A., Kleijn, D., & Kovács-Hostyánszki, A. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, *22*, 1083–1094.

Maskell, L. C., Crowe, A., Dunbar, M. J., Emmett, B., Henrys, P., Keith, A. M., Norton, L. R., Scholefield, P., Clark, D. B., & Simpson, I. C. (2013). Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. *Journal of Applied Ecology*, *50*, 561–571.

Mason-D'Croz, D., Bogard, J. R., Sulser, T. B., Cenacchi, N., Dunston, S., Herrero, M., & Wiebe, K. (2019). Gaps between fruit and vegetable production, demand, and recommended consumption at global and national levels: An integrated modelling study. *The Lancet Planetary Health*, *3*, e318–e329.

O'Mara, F. P. (2012). The role of grasslands in food security and climate change. *Annals of Botany*, *110*, 1263–1270.

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., & Settele, J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*, 220–229. https://doi.org/10.1038/nature20588

Pretty, J. (2018). Intensification for redesigned and sustainable agricultural systems. *Science*, *362*, eaav0294. https://doi.org/10.1126/science.aav0294

Pywell, R. F., Bullock, J. M., Walker, K. J., Coulson, S. J., Gregory, S. J., & Stevenson, M. J. (2004). Facilitating grassland diversification using the hemiparasitic plant Rhinanthus minor. *Journal of Applied Ecology*, *41*, 880–887.

Pywell, R. F., Heard, M. S., Woodcock, B. A., Hinsley, S., Ridding, L., Nowakowski, M., & Bullock, J. M. (2015). Wildlife-friendly farming increases crop yield: Evidence for ecological intensification. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151740.

R Development Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0. http://www.R-project.org

Ray, D. K., Ramankutty, N., Mueller, N. D., West, P. C., & Foley, J. A. (2012). Recent patterns of crop yield growth and stagnation. *Nature Communications*, *3*, 1–7.

Schweiger, O., Klotz, S., Durka, W., & Kühn, I. (2008). A comparative test of phylogenetic diversity indices. *Oecologia*, *157*, 485–495.

Seppelt, R., Arndt, C., Beckmann, M., Martin, E. A., & Hertel, T. W. (2020). Deciphering the biodiversity–production mutualism in the global food security debate. *Trends in Ecology & Evolution*, *35*, 1011–1020.

Simpson, E. H. (1951). The interpretation of interaction in contingency tables. *Journal of the Royal Statistical Society, Series B: Statistical Methodology*, *13*, 238–241.

Srivastava, D. S., Cadotte, M. W., MacDonald, A. A. M., Marushia, R. G., & Mirotchnick, N. (2012). Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters*, *15*, 637–648.

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 20260–20264.

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S., & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature*, *546*, 73–81.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, *277*, 1300–1302.

Tsirogiannis, C., & Sandel, B. (2016). PhyloMeasures: A package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*, *39*, 709–714.

Venail, P., Gross, K., Oakley, T. H., Narwani, A., Allan, E., Flombaum, P., Isbell, F., Joshi, J., Reich, P. B., & Tilman, D. (2015). Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Functional Ecology*, *29*, 615–626.

Westbury, D. B. (2004). Rhinanthus minor L. *Journal of Ecology*, *92*, 906–927.

Westbury, D. B., Davies, A., Woodcock, B., & Dunnett, N. (2006). Seeds of change: The value of using Rhinanthus minor in grassland restoration. *Journal of Vegetation Science*, *17*, 435–446.

Willett, W., Rockström, J., Loken, B., Springmann, M., Lang, T., Vermeulen, S., Garnett, T., Tilman, D., DeClerck, F., & Wood, A. (2019). Food in the Anthropocene: The EAT–Lancet Commission on healthy diets from sustainable food systems. *The Lancet*, *393*, 447–492.

Winter, M., Devictor, V., & Schweiger, O. (2013). Phylogenetic diversity and nature conservation: Where are we? *Trends in Ecology & Evolution*, *28*, 199–204.

Zavaleta, E. S., Pasari, J. R., Hulvey, K. B., & Tilman, G. D. (2010). Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 1443–1446.

Zou, Y., De Kraker, J., Bianchi, F. J., Xiao, H., Huang, J., Deng, X., Hou, L., & Van Der Werf, W. (2020). Do diverse landscapes provide for effective natural pest control in subtropical rice? *Journal of Applied Ecology*, *57*, 170–180.

SUPPORTING INFORMATION

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

Data S1: Additional information on methods and supplementary figures.

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