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RESEARCH ARTICLE

Taxon-specific response of natural enemies to different flower strip mixtures

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Abstract

1. Flower strips are a prominent agri-environmental scheme with the central objective to promote biodiversity and maintain associated ecosystem services. The promotion of natural enemies by increasing resource availability through flower strips is a promising approach for integrated pest management.
2. In a 3-year field study, two annual and two perennial flower strip mixtures, as well as a grass mixture, were tested regarding their attractiveness for natural enemies at three different study sites in Germany. Natural enemies were sampled annually in nine sampling rounds at a 10-day rhythm using sweep netting and pitfall traps. To assess available floral resources, we estimated the species-specific flower cover and classified species into flower types.
3. Flower strip mixtures differed in their attractiveness to natural enemies. Treatment effects on arthropod activity density were most pronounced in the second and third year. Overall, perennial were more attractive than annual flower strip mixtures for most natural enemies, however, the response to flower strip mixtures varied significantly among taxa. For example, perennial flower strips showed a two- to fourfold increase of plant-dwelling spider and parasitoid wasp activity density as well as higher numbers of juvenile stages of predatory bugs and rove beetles compared to annual flower strips. In contrast, annual flower strip mixtures showed the highest attractiveness for ground beetles. Moreover, different natural enemy taxa were associated with varying flower strip characteristics such as flower type proportion, herbivore availability and plant species richness.
4. *Synthesis and applications*. We found taxon-specific responses of natural enemies to different flower strips, which provide guidance for the floral composition of flower strips in order to maximize their effectiveness for natural pest control. We suggest the use of perennial mixtures with high proportion of flower heads (Asteraceae) and disk flowers (esp. Apiaceae, Rubiaceae, Brassicaceae) in particular, but also flag blossoms (Fabaceae) as these flower types were positively associated with several natural enemy groups. However, since we found mixed

responses to flower types, specific flower strip composition will ultimately depends on its objective.

KEYWORDS
agri-environmental schemes, beneficial arthropods, ecosystem services, flower strip mixtures, habitat management, natural enemies, natural pest control

1 | INTRODUCTION

Modern agriculture is facing major environmental and societal challenges due to a growing human population and its increasing demand for food (Godfray et al., 2010). Although the current global agricultural area would be sufficient to feed the predicted world population in 2050, this would require significant interventions (e.g. wide adoption of plant-based diets, radical reduction of food waste; Berners-Lee et al., 2018). At present, however, agriculture covers approximately half of Earth's ice-free land area (Poore & Nemecek, 2018) and its intensification as well as ongoing expansion are considered main drivers of jeopardizing biodiversity and associated ecosystem services (Kleijn et al., 2008; Matson et al., 1997). Natural pest control and pollination are two key ecosystem services with an estimated economic value of 253 billion dollars per year (Gallai et al., 2009; Neumann et al., 2015), highlighting the urgent need for effective and environmentally friendly solutions that can counteract biodiversity loss with a minimal sacrifice in arable land to ensure food sovereignty (Knapp et al., 2023).

In this context, incorporation of specific flowering plants (e.g. flower strips) into arable land is an effective solution that can contribute to increased provision of ecosystem services and therefore to a more sustainable production (Albrecht et al., 2020; Bommarco et al., 2013). In the EU, flower strips are a measure within the agri-environmental schemes (AES), a governmental program that financially supports farmers that implement environmental friendly farming practices (Batary et al., 2015). Despite direct compensation, implementation of flower strips by farmers is still insufficient and among the most disliked practices in the EU (Kleijn et al., 2019). Drawbacks such as loss of productive area and concerns about higher weed and/or pest pressure seem to outweigh the benefits and mitigate the acceptance of these schemes (Kleijn et al., 2019). Moreover, decision support for farmers regarding the choice of flower strip mixtures based on their functions (e.g. enhanced natural pest control) is either absent or based on anecdotal experiences rather than scientific data (Lundin et al., 2019). Therefore, the focus of research has shifted from evaluating exclusively ecological benefits to additionally incorporate economic benefits of AES to increase adoption by farmers (Albrecht et al., 2020; Cresswell et al., 2019). Especially the improvement of natural pest control has gained increasing interest with the main goal of reducing pesticide inputs while maintaining or even increasing crop yield (Lundin et al., 2023; Scheper et al., 2021).

Many predators and parasitoids of important crop pests rely on floral food resources, such as nectar and pollen, to complete their life cycle or to bridge times of prey shortage (Wäckers & van Rijn, 2012). In this context, flower strips can improve habitat quality and increase local abundance of natural enemies (Landis et al., 2000). Beside the supply of floral food, flower strips also offer alternative prey, shelter, oviposition and overwintering habitats, which further enhances their ecological value (Ganser et al., 2019; Holland et al., 2016). One of the key factors influencing local populations of natural enemies is the selection of suitable flower strip mixtures (Albrecht et al., 2020). This is because both the morphological and physiological characteristics of each plant species within a mixture can differ (e.g. flower shape/colour, depth of nectaries, and nectar accessibility and content) and will directly affect the attractiveness of a plant mixture for natural enemies (Wäckers & van Rijn, 2012).

While several studies have proven that flower strips have positive effects on natural enemies compared to low quality habitats such as arable land (Albrecht et al., 2020), there are only few studies comparing different flower strip mixtures and their effects on multiple natural enemy taxa (e.g. Boetzl et al., 2021). However, since these mixtures vary greatly in characteristics such as temporal continuity, species richness, species composition and proportion, studies that attempt to understand the complex interactions between flower strips and natural enemies are urgently needed. Therefore, we examined four different, commercially available flower strip mixtures comprising a broad range of characteristics over three consecutive years to shed light on the question which of these mixtures are most attractive for natural enemy taxa and thus most suitable to increase natural pest control.

2 | MATERIALS AND METHODS

2.1 | Study site and design

Our study was conducted from April 2020 to August 2022 at three sites in the federal state of North Rhine-Westphalia, Germany. Soil types at study sites comprised a sand soil near Lippetal, a silt soil at the experimental research station of the South Westphalia University of Applied Sciences, and a clay soil near Ense. At all study sites, we received permission from the respective farmer to conduct our study on their land. We hereafter refer to the study sites by their soil type. For detailed site description, general soil properties and annual weather conditions see Tables S1 and S2.

In April 2020, five plant mixtures (hereafter referred to as "treatments") were mechanically sown at a seeding rate of 10 kg/ha at each study site. At each site, sixteen 252 m^2 (28 × 9 m) plots were arranged in a fully randomized plot design with each treatment replicated three to four times (48 plots across sites; see Figure S1). A 3-m wide sown grass strip (*Lolium perenne*) that was regularly mulched to prevent any plants from flowering separated the plots. Treatments included two annual flower strip mixtures (comprising 11 and 13 plant species, referred to as 'annual flower strip 1' and 'annual flower strip 2', respectively), two perennial flower strip mixtures (comprising 30 and 51 plant species, referred to as 'perennial flower strip 1' and 'perennial flower strip 2', respectively), and a perennial field margin vegetation serving as a control (comprising 1–4 grass species, referred to as 'field margin'). These commercially available mixtures (provided by Feldsaaten Freundenberger®) were chosen to cover a broad range of plant community parameters such as temporal continuity, species richness, plant species proportion and composition. For detailed information on the different plant mixtures see Table S3.

The re-establishment of the annual flower strips included mulching, soil tillage for mechanical weed control (grubber and rotary harrow) and re-sowing of the mixture at the end of April 2021 and 2022. Perennial flower strip mixtures were topped at 15 cm once in March 2022 and received no further applications. The field margin vegetation consisted of a single grass species in 2020, but was complemented with three additional grass species in autumn 2020, as a dense field margin vegetation could not be achieved in summer 2020. Following this, no further management of the perennial flower strips and field margin vegetation was conducted. Due to high weed pressure at the silt soil, all plant mixtures were re-established in late spring 2021. Therefore, no data are available for the silt soil in 2021 (Figure 1).

2.2 | Sampling of arthropods

The attractiveness of the different plant mixtures to natural enemies was determined by recording the activity density of nine important predator/parasitoid groups (i.e. natural enemies) in the main blooming period of the mixtures from June to August/September across the study period (2020–2022). Each year, sampling was conducted at nine sampling rounds at 10-day intervals. Aphidophagous hoverflies, predatory bugs, parasitoid wasps and plant-dwelling spiders were sampled using standardized sweep netting along a transect (28 × 1 m) along the length of each respective plot (net diameter: 30 cm; 40 sweeps per plot). Ground beetles, rove beetles, and ground-dwelling spiders were sampled using pitfall traps (two traps per plot at a distance of 9 m; polystyrene cups of 9 cm diameter filled with 60% (v/v) propylene glycol). Individuals of two pitfall traps per plot were pooled for further analysis. Ladybirds and lacewings were sampled using both sweeping and pitfall traps. Samples were either frozen at −30°C for sweep net samples or stored at +7°C in the dark for pitfall trap samples until processing. All captured predatory or parasitoid arthropods were classified into one of the nine above-mentioned functional groups. To improve data quality in the second and third study year, we considered the active life stages separately (adult & larvae) and identified individuals at different taxonomic levels (e.g. superfamily for parasitoid wasps, species level for ladybirds), depending on variation in diet of functional groups and taxonomic expertise. Moreover, for the sweep net samples, we assessed overall activity density of herbivores (e.g. aphids), which can act as prey. Detailed information on sampling methods and dates as well as taxonomic resolution of each group are provided in Supporting Information File S1 and Tables S4 and S5. Sampling of arthropods was conformed to the legal requirements of the state of NRW, Germany.

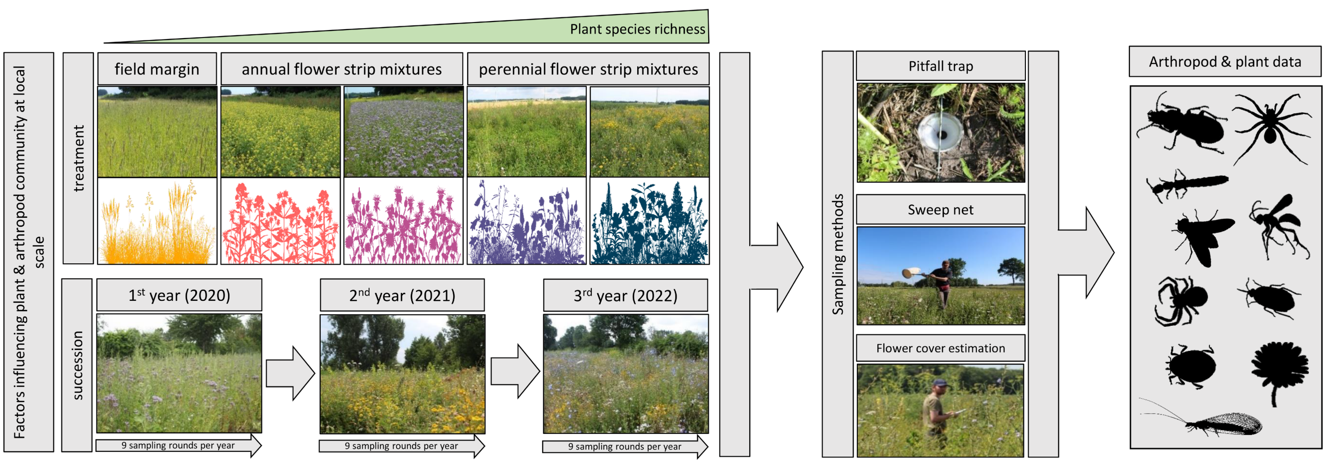

FIGURE 1 Study design. Activity density of nine natural enemy groups (from left top to right bottom: Ground beetles, ground-dwelling spiders, rove beetles, hoverflies, parasitoid wasps, plant-dwelling spiders, predatory bugs, ladybirds, and lacewings) and flower cover of vascular plants were recorded in five different plant mixtures over 3 years at three study sites using different sampling methods. Icons of the plant mixtures represent the respective treatment. Plant Icons are courtesy of the Integration and Application Network (ian.umces.edu/media-library). Photos and arthropod icons were provided by Simon Blümel.

2.3 | Assessment of flower cover and flower type

Flower availability of each flowering plant species (including plants that were not part of the mixtures but spontaneously emerged) was determined by estimating species-specific flower cover (%) per plot on the day of arthropod sampling. We defined flower cover as the coverage of open flowers of a given plant species in relation to the total area of the plot. For the eudominant weed *Chenopodium album* and all wind pollinated plant species (including the four grass species of the field margin mixture), we estimated the cover of the whole plant instead of the flower cover. To minimize variability of this method, estimations were performed by the same person throughout the entire study period. To account for differences in flower availability (blooming period) of each plant species over the sampling period, we used the average flower cover for analysis. Since flower traits, such as resource accessibility, determine the attractiveness of plants for natural enemies (Wäckers & van Rijn, 2012), we classified each plant species into eight flower types as proposed by Kugler (1970): (1) disk flowers, (2) flower heads, (3) lip flowers, (4) bell shaped flowers, (5) funnel flowers, (6) flag blossoms, (7) stalk disk flowers and (8) wind-pollinated plants. We used the Biolflor database (Klotz et al., 2002) to assign plant species to flower type. The flower type of each recorded plant species is listed in Table S3.

2.4 | Statistical analysis

We performed generalized linear mixed effect modelling (GLMM) to assess the impact of plant mixtures on the activity density of the different natural enemy groups in a first group of GLMMs. Here, number of individuals of each natural enemy group (pooled across sampling rounds per year) was used as the response variable which was modelled as a negative binomial error distribution. Plant mixture was used as fixed effect and study site as random intercept. The relations between certain plant mixture characteristics (e.g. cover of specific flower type, herbivore density) and the different natural enemy groups were analysed utilizing a second group of GLMMs. Here, natural enemies were used as response variable. Individual plant mixture characteristics were scaled and used as fixed effect; year, treatment and study site as random intercept. Moreover, we used a third group of GLMMs to analyse the impact of study year on the natural enemy groups, which were continuously recorded over 3 years. These GLMMs used natural enemies as response variable, year and plant mixtures as well as their interaction as fixed effects, and study site was random intercept.

All models were checked by visual inspection as well as quality of fit characterizing quantities and found to fulfil model assumptions. The Akaike Information Criterion (AIC_c; corrected for small sample size) was particularly used for model selection between competing models in the second group of GLMMs. All GLMMs were performed in R versions 4.2.2 (R Core Team, 2022). We used the 'glmmTMB'-function with family parameter 'nbinom2()' using the log-link function from the R-package 'glmmTMB' version 1.1.5 (Brooks et al., 2017). For statistical inference of fixed effects, we used the methods suggested by Hothorn et al. (2008) and Bretz et al. (2010) for significant effects of a priori selected parameters relevant to the hypotheses implemented in the glht method for Tukey contrasts from the R-package 'multcomp' version 1.4.22 (Hothorn et al., 2008).

A few pitfall traps were disturbed by large mammals, which resulted in missing data points (3% of all trap samples in 2020; $<1\%$ of all trap samples in 2021, and none in 2022). In case of missing data points, only one out of two pitfall traps per plot and sampling round were disturbed. Therefore, we decided to impute the missing data points by multiplying the undisturbed pitfall trap by factor two. To assess the impact of this procedure, we compared models with this imputation procedure to models in which missing data points were treated as zeros for the sampling year 2020 (most missing data points). The comparison revealed no substantial change in the results of the GLMMs, which highlight that the number of missing data points in our dataset is negligible (see Table S6).

3 | RESULTS

Over 3 years, we collected 132,265 arthropod individuals of nine natural enemy groups. Within sweep net samples, parasitoid wasps were the most abundant group accounting for 52% (25,389 individuals) of all collected individuals followed by predatory bugs (19%; 9318), plant-dwelling spiders (16%; 7663), hoverflies (8%; 3717), ladybirds (4%; 1855) and lacewings (1%; 493). Catches in pitfall traps were dominated by ground-dwelling spiders (46%; 38,236) followed by ground beetles (36%; 30,426), rove beetles (17%; 14,168), ladybirds (1%; 836) and lacewings (<1%; 164).

3.1 | Effects of plant mixtures on natural enemies

Total number of natural enemies showed no differences among flower strips, except for the field margin, which was less attractive in the second and third year. A taxon-specific analysis, however, revealed that the five plant mixtures differed in their attractiveness to natural enemy groups (Figures 2a and 3b–j). Treatment effects on the different functional groups were most pronounced in the second and third year. Both perennial flower strip mixtures showed the highest attractiveness for parasitoid wasps, plant-dwelling spiders, rove beetle larvae and predatory bug nymphs (Figures 3 and 4). When considering the two dominant subgroups of parasitic wasps separately, data show that especially chalcid wasps had high densities in perennial mixtures, while for ichneumonid wasps results were mixed (Figure 4c,d). Total number of predatory bugs were highest in perennial flower strip 2. This was even stronger when analysing only the nymphs of predatory bugs (Figure 4e). In contrast, annual flower strips showed the highest attractiveness for ground beetles (second and third year) and ground-dwelling spiders (third year). When excluding the eudominant ground beetle species *Harpalus rufipes* (55% of all ground beetle individuals), differences among flower strips were less pronounced but still present (Figure 4b). Hoverflies, lacewings and total number of

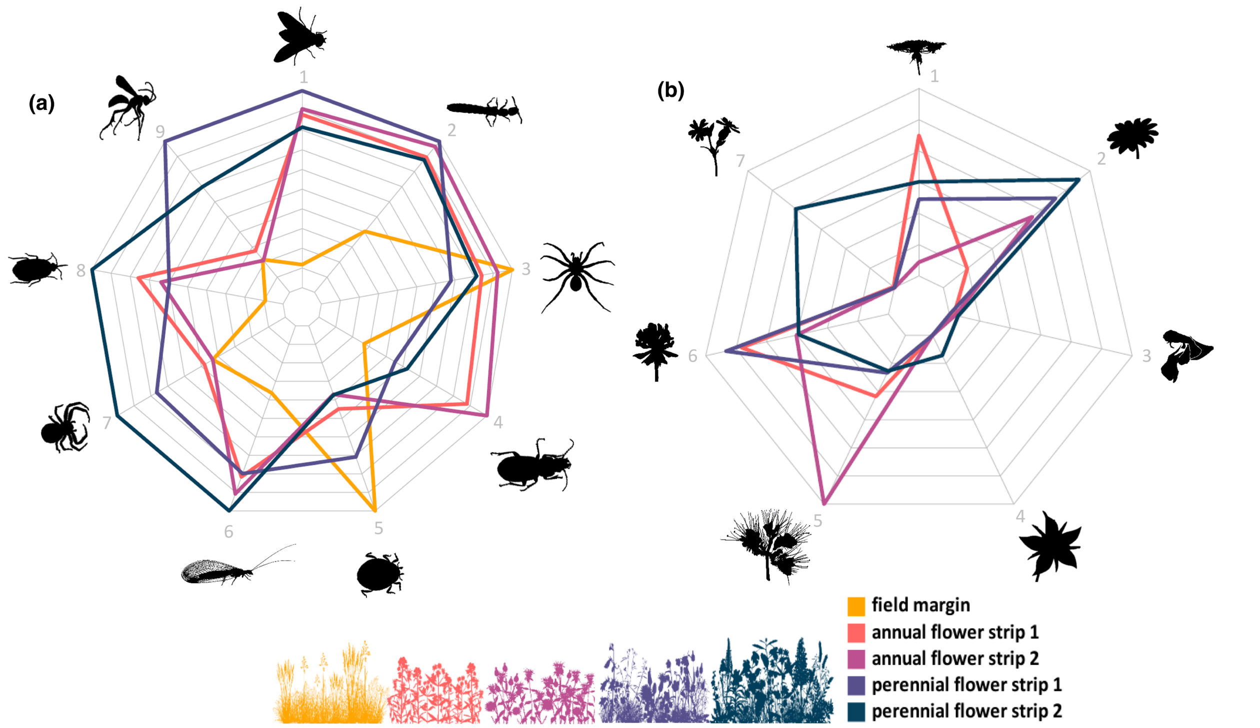

FIGURE 2 Distribution of the different functional groups of natural enemies among plant mixtures (a) and average proportion (%) of the flower cover of the different flower types (b) across three study years. Natural enemy groups in (a) are arranged clockwise from top: (1) hoverflies, (2) rove beetles, (3) ground-dwelling spiders, (4) ground beetles, (5) ladybirds, (6) lacewings, (7) plant-dwelling spiders, (8) predatory bugs and (9) parasitoid wasps. Flower types in (b) are arranged clockwise from top: (1) disk flowers (2) flower heads, (3) lip flowers, (4) bell shaped flowers, (5) funnel flowers, (6) flag blossoms and (7) stalk disk flowers. We excluded wind pollinated plants since the estimation method of cover differed (but see Figure S3). Each interval equals 10% (a) or 2.5% (b) increments starting from the centre of the radar chart. Percentages of treatments for each natural enemy group are scaled to the highest catch. Plant icons are courtesy of the Integration and Application Network (ian.umces.edu/media-library). Arthropod icons were provided by Simon Blümel.

rove beetles did not differ in activity density among flower strips, but the field margin was least attractive in at least two study years (Figure 3f,g,i). However, the field margin showed the highest attractiveness to polyphagus ladybirds (dominant species *Tytthaspis sedecimpunctata*; 76%) while numbers of predatory ladybirds were higher in flower strips in the last year, especially in perennial flower strip 1 (Figure 4f,g). Numbers of ground-dwelling spiders were highest in the field margin in the first year but decreased continuously and were lowest in the third year as compared to the flower strips. Finally, herbivore density were higher in perennial mixtures compared to annuals and the field margin in the third but not in the second year. Study year affected each functional group of natural enemies except for total number natural enemies. However, total number natural enemies but also parasitoid wasps, plant-dwelling spiders, hoverflies as well as all three ground-dwelling arthropod groups (Figure 3h–j) were impacted by the interaction between study year and treatment. Information on statistics are shown in Tables S6 and S8.

3.2 | Proportion of flower types

Cover of flower types varied across flower strip mixtures (Figure 2b). The most dominant flower types were making up 71% of the total flower cover (wind-pollinated plants excluded) and comprised flag blossoms (27%), flower heads (26%) and disk flowers (18%). The field margin mixture consisted exclusively of wind-pollinated grass species. Annual flower strip mixture 1 had a high proportion of disk flowers (especially *Sinapis alba*, *Raphanus sativus*) and flag blossoms (especially *Trifolium*/*Meliotus* species) with an average cover of 11 and 12%, respectively. Annual flower strip mixture 2 was dominated by funnel flowers (15% cover; especially *Phacelia tanacetifolia*) and flower heads (9%; especially *Centaurea cyanus*). Both perennial flower strip mixtures had high proportion of disk flowers (different Apiacaea/Rubiacae species) and flower heads (*Cichorium intybus*, *Achillea millefolium*, *Anthemis tinctoria* and *Leucanthemum* species). However, perennial flower strip mixture 1 had the highest cover of flag blossoms (13%; especially *Trioflium*/*Meliotus* species) and perennial flower strip mixture 2 had the highest proportion of stalk disk (10%; especially *Silene* species), bell shaped (2%) and lip flowers (1%; Figure 2b) compared to the other mixtures. Moreover, while both annuals had an annually increasing cover of non-mixture wind-pollinated herbs (especially *Chenopodium album*), perennial non-mixture plants were mainly wind-pollinated grass species. For a graphical representation of the annual change of flower types as well as the average proportion of wind-pollinated plants among plant mixtures see Figures S2 and S3.

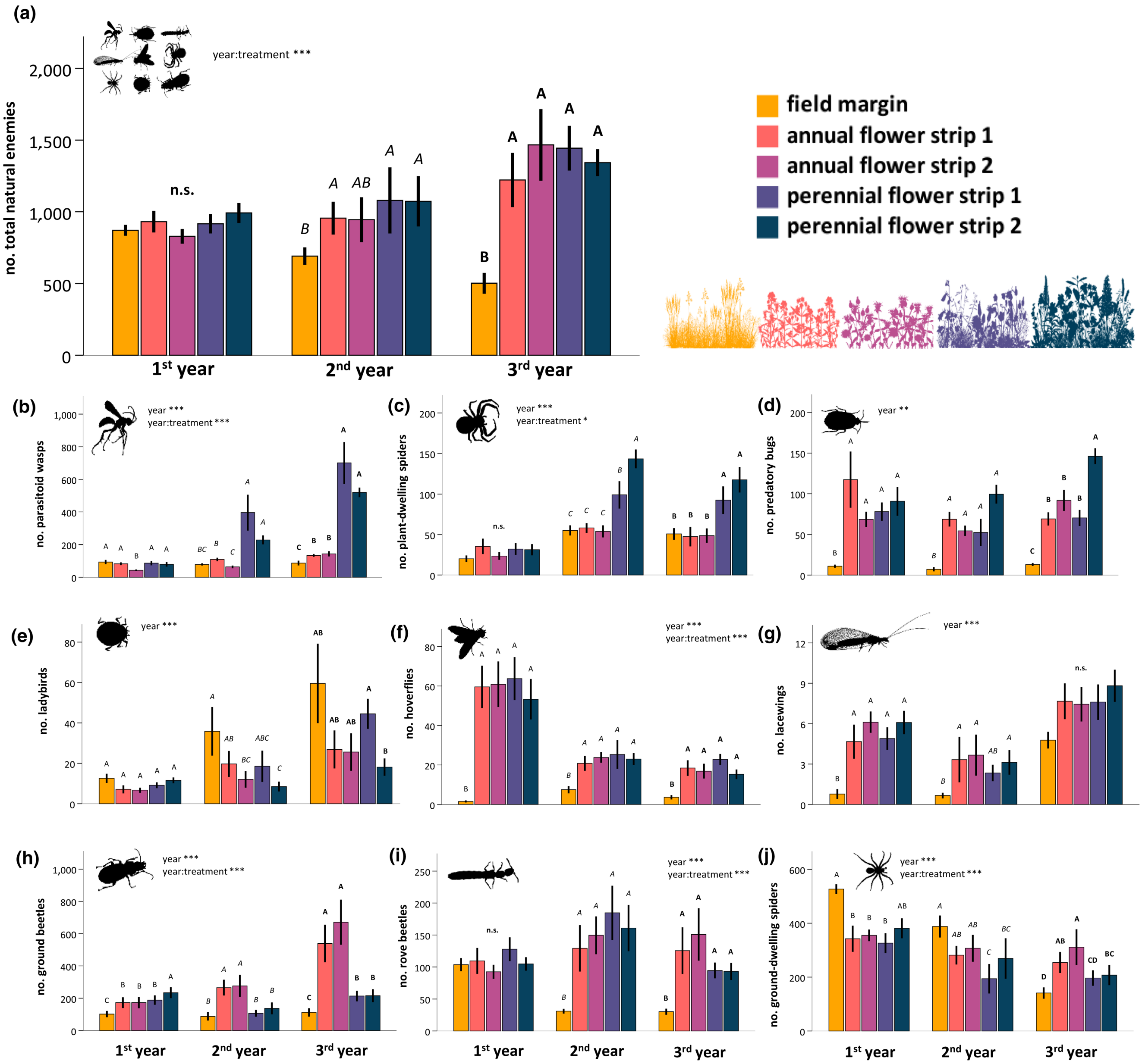

FIGURE 3 Activity density of the different functional groups of natural enemies in five different plant mixtures over 3 years (2020–2022). (a) total number of natural enemies, (b) parasitoid wasps, (c) plant-dwelling spiders, (d) predatory bugs, (e) ladybirds, (f) hoverflies, (g) lacewings, (h) ground beetles, (i) rove beetles and (j) ground-dwelling spiders. Different letters of the same font indicate statistically significant differences (GLMM, $p < 0.05$) among treatments within one sampling year. n.s. = not significant. Significant effects of study year as well as interaction between study year and treatment are indicated beside the respective arthropod icon (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).Error bars represent the SE. Images are courtesy of the Integration and Application Network (ian.umces.edu/media-library). Arthropod icons were provided by Simon Blümel. For statistics, see Tables S6 and S8.

3.3 | Associations between plant mixture characteristics and natural enemies

In consistence with the varying responses to different plant mixtures, responses of natural enemy groups to the several plant mixture characteristics (i.e. predictor variables) were also taxon-specific (Figures 5 and 6). For example, total flower cover was positively associated with activity density of several plant-dwelling natural enemy groups (hoverflies, parasitoid wasps, predatory bugs and plant-dwelling spiders) and total number of natural enemies but was negatively associated with both subgroups of ladybird (predatory and polyphagus) as well as herbivores. However, ladybirds, especially polyphagus ladybirds but also herbivores, lacewings and ground beetles were positively affected by the cover of wind-pollinated plants. In contrast, cover of wind-pollinated plants was negatively associated with ground beetles without *H. rufipes*, hoverflies, parasitoid wasps, rove beetles as well as total number of natural enemies. Overall, relations between the cover of flower heads and all natural enemy groups were either positive or neutral (except for

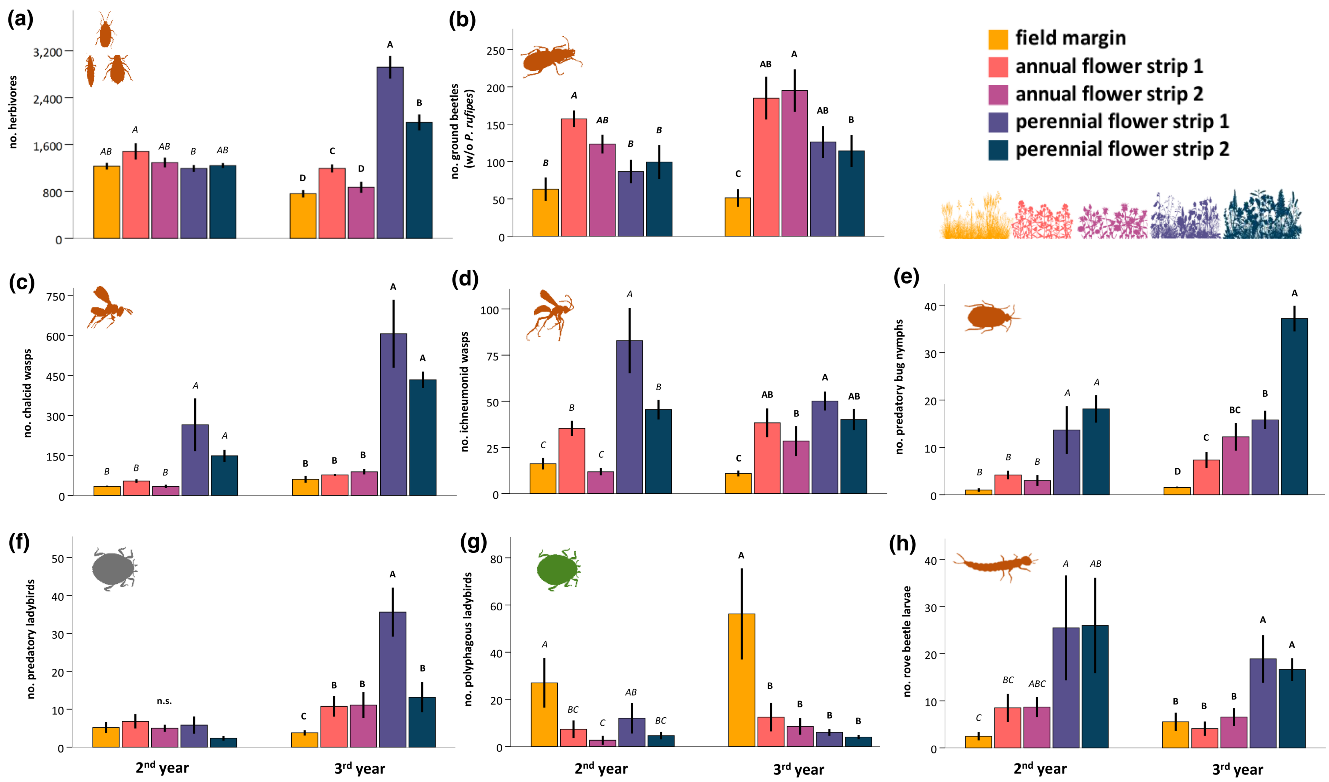

FIGURE 4 Activity density of selected functional subgroups of natural enemies and herbivores in five different plant mixtures over 2 years (2021–2022). (a) Herbivores, (b), ground beetles without *Harpalus rufipes*, (c) chalcid wasps, (d) ichneumonid wasps, (e) predatory bug nymphs, (f) predatory ladybirds, (g) polyphagous ladybirds and (h) rove beetles larvae. Different letters of the same font indicate statistically significant differences (GLMM, $p < 0.05$) among treatments within one sampling year. n.s. = not significant. Error bars represent the SE. 1st study year is not shown here since data on subgroups are only available for the second and third year (see Section 2). Images are courtesy of the Integration and Application Network (ian.umces.edu/media-library). Arthropod icons were provided by Simon Blümel. For statistics, see Table S6.

polyphagus ladybirds), with strongest effects on parasitoid wasps and plant-dwelling spiders. Flag blossoms had contrasting effects on natural enemies. While the activity density of lacewings and ground beetles was negatively associated with flag blossoms, predatory bugs and plant-dwelling spiders showed a positive relation. Different flower types exhibited mixed effects on the two subgroups of parasitoid wasps, with flag blossoms showing contrasting associations with chalcid and ichneumonid wasps (Figure 6b). Disk flowers had no effect on chalcid wasps but a strong positive effect on ichneumonid wasps as well as on rove beetles, ground beetles and total number of natural enemies. Moreover, disk flowers showed a negative relation with the activity density of herbivores. Herbivore density as a predictor variable had a strong positive association with predatory but not polyphagous ladybirds, total number of natural enemies and ground-dwelling spiders. Finally, plant species richness showed strong positive association with the density of predatory bugs, rove beetles and their juvenile stages as well as with ichneumonid wasps. Information on statistics are shown in Table S7.

4 | DISCUSSION

In recent years, the purpose of flower strips in agricultural landscapes has shifted from an exclusively protective to a multifunctional usage that additionally considers economic perspectives (Ekroos et al., 2014). Especially the improvement of ecosystem services through flower strips has gained increasing interest in research with the aim of combining ecological and economic goals. In order to identify flower strip mixtures that maximize pest control service, a detailed analysis of the effects of different flower strip mixtures and their respective plant species composition on different natural enemy groups is required.

Our three-year data revealed that the tested plant mixtures differ in terms of attractiveness to natural enemies. Responses to the mixtures and their specific characteristics (e.g. flower types) varied greatly between and even within functional groups of natural enemies (e.g. cf. predatory and polyphagus ladybirds, Figure 4f,g). These results are supported by recent studies, which also show a high taxon-specific response of natural enemies to flower plantings (Boetzl et al., 2021; Lundin et al., 2023; Scheper et al., 2021; Warzecha et al., 2018). When considering natural enemies as a single functional group (all individuals taken together), differences between flower strips were neutralized due to contrasting responses to the plant mixtures (e.g. cf. ground beetles and parasitoid wasps, Figure 3b,h), highlighting the importance of a taxon-specific approach to prevent misinterpretation of data and to understand which factors promote specific functional groups.

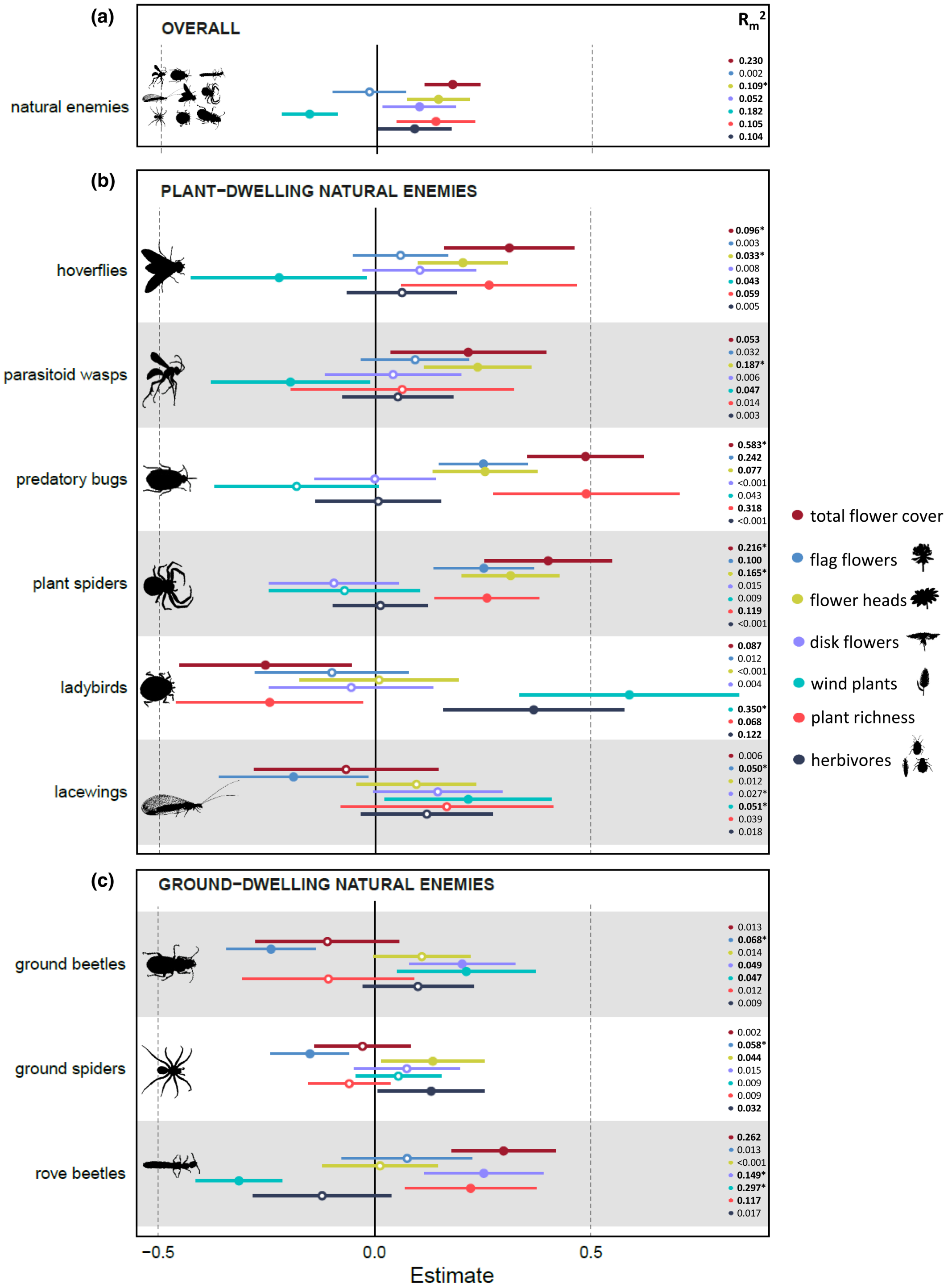

FIGURE 5 Response of different functional groups of natural enemies on seven plant mixture characteristics. (a) Total number of natural enemies, (b) plant-dwelling and (c) ground-dwelling natural enemies. Estimates with filled dots and bold marginal R^2 value (R_m^2) indicate statistically significant association (GLMM, $p < 0.05$). Asterisks indicate $\Delta AIC_c < 2$. Herbivores were excluded from model comparison since data are only available for 2 years. Error bars represent the SE. Icons are courtesy of phylopic.org, the Integration and Application Network (ian.umces.edu/media-library) or were provided by Simon Blümel. For statistics, see Table S7.

Observed effects on natural enemy taxa were most pronounced in the 2nd and 3rd year, possibly due to successional shifts in flower type composition and proportion in perennial flower strips (for annual plant mixture specific flower type composition see Figure S2). Perennial flower strip mixtures were more attractive than annual flower strip mixtures for most of the natural enemy taxa studied here and thus assumed to be more suitable for optimizing natural pest control. The perennial field margin vegetation (control) was least attractive for most of the investigated natural enemy groups, especially for those, which rely on the presence of floral food resources

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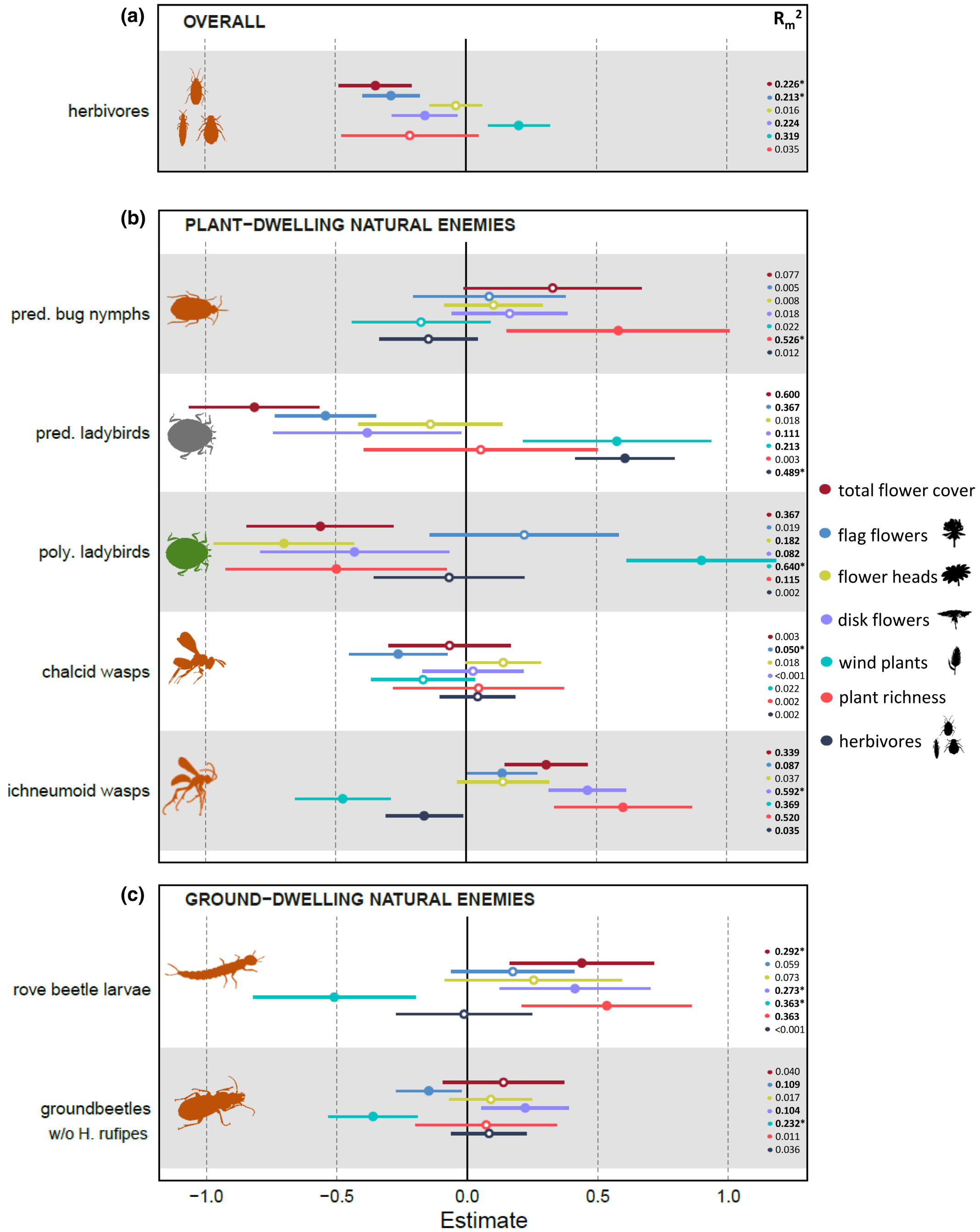

FIGURE 6 Response of different selected functional subgroups of natural enemies and herbivores on seven plant mixture characteristics. (a) Total number of herbivores, (b) plant-dwelling and (c) ground-dwelling natural enemies. Estimates with filled dots and bold marginal R^2 value (R_m^2) indicate statistically significant association (GLMM, $p < 0.05$). Asterisks indicate $\Delta AIC_c < 2$. Error bars represent the SE. Icons are courtesy of phylopic.org, the Integration and Application Network (ian.umces.edu/media-library) or were provided by Simon Blümel. For statistics, see Table S7.

(e.g. hoverflies & predatory bugs). However, undisturbed grass dominated habitats can support other taxa that were not within the scope of this study such as orthopterans (Boetzl et al., 2021).

Greater temporal continuity of flower strip mixtures and the associated soil dormancy and permanent ground cover allows arthropods, especially those that are less mobile, to overwinter or reproduce (Frank & Reichhart, 2004). In our study, higher numbers of juvenile stages of predatory bugs and rove beetles in the perennial mixtures support this assumption (Figure 4e,h). However, temporal continuity alone cannot be the single explanatory factor, as the field margin vegetation was also a perennial and undisturbed habitat and did not show these positive effects on juvenile predatory bugs and rove beetles. Thus, we hypothesize additive effects between temporal continuity and plant mixture characteristics (e.g. flower types).

Moreover, we argue that higher plant species richness in perennials may increases the probability of a mixture to perform better under varying site-specific conditions. In real-world landscapes, the establishment of a flower mixture is affected by a complex interplay of local factors. Variations in soil parameters, land-use history, weed pressure, interspecific interactions between plants, flower strip management and weather conditions can make predictions of the outcome a complex task (Scheper et al., 2021). However, the successful establishment of a sown flower mixture ultimately determines their effectiveness in promoting ecosystem services. Therefore, it seems inevitable to identify plant species and mixtures, which perform well under a broad range of site conditions, or to tailor mixtures to the local conditions in order to find local solutions.

Our study makes an important contribution to the optimization of flower strips for natural pest control. Nevertheless, in the following we want to point out some limitations. First, high attractiveness of flower strips for natural enemies serves as an indicator but may not directly translated into an increased natural pest control in adjacent croplands. Second, although plot designs can be a powerful approach to compare several treatments regarding their attractiveness (Lundin et al., 2019; Warzecha et al., 2018), it represents an artificial experimental matrix and may produce slightly different outcomes compared to more realistic field scenarios. Third, arthropod sampling was limited to the main blooming period of flower strip mixtures in summer. Considering the second and third argument, one can expect that the observed positive effects of specific flower strip mixtures would be even greater if they were not in direct proximity to other high quality habitats (e.g. other flower strip mixtures) or if other seasons and their associated challenges for arthropods (e.g. finding suitable overwintering habitat in winter) had been considered. Especially the direct proximity of annual to perennial plots and the exclusion of other seasons than summer in our sampling scheme may overestimated the value of annual and underestimate the value of perennial flower strip mixtures.

To understand the mechanisms underlying the observed differences in flower strip attractiveness, we additionally investigated the relation between several plant mixture characteristics (e.g. flower cover) and natural enemies. Overall we found that total number of natural enemies were positively associated with total flower cover and negatively with the cover of wind-pollinated plants, supporting the general assumption, that flowering plants can increase the abundance of a broad range of beneficial arthropods in agricultural landscapes (Wäckers & van Rijn, 2012). Even though, this trend held true for most of the natural enemies when analysing groups separately, ladybirds, lacewings and ground beetles showed a (partially) contrasting response. Moreover, we found contrary effects of flower types within natural enemy groups. In this context, ichneumonid wasps were positively associated with flag blossoms, while chalcid wasps showed a negative relation. These findings are in line with another recent study that showed contrasting associations between flower types and beneficial arthropods (Scheper et al., 2021).

Adults of hoverflies and predatory bugs whose diet is directly linked to nectar and/or pollen (Wäckers & van Rijn, 2012) were positively associated with total flower cover and showed the strongest and most consistent positive effects to flower strips compared to the field margin vegetation (Figure 3d,f). Tschumi et al. (2015, 2016) showed similar results for these taxa when comparing annual flower strips and winter wheat strips. Activity densities of parasitoid wasps, predatory bugs, plant dwelling spiders and ground beetles showed the strongest treatment-related effects among the different flower strip mixtures, suggesting that these taxa have a great potential to be locally enhanced through the establishment of suitable flower strip mixtures. Therefore, we will discuss results for these groups in detail.

Parasitoid wasps were more abundant in the perennial mixtures, probably due to higher proportion of plant species with disk flowers, flower heads and flag blossoms (Figures 2b and 3b). Apiaceae with species such as *Foeniculum vulgare*, *Daucus carota*, and *Pastinaca sativa* are species with disk flowers and were frequently blooming in both perennial mixtures. Their flowers have easily accessible nectar well known to support nectar-feeding wasps (Campbell et al., 2012; Tooker & Hanks, 2000; Wäckers & van Rijn, 2012). Here, we found a strong positive relation between disk flowers and Ichneumonid wasps (Figure 6b). Moreover, parasitic wasps showed a positive relation to flower heads including Asteraceae with species such as *A. millefolium*, *Anthemis tinctoria* and *Leucanthemum vulgare*, which agrees with other studies showing that Asteraceae are highly attractive to parasitic wasps (Fiedler & Landis, 2007a, 2007b; Lundin et al., 2019; Rowe et al., 2021). Plant species with extrafloral nectar (EFN) such as *Centaurea cyanus* and *Helianthus annuus* are known to support parasitoids (Bugg et al., 1989). However, since annual flower strip mixture 2 had a high cover of *C. cyanus* and to a lower extent *H. annuus* but had the lowest number of parasitoid wasps compared to the other mixtures, EFN did not seem to play an important role for parasitoids in the presence of other available food resources.

Predatory bugs were dominated by flower bugs (Anthocoridae; 90%). Perennial flower strip 2 were more attractive than all other plant mixture in the second and third year (Figures 3d and 4e). Sampling data on flower bugs from Bosco and Tavella (2008, 2013) and unpublished results from Van Rijn (see Wäckers & van Rijn, 2012) suggest that they preferably use flowers within the plant families of Fabaceae and Asteraceae. Wäckers and van Rijn (2012) argue that these flowers can act as a nectar source and additionally as a place to hide due to their deeper and wider corollas. Indeed, we found a positive relation between flower bugs and flag blossoms, which comprises Fabaceae, and flower heads, which comprises Asteraceae (Figure 5b). Bosco and Tavella (2013), however, showed that the flower preferences of flower bugs were species-specific, potentially explaining the fact, that even though both perennial mixtures had a relatively high proportion of flag blossoms and flower heads, perennial flower strip 2 was more attractive to flower bugs since the actual species composition among these treatments were clearly distinct. For example, in the third year at the sand soil site, we found about twice as much flower bugs in perennial flower strip 2 (dominated by Asteraceae species *Anthemis tinctoria* (Ø 15% flower cover) and *Leucanthemum vulgare* (Ø 12% flower cover)) compared to perennial flower strip 1 (dominated by the plant species *Achillea millefolium* (Ø 40% flower cover)).

Plant-dwelling spiders were most abundant in both perennial flower strip mixtures (Figure 3c). These results are congruent with findings that perennial flower strips can increase overwintering success of spiders compared to annual flower strips (Ganser et al., 2019). Especially large free-hunting spiders, that is those that do not build webs (e.g. crab spiders, the most abundant spider family in our study accounting for 49% of all plant-dwelling spiders), benefit more from undisturbed perennial habitats than small web-building species (e.g. money spiders (Linyphiidae), most dominant family in the group of ground-dwelling spiders, 60%). It is assumed that populations of large free-hunting spiders regenerate slower after disturbance (e.g. tillage) and take longer to recolonize disturbed habitats than small web-builders (Schmidt & Tscharntke, 2005). However, temporal continuity alone cannot conclusively explain the results, as the field margin also represents an undisturbed perennial habitat. Crab spiders are known to use flowers as their hunting ground (Schmalhofer, 1999) or even feed on nectar (Taylor & Pfannenstiel, 2008). Here, we found that plant-dwelling spiders were associated with the flower type flag blossoms and flower heads as well as plant species richness (Figure 5b). An increased plant species richness in both perennials may have influenced diversity and complexity of vertical structure of the vegetation, which is shown to positively affect spider density (Garratt et al., 2017; Mestre et al., 2018).

Ground beetles were positively affected by annual flower strips (Figure 3h). A recent review on the effects of intensive tillage on ground beetles showed that responses can be extremely variable and depend on the respective species (Müller et al., 2022). Moreover, Boetzl et al. (2021) reported that newly established flowering fields have a higher ground beetle species richness than established perennial ones. The eudominant ground beetle species in our study, *Harpalus rufipes* (55% of all ground beetle individuals), is known as an omnivorous species feeding on a variety of invertebrates and plant seeds (Luff, 1980). Studies on seed consumption of *H. rufipes* larvae revealed that they prefer seeds of specific plant species such as *Chenopodium album* (Luff, 1980; Saska et al., 2019). This weed species was dominant in our plots with an annually increasing cover in the annual mixtures, but was absent in the perennials after the first year and thus could be an explanation for the observed effect. This assumption is supported by the finding that ground beetles were positively correlated with wind-pollinated plants (including *C. album*), while the exclusion of *H. rufipes* from analysis resulted in an opposite effect of wind-pollinated plants on ground beetles (Figures 5c and 6c). In addition, the magnitude of the negative impacts of tillage on *H. rufipes* is mainly determined by timing and intensity of tillage (Müller et al., 2022; Shearin et al., 2007). In contrast to the study of Shearin et al. (2007), tillage (grubber and rotary harrow) in the annual mixtures at our study sites was conducted in spring and not in late summer. In summer, the first instar larvae of *H. rufipes*—and therefore their most vulnerable life stage—is already active, which could increases the probability of fatal damage (Luff, 1980).

Considering the described taxon-specific responses of natural enemies to flower strip mixture and their associated characteristics, we suggest that an improvement of effectiveness of flower strips requires a local adaption of the flower strip mixture to the respective crops, pests and their specific natural enemies. Flower strips that aim to provide multiple beneficial functions (e.g. pollination, natural pest control and nature conservation) simultaneously will face a trade-off between multifunctionality and the effectiveness of individual functions. Accordingly, flower strips designed for specific applications (e.g. the control of a specific pest) can help maximizing their effectiveness, which in turn is expected to enhance adoption by farmers.

5 | CONCLUSIONS

Our study provides novel insights into the complex configuration of flower strip mixtures in order to optimize their effectiveness as a pest control measure. Several factors, acting in isolation or additive, are determining the attractiveness of a plant mixture for natural enemies. These factors comprise floral resource suitability (e.g. flower type), alternative prey availability and temporal continuity. Responses of natural enemies to flower strip mixtures and flower types were highly taxon-specific and varied significantly between as well as within functional groups. Therefore, composition of flower strip mixtures should be based on an explicit objective (e.g. natural pest control of aphids in a specific crop) that takes into account farm-specific variables (e.g. soil type).

AUTHOR CONTRIBUTIONS

Simon Blümel and Verena Haberlah-Korr conceived the ideas and designed methodology; Simon Blümel collected the data; Simon Blümel and Nicolai Bissantz analysed the data and Simon Blümel led the writing of the manuscript. Lukas Beule, Nicolai Bissantz, Wolfgang H. Kirchner and Verena Haberlah-Korr contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dbrv15f7p (Blümel et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1. Study design. Plots were arranged in a fully randomized plot design with each treatment replicated three to four times (48 plots across sites).

Figure S2. Distribution of the average proportion (%) of the flower cover of the different flower types in each study year.

Figure S3. Average proportion (%) of wind-pollinated plants in the different plant mixtures over 3 years (2020–2022).

Table S1. Study site description and general soil properties.

Table S2. Temperature and precipitation values for each study year for the respective study site.

Table S3. General information and plant species composition of the five tested plant mixtures at sowing.

Table S4. Sampling scheme of arthropod and plant data.

Table S5. Information on the taxonomic resolution and life stage of each functional group.

Table S6. Summary of results of the first group of generalized mixed effect models testing the effects of different plant mixtures on several natural enemy groups and herbivores.

Table S7. Summary of results of the second group of generalized mixed effect models testing the effects of different flower types, total flower cover and plant species richness on several natural enemy groups and herbivores.

Table S8. Summary of results of the third group of generalized mixed effect models testing the effects of year, treatment and their interaction on the different natural enemy groups.

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