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RESEARCH ARTICLE

Multispecies crop mixtures increase insect biodiversity in an intercropping experiment

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Abstract

1. Recent biodiversity declines require action across sectors such as agriculture. The situation is particularly acute for arthropods, a species-rich taxon providing important ecosystem services. To counteract the negative consequences of agricultural intensification, creating a less hostile agricultural 'matrix' through growing crop mixtures can reduce harm for arthropods without yield losses.
2. While grassland biodiversity experiments showed positive plant biodiversity effects on arthropods, experiments manipulating crop diversity and agrochemical input used to study arthropods are lacking.
3. Here, we experimentally manipulated crop diversity (1–3 species, fallows), crop species (wheat, faba bean, linseed and oilseed rape) and agrochemical input (high vs. low) and studied responses of arthropod biodiversity. We tested whether arthropod responses were affected by crop diversity, mixtures and management. Additionally, we measured crop biomass.
4. Crop biomass increased with crop diversity under high-input management, while under low management intensity, biomass was highest in two-species mixtures.
5. Increasing crop diversity positively affected arthropod abundance and diversity, under both low- and high-input management. Crop mixtures containing faba bean, linseed or oilseed rape had particularly high arthropod diversity.
6. Mass-flowering crops attracted more arthropods than legumes or cereals. Integrating intercropping into agricultural systems could increase flower visits by insects up to 1.5 million per hectare, thus likely also supporting pollination and pest-control ecosystem services.
7. Flower visitor network complexity increased in mixtures containing linseed and faba bean and under low-input management.
8. Intercropping can counteract insect declines in farmland by creating beneficial matrix habitat without compromising crop yield.

KEYWORDS
agricultural landscapes, agroecosystem biodiversity, arthropods, biodiversity conservation, crop identity, flower visitors, intercropping, matrix quality, mixed cropping

1 | INTRODUCTION

Arthropods and especially flower-visiting insects provide a range of important ecosystem services. Since more than one-third of the global food production comes from crops that depend on pollinators (Klein et al., 2007), increasing cropping system diversity in space or time may help to balance environmental sustainability and agricultural production. Modern agricultural landscapes are often dominated by large expanses of crop monocultures (Eurostat, 2018), where food or habitat resources for flower-visiting arthropods are generally scarce (Nicholls & Altieri, 2013). Some mass-flowering crops, such as oilseed rape (canola) or sunflower, can support some flower visitor species, but only for limited time periods (Westphal et al., 2003) and without providing safe sites for reproduction and hence population growth. Herbicide application removes weeds efficiently from agricultural fields and thus leads to clean landscapes where only a fraction of species can survive due to habitat and resource losses (Nicholls & Altieri, 2013). Input of other agrochemicals, such as fertilizers, insecticides and fungicides increase yield, but often at the expense of overall agrobiodiversity, potentially contributing substantially to recent insect declines (Benton et al., 2002; Dicks et al., 2021; Tscharntke et al., 2005).

There are, however, countermeasures focussing on the concept of sustainable intensification, a process (or system) where yields are increased without harmful environmental impacts. Integrated pest management and conservation agriculture (including diversified crop rotations) have been practised for a long time already with not only positive but also negative effects on biodiversity (Beillouin et al., 2021; Dainese et al., 2019; Lichtenberg et al., 2017). One approach to support biodiversity in agriculture is intercropping (Martin-Guay et al., 2018; Wuest et al., 2021), where two or more crop species are grown on the same piece of land. As large expanses of cropland worldwide are dominated by cereal monocultures, growing mixtures of cereals with another crop (e.g. legumes) may have positive impacts on the quality of the matrix (Perfecto et al., 2009) in which natural habitats are embedded.

Intercropping has been shown to increase flower visitor or natural enemy abundance and diversity (Brandmeier et al., 2021; Norris et al., 2018) while at the same time enhancing yield stability and productivity (Li et al., 2020; Raseduzzaman & Jensen, 2017; Yu et al., 2015) or reducing needs for chemical fertilizers when cereals are intercropped with legumes (Hauggaard-Nielsen et al., 2008). Despite these benefits, intercropping has remained surprisingly unpopular in industrialized countries, though it is widely used in low-input tropical agroecosystems (Hauggaard-Nielsen et al., 2009) and in traditional smallholder farming systems in the Global South (Brooker et al., 2015). When implemented at larger scales in the landscape, intercropping may be an important measure to support arthropod populations by increasing the availability of food and nesting resources.

Flower visitor species richness and composition depend on the local plant community (Biesmeijer et al., 2006), and it has been shown that not only crop diversity but also crop identity affects arthropods (Meyer et al., 2019). Additional community attributes such as interaction network complexity can help to understand relationships between crop diversity and ecosystem functioning, such as pollination success or crop yield (Saunders & Rader, 2019). Beyond the effects of crop diversity and identity, a large body of literature has examined the effects of management intensity (e.g. organic vs. conventional farming) on flower visitors (for recent reviews, see Kennedy et al., 2013; Lichtenberg et al., 2017). However, only few studies so far compared flower visitors in crop monocultures and mixtures under high- versus low-input management (Brandmeier et al., 2021).

Here, we set up a fully factorial experiment with the following three factors: (i) management intensity (high vs. low input of pesticides and fertilizer), (ii) crop diversity (0, 1, 2 or 3 crop species) and (iii) crop identity (wheat, faba bean, linseed and oilseed rape). An increasing number of crop species (crop species richness) per se can be expected to increase arthropod diversity and abundance due to bottom-up effects, as has been shown in grassland biodiversity experiments (Scherber et al., 2010; hypothesis 1). Additionally, the identity of the crop species will likely affect diversity, abundance and plant–flower visitor network structure, due to differences in floral resource provisioning (Losapio et al., 2019; Maia et al., 2019; Hypothesis 2). Finally, management intensity (fertilizer and herbicide input) can be hypothesized to decrease arthropod abundance and richness (hypothesis 3), due to indirect effects (reduced weed abundance, microclimate; Brühl & Zaller, 2021; Dupont et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Experimental design

We set up a field experiment as part of a series of multiyear intercropping trials conducted at the agricultural research station of the Julius Kühn Institute in 2019 in Münster, Germany (51°58′32.5″N 7°33′57.4″E; (Brandmeier et al., 2021). The site was bordered by a woodland, crop fields and grassland, and residential developments. Intensively farmed cereal fields were abundantly present in the wider landscape surrounding the site. We manipulated the number of crop species (crop diversity), crop species identity and management intensity in a randomized blocks design (Figures S1 and S2). The full experimental design had $N = 240$ plots (including monocultures, two- and three-species mixtures with barley and pea). Here, we focus on a subset of $N = 104$ plots on which pollinator sampling was done. Plots were sown with monocultures or mixtures of summer wheat (*Triticum aestivum* L.), faba bean (*Vicia faba* L.), linseed (*Linum usitatissimum* L.) and oilseed rape (*Brassica napus* L.) in a substitutive design (Table S1), that is mixture proportions added to 100 per cent. A total of 104 plots, each measuring 3×4 m, were sown at random in four replicate blocks with a sowing machine (Wintersteiger Plotseed S) at a row spacing of 12.5 cm with eight rows per metre at a sowing depth of 3.5 cm on 14 May 2019. We assigned management intensity at random to half-blocks: One half of each block received high-intensity management, consisting of (i) one pre-emergence spray of herbicides (4.4 L/ha Stomp Aqua with 455 g/L Pendimethalin as active agent) and (ii) nitrogen fertilizer applied as a solution of urea and ammonium nitrate (70 kg N/ha); the other half received no treatment (low intensity). We adjusted application levels to the common amounts for our region, but reduced fertilizer quantity to account for legumes in our mixtures. Arthropods were sampled using either pan traps (all plots) or flower visitor observations (a subset of plots not containing oilseed rape; Table S1). Permits for insect sampling were obtained from the city of Münster (Amt für Grünflächen und Umweltschutz) via the Julius Kühn Institute (Institute for Plant Protection in Horticulture and Forests).

2.2 | Flower visitor observations

Observations were carried out between 2 and 10 July at appropriate weather conditions (warm, sunny and dry). One square metre of each plot was observed for 15 min during each observation run. In one block of the experiment, we managed to accomplish two observation runs, while plots in all other blocks were only visited once due to time limitations and the rapid ripening of linseed flowers. At each observation run, we assessed the numbers of flower visits and flower visitor taxon at the lowest possible taxonomic resolution (species, family, order). Observations were done on monocultures of wheat, faba bean and linseed, their two- and three-species mixtures, and also on bare-ground control plots, where weeds had established (Table S2). The plant species visited was noted regardless of whether the plant was a crop or a weed species. Each contact with floral organs was counted as one visit. If the ears of wheat plants had been visited, this was also counted as a flower visit, as it has been shown that hoverflies and bees sometimes also visit wind-pollinated plants (Saunders, 2018). For data analyses, we summed all observations per crop diversity (four levels, see Staab et al., 2015) and per crop mixture (eight levels).

2.3 | Pan traps

Pan traps were installed during four time periods (28 June–1 July, 5–8 July, 12–15 July and 23–26 July) as an indirect measure of arthropod abundance (Scherber & Beduschi, 2021). We had to exclude the third sampling period, because heavy rain had flooded the traps. We used plastic bowls sprayed with UV yellow paint (Montana Black infra yellow, European Aerosols GmbH, Heidelberg, Germany), filled with water and a drop of detergent (Frosch, Werner & Mertz GmbH, Germany). Traps were placed at ground level in the vegetation of each plot and were left active for 72 h; then, we transferred arthropods into 70% ethanol in the field and sorted them up to the lowest possible taxonomic level in the laboratory using binoculars (Leica EZ4-HD; for details, see Table S3). We summed the abundances from all three sampling periods for each level of crop diversity (four levels—0, 1, 2 or 3 species) and per crop mixture (13 different mixtures, Table S1).

2.4 | Crop biomass sampling and weed assessment

We harvested crop biomass from 17 July to 9 August from crops and weeds on a randomly selected subplot of 40 × 40 cm of each plot. All biomass material was hand-harvested at 1 cm above ground for crop species separately and for weed species combined (not species-specific). Biomass material was oven-dried for 48 h at 70°C, weighed immediately afterwards (Sartorius Industry) and extrapolated to g/m^2. The cover and presence of weed species was assessed visually from 18 June—4 July on one randomly selected 1-m^2 quadrat for each plot.

2.5 | Statistical analyses

Flower visitor diversity and arthropod diversity were expressed as Shannon's entropy (Jost, 2007) and its numbers equivalent (exponential of Shannon's diversity), calculated using the package *vegan* (Oksanen et al., 2019). The numbers equivalent allows to compare species richness values corrected for differences in abundance. Data analysis was done in R (version 3.6.1) operated via RStudio (Posit team, 2022). For all response variables, we checked distributional assumptions using the *fitdistrplus* package (Delignette-Muller & Dutang, 2015) and inspected model residuals for constant variance. The numbers equivalents of flower visitor diversity and arthropod diversity were count data and therefore analysed using generalized linear mixed-effects models with a Tweedie family of distributions (Dunn & Smyth, 2008). A generalized Poisson distribution (Consul & Famoye, 1992) was used to model total arthropod abundances. Because of the hierarchical experimental design, we included blocks and management nested within blocks, as a random effect to account for spatial nonindependence. Models were fitted using the *glmmTMB* package in R (Brooks et al., 2017). The fixed effects in the models were either (i) crop diversity*management or (ii) crop mixture*management, fitted in separate models.

Plant–flower visitor networks were constructed using the bipartite package (Dormann et al., 2009). First, the *plotweb*() function was used to construct individual networks for each crop mixture and management intensity, resulting in 16 networks. Additionally, we calculated network metrics, using the *networklevel*() function, for data pooled per block, crop mixture and management intensity (resulting in $N = 64$ data points). The effects of crop mixture and management on these network metrics were then analysed using the same model structure as above, but using generalized Poisson or Maxwell-Conway Poisson errors (Huang, 2017). We used the number of interactions, number of flower visitor species and Shannon's diversity of interactions as metrics to describe the networks, as more complex indices need a minimal network size to function reliably (Dormann et al., 2009), which was not the case in this study.

The number of flower visits and the total number of arthropod individuals were analysed as described above with generalized Poisson errors. Crop biomass was analysed using a Tweedie family. Means were compared using Type II Wald chi-squared tests from the *car* library (Fox & Weisberg, 2019). In all models containing factors as explanatory variables, we used successive difference contrasts (Venables & Ripley, 2002) to compare means (e.g. mono- vs. 2 and 2- vs. 3-species mixtures).

3 | RESULTS

3.1 | Arthropod community

In pan trap samples, the most frequent taxa were Diptera (excluding Syrphid flies), wasps, Coleoptera, Thysanoptera and Auchenorrhyncha. In pollinator networks, the arthropod community was dominated by the bumblebee species *Bombus lapidarius* and *B. terrestris* and the hoverfly species *Syrphus ribesii* and *Episyrphus balteatus*. A detailed overview of the taxonomic composition is given in Tables S3 and S4.

3.2 | Arthropod diversity in monocultures, two- and three-species mixtures

In fertilized plots that had received a herbicide treatment (high management intensity), arthropod and flower visitor diversity increased with increasing crop diversity (Figure 1, Tables S5 and S6). Except for three-species mixtures, arthropod diversity was always higher if no fertilizers or herbicides had been applied (low management intensity).

3.3 | Effects of crop and mixture identity on arthropod diversity

Observation data showed that the presence of faba bean and linseed, in monoculture or mixture, leads to an increase in flower visitor diversity (Figure 2a). Pan trap data showed that arthropod diversity was influenced by an interaction between crop mixture and management: Arthropod diversity was highest in linseed-oilseed rape mixtures, faba bean-oilseed rape mixtures and linseed monocultures under low-intensity management; and in oilseed rape monocultures and wheat-faba bean-linseed mixtures under high-intensity management (Figure 2b). Both methods show that crop mixtures significantly increased arthropod diversity (Tables S5 and S6).

3.4 | Plant–flower visitor networks and network metrics

The number of flower visits was higher under low-intensity than under high-intensity management (Table S7). On untreated (low-intensity management) plots, fewest visits were observed on wheat monocultures (35 visits) and fallow ('no crop') plots (53 visits). Number of visits increased when linseed was present. Wheat-faba bean-linseed mixtures were visited most frequently (612 visits, Figure 3a, Table S7).

Under high-intensity management, fewest visits were observed when no flowering crop was sown (i.e. two visits on wheat monocultures and 16 visits on 'no crop' plots). With increasing proportion of linseed (from 33% in three-species mixtures and 50% in two-species mixtures to 100% in monocultures), more visits were observed (i.e. 353 visits in linseed monocultures, Figure 3b, Table S7). Overall, bees mainly visited linseed, while hoverflies mainly visited weeds and faba beans.

The mean number of interactions as well as the number of flower visitor species and Shannon's diversity of interactions was lowest in high-intensity wheat monocultures and no crop plots. Values for all indices increased considerably in mixtures containing linseed as well as in linseed monocultures. Shannon's diversity of interactions

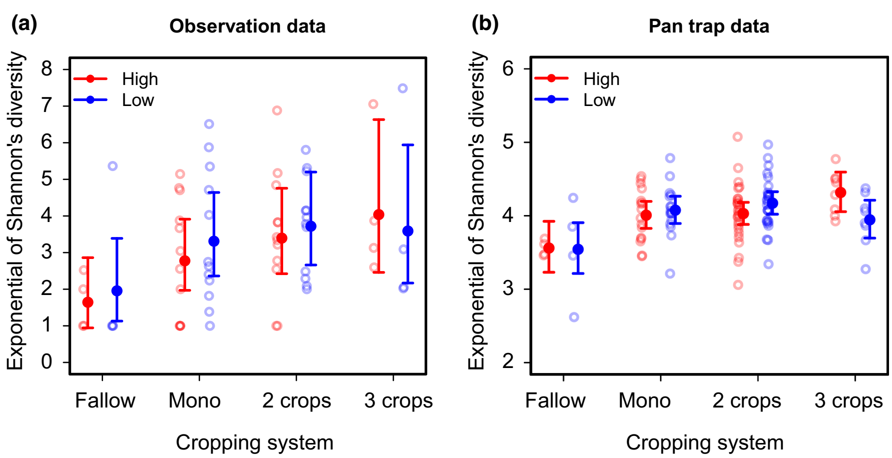

FIGURE 1 Biodiversity responses to increased crop diversity within cropping systems. (a) Flower visitor and (b) arthropod diversity for four different cropping systems (Fallow: no crop was sown, but weeds were present; Mono: crop monoculture, 2 crops; two-species mixture; 3 crops: three-species mixture) for high (red) and low (blue) management intensity. Graphs show raw data (open circles) and model fits (filled circles) with 95% confidence intervals, predicted from generalized linear mixed-effects models from a, flower visitor observations ($N = 64$; Cropping system: $\chi^2 = 13.06$, $p = 0.005$) and b, pan traps ($N = 104$; Cropping system: $\chi^2 = 16.08$, $p = 0.001$).

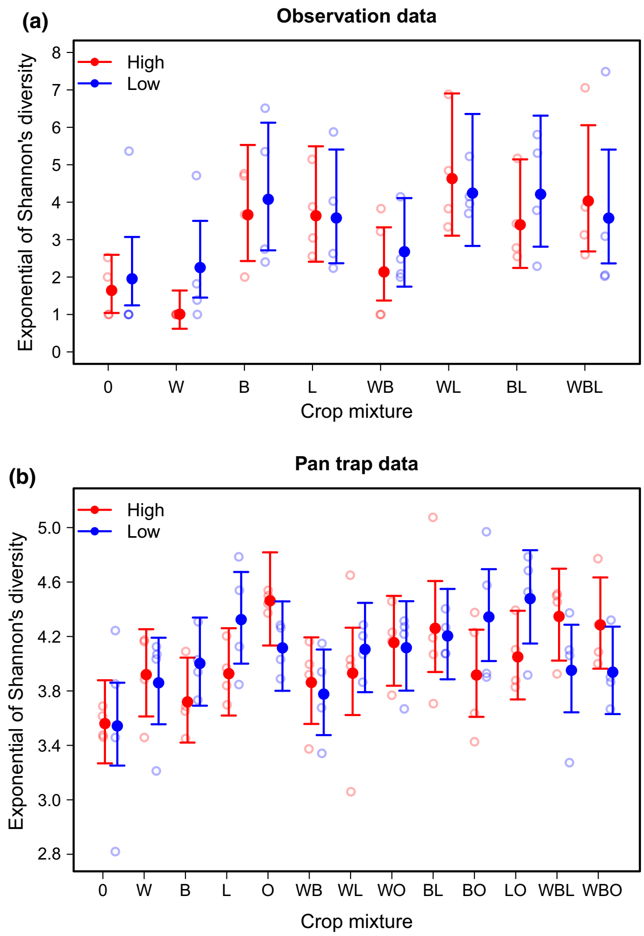

FIGURE 2 Biodiversity responses to crop mixtures. (a) Flower visitor and (b), arthropod diversity for a range of crop mixtures (0, fallow where no crop was sown; W, wheat; B, faba bean; L, linseed; O, oilseed rape; WB, wheat-faba bean; WL, wheat-linseed; WO, wheat-oilseed rape; BL, faba bean-linseed; BO, faba bean-oilseed rape; LO, linseed-oilseed rape; WBL, wheat-faba bean-linseed; and WBO, wheat-faba bean-oilseed rape) for high (red) and low (blue) management intensity. Graphs show raw data (open circles) and model fits (filled circles) with 95% confidence intervals, predicted from generalized linear mixed-effects models for (a), flower visitor observations ($N = 64$; Crop mixture: $\chi^2 = 60.66$, $p < 0.001$) and (b), pan traps ($N = 104$; Crop mixture: $\chi^2 = 40.98$, $p < 0.001$).

was also high in faba bean monocultures. In most cases, values were higher for low compared with high-intensity management (Figure 4, Tables S8 and S9).

3.5 | Arthropod abundances

Flower visitor observations showed that abundances were usually higher under low-intensity management (Figure 5a,b), while pan trap data (all arthropods) showed a reversed trend (Figure 5c,d). Pan traps which were placed on linseed plots contained fewer arthropods than traps on plots sown with other crops. Conversely, observations on plots containing linseed showed highest numbers of flower visits (Tables S10 and S11).

3.6 | Crop biomass

Crop biomass was influenced by an interaction between crop mixture and management, but not by crop diversity (Tables S12 and S13). Under high management intensity, crop biomass increased with crop diversity, while under low management intensity, biomass was highest in two-species mixtures. Notably, biomass was low in oilseed rape monocultures and in mixtures containing oilseed rape (except linseed-oilseed rape mixtures, Figure S3).

4 | DISCUSSION

Data from our agricultural field experiment show the importance of increased crop diversity in cropping systems for arthropod diversity and abundances. Independent of the sampling methods employed, we consistently found that higher crop diversity increased arthropod and flower visitor diversity (hypothesis 1). Crop identity played an important role as well, as some mixtures had more arthropods or were visited more frequently than others (hypothesis 2). In our study, especially linseed was visited often, both in mixtures and in monocultures. This suggests that when a mass-flowering crop is available, this crop is more important than other less conspicuous crops (in our case faba bean) or weeds, masking their effects. Consequently, plant–flower visitor networks that we analysed here were dominated by linseed; when this crop was available, we found particularly many interactions, a high number of flower visitor species and therefore also a high Shannon's diversity of interactions.

The intensity of agrochemical input had only limited effects in our study (hypothesis 3), likely because the applied rates of pre-emergence herbicide and fertilizer were still very low in comparison with high-intensity monocropping. In fact, our own observations in intercropping trials so far have shown that intercropping allows for a 'system shift', where not really much management is necessary once the crops are sown; legumes will respond negatively to fertilizer, and herbicides (usually targeting either mono- or dicots) are inapplicable in mixtures after sowing. Some crop monocultures, such as linseed, showed particularly high insect abundances and diversity if they had been treated with pre-emergence herbicide and fertilizer, likely because they contained fewer weeds and higher flower density (personal observations). Increasing weed abundance in fields where no flowering crops are present (i.e. wheat monocultures) can maintain flower visitor populations and ensure pollination services (Bretagnolle & Gaba, 2015). While, in the present study, we did not explicitly perform pollinator exclusion experiments to measure pollination success, we have done so previously (Brandmeier et al., 2021) and shown that (at least for wheat/faba bean in intercropping) the increases in flower visitor abundance also lead to better pollination services.

As an alternative to accepting tolerable levels of weed densities in the field (Nicholls & Altieri, 2013), intercropping could be deliberately integrated also into conventional farming systems. Our predictions indicate that the number of flower visits could increase from

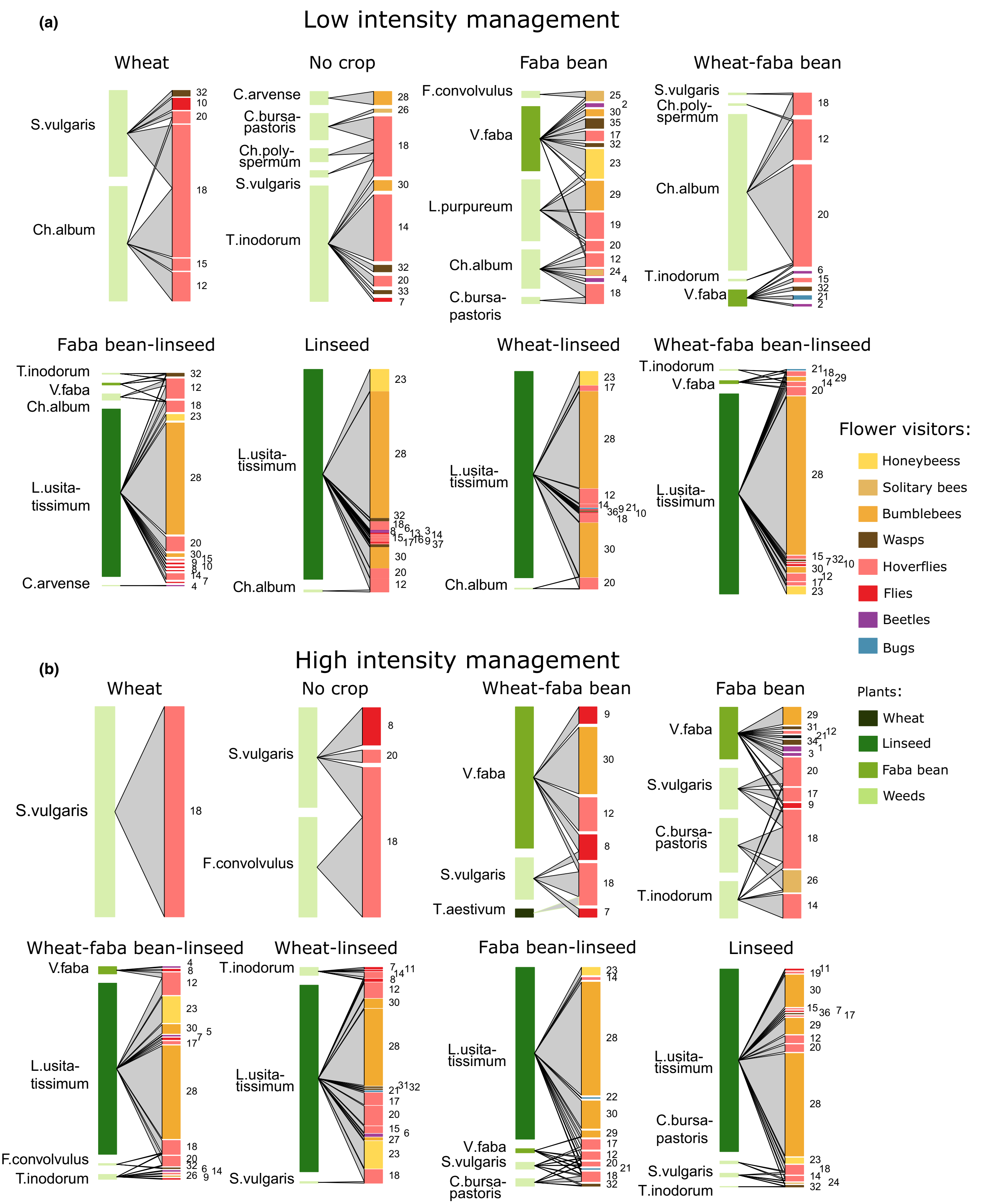

FIGURE 3 Bipartite plant–flower visitor networks for plots sown with different crop mixtures for (a), low- and (b), high-intensity management. Networks were generated by summing all visits for each group. $N = 4$ for each crop mixture and management intensity. Left section in networks represents plant species, and right section represents flower visitors (see Table S4). Small bars indicate fewer visits than wider bars. Networks are sorted by total number of visits, starting with the fewest (upper left network) and ending with the most (lower right network) within the two types of management intensity.

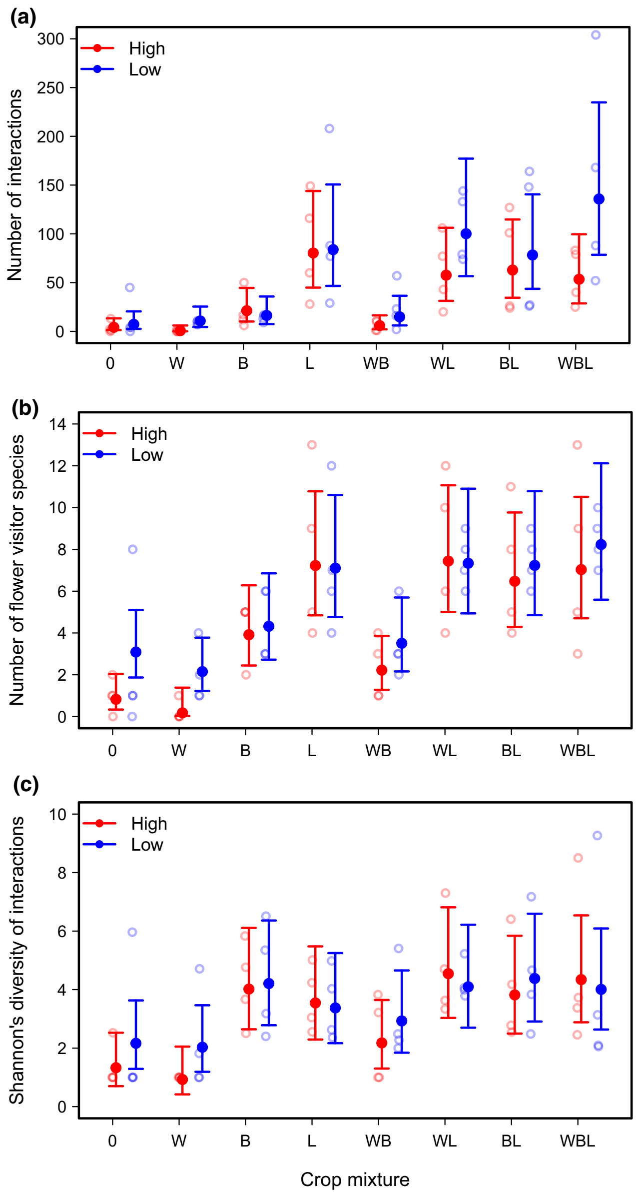

FIGURE 4 Bipartite plant–flower visitor network indices in response to crop mixtures. Graphs show data points (open circles), model predictions (filled circles) and 95% confidence intervals from generalized linear mixed-effects models for each crop mixture (0, fallow where no crop was sown; W, wheat; B, faba bean; L, linseed; WB, wheat-faba bean; WL, wheat-linseed; BL, faba bean-linseed; WBL, wheat-faba bean-linseed) under high (red) and low (blue) management intensity. $N=4$. (a) Number of interactions (Crop mixture: $\chi^2=176.65$, $p<0.001$; Crop mixture: Management: $\chi^2=17.04$, $p=0.017$), (b) number of flower visitor species (Crop mixture: $\chi^2=95.79$, $p<0.001$) and (c) Shannon's diversity of interactions (Crop mixture: $\chi^2=47.61$, $p<0.001$).

about 4700 visits/ha in wheat monocultures up to 566,000 visits/ha in wheat-bean-linseed mixtures. In low-input systems (comparable to organic farming), the number of visits could be as high as 1.5 million visits/ha in wheat-faba bean-linseed mixtures. Of course, such extrapolations from small plot sizes to field scale are ambitious, but at least they show the potential benefits of intercropping at larger scales.

Previous studies showed that ecosystem service delivery is positively influenced by the richness of service-providing organisms such as flower visitors (Dainese et al., 2019). Although honeybees (mainly the European honeybee *Apis mellifera* L.) are kept worldwide to provide crop pollination, other insects (such as wild bees, flies, beetles and wasps) have been reported to contribute more to total pollination than previously thought (Page et al., 2021; Rader et al., 2016). Floral abundance and richness are important for crop pollination services delivered by unmanaged flower visitors (Garibaldi et al., 2014; Kremen et al., 2007); thus, wild pollinator communities should be supported by increasing the floral abundance and richness in their environment. Obviously, monocultures of mass-flowering crops such as linseed or oilseed rape can serve as a food resource for particular taxa (*Bombus*) and for a limited period of time, but floral abundance can be increased using crop mixtures, too (comparing mixtures to cereal monocultures). The advantage of crop mixtures compared with a mass-flowering monoculture is that the monoculture (e.g. oilseed rape) has to be treated with higher amounts of fertilizers and pesticides. In mixtures, these amounts have to be reduced, especially if legumes are present. This could potentially lead to a system change in agriculture, leading away from intensively treated monocultures to less intensively treated mixtures.

Pollinators, as mobile organisms, respond to cropping system diversification at different spatial scales. Diversification methods have already been shown to benefit flower visitors and pollination services by enhancing floral diversity at the local scale (Albrecht et al., 2007; Garibaldi et al., 2014; Isbell et al., 2017). At the landscape scale, an increasing distance from a natural habitat may lead to lower wild bee richness, visitation numbers and fruit set (Garibaldi et al., 2011). Therefore, integrating flower-rich agricultural fields into conventional farming can provide important resources and improve the matrix quality (Perfecto et al., 2009) for flower visitors as well as other arthropods.

Our pan trap sampling showed that crop identity affected arthropod diversity and abundances. In oilseed rape monocultures and mixtures (especially wheat-oilseed rape and wheat-faba bean-oilseed rape mixtures), arthropod abundances were high, while plots including linseed attracted less individuals. These results can be explained by the poor crop performance of oilseed rape, which suffered from the late sowing date and only grew sparsely on some plots. Thus, plots with oilseed rape contained more bare ground and pan traps were more easily visible, leading to a higher attraction than in, for example, linseed plots. As is common for plot-based studies in randomized block designs, potential spillover effects among neighbouring plots were minimized by randomization, and we accounted for such spatial nonindependence in our statistical models using random effects for blocks and management.

While pan traps are suggested to be an efficient method for large-scale agricultural systems and to reduce collector biases (Westphal et al., 2008), they are taxon-specific and the catching success depends on colour (Moreira et al., 2016). Thus, for plot-based trials, we conclude that flower visitor observations seem to

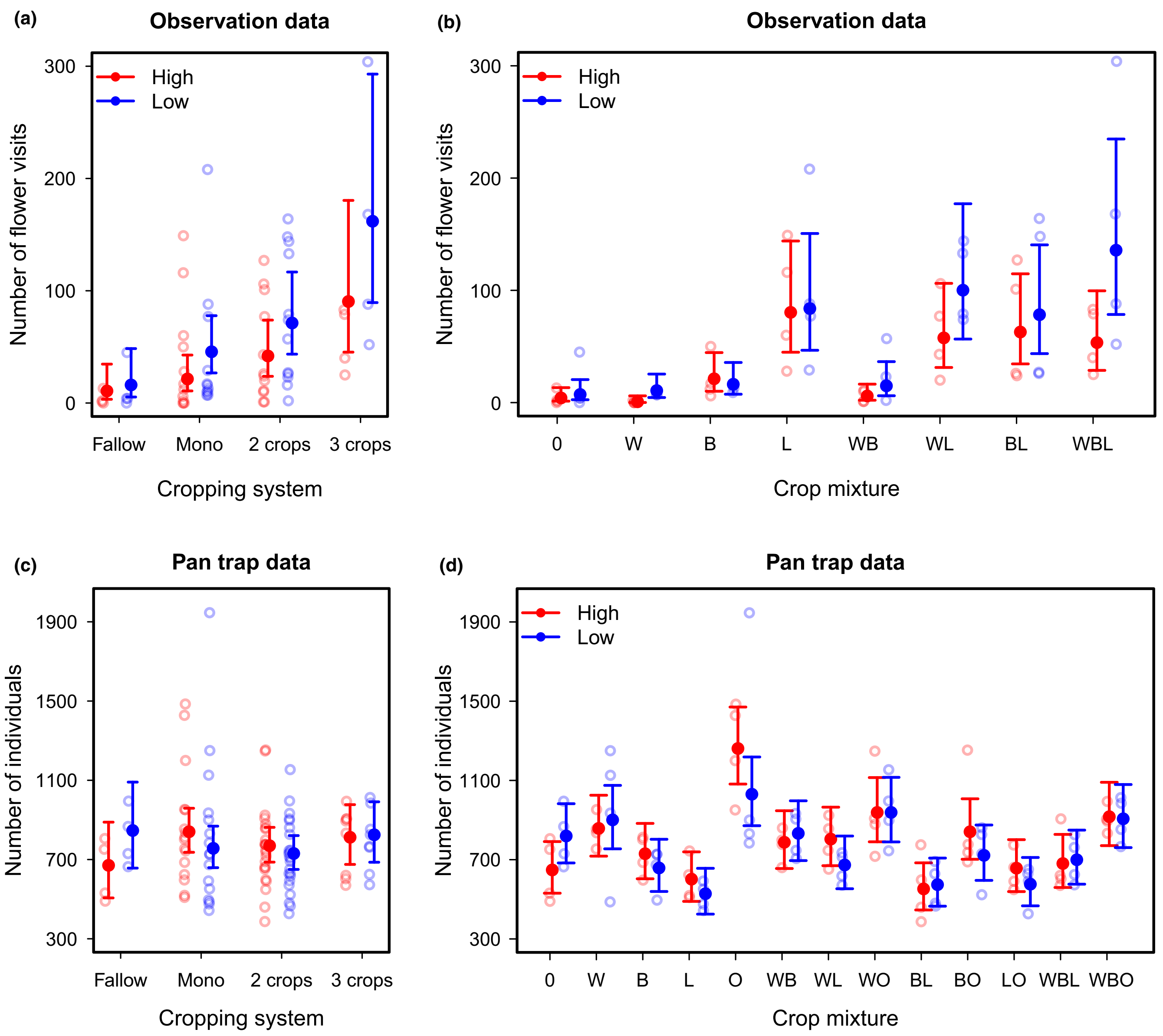

FIGURE 5 Number of visits and arthropod numbers in response to (a, c) four different cropping systems (Fallow: no crop was sown; Mono: crop monoculture, two crops; two-species mixture; 3 crops: three-species mixture) and (b, d) different crop mixtures (0, fallow; W, wheat; B, faba bean; L, linseed; O, oilseed rape; WB, wheat-faba bean; WL, wheat-linseed; WO, wheat-oilseed rape; BL, faba bean-linseed; BO, faba bean-oilseed rape; LO, linseed-oilseed rape; WBL, wheat-faba bean-linseed; and WBO, wheat-faba bean-oilseed rape) for high (red) and low (blue) management intensity. Graphs show raw data (open circles) and model fits (filled circles) with 95% confidence intervals, predicted from generalized linear mixed-effects models from (a, b) flower visits ($N=64$; Cropping system: $\chi^2=35.36$, $p<0.001$; Management: $\chi^2=8.68$, $p=0.003$ and Crop mixture: $\chi^2=176.65$, $p<0.001$; Crop mixture: Management: $\chi^2=17.04$, $p=0.017$) and (c, d) all arthropods caught in pan traps ($N=104$; Crop mixture: $\chi^2=145.06$, $p<0.001$).

be more appropriate (see also Venjakob et al., 2016). The observed subplot represents a sufficient part of the whole plot, and we were able to generate plant–flower visitor networks from qualitative observation data (Nielsen et al., 2011). On the contrary, observations can also be rather time-consuming and may lead to biases when conducted by multiple observers (Westphal et al., 2008), which was not the case in our study (we always used the same observers). Using high-resolution camera traps could be an efficient and standardized method to simultaneously assess flower visits on multiple plots. Indeed, we employed such a camera trapping setup on the same site; these results will be reported elsewhere. When using high-technology cameras or camera traps with adequate resolution, flower visitors can be determined up to species or family level (Droissart et al., 2021) with low sampling effort. We acknowledge that the taxonomic resolution in the present study was limited; future studies could, for example, employ DNA metabarcoding approaches, especially for taxa that are difficult to distinguish under field conditions.

5 | CONCLUSIONS

Based on our multifactorial intercropping trial, we suggest to integrate intercropping into agricultural systems, as arthropod diversity can clearly benefit from increased crop diversity, especially also under high-intensity management. Based on our experiments and also on results from our own previous study at the same location (Brandmeier et al., 2021), we conclude that a full mixing of crops at adequate densities (50:50 or others, depending on crop competitive performance) can be beneficial for both crop yields and biodiversity enhancement. Thinking intensive farming and intercropping together can transform European farmland into a more insect-friendly matrix. Additionally, the choice of crops is relevant; bringing in some mass-flowering crops at 10%–50% density can provide important 'stepping stone' resources for arthropods, at least during the growth period. In-field diversification through intercropping should thus become part of everyday's agricultural landscapes.

AUTHOR CONTRIBUTIONS

Jana Brandmeier, Hannah Reininghaus and Christoh Scherber conceived the ideas and designed methodology; Jana Brandmeier and Hannah Reininghaus collected the data; all authors analysed the data, wrote the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.f4qrfj71v (Scherber et al., 2023).

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SUPPORTING INFORMATION

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

Figure S1. Experimental design of the DIVERSify field trial in 2019.

Figure S2. Details on the field site and the experimental plots.

Figure S3. Crop biomass as a function of (a) crop diversity within cropping systems (Fallow: no crop was sown; Mono: crop monoculture, 2 crops; two-species mixture; 3 crops: three-species mixture) and (b) crop mixtures (0, fallow where no crop was sown; W, wheat; B, faba bean; L, linseed; O, oilseed rape; WB, wheat-faba bean; WL, wheat-linseed; WO, wheat-oilseed rape; BL, faba bean-linseed; BO, faba bean-oilseed rape; LO, linseed-oilseed rape; WBL, wheat-faba bean-linseed; WBO, wheat-faba bean-oilseed rape) for high (red) and low (blue) management intensity.

Table S1. Overview of crops, crop mixtures, varieties and sowing densities for plots on which data collection was carried out.

Table S2. List of weed species that grew on the experimental plots.

Table S3. List of arthropods caught in pan traps.

Table S4. Information about flower visitors present in networks (see Figure 3).

Table S5. Chi-square (χ^2) values, degrees of freedom (df), significance levels and family distributions for generalized linear mixed-effects models on (a) flower visitor (observation data) and (b) arthropod diversity (pan trap data).

Table S6. Model summaries using successive difference contrasts showing coefficients for generalized linear mixed-effects models on (a) flower visitor diversity (observation data) and (b) arthropod diversity (pan trap data) vs. crop diversity (Div), crop mixture (Mix, ordered factor: ordered by expected number of flowers) and management (high vs. low intensity).

Table S7. Total number of flower visits corresponding to the networks in Figure 3 for each crop mixture for high and for low intensity management ($N = 4$).

Table S8. Chi-square (χ^2) values, degrees of freedom (df), significance levels and family distributions for generalized linear mixed-effects models on network metrics.

Table S9. Model summaries using successive difference contrasts showing coefficients for generalized linear mixed-effects models on network metrics vs. crop mixture (Mix, ordered factor: ordered by expected number of flowers) and management (high vs. low intensity).

Table S10. Chi-square (χ^2) values, degrees of freedom (df), significance levels and family distributions for generalized linear mixed-effects models on flower visitor abundance (observation data) and total arthropod abundance (pan trap data).

Table S11. Model summaries using successive difference contrasts showing coefficients for generalized linear mixed-effects models on a) number of flower visits (observation data) and b) total number of individuals (pan trap data) vs. crop diversity (Div), crop mixture (Mix, ordered factor: ordered by expected number of flowers) and management (high vs low intensity).

Table S12. Chi-square (χ^2) values, degrees of freedom (df), significance levels and family distributions for generalized linear mixed-effects models on crop biomass.

Table S13. Model summaries using successive difference contrasts showing coefficients for generalized linear mixed-effects models on crop biomass vs. crop diversity (Div), crop mixture (Mix, ordered factor: ordered by expected number of flowers) and management (high vs low intensity).

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