ORIGINAL ARTICLE

Insect Conservation
and Diversity

Royal Entomological Society

A novel farmland wildflower seed mix attracts a greater abundance and richness of pollinating insects than standard mixes

Rachel N. Nichols[1] | John M. Holland[2] | Dave Goulson[1]

[1]School of Life Sciences, John Maynard Smith (JMS) Building, University of Sussex, Brighton, UK

[2]Game and Wildlife Conservation Trust, Hampshire, UK

Correspondence
Rachel N. Nichols, School of Life Sciences, John Maynard Smith (JMS) Building, University of Sussex, Falmer, Brighton, BN1 9QG, UK.
Email: r.nichols@sussex.ac.uk

Abstract

1. Wildflower strips are a popular agri-environment scheme (AES) implemented on farmland to provide forage for insect pollinators. The standard seed mixtures were often formulated without a clear evidence base, and subsequent field trials to assess their attractiveness to insects are commonly carried out at low taxonomic resolution (e.g., pooling all 'solitary' bees).

2. We created two novel wildflower mixes: a wild bee mix based on primary research (WB) and one on literature-based evidence (LT). We trialled our novel mixes against two standard AES wildflower mixes: a Fabaceae-heavy mix (FAB); a diverse wildflower mix (WF); plus a fallow plot (control). Our aim was to determine which mix attracted the highest overall insect pollinator abundance and highest species richness for wild bees.

3. Our WB mix attracted both the highest number of total insect visitors, and the highest wild bee abundance and richness. WB attracted significantly more bumblebees (abundance and richness) than the typical low diversity, Fabaceae-heavy mix (FAB); and significantly greater solitary bee abundance, than all other treatments.

4. Only 11 'key' wildflower species were required to cater to all wild bee species recorded during the study, eight of which were sown species. *Taraxacum officinale* agg., *Cirsium vulgare*, *Daucus carota* and *Geranium pyrenaicum* received the highest numbers of wild bee species visits.

5. In conclusion, we suggest a novel wildflower seed mix based on primary research has the potential to provide more attractive forage for both wild bees and other insect pollinators compared to current AES mixes.

KEYWORDS
agri-environment scheme, bumblebees, flower strip, solitary bees, wild bees

INTRODUCTION

Land-use change brought about by agricultural intensification is generally considered to be the main driver of farmland biodiversity decline, as semi-natural habitats and weeds have become increasingly scarce (Foley et al., 2005; Potts et al., 2010). To counteract the negative effects of modern farming practices, agri-environment schemes (AES) have been implemented throughout the Western world in an

attempt to restore biodiversity in agricultural landscapes (Harmon-Threatt & Hendrix, 2015; Howlett et al., 2021; Lindenmayer et al., 2012; Scheper et al., 2015).

Wildflower strips are a popular AES employed on farmland throughout Europe to provide forage for wild pollinators and insect predators of crop pests (Ouvrard et al., 2018; Tschumi et al., 2016). These strips have the potential to provide a diverse resource for the insect community, as both food for adults foraging on pollen and nectar (e.g., bees), or as host plants for insect larvae (e.g., Lepidoptera; Curtis et al., 2015). Different flower species produce pollen and nectar of varying nutritional components, qualities, and quantities. The main nutritional component of nectar is carbohydrate in varying quantities (Hicks et al., 2016), while pollen is a source of protein and lipids (Jeannerod et al., 2022). Insects such as bees must not only consume sufficient quantities of food to meet their own energy expenditure requirements, but must also obtain an adequate and diverse range of nutrients to feed their larvae. Where nutritional components are missing, evidence suggests reproductive success is decreased (Brunner et al., 2014; Génissel et al., 2002).

Wildflower strips are typically created adjacent to crops in field margins, comprised of non-competitive grasses and wildflower species. These wildflower seed mixes differ in the number of wildflower species and in their target taxa. For example, mixes can contain as few as 4–6 species (DEFRA, 2013), or in excess of 50 species (Warzecha et al., 2018) and may not always include grasses depending on the country and region. Some mixes contain a high proportion of Fabaceae species that have the potential to attract specialist pollinators (Carvell et al., 2007; Kleijn et al., 2018), while others contain a higher proportion of Apiaceae and Asteraceae species that attract short-tongued generalists (Kleijn et al., 2018). Mixes can also be specialised to a geographical region, for example, there is a specific list of species allowed to be sown on the Swiss plateau through AES (Tschumi et al., 2016).

Studies measuring the impact of wildflower strips on pollinating insect abundance or diversity typically assess a single seed mix (Carvell et al., 2011; Haaland & Bersier, 2011; Ouvrard et al., 2018), or compare multiple seed mixes that are available locally through AES agreements (Grass et al., 2016; Warzecha et al., 2018). Examples include early research showing that a (Fabaceae-heavy) pollinator-targeting mix was more effective at providing bumblebee forage than a grass-only seed mix or natural regeneration (Carvell et al., 2007); while recent research comparing multiple wildflower seed mixes found that it was the presence of 'key plant species' rather than floral diversity that attracted the highest insect richness (Warzecha et al., 2018). Few studies have considered novel or bespoke seed mixes (though see Griffiths-Lee et al., 2022; Uyttenbroeck et al., 2017), nor do they include the evidence base for selecting certain species for a flower mix. Uyttenbroeck et al. (2017) created four bespoke seed mixes of varying functional diversity (FD) levels and found that FD had no effect on pollinator abundance or richness, but that pollinator visitations could occasionally be explained by floral abundance of specific plant species. Moreover, studies have historically focused on single insect groups, such as just *Bombus* species or

butterflies (Carvell et al., 2007; Haaland & Bersier, 2011). More recently, solitary bees, hoverflies, and non-bee species (Howlett et al., 2021; Warzecha et al., 2018; Wood et al., 2017), along with the wider insect community (Grass et al., 2016; Ouvrard et al., 2018) have also been taken into consideration. For example, Scheper et al. (2021) trialled two seed mixes, one targeting long-tongued pollinators such as bumblebees, and another targeting more generalist species and predators such as hoverflies. Their study found that bumblebee abundance was positively associated with the amount of Fabaceae cover, while hoverflies were positively associated with Apiaceae cover. Therefore, it is timely to further consider the wider insect community and its interaction with novel seed mixes.

In this study we assess the whole flower-visiting insect community as well as focusing on wild bees. We compared two standard AES wildflower seed mixes with our own two novel wildflower seed mixes and with unsown fallow plots. Our novel seed mixes were designed to attract maximum wild bee visitations, but had the potential to also attract a broad range of insect pollinators (Nichols et al., 2022a). The aims of our study, therefore, were to:

1. Identify which wildflower mix attracted (a) the highest number of insect pollinators; and (b) the highest wild bee abundance and richness;
2. Determine which wildflowers were key resources for wild bees.

MATERIALS AND METHODS

Creating wildflower mixes

We created two novel wildflower mixes (see Nichols et al., 2022a, for details on the selection process used, which is summarised here). First, we used the existing literature to select wildflowers that were shown to be key resources for a diversity of solitary bees within agricultural settings (Howlett et al., 2021). Second, we created a novel mix through primary research on a wildflower farm (Nichols et al., 2019), selecting the wildflowers that attracted the highest richness of wild bees. Plant species were placed into categories according to their flowering phenology: late-spring, early-summer, mid-summer, and late-summer to ensure we had at least 1–2 species flowering within each period (Williams et al., 2015), and any species that were unavailable were removed. We also included four annual cornfield species to both mixes to act as a 'nursery' in the first year: poppy (*Papaver rhoeas*), corn marigold (*Glebionis segetum*), cornflower (*Centaurea cyanus*) and corncockle (*Agrostemma githago*). Our final literature-based mix (LT) contained 17 wildflower species, and our primary research-based wild bee mix (WB) contained 16 wildflower species. We also used two standard AES mixes available in the United Kingdom (UK): a Fabaceae-focused mix of six species (FAB), and a typical wildflower mix of 12 species (WF). All mixes were created with 20:80 ratio of wildflowers to non-competitive grasses, except for FAB which was made with 100% wildflower seeds following normal farming practice (see Supplementary Information S1 for seed mix details).

Study site

The study was conducted in a single field on two farms: Church Farm, Oxfordshire (51°38′14.4348″N, 1°11′5.4528″W) and Lee Farm, West Sussex (50°53′0.2112″N, 0°28′24.1464″W). The farms were of different soil type and the fields had received different management prior to our experiment commencing. Church Farm has freely-draining, base-rich loamy soil of high fertility, and the field had recently been in production. It also had a high abundance of aggressive weeds (e.g., *Cirsium vulgare, Alopecurus myosuroides*). Lee Farm had lime-rich loamy soils over chalk, the field had been out of production for 2–3 years, and any natural regeneration had been cut and ploughed yearly, breaking up any perennial thistles and encouraging annuals. Seed mixes were sown in 2018 on 4th and 5th September respectively. Both sites were cultivated and sprayed-off using glyphosate herbicide as ground preparation to aid establishment. The ground was then rolled, seeds were broadcast sown by hand, and then rolled again to ensure sufficient seed-to-soil contact.

Seed mixes were sown in 20 × 5 m contiguous plots. Our treatment consisted of four different seed mixes: FAB, WF, LT, WB; and a fallow (control). Each treatment was replicated 5 times on each farm, therefore each farm had 25 20 × 5 m plots. Seed mixes were allocated to plots using a Latin-square-type design to ensure no mix was next to itself. Plots were then marked by a GPS device to store and re-find the plot locations for surveys.

All plots on a farm were managed the same way, but cuts were performed according to need on each farm. Church Farm was cut in May 2019 when thistles began to take over the plots, and then in June during both 2020 and 2021 when plants started to collapse under their own weight. Lee Farm was cut in July in both 2019 and 2020 when growth began to collapse. Both farms were also then cut during the autumn months in 2019 and 2020 once the majority of plants had seeded and growth could be removed.

Floral and insect surveys

Surveys were conducted from April to August in 2019, 2020 and 2021. They were conducted every 2–3 weeks, providing a total of eight survey rounds each year. Farms were surveyed on two separate days close to one another for each of the eight survey periods. Surveys were not conducted on a farm if they would occur immediately after a cut, since nothing would be in flower. During each survey, each plot was walked centrally lengthways and insects visiting flowers seen 2 m either side were identified to group-level on the wing. Bees and hoverflies were then further identified to species-level. Those that could not be identified to species-level on the wing were captured for identification in the lab by RNN. Specimens that were not able to be identified by RNN were sent to Steven Falk and Ellen Rotheray for identification. Flower species seen 2 m either side were also noted and the estimated abundance of open flowers in the plot recorded (Campbell et al., 2017; Wood et al., 2017). 'Flower' was defined as either a single flower, flowers on an umbel or spike, or a capitulum

(Heard et al., 2007). A maximum of 10 minutes was allowed for each plot. Surveys were conducted between 08:30 and 17:00 when the temperature was above 13°C with at least 60% clear sky, or above 17°C in any sky conditions, and not raining (Pollard & Yates, 1993).

Data analysis

All data analysis was handled in R version 4.0.3 (R Core Team, 2020). Zero-inflated Generalised Linear Mixed Models were built using the *glmmTMB* package (Brooks et al., 2017). Shannon's Diversity index was calculated for the 'plant diversity' of each plot for every survey conducted and included as an explanatory variable (Griffiths-Lee et al., 2022) in each model to improve model fit. 'Survey round' was also included as an explanatory variable in each model. 'Replicate' nested within 'farm' was included as a random variable in each model. Models testing insect 'richness' were built with a 'Poisson' log link, and models testing insect 'abundance' were built using a 'negative binomial' family after conducting residual plot diagnostic checks. An ANOVA was then performed on each model and its null, reported as χ^2 values, and post hoc Tukey tests were conducted to see where the significance lay when appropriate. All figures were created using *ggplot2* (Wickham, 2016).

First, the plant and insect abundance heatmap was created by calculating the total abundance of the flowers and all insects visiting each flower, per plot, averaged across replicates, survey periods, mixes, farms, and years.

Next, we assessed the treatment effect on insect visitation. All insect visits were summed for each plot, per survey round, per farm, per year (hereon referred to as total insect abundance). A model was built to test the effect of 'treatment' and 'survey year', and their interaction, as predictor variables.

Following this, we built models to determine the effect of 'treatment' and 'survey year', and their interaction, on wild bee abundance and richness (also considering solitary bees and bumblebees separately). The number of wild bees (abundance), and the number of wild bee species (richness) were summed for each plot, per survey round, per farm, per year.

To identify the plant species most significantly visited by wild bees, we calculated their species strength. First, insect visits to each wildflower species were pooled across treatments and years. 'Species strength' is defined as the sum of dependencies (proportion of visits) of flower visitors relying on a specific plant species, and was calculated on the pooled data using the 'strength' function in the *bipartite* package (Dormann, 2011). To identify the minimum plant species composition needed to cover all wild bee species (hereafter 'key wildflower species'), we first took the plant species attracting the highest number of wild bee species and subsequently added plant species attracting most of the remaining wild bee species until all wild bee species were covered. Seed mixture potential was defined as the percentage of key wildflower species within each plot (Warzecha et al., 2018). A Linear Model was built to test the effect of 'treatment' on the 'percentage' of key plant species in each plot, and the result is reported as an *F*-statistic.

The wild bee-plant visitation network was calculated after identifying abundance of each wild bee species visiting each plant species over the whole 3-year experiment, removing any species that were seen less than three times, and then analysed and visualised with the 'computeModules' and 'plotModuleWeb' functions, in the *bipartite* package.

RESULTS

Overall visitation network

A total of 4002 insects were recorded making flower visits to the plots over the 3 years. Visits to flowers were dominated by Diptera (flies; excluding hoverflies; 28.1% of all visits), followed by Coleoptera (beetles; 20.6%) and *Bombus* spp. (bumblebees; 20.0%). Non-corbiculate wild bees (solitary bees) accounted for 14.8% of visits, and Syphridae (hoverflies) made up 8.6% of visits. The remaining 7.9% of visits were made up of *Apis mellifera* (honeybees), Lepidoptera (butterflies), and solitary wasps.

We recorded 79 flower species across 21 families in the plots, including 28 sown and 51 spontaneous species (see Nichols et al., 2022a, for details on success of sown plant species). Insect visits were recorded to 55 flower species across 15 families, with 75.5% of visits to 26 sown species and 24.5% of visits to 29 spontaneous species (Figure 1). Insect visits were predominantly made to Asteraceae species (58.0%), followed by Apiaceae (14.2%) and Fabaceae (7.5%) species (see Supplementary Information S2 for full list of plant–insect interactions).

There were 1390 visits made to flowers by wild bees. Of the bees recorded, 1124 (80.9%) were identified to species level: 798 bumblebees across six species, and 326 solitary bees across 34 species. Bumblebee
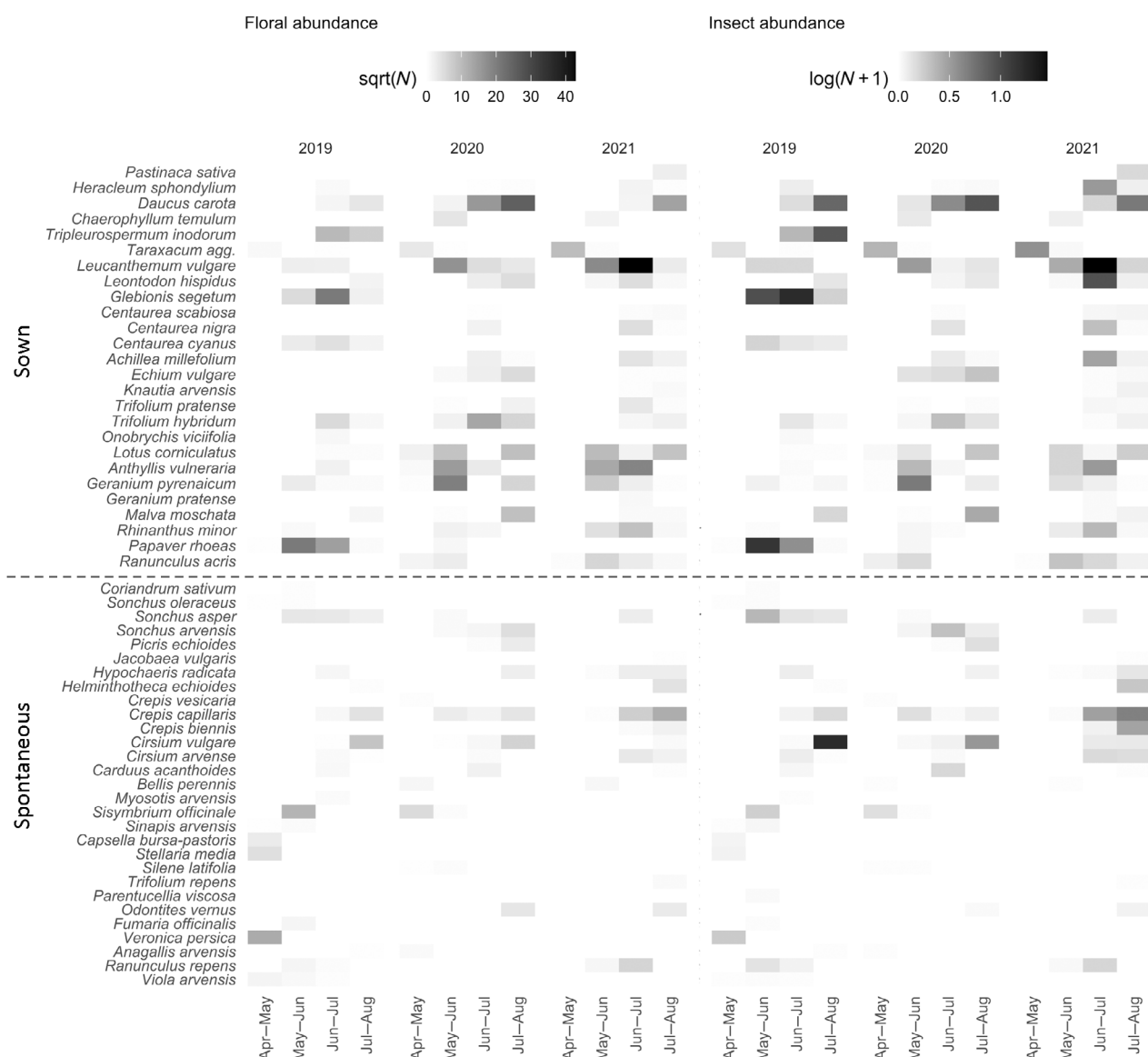

FIGURE 1 Flower and insect counts for each plant species visited. Counts summed for each plant species within each plot for the survey period, and then averaged between replicates, farms, and years. Mean number of flowers observed (square-root-transformed) and mean insect abundance (log-transformed) per flower species (each calculated per 80 m^2).
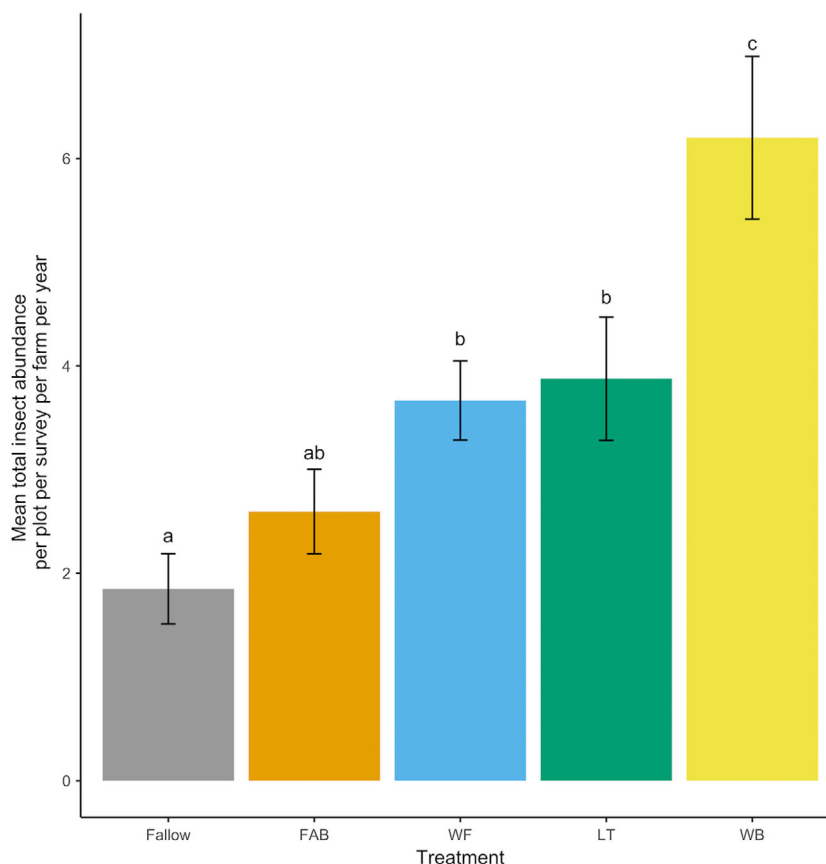
FIGURE 2 Total insect visits to each treatment. Mean total insect abundance per treatment, summing values for each plot, averaging across replicates, survey periods, farms and years. Significance (post hoc Tukey) of treatments denoted by lettering (±SE).

visits were recorded mainly to Fabaceae species (29.7%), Asteraceae species (27.9%), and Papaveraceae (26.0%); whereas solitary bee visits were heavily focused on Asteraceae species (58.9%), followed by Apiaceae (12.4%) and Geraniaceae (9.5%).

Bumblebees visited 33 flower species, with visits predominantly made to *Papaver rhoeas* (25.9% of bumblebee visits) over the 3 years, followed by *Cirsium vulgare* (18.3%) and *Anthyllis vulneraria* (15.1%). Honeybees visited just 16 species, with most visits to *Cs. vulgare* (47.5%). Solitary bees visited the highest number of flower species (38), with visits predominantly to *Taraxacum officinale* agg. (13.9%), *Daucus carota* (9.5%), *Geranium pyrenaicum* (9.5%) and *Leucanthemum vulgare* (9.3%). Hoverflies visited the second highest number of flower species (37), with visits directed to *Lc. vulgare* (20.2%) and *Crepis capillaris* (18.1%). Other flies visited 36 flower species, with visits split mainly between *D. carota* (26.4%), *Lc. vulgare* (16.9%), and *Glebionis segetum* (14.0%). Beetles visited 23 flower species, with visits predominantly made to *G. segetum* (21.6%), *Leontodon hispidus* (13.5%) and *Lc. vulgare* (12.0%) (see Supplementary Information S3 for pollinator visitation network analysis).

Treatment effect on visitations

Treatment had a significant effect on total insect abundance (GLMM: $\chi^2 = 52.4$, $p < 0.001$; Figure 2), with the WB mix attracting significantly more insect visitors than all other treatments, when controlling for plant diversity. Additionally, although WF and LT attracted significantly lower insect abundances than WB, they attracted significantly greater numbers than the fallow control. There was no significant difference between the fallow plots or FAB mix in terms of insect abundance (see Supplementary Information S4 for insect abundance of each insect group).

There was also a significant interaction effect of treatment × year on total insect abundance (GLMM: $\chi^2 = 15.9$, $p = 0.044$), though no effect of year alone on total insect abundance (GLMM: $\chi^2 = 3.36$, $p = 0.186$).

Treatment also had a significant effect on total wild bee abundance and richness, with the WB mix attracting significantly greater abundance (GLMM: $\chi^2 = 42.0$, $p < 0.001$), and richness (GLMM: $\chi^2 = 31.4$, $p < 0.001$), compared to all other treatments, when controlling for plant diversity. Breaking down the wild bee abundance into solitary bee and bumblebee counts (Figure 3), there were significantly more solitary bee counts on the WB treatment than all other treatments (after post hoc Tukey analysis) (GLMM: $\chi^2 = 25.6$, $p < 0.001$), and there was no significant difference in solitary bee abundance between the fallow plots and FAB, WF or LT mixes. Similarly, there were significantly more bumblebee counts on the WB mix than on the Fallow, FAB and LT treatments (GLMM: $\chi^2 = 27.8$, $p < 0.001$). There was no significant difference in bumblebee abundance between the fallow plots and the FAB or LT mixes.
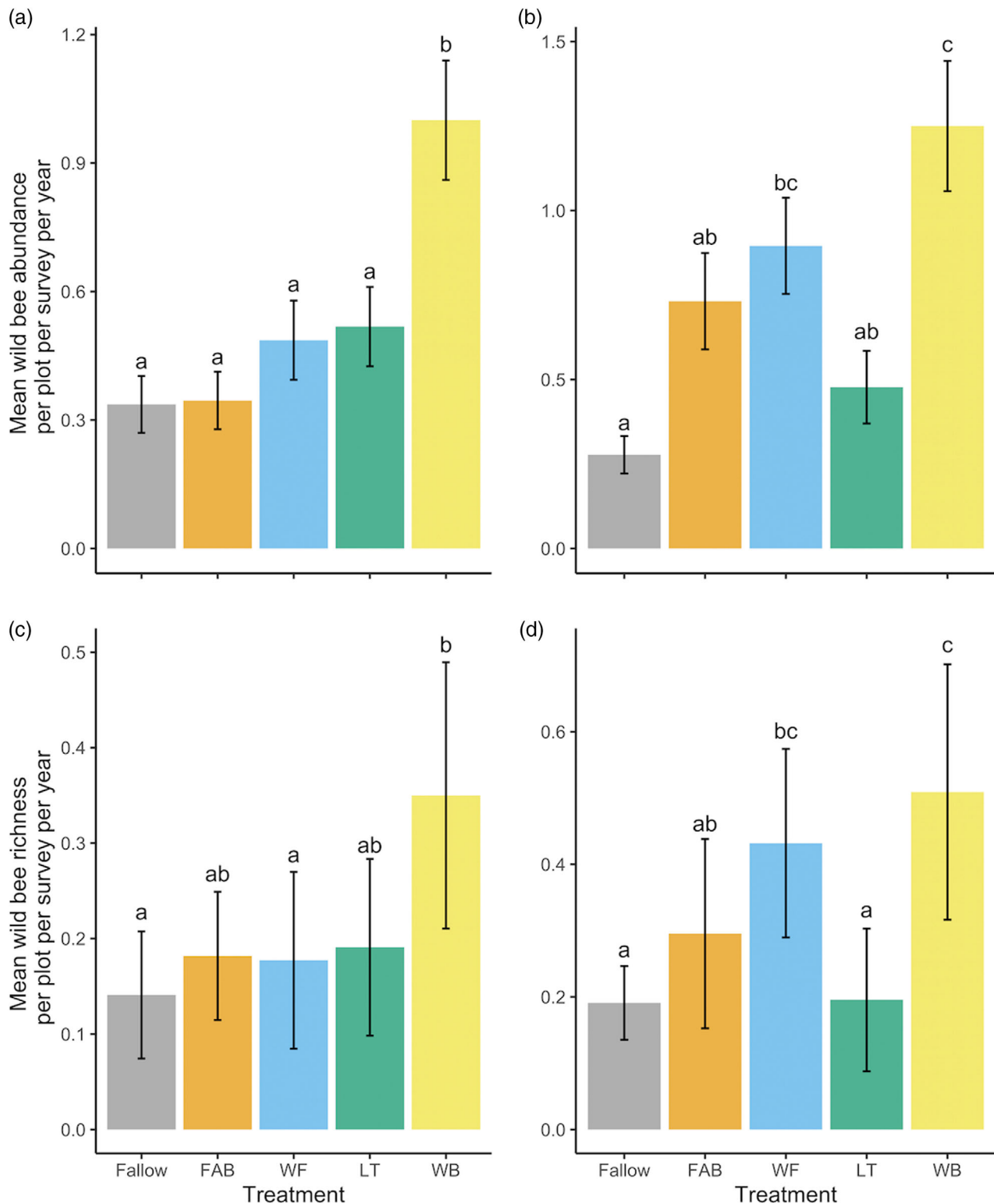
FIGURE 3 Solitary bee and bumblebee visits to each treatment. Mean wild bee abundance for (a) solitary bees and (b) bumblebees; and mean wild bee richness for (c) solitary bees and (d) bumblebees; calculated for each treatment summing values for each plot, averaging across replicates, survey periods, farms and years. Significance (post hoc Tukey) denoted by lettering (±SE).

Likewise, there were significantly more solitary bee species on the WB treatment than on the Fallow or WF plots (GLMM: $\chi^2 = 13.7$, $p = 0.008$), once more with mixes FAB, WF and LT attracting no more solitary bee species than the fallow plots. There were also significantly more bumblebee species on the WB mix than on the Fallow, FAB and LT treatments (GLMM: $\chi^2 = 26.7$, $p < 0.001$).
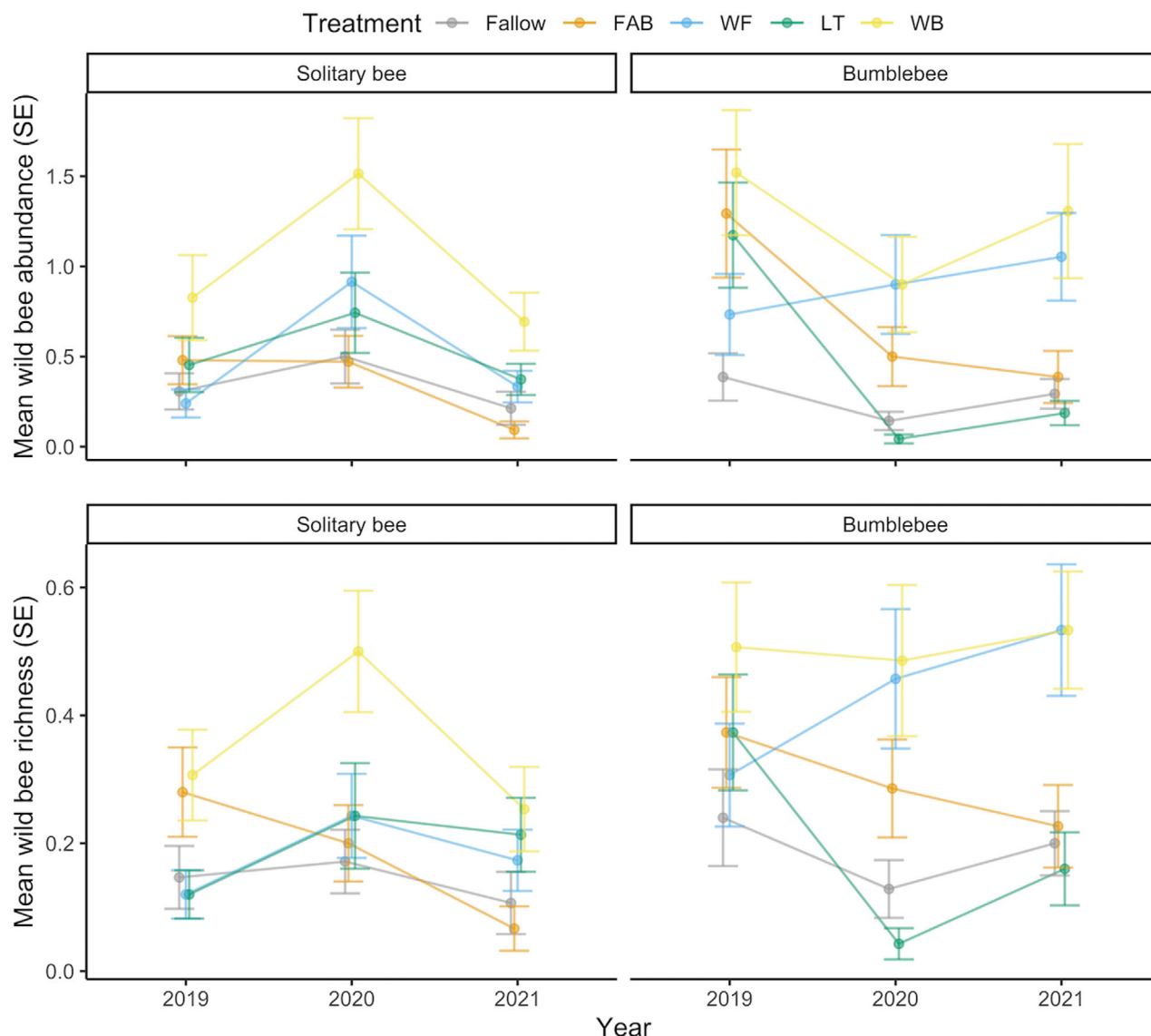
NEW WILDFLOWER MIX ATTRACTS MORE BEES

Insect Conservation
and Diversity

Royal
Entomological
Society

7

FIGURE 4 Wild bee abundance and richness per year per treatment. Mean solitary bee and bumblebee abundance and richness, calculated for each treatment, summing each plot, averaging across replicates, survey periods, and farms, per year (±SE).

There was a significant interaction effect of treatment × year on wild bee abundance (GLMM: $\chi^2 = 21.1$, $p = 0.007$). This could be explained when separating the two taxa. Both solitary bees (GLMM: $\chi^2 = 16.5$, $p = 0.036$) and bumblebees (GLMM: $\chi^2 = 25.9$, $p = 0.001$) showed significant interaction effects of treatment × year, but solitary bees had significantly higher abundance during the 2020 survey than the 2019 or 2021 surveys (GLMM: $\chi^2 = 16.5$, $p < 0.001$; Figure 4), with WB mix showing the highest abundance overall; whereas bumblebees had significantly higher abundance during 2019 survey than in 2020 or 2021 (GLMM: $\chi^2 = 17.2$, $p < 0.001$).

There was also a significant interaction effect of treatment × year on wild bee richness (GLMM: $\chi^2 = 20.5$, $p = 0.009$). When separating the two taxa, there was no significant interaction effect of treatment × year on solitary bee richness (GLMM: $\chi^2 = 13.2$, $p = 0.104$), though there was an effect of year alone (GLMM: $\chi^2 = 8.56$, $p = 0.014$), potentially explained by the peak in solitary bee richness seen in the WB mix during the 2020 survey. Whereas there was a significant

interaction effect of treatment × year on bumblebee richness (GLMM: $\chi^2 = 28.1$, $p < 0.001$), potentially caused by the high and increasing levels of bumblebee richness in the WB and WF mixes, compared to the low and decreasing levels in the other treatments from year to year. By contrast, there was no significant effect of year alone on bumblebee richness (GLMM: $\chi^2 = 3.60$, $p = 0.166$).

The FAB mix was the only mix to show a consistent decline in both solitary bee and bumblebee abundance and richness from 2019 to 2021 (Figure 4), while the WF mix showed a general increase in bumblebee abundance and richness from 2019 to 2021. Solitary bee abundance and richness remained the highest in the WB mixes for all 3 years.

Key wildflower species for wild bees

Wildflower species visited by wild bees were ranked according to their species strength (Table 1). The top four plant species (Cs. vulgare,

TABLE 1 Plant species visited by wild bees over the 3-year study

Flower species	Species strength	No. of visitors	Origin	No. of surveys (/8) in flower
Taraxacum agg.	**5.53**	**83**	**Sown**	**6**
Cirsium vulgare	**4.61**	**157**	**SB**	**5**
Daucus carota	**4.55**	**59**	**Sown**	**7**
Geranium pyrenaicum	**3.90**	**76**	**Sown**	**7**
Crepis capillaris	**2.46**	**40**	**SB**	**6**
Leontodon hispidus	**1.81**	**19**	**Sown**	**6**
Sisymbrium officinale	**1.71**	**14**	**SB**	**6**
Trifolium hybridum	**1.55**	**50**	**Sown**	**5**
Echium vulgare	**1.50**	**51**	**Sown**	**5**
Papaver rhoeas	**1.46**	**233**	**Sown**	**7**
Tripleurospermum inodorum	**1.28**	**21**	**Sown**	**6**
Cirsium arvense	0.87	10	SB	5
Leucanthemum vulgare	0.85	61	Sown	7
Glebionis segetum	0.74	44	Sown	6
Veronica persica	0.63	10	SB	4
Ranunculus acris	0.56	18	Sown	7
Centaurea cyanus	0.54	32	Sown	6
Anthyllis vulneraria	0.49	121	Sown	7
Lotus corniculatus	0.45	71	Sown	7
Sonchus asper	0.42	12	SB	7
Centaurea scabiosa	0.39	8	Sown	3
Chaerophyllum temulum	0.35	11	Sown	5
Stellaria media	0.34	5	SB	4
Capsella bursa-pastoris	0.34	5	SB	3
Rhinanthus minor	0.30	51	Sown	7
Ranunculus repens	0.29	3	SB	8
Carduus acanthoides	0.23	18	SB	6
Centaurea nigra	0.19	17	Sown	5
Helminthotheca echioides	0.16	5	SB	3
Sonchus arvensis	0.16	11	SB	5
Trifolium pratense	0.15	8	Sown	7
Hypochaeris radicata	0.15	11	SB	5
Crepis biennis	0.12	5	SB	3
Odontites vernus	0.12	8	SB	2
Onobrychis viciifolia	0.10	3	Sown	5
Coriandrum sativum	0.09	1	SB	1
Sinapis arvensis	0.09	1	Sown	4
Achillea millefolium	0.08	9	Sown	4
Parentucellia viscosa	0.08	2	SB	1
Picris echioides	0.07	8	SB	3
Knautia arvensis	0.07	3	Sown	4
Viola arvensis	0.06	2	SB	8
Heracleum sphondylium	0.04	5	Sown	3
Malva moschata	0.03	5	Sown	5
Fumaria officinalis	0.03	1	SB	5

(Continues)

TABLE 1 (Continued)

Flower species	Species strength	No. of visitors	Origin	No. of surveys (/8) in flower
Trifolium repens	0.03	1	SB	4
Anagallis arvensis	NA	1	SB	6

Note: 'Species strength' refers to the sum of dependencies (proportion of visits) of flower visitors relying on a specific plant species (only of wild bees that were identified to species level), 'No. of visitors' refers to counts of all wild bees to each species, and 'Origin' refers to whether the plant grew spontaneously from the seedbank (SB) or was sown in a mix (sown). The 'top 11' species that attracted all 40 wild bee species are in bold.

TABLE 2 Total wild bee visits over 3-year study to different plant species

Apr–May	%	May–Jun	%	Jun–Jul	%	Jul–Aug	%
Solitary bee visits							
Taraxacum agg.	69.9	**Geranium pyrenaicum**	25.0	**Glebionis segetum**	19.0	Crepis capillaris	18.4
Veronica persica	8.8	**Leucanthemum vulgare**	19.4	**Daucus carota**	16.8	**Daucus carota**	16.7
Sisymbrium officinale	7.1	Crepis capillaris	8.9	**Leucanthemum vulgare**	9.2	**Leontodon hispidus**	11.4
Capsella bursa-pastoris	4.4	**Ranunculus acris**	8.9	Carduus acanthoides	7.1	**Tripleurospermum inodorum**	8.8
Stellaria media	4.4	**Papaver rhoeas**	7.2	**Papaver rhoeas**	6.5	**Geranium pyrenaicum**	7.9
Bumblebee visits							
Lotus corniculatus	60.0	**Papaver rhoeas**	46.5	**Papaver rhoeas**	25.3	Cirsium vulgare	55.9
Anthyllis vulneraria	20.0	**Anthyllis vulneraria**	20.8	**Anthyllis vulneraria**	23.6	**Lotus corniculatus**	11.7
Taraxacum agg.	20.0	**Lotus corniculatus**	10.4	**Rhinanthus minor**	14.4	Echium vulgare	9.3
		Geranium pyrenaicum	6.3	**Trifolium hybridum**	12.2	Odontites vernus	3.2
		Rhinanthus minor	4.7	**Centaurea nigra**	3.9	**Trifolium hybridum**	2.4

Note: The percentage of total solitary bee and bumblebee visits to each flower species within each survey period, listing the five most commonly visited species within each survey period. Sown species are bold.

T. officinale agg., *D. carota*, *G. pyrenaicum*) attracted 34 of the 40 wild bee species recorded, and the 'top 11' species accounted for all 40 species and 57.8% of all wild bee visits. The top 11 plant species included eight sown, and three spontaneous. Sown *T. officinale* agg. had the highest species strength, as it attracted 14 species of solitary bee, one species of bumblebee, and a total of 83 wild bees over the 3-year study. Each treatment was assessed for the percentage of 'top 11' wildflower species recorded at the plot level, and a significant difference was identified between treatments ($F_{4,45} = 9.61$, $p < 0.001$). Post hoc analysis showed the WB mix had significantly more of the 'top 11' key plant species per plot than any other treatment.

Taking the 12 most successful sown plant species in terms of their abundances across both farms (*Anthyllis vulneraria*, *D. carota*, *G. pyrenaicum*, *Lotus corniculatus*, *Ln. hispidus*, *Lc vulgare*, *Malva moschata*, *Rananculus acris*, *Rhinanthus minor*, *Trifolium hybridum*. *T. officinale* agg., and *Tr. pratense*; Nichols et al., 2022a), only 5/12 species were included in the 'top 11' plants for wild bees (Table 1). By contrast, these 12 species attracted 33 out of the 40 wild bee species recorded and 44.7% of all wild bee visits. They also attracted 46.3% of total insect visits, and encompassed visits from all insect pollinator groups.

Bumblebees relied heavily on sown species during the 3-year study (Table 2). Only two species growing from the seedbank were identified as being highly preferred foraging plants for bumblebees during the Jul–Aug survey period (*Cs. vulgare* and *Odontites vernus*).

Both *L. corniculatus* and *A. vulneraria* remained consistently highly visited forage plants for bumblebees across the season, with *P. rhoeas* being key during both May–Jun and Jun–Jul survey periods.

Solitary bees, on the other hand, relied upon a greater number of species growing from the seedbank across the season. They relied most heavily upon sown *T. officinale* agg. during the Apr–May survey period, but other significant forage species all germinated from the seedbank during this early period (*Veronica persica*, *Sisymbrium officinale*, *Capsella bursa-pastoris*, and *Stellaria media*). *Geranium pyrenaicum*, *Lc. vulgare*, *D. carota* and *P. rhoeas* were all sown species identified as highly visited forage plants in more than one survey period, along with *Cr. capillaris* from the seedbank. Alongside *P. rhoeas*, another cornfield annual, *G. segetum*, was also highly visited by solitary bees.

Analysis of the structure of the plant–wild bee flower visitation network showed that the network was modular (Figure 5). Modularity analysis detected five modules when looking at wild bee species that were recorded a minimum of three times. *Andrena* species were largely grouped together in module 5, which was formed of earlier flowering plant species such as *T. officiniale* agg., *V. persica*, *Sinapsis arvensis* and *Chaerophyllum temulum*. Unexpectedly, *Tr. hybridum* is also included within this group. *Lasioglossum calceatum* and *L. malachurum* formed their own module (3) associated strongly with Asteraceae species (*G. segetum*, *Lc. vulgare* and *Tripleurospermum inodorum*). *Bombus* species can be found across three modules, with *B. hortorum* and *B. pascuorum* forming one module, both visiting *A. vulneraria*, *Tr. pratense*, and
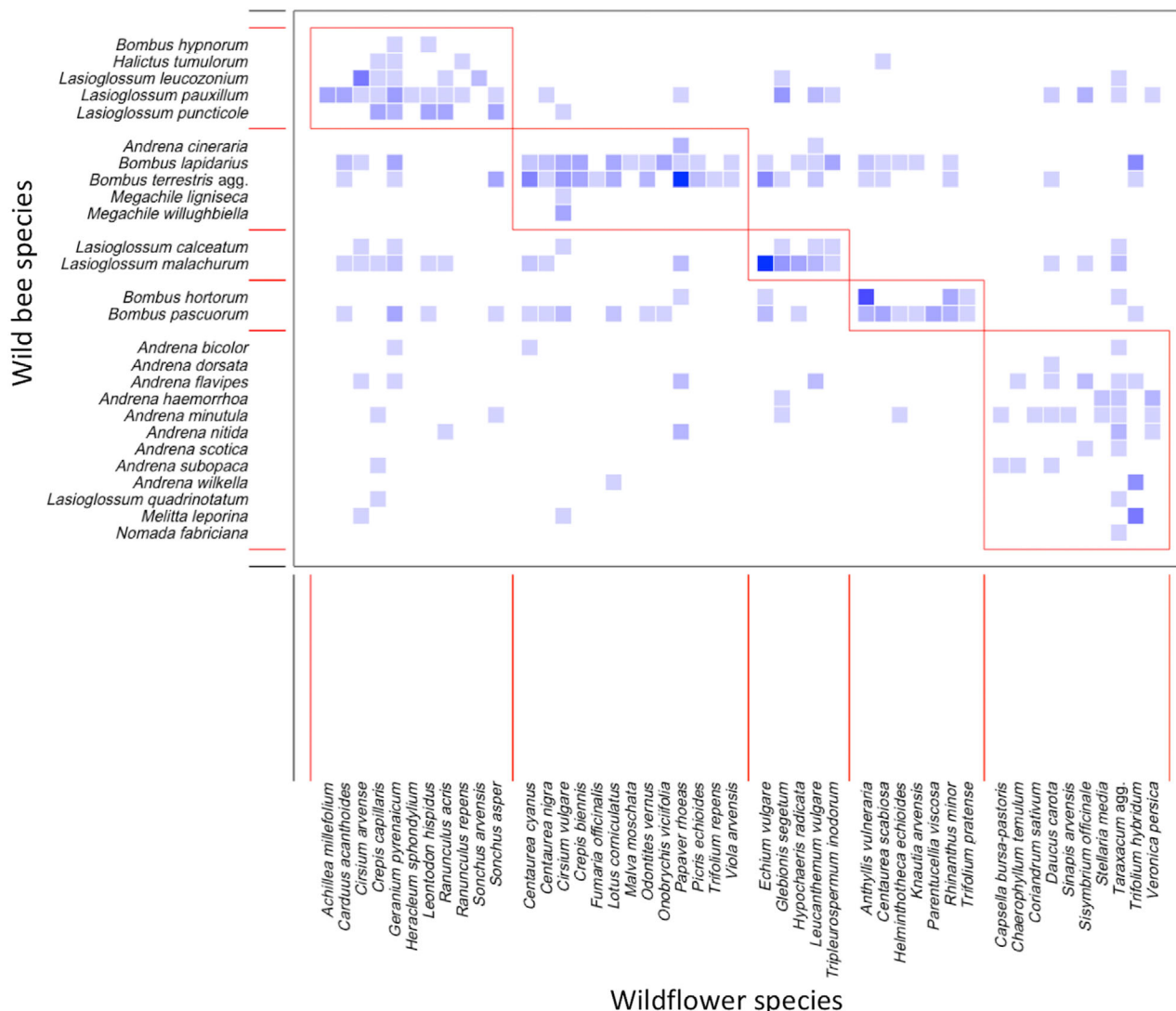
FIGURE 5 Modules detected in the plant–wild bee flower visitation network. Results of modularity analysis of wild bee visitations (>2 records). Wild bees are displayed in columns and plants in rows. The blue rectangles show observed interactions with more frequent interactions shown by darker colour. Modules are numbered as 1–5 from the top-left to the bottom-right.

Rhinanthus minor. Bombus terrestris and *B. lapidarius* are combined with three larger solitary bees (two *Megachile* species and *A. cineraria*), forming a module that included the highest number of plant species. Finally, *B. hypnorum* joins the remaining Halictidae species, with most species visiting *G. pyrenaicum* and *Heracleum sphondylium* (see Supplementary Information S5 for all observed plant–wild bee interactions).

DISCUSSION

Treatment effect on visitations

Wildflower seed mixes created through regional primary research could be considered for future AES. Seed mixes are typically produced to either follow specific AES guidelines (Schmidt et al., 2020; Warzecha et al., 2018), the local abiotic conditions (e.g., soil type; Haaland & Bersier, 2011; Nowakowski & Pywell, 2016), or to target a specific taxa or insect group (Carvell et al., 2011; Kleijn et al., 2018). Here we showed that a mix created through primary research to attract a target insect group (wild bees) was successful, despite being sown on two farms with different soil types, management histories, and different seed banks (Nichols et al., 2022a). Studies have previously shown that targeted AES are better at producing optimal abundance and diversity of a target taxa than general AES (Carvell et al., 2011; Wood, Holland, & Goulson, 2015a; Wood, Holland, Hughes, & Goulson, 2015b). Our WB mix was not only successful at attracting the highest abundance and richness of wild bees compared to the other treatments, but also the highest total insect abundance, suggesting it was attractive to other taxa as well (Ouvrard et al., 2018). Although conducting region-specific primary research to identify key species is far costlier than adhering to a generic national seed mix, it should be considered if we are to better support the wider pollinator community.

We suggest that Fabaceae-heavy seed mixes such as the one trialled in this study and that have been widely used by farmers should be updated to include a broader range of species. When composed of only 4–6 wildflower species (as recommended; DEFRA, 2013), this mix not only lost floral abundance rapidly as grasses became predominant (Carvell et al., 2007; Nichols et al., 2022a), but it performed poorly in terms of overall abundance of insect visitors, and wild bee visitors. Early research showed that the Fabaceae-heavy mixes could attract high bumblebee abundance and support specialist species (Carvell et al., 2007; Pywell et al., 2006). By contrast, our results showed the Fabaceae mix was statistically no better than a fallow plot for attracting bumblebees (though see Cole et al., 2022 for contrasting evidence of a low diversity Fabaceae mix). Only one species typically included in the mix, *Tr. hybridum*, was found to be an attractive plant for wild bees (in the 'top 11' species). Therefore, we suggest that the mix is updated, and instead, species that attracted very few wild bees (e.g., *O. vicifollium*) are removed, and replaced with a Fabaceae that did attract bumblebees (e.g., *Anthyllis vulneraria*). Additional key species that attracted high diversity of other wild bees across the whole spring–summer season (e.g., *D. carota*, *G. pyrenaicum*, *T. official* agg.) could replace the less attractive *M. moschata* and *C. nigra*. This would create a low diversity, low-cost AES seed mix that delivers greater benefit for a wider range of pollinators.

The nutritional components of pollen and nectar varies widely between plant species and families (Hanley et al., 2008; Jeannerod et al., 2022), which can in turn limit the growth and survival of bee broods. Brunner et al. (2014) found that a diet consisting of just *Taraxacum spp.* resulted in failure to lay eggs in *B. terrestris* micro-colonies; while Austin and Gilbert (2021) found *Osmia bicornis* larvae survival was positively correlated with carbohydrate quantity. Therefore, bee species benefit from a diverse diet in which pollen and nectar are sourced from a variety of plant species in order to obtain all essential amino acids and sufficient quantities of sugar nectar (Hanley et al., 2008; Jeannerod et al., 2022; Vaudo et al., 2015). Although our novel WB mix was found to attract the greatest abundance of insect pollinators, we did not record if visits were made for pollen or nectar foraging/collection. Therefore, it is difficult to attribute a nutritional benefit to the seed mix or specific plant species within it. Additionally, all foragers recorded were adult forages, therefore it is unclear if they were foraging for their own consumption, or collecting to provide for offspring. As the protein and carbohydrate contents of food can have a big effect on the reproductive success, this should be considered when forming a wildflower seed mix (Jeannerod et al., 2022).

Finally, we encourage creating mixes that can cater to both solitary bees and bumblebees within a single mix (so long as the species included do not require very different management strategies). Our modularity analysis showed that species from both taxa foraged relatively separately, reducing competition between small solitary bees and larger solitary bees and bumblebees. Therefore, if there is only space or financial benefit from sowing a single wildflower strip on farmland, we have shown that all wild bees can be catered for within it.

Sown species

Sown species were a significant resource for insect pollinators on farmland. Certain sown species attracted high numbers of insect visitors, and eight of our 'top 11' plant species for wild bees were sown species. *Daucus carota*, *G. segetum*, *G. pyrenaicum*, *Lc. vulgare*, and *T. officinale* agg. were all shown to either be highly visited sown species, attracting high overall insect abundances or a high abundance and richness of wild bees (as seen in previous studies: Dicks et al., 2002; Klecka et al., 2018; Nichols et al., 2019; Ouvrard et al., 2018; Warzecha et al., 2018; Wood et al., 2017). Asteraceae species have been shown to hold some of the highest nectar and pollen quantities due to their capitulum of tiny florets (Hicks et al., 2016). Similarly, *D. carota* has relatively low quantities of nectar sugar per flower, but as the flowers are grouped *en masse* in umbellifers, and flower in high abundance, it provides large overall quantities of nectar (Hicks et al., 2016). This in turn reduces flight time and energy expenditure for adult foragers, allowing them to provide large quantities of nectar to the brood in a shorter time frame, making these species valuable resources to bees as well as other insects.

Bumblebees were particularly reliant on sown species, with few spontaneous species receiving high numbers of visits. The only plant species visited by bumblebees in the trial plots during the early season surveys were sown species (*Tr. hybridum*, *A. vulneraria*, *T. officinale*), indicating that spontaneous species found on farmland during this period could be relatively unattractive to bumblebees (Falk & Lewington, 2015; Wood, Holland, & Goulson, 2015a; Wood, Holland, Hughes, & Goulson, 2015b).

Solitary bees relied upon a diverse range of sown species within Asteraceae, Apiaceae, Geraniaceae and Ranunculaceae. Although solitary bees are known to often rely upon spontaneous plants in farmland (McHugh et al., 2022; Wood et al., 2017), our study shows that they will also readily use sown plants. *Geranium pyrenaicum* was particularly significant to species within the Halictidae family, while *T. officinale* agg. provided forage for a wide range of *Andrena* spp. *Taraxacum officinale* agg., although sown in our mixes, is historically considered a horticultural (Tilman et al., 1999) and organic-farming weed (Carr, 2017), and not a weed of concern in modern farming, and is not regularly included in European wildflower seed mixes (Nichols et al., 2022a). Here we showed the importance of including it in a seed mix, as it not only had the highest species strength for wild bees, but it was the only sown species in relatively high abundance during the early-season surveys (Nichols et al., 2022a), therefore providing substantial nectar and pollen to early emerging species (Hicks et al., 2016).

We suggest that cornfield annuals are added to future wildflower seed mixes. *Papaver rhoeas* and *G. segetum* were shown to be attractive to wild bees and other insect pollinators, likely due to their high yielding pollen rewards (Hicks et al., 2016). As they are not long-lasting, they should not be relied upon to provide forage for insects year-on-year. By contrast, they can act as a 'nursery', suppressing the growth of weeds and allowing the perennial mix to establish during the first year (Emorsgate Seeds, 2021; Nichols et al., 2022a). They

may be a better nurse crop than grasses as they are unlikely to persist, unlike grasses which can become too predominant, especially on fertile soils. Further research is needed as to whether grasses should be included in seed mixes, as many recent European studies trialling seed mixes appear to not include grasses (Scheper et al., 2021; Schmidt et al., 2020; Schoch et al., 2022) or are recommended at a lower proportion (pers. comm., J. Bijkirk).

Spontaneous species

Spontaneous species played a particularly important role for solitary bees, however, the inclusion of 'weeds' in a wildflower seed mix should be carefully considered. Both *Cr. capillaris* and *Cs. vulgare* grew spontaneously in the plots and were highly visited by wild bees, as seen in other studies (Balfour & Ratnieks, 2022; Carvell et al., 2007; McHugh et al., 2022; Nichols et al., 2019). This is most likely due to high nectar sugar quantities (Hicks et al., 2016), however, some spontaneous species such as *Cs. vulgare*, are injurious weeds, competing with crops (DEFRA, 2003; Maskell et al., 2020). Nevertheless, many species of annual arable plants arable are relatively uncompetitive, even at high densities, (Marshall et al., 2003). Herbicides also differ in their efficacy on different species offering an opportunity for selective weed control, while crops also differ in their ability to compete with weeds. The challenge is therefore to manage weed populations to benefit biodiversity (Storkey & Westbury, 2007) and ensure that they do not cause a greater ecosystem disservice than benefiting biodiversity (Tschumi et al., 2018).

Recommendations for further research

Insect–plant interactions are shaped by complex ecological mechanisms related to the functioning of the entire ecosystem. These mechanisms influence the quantity and quality of food resources offered to pollinators by plants that grow in different habitats. We conducted this study on only two farms, with particular geology, climate, and flora. Therefore, it is unknown if similar results would be obtained in other agricultural environments. We suggest primary research into flower species favoured by insect visitors is carried out in other areas, both nationally and globally, before 'pollinator targeting' seed mixes are sown. This ensures that the species sown are more likely to attract their target taxa, not only encouraging farmers to continue conservation efforts, but also saving financial resources by only planting the most useful species. Additionally, the nutritional benefits of these plant species should also be considered when designing seed mixes in the future.

We suggest our mix is trialled across a wider range of soil types, assessed over a longer time period, using larger sized plots that are more akin in real field margins (Ouvrard et al., 2018). Additionally, short-term trials such as these are primarily assessing the attractiveness of the mix to local insect pollinator communities. More extensive and longer-term trials would be needed to determine if they can increase the community diversity and abundance.

There is always the possibility that wildflower strips are simply redistributing local insects in an area, or if they are boosting population numbers. Therefore, this mix should be trialled as an AES to test its cost, viability, and its long-term impact on insect pollinator populations.

Finally, although we have recorded non-bee visitors during our study, giving us a better picture of plant species required to support the greater insect pollinator community on farmland, these were adult foragers. Non-bee pollinators also require suitable resources for larvae, such as hostplants (Curtis et al., 2015). Over 65% of insect visits recorded to flowers were from non-bee species, and although most non-bee species provide a lower pollen deposition rate per visit than bees, due to their greater numbers they are likely to be important for the continued pollination service provided to both wildflowers and crops (Rader et al., 2016). Therefore, to achieve a continued pollination service, it is vital all life-stages are taken into consideration when forming a seed mix, as the functioning of the population depends on the nutritional requirements of juveniles being met. It may be that larval resources limit their populations on farmland, so that providing more floral resources may not increase the population. We identified plant species that attracted high abundances of adult non-bee insect pollinators (e.g., *D. carota*, *T. inodorum*, *Lc. vulgare*, *Ln. hispidus*, *G. segetum*, and *P. rhoeas*), and it would be interesting to investigate further the resources required to also support additional life-stages of non-bee insect pollinators.

AUTHOR CONTRIBUTIONS

Rachel Nichols: Data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); writing – original draft (lead). **John Holland:** Conceptualization (supporting); methodology (equal); supervision (supporting); writing – review and editing (equal). **Dave Goulson:** Conceptualization (lead); methodology (equal); supervision (lead); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors have no competing interests to declare that are relevant to the content of this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study (Nichols et al., 2022b) are openly available in NERC EDS Environmental Information Data

Centre: https://doi.org/10.5285/ca785f4c-5e45-4743-83bb-e30dd620de2e

ORCID

Rachel N. Nichols https://orcid.org/0000-0002-0149-1820

REFERENCES

Austin, A.J. & Gilbert, J.D. (2021) Solitary bee larvae prioritize carbohydrate over protein in parentally provided pollen. *Functional Ecology*, 35(5), 1069–1080.

Balfour, N.J. & Ratnieks, F.L.W. (2022) The disproportionate value of 'weeds' to pollinators and biodiversity. *Journal of Applied Ecology*, 59, 1209–1218. Available from: https://doi.org/10.1111/1365-2664.14132

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9(2), 378–400. Available from: https://doi.org/10.32614/rj-2017-066

Brunner, F.S., Schmid-Hempel, P. & Barribeau, S.M. (2014) Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris*. *Proceedings of the Royal Society B: Biological Sciences*, 281(1786), 20140128.

Campbell, A.J., Wilby, A., Sutton, P. & Wäckers, F.L. (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture, Ecosystems & Environment*, 239, 20–29. Available from: https://doi.org/10.1016/J.AGEE.2017.01.005

Carr, P.M. (2017) Guest editorial: conservation tillage for organic farming. *Agriculture (Switzerland)*, 7, 19. Available from: https://doi.org/10.3390/agriculture7030019

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44(1), 29–40. Available from: https://doi.org/10.1111/j.1365-2664.2006.01249.x

Carvell, C., Osborne, J.L., Bourke, A.F.G., Freeman, S.N., Pywell, R.F. & Heard, M.S. (2011) Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. *Ecological Applications*, 21(5), 1760–1771. Available from: https://doi.org/10.1890/10-0677.1

Cole, L.J., Baddeley, J.A., Robertson, D., Topp, C.F.E., Walker, R.L. & Watson, C.A. (2022) Supporting wild pollinators in agricultural landscapes through targeted legume mixtures. *Agriculture, Ecosystems and Environment*, 323, 107648. Available from: https://doi.org/10.1016/j.agee.2021.107648

Curtis, R.J., Brereton, T.M., Dennis, R.L., Carbone, C. & Isaac, N.J. (2015) Butterfly abundance is determined by food availability and is mediated by species traits. *Journal of Applied Ecology*, 52(6), 1676–1684. Available from: https://doi.org/10.1111/1365-2664.12523

DEFRA. (2003) *The Weeds Act 1959, Preventing the spread of harmful weeds*. Department for Environment, Food and Rural Affairs.

DEFRA. (2013) *Entry level stewardship environmental stewardship handbook*. Available at: http://publications.naturalengland.org.uk/file/2781958 [Accessed October 25, 2018]

Dicks, L.V., Corbet, S.A. & Pywell, R.F. (2002) Compartmentalization in plant–insect flower visitor webs. *Journal of Animal Ecology*, 71, 32–43.

Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, 1(1), 1–20 Available at: http://www.iaees.orgArticle [Accessed March 29, 2022]

Dormann, C.F., Gruber, B. & Fründ, J. (2008) *Introducing the bipartite package: Analysing ecological networks* (Vol. 8). Available at: http://erzuli.ss.uci.edu/R.stuff [Accessed March 29, 2022]

Emorsgate Seeds. (2021) *Cornfield annuals as nurse cover*. Available at: https://wildseed.co.uk/page/cornfield-annuals-as-nurse-cover [Accessed November 16, 2021]

Falk, S.J. & Lewington, R. (2015) *Field guide to the bees of Great Britain and Ireland (first)*. London: Bloomsbury Publishing.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. et al. (2005) Global consequences of land use. *Science*, 309(5734), 570–574. Available from: https://doi.org/10.1126/science.1111772

Génissel, A., Aupinel, P., Bressac, C., Tasei, J.N. & Chevrier, C. (2002) Influence of pollen origin on performance of Bombus terrestris micro-colonies. *Entomologia Experimentalis et Applicata*, 104(2–3), 329–336.

Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V. et al. (2016) Much more than bees-wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. *Agriculture, Ecosystems and Environment*, 225, 45–53. Available from: https://doi.org/10.1016/j.agee.2016.04.001

Griffiths-Lee, J., Nicholls, E. & Goulson, D. (2022) Sown mini-meadows increase pollinator diversity in gardens. *Journal of Insect Conservation*, 26, 299–314. Available from: https://doi.org/10.1007/s10841-022-00387-2

Haaland, C. & Bersier, L.-F. (2011) What can sown wildflower strips contribute to butterfly conservation?: an example from a Swiss lowland agricultural landscape. *Journal of Insect Conservation*, 15(1–2), 301–309. Available from: https://doi.org/10.1007/s10841-010-9353-8

Hanley, M.E., Franco, M., Pichon, S., Darvill, B. & Goulson, D. (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology*, 22(4), 592–598. Available from: https://doi.org/10.1111/j.1365-2435.2008.01415.x

Harmon-Threatt, A.N. & Hendrix, S.D. (2015) Prairie restorations and bees: the potential ability of seed mixes to foster native bee communities. *Basic and Applied Ecology*, 16(1), 64–72. Available from: https://doi.org/10.1016/j.baae.2014.11.001

Heard, M.S., Carvell, C., Carreck, N.L., Rothery, P., Osborne, J.L. & Bourke, A.F.G. (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. *Biology Letters*, 3(6), 638–641. Available from: https://doi.org/10.1098/rsbl.2007.0425

Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E. et al. (2016) Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows. *PLoS One*, 11(6), e0158117. Available from: https://doi.org/10.1371/journal.pone.0158117

Howlett, B.G., Todd, J.H., Willcox, B.K., Rader, R., Nelson, W.R., Gee, M. et al. (2021) Using non-bee and bee pollinator–plant species interactions to design diverse plantings benefiting crop pollination services. In: *Advances in ecological research*, Vol. 64. London, UK: Academic Press, pp. 45–103. Available from: https://doi.org/10.1016/bs.aecr.2020.11.002

Jeannerod, L., Carlier, A., Schatz, B., Daise, C., Richel, A., Agnan, Y. et al. (2022) Some bee-pollinated plants provide nutritionally incomplete pollen amino acid resources to their pollinators. *PLoS One*, 17(8), e0269992. Available from: https://doi.org/10.1371/journal.pone.0269992

Klecka, J., Hadrava, J., Biella, P. & Akter, A. (2018) Flower visitation by hoverflies (Diptera: Syrphidae) in a temperate plant–pollinator network. *PeerJ*, 6, e6025. Available from: https://doi.org/10.7717/peerj.6025

Kleijn, D., Linders, T.E.W., Stip, A., Biesmeijer, J.C., Wäckers, F.L. & Bukovinszky, T. (2018) Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. *Methods in Ecology and Evolution*, 9, 1727–1738. Available from: https://doi.org/10.1111/2041-210X.13017

Lindenmayer, D., Wood, J., Montague-Drake, R., Michael, D., Crane, M., Okada, S. et al. (2012) Is biodiversity management effective? Cross-sectional relationships between management, bird response and

vegetation attributes in an Australian agri-environment scheme. *Biological Conservation*, 152, 62–73. Available from: https://doi.org/10.1016/j.biocon.2012.02.026

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. & Ward, L.K. (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research*, 43(2), 77–89. Available from: https://doi.org/10.1046/j.1365-3180.2003.00326.x

Maskell, L.C., Henrys, P., Pescott, O.L. & Smart, S.M. (2020) Long-term trends in the distribution, abundance and impact of native "injurious" weeds. *Applied Vegetation Science*, 23(4), 635–647. Available from: https://doi.org/10.1111/avsc.12518

McHugh, N.M., Bown, B., McVeigh, A., Powell, R., Swan, E., Szczur, J. et al. (2022) The value of two agri-environment scheme habitats for pollinators: annually cultivated margins for arable plants and floristically enhanced grass margins. *Agriculture, Ecosystems and Environment*, 326, 107773. Available from: https://doi.org/10.1016/j.agee.2021.107773

Nichols, R.N., Goulson, D. & Holland, J.M. (2019) The best wildflowers for wild bees. *Journal of Insect Conservation*, 23(5–6), 819–830. Available from: https://doi.org/10.1007/s10841-019-00180-8

Nichols, R.N., Holland, J.M. & Goulson, D. (2022a) Can novel seed mixes provide a more diverse, abundant, earlier, and longer-lasting floral resource for bees than current mixes? *Basic and Applied Ecology*, 60, 34–47. Available from: https://doi.org/10.1016/j.baae.2022.02.002

Nichols, R.N., Holland, J.M. & Goulson, D. (2022b) *Insect visitations to wildflower seed mix trials on farms in West Sussex and Oxfordshire from 2019–2021*. NERC EDS Environmental Information Data Centre. https://doi.org/10.5285/ca785f4c-5e45-4743-83bb-e30dd620de2e

Nowakowski, M. & Pywell, R. (2016) *Habitat creation and management for pollinators*. Wallingford, UK: Centre for Ecology & Hydrology.

Ouvrard, P., Transon, J. & Jacquemart, A.-L. (2018) Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodiversity and Conservation*, 27(9), 2193–2216. Available from: https://doi.org/10.1007/s10531-018-1531-0

Pollard, E. & Yates, T.J. (1993) *Monitoring butterflies for ecology and conservation: the British butterfly monitoring scheme*. London, UK: Chapman & Hall.

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25(6), 345–353. Available from: https://doi.org/10.1016/J.TREE.2010.01.007

Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H. et al. (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation*, 129(2), 192–206. Available from: https://doi.org/10.1016/J.BIOCON.2005.10.034

R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/ [Accessed January 14, 2022]

Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R. et al. (2016) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, 113(1), 146–151. Available from: https://doi.org/10.1073/pnas.1517092112

Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M. et al. (2015) Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology*, 52(5), 1165–1175. Available from: https://doi.org/10.1111/1365-2664.12479

Scheper, J., Bukovinszky, T., Huigens, M.E. & Kleijn, D. (2021) Attractiveness of sown wildflower strips to flower-visiting insects depends on seed mixture and establishment success. *Basic and Applied Ecology*, 56, 401–415. Available from: https://doi.org/10.1016/j.baae.2021.08.014

Schmidt, A., Kirmer, A., Kiehl, K. & Tischew, S. (2020) Seed mixture strongly affects species-richness and quality of perennial flower strips on fertile soil. *Basic and Applied Ecology*, 42, 62–72. Available from: https://doi.org/10.1016/j.baae.2019.11.005

Schoch, K., Tschumi, M., Lutter, S., Ramseier, H. & Zingg, S. (2022) Competition and facilitation effects of semi-natural habitats drive Total insect and pollinator abundance in flower strips. *Frontiers in Ecology and Evolution*, 10, 1–11. Available from: https://doi.org/10.3389/fevo.2022.854058

Storkey, J. & Westbury, D.B. (2007) Managing arable weeds for biodiversity. *Pest Management Science: Formerly Pesticide Science*, 63(6), 517–523. Available from: https://doi.org/10.1002/ps.1375

Tilman, E.A., Tilman, D., Crawley, M.J. & Johnston, A.E. (1999) Biological weed control via nutrient competition: potassium limitation of dandelions. *Ecological Applications*, 9, 103–111.

Tschumi, M., Albrecht, M., Bärtschi, C., Collatz, J., Entling, M.H. & Jacot, K. (2016) Perennial, species-rich wildflower strips enhance pest control and crop yield. *Agriculture, Ecosystems & Environment*, 220, 97–103. Available from: https://doi.org/10.1016/J.AGEE.2016.01.001

Tschumi, M., Ekroos, J., Hjort, C., Smith, H.G. & Birkhofer, K. (2018) Predation-mediated ecosystem services and disservices in agricultural landscapes. *Ecological Applications*, 28(8), 2109–2118. Available from: https://doi.org/10.1002/eap.1799

Uyttenbroeck, R., Piqueray, J., Hatt, S., Mahy, G. & Monty, A. (2017) Increasing plant functional diversity is not the key for supporting pollinators in wildflower strips. *Agriculture, Ecosystems & Environment*, 249, 144–155. Available from: https://doi.org/10.1016/J.AGEE.2017.08.014

Vaudo, A.D., Tooker, J.F., Grozinger, C.M. & Patch, H.M. (2015) Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, 10, 133–141. Available from: https://doi.org/10.1016/j.cois.2015.05.008

Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2018) Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, 11(1), 32–41. Available from: https://doi.org/10.1111/icad.12264

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag. Available at: http://ggplot2.org [Accessed xxxx]

Williams, N.M., Ward, K.L., Pope, N., Isaacs, R., Wilson, J., May, E.A. et al. (2015) Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecological Applications*, 25, 2119–2131.

Wood, T.J., Holland, J.M. & Goulson, D. (2015a) Pollinator-friendly management does not increase the diversity of farmland bees and wasps. *Biological Conservation*, 187, 120–126. Available from: https://doi.org/10.1016/J.BIOCON.2015.04.022

Wood, T.J., Holland, J.M., Hughes, W.O.H. & Goulson, D. (2015b) Targeted agri-environment schemes significantly improve the population size of common farmland bumblebee species. *Molecular Ecology*, 24(8), 1668–1680. Available from: https://doi.org/10.1111/mec.13144

Wood, T.J., Holland, J.M. & Goulson, D. (2017) Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, 54(1), 323–333. Available from: https://doi.org/10.1111/1365-2664.12718

SUPPORTING INFORMATION

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

Supplementary Information S1. Supplementary Table S1. Seed mix composition as provided by Emorsgate Seeds. LT, WB, and WF were sown at a rate of 20% wildflower to 80% grasses, and FAB was sown

at 100% wildflower. For ease, only the wildflower species are included in the table.

Supplementary Information S2. Supplementary Table S2. Insect visits to flowers spreadsheet. Insects identified to species or genus seen on a flower are noted as abundances. Flower species are displayed down the column on the left and insect species are across the top in a single row.

Supplementary Information S3. Supplementary Figure S3. Flower visitation network of plants and insects. A pollinator visitation network of all insects was visualised using the 'plotweb' function in the *bipartite* package (Dormann et al., 2008). Insect groups are displayed on the right and the width of the boxes is proportional to the number of individuals observed. Flower species are displayed on the left and box width is proportional to the number of flower visits observed. The width of the connecting lines is proportional to the number of interactions observed between each plant–insect group pair.

Supplementary Information S4. Supplementary Figure S4. Total insect visits to each treatment. Mean total insect abundance per treatment, summing values for each plot, averaging across replicates, survey periods, farms and years for each insect group. Significance (post hoc Tukey) of treatments denoted by lettering.

Supplementary Information S5. Supplementary Figure S5. Wild bee-flower visitation network. Wild bee species are displayed in rows and flowers in columns. The black square shows an observed interaction was recorded.