RESEARCH ARTICLE

Functional traits driving pollinator and predator responses to newly established grassland strips in agricultural landscapes

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Abstract

1. Agricultural biodiversity and associated ecosystem functions are declining at alarming rates due to widespread land use intensification. They can only be maintained through targeted landscape management that supports species with different habitat preferences, dispersal capacities and other functional traits that determine their survival. However, we need better understanding whether short-term measures can already improve functional diversity in European agroecosystems.

2. We investigated spatio-temporal responses of bees (solitary bees, bumblebees and honey bees), hoverflies, carabid beetles and spiders to newly established grassland strips in Lower Austria over 3 years, and along a distance gradient to old grasslands. Specifically, we asked if new grasslands, compared to old grasslands and cereal fields, serve as temporal dispersal habitat or corridor, and how species-specific traits affect dispersal patterns. Using a trait-based functional diversity approach, we investigated year and distance effects for nine selected key traits per taxon (e.g. body size, feeding guild and habitat preferences).

3. Our results show that the functional diversity of predators and pollinators (i.e. functional richness and evenness), as well as community-weighted means of selected key traits in new grasslands significantly differed from adjacent cereal fields, but only slowly adjusted to adjacent old grasslands. These effects significantly decreased with increasing distance to old grasslands for carabids and spiders, but not for mobile bees and hoverflies.

4. *Synthesis and applications.* Over 3 years, newly established grassland strips supported larger sized and actively foraging/hunting species in the agricultural landscape. Adjacent crops likely benefit from such measures through enhanced functional diversity and related ecosystem services. However, our results also suggest that 3-year period is too short to enhance the occurrence of pollinators and epigeic predators in new grasslands. Agri-environment measures need to be complemented by the conservation of permanent habitats to effectively maintain species and functional diversity. Our findings should be acknowledged by European policy and agricultural decision makers for the design of more effective

agri-environment schemes, taking into account trait-dependent species responses to land use change.

1 | INTRODUCTION

Biodiversity loss in agricultural landscapes has been driven by rapid land use expansion and intensification, leading to the decline of ecosystem functions and services such as pollination and biological pest control (Batáry et al., 2015; Cole et al., 2020). In Europe, semi-natural grasslands created by traditional farming practices present important refuges for a variety of species (Ekroos et al., 2013; Holland et al., 2016; Öckinger et al., 2018), yet have the worst conservation status among all ecosystems (Pe'er et al., 2014). Many functionally important organisms can only survive or spread in agricultural landscapes through the presence of such extensive and persistent habitats. Since the abolition of subsidized arable set-aside in Europe in 2008, the amount of semi-permanent set-aside land is sharply decreasing, causing a sudden loss in habitat availability and biodiversity in agricultural landscapes (Pe'er et al., 2014). Current agri-environmental schemes are criticized for not responding effectively to habitat and biodiversity decline due to lacking landscape-level habitat management and poor policy design (Cole et al., 2020; Gallé et al., 2019; Pe'er et al., 2020).

In the European Union (EU), a Common Agricultural Policy (CAP) has been enacted to achieve higher sustainability in EU agriculture by providing financial support to farmers through agri-environment schemes (AES). The EU CAP budget for 2021–2027 is 365 billion EUR, a third of the overall EU budget for this period (EC, 2018). AES funds support the design and implementation of agri-environment measures to meet objectives such as the protection or enhancement of biodiversity by improving landscape and habitat quality (Cole et al., 2020). However, AES have often been criticized for diluting conservation and restoration targets (Pe'er et al., 2014), leading to ongoing decline of high-diversity grasslands and high nature value farmland regions (Pe'er et al., 2020). The same trend is observed in Austria (Grandl et al., 2016), the country with the second highest per-ha contribution to the Common Agricultural Policy's AES (Batáry et al., 2015). The effectiveness of AES measures largely depends on their spatial and temporal extent and shows negative effects on biodiversity due to insufficient diversity and continuity of resources (Boetzl et al., 2020; Cole et al., 2020). In Austria, the implementation of grassland management with higher species diversity and longer maturities than in currently available AES (Grandl et al., 2016) has been identified as a necessary complement of the AES strategy to counteract ongoing biodiversity loss (Hülber et al., 2017). Increasing evidence suggests that even small uncultivated habitat fragments such as vegetation strips provide source populations for beneficial arthropod groups and thereby enhance species dispersal and

associated ecosystem functions in the agricultural matrix (Ekroos et al., 2013; Öckinger & Smith, 2007). However, their contribution to landscape-scale species richness, functional diversity and related ecosystem services remains poorly understood (Cole et al., 2020; Gallé et al., 2019; Pe'er et al., 2020).

Species-specific ecological traits are the ultimate driver of different species responses to agricultural landscape structure and management (Ekroos et al., 2013). The functional characteristics of different species such as life history, habitat preferences and dispersal capacity influence ecosystem functioning by mediating changes in trophic interactions, and through responses to changes in the local environment (Wood et al., 2015). Thus, ecological studies are increasingly moving towards trait-based approaches, as the evidence mounts that functional trait diversity, rather than taxonomic or species diversity per se, drives ecosystem service delivery of arthropods (Cadotte et al., 2011; Finney & Kaye, 2017; Perović et al., 2018). Next to honeybees, bumble bees and solitary wild bees are the most important insect pollinators in agricultural landscapes and depend on continuous floral resources (Wintermantel et al., 2019), whereas hoverflies contribute significantly to both pollination and biological pest control and have also been shown to benefit from increased floral resource availability (Dunn et al., 2020). Many carabid beetles and all spiders are polyphagous predators commonly found in agricultural landscapes (Gallé et al., 2019), and are among the most important biological control agents of winter wheat pests (Diekötter et al., 2010). Understanding trait-specific responses of biodiversity to changes in the environment is crucial for predicting species movement (Schleuning et al., 2020) and thus assessing the potential agricultural management to promote species dispersal and related ecosystem functions in the agricultural matrix (Cole et al., 2020; Wood et al., 2015).

Ecosystem functions are provided at different scales, depending on the mobility, foraging activity and habitat requirements of species. From a landscape perspective, species with low mobility and/or specific habitat requirements benefit from higher landscape heterogeneity, while less mobile and generalist species react less sensitive to new grasslands (Alignier & Aviron, 2017; Öckinger et al., 2018). Central place foragers like solitary wild bees show stronger distance decay in abundance and species richness (Jauker et al., 2013), compared to species without brood-care behaviour and with less specific habitat requirements like hoverflies (Ekroos et al., 2013). For carabids, carnivorous species respond faster to newly established grasslands and reach remote sites earlier than phytophagous species (Gallé et al., 2019; Purtauf et al., 2005). Apart from diet, body size is an important predictor for dispersal and functionality

of pollinators and predators, as large predators consume higher amounts of larger pests, but also have more limited dispersal abilities (Boetzl et al., 2020), and larger pollinators have higher resource demands and flight capacities (Willmer & Finlayson, 2014; Wintermantel et al., 2019). These species-specific responses to habitat heterogeneity and resource availability determine community functionality (Gallé et al., 2019) and the conservation effectiveness of agricultural management measures (Hülber et al., 2017) such as the newly established, high-diversity grassland strips of this study.

Species distributions can be facilitated by the introduction of additional habitat types that support their dispersal, foraging and survival within the landscape. In this study, we quantified the potential corridor effect of newly established, high-diversity grassland strips (hereafter: new grasslands) that have been identified as a necessary complement to promote the conservation effectiveness of currently available AES (Grandl et al., 2016; Hülber et al., 2017). Over a period of three consecutive years, the distribution of pollinators and predators to these new grasslands was recorded along distance gradients from old, semi-natural habitats and in relation to surrounding crop habitats and functional traits. Higher functional diversity has been demonstrated to be more closely correlated to agroecosystem services than other diversity measures such as species richness (Finney & Kaye, 2017). Trait-based functional diversity approaches like this study offer a way to assess changes in community multifunctionality between agroecosystems (Gallé et al., 2019). We addressed two open research questions and related hypotheses: (a) Do newly established grasslands serve as dispersal habitats within the wider agricultural matrix? and (b) how do spatial and temporal dispersal patterns differ related to species-specific traits? We hypothesized that (H1) pollinators and predators will disperse differently from old to new grasslands with increasing distance and time (indicating potential corridor effects of new grasslands), as well as compared to agricultural habitat types (indicating habitat suitability); and that (H2) species-specific traits such dispersal capacity (i.e. body size), feeding and habitat preferences drive their responses to new grassland over space and time.

2 | MATERIALS AND METHODS

2.1 | Study area and establishment of grassland strips

The study was conducted in Lower Austria, in the region of Sieghartskirchen. Five study locations were selected in the vicinity of the villages Ollern (48°16′02.5″N, 16°05′07.9″E) and Elsbach (48°15′08.3″N, 16°02′56.9″E). The study area is characterized by small scale but mostly intensified agriculture surrounded by heterogeneous landscapes and the protected forest area of the Wienerwald Biosphere Reserve (mean annual air temperature and precipitation: 9.9°C, 673 mm). In our study area, we selected five study locations along the transition zone between extensively managed, semi-natural meadows (hereafter: old grassland; OG) and
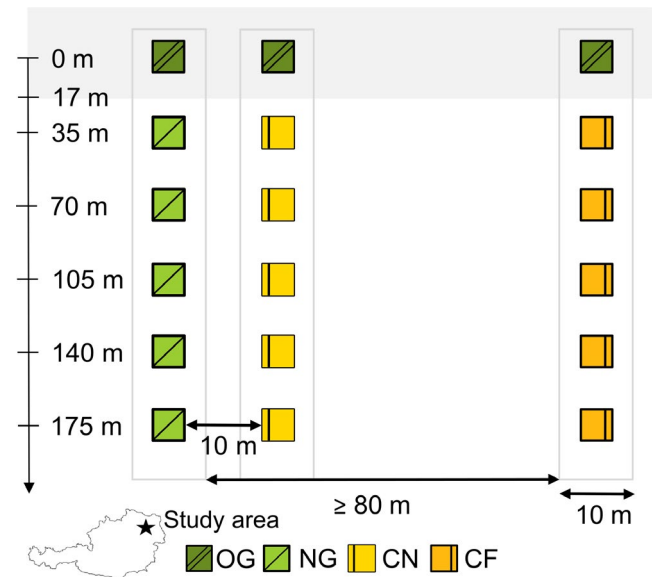

FIGURE 1 Exemplary representation of the study design of each of the five study locations in our study area, each consisting of three, 10-m wide transects (NG = newly established grassland; CN = adjacent cereal field near to NG; CF = control cereal field far from NG), and containing six sampling sites at an increasing distance to the directly adjacent old grassland (OG), indicated by the grey box on top, with a total of 90 sampling sites. The first site of each transect was located in OG (reference site)

intensively managed crop fields. In each location, we established three transects directly adjacent to each OG: new grasslands (NG), directly adjacent cereal fields near NG (CN) and more remote cereal fields far from NG (CF). Each of the resulting 15 transects contained six sampling sites (total of 90 sampling sites at regular distances of 35 m). With this set-up (Figure 1), we investigated the occurrence and spread of pollinating insects and predatory arthropods over a period of three consecutive years (2017–2019).

We established the NG transects prior to the study in August 2016, using a seed mixture of 41 plant species (with 34.0% grass species, 51.2% herbaceous plants and 14.6% legumes) to mimic the plant composition of previously investigated old grasslands. For this, we analysed 28 samples of *Filipendulo-Arrhenatheretum* and 54 samples of *Ranunculobulbosi-Arrhenatheretum* grasslands from the study area (Hülber et al., 2017). Based on these samples, we selected the 50 most frequent plant species (i.e. occurring in more than 25% of the samples), and used 41 plants for the final seed mixture that were available in sufficient quantity (Appendices S1 and S2). The new grasslands were managed through one yearly mowing event in August, and old grasslands were mown twice per year in June and August.

2.2 | Arthropod sampling and trait selection

We recorded arthropods on a total of 90 sampling sites over the years 2017, 2018 and 2019 (total of 270 site–year combinations).

Epigeic predators were recorded with two pitfall traps per sampling site (4 m apart). Pitfall traps were covered with a solid metal roof and exposed to the field for 1 week. The glass traps contained a 1:2 mixture of propylene glycol and water (Knapp et al., 2016). In total, three pitfall-trap surveys at 2-week intervals were carried out between 5 April and 30 May each year to cover the main activity peak of ground-dwelling arthropods (i.e. total of 1,620 samples for epigeic predators).

Pollinators were recorded through a combination of standardized point counts and sweep-netting (10 min per sampling site), during conditions of at least 15°C with no rain (dry vegetation), low wind force (below 10 km/hr) and low cloud cover (below 30%). Easily identifiable individuals were recorded directly and temporally kept to avoid pseudo-replication, while more cryptic species were collected with hand-nets for later identification. We counted the number of observed individuals for each recorded species. In total, four surveys at monthly intervals were carried out between 3 May and 25 August each year, until the end of the annual pollinator activity peak (i.e. total of 1,080 samples for pollinators).

All recorded species of carabids, spiders, bees (solitary wild bees, bumblebees and honey bees) and hoverflies were assigned to coded traits (Appendices S3 and S17), from which four key categories were selected for analysis of functional groups: (A) Body size: representing a continuous measure of mean thorax length in mm that was transformed to a range between 0 and 1, and interpreted as a proxy for dispersal abilities; (B) Feeding preference: reflecting the degree of zoophagous foraging in adult carabids and for hoverfly larvae (phytophagous: 0; polyphagous or saprophagous: 0.5; and zoophagous or predatory: 1); degree of hunting activity in spiders (weavers: 0; ground hunters: 0.5; and ambush hunters: 1); and the number of floral resources used by bees (oligolectic: 0 and polylectic: 0.5), which were interpreted as a proxy for species contribution to pest control of pollination services (Gallé et al., 2019); and available census data of carabids and spiders (Zulka, Paill &Trautner, unpubl. database) were used to identify probabilities of species recorded in (C) arable lands or (D) forests in Austria, according to EUNIS habitat classifications (EEA, 2014), to account for potential spillover effects of the nearby forests and the potential occurrence or survival of species across habitat types. Since adult hoverfly species cannot be assigned to distinct feeding preferences, partly because of lacking data and the dependence of feeding preferences on larval development, we used feeding preferences of predatory hoverfly larvae (Dunn et al., 2020). Honey bees were included in the analyses to assess effects on the whole pollinator community, since both honey bees and wild bees depend on continuous floral resources and potential benefit from new grasslands (Willmer & Finlayson, 2014; Wintermantel et al., 2019).

2.3 | Data analyses

Statistics were conducted with the software R (R Development Core Team, 2018, version 3.5.0). For the analysis of functional diversity

along the investigated gradients, all arthropods were considered which could be identified up to species level and assigned to a priori selected traits. For analyses, data were pooled for the 90 sampling sites and 3 years for predators (three survey periods per site and year) and pollinators (four survey periods per site and year).

First, we calculated multidimensional functional diversity (FD) of the species communities to compare different functional diversity measures and community-weighted mean (CWM) values of traits across different habitat types using the R package FD by Laliberté and Legendre (2010). We calculated the complementary functional diversity indices functional richness and functional evenness (Villéger et al., 2008), as well as community-weighted means of selected key traits for body size (linked to dispersal and food intake), feeding preference (linked to ecosystem services) and habitat preference (linked to survival).

Among the functional diversity measures, the multidimensional functional richness (FRic) index of Villéger et al. (2008) measures the amount of functional space occupied by a community. FRic is also known as the convex hull volume, which is defined by the most extreme trait values within a community. It is low when the amount of niche space occupied by a community is small. The functional evenness (FEve) index measures the regularity of the distribution of abundances in multidimensional trait space and identifies whether the resources, that is, functional niches, are evenly exploited by the species (Villéger et al., 2008). It will be lower when the filled niche space is unevenly populated, for example, when abundance is less evenly distributed among species or when functional distances among species are less regular (Mouchet et al., 2010; Villéger et al., 2008). Functional richness and evenness were calculated for the same species communities but vary independently of each other. Community-weighted means (CWM) of classified traits represent the average of trait values weighted by the relative abundances of each species, for each trait at each sampling site (Lavorel et al., 2008).

Second, we used linear mixed effect models to test how selected functional traits changed between habitat types (OG, NG, CN, CF), as well as depending on distance to semi-natural habitats (distance of sampling site to OG), and time (three survey years). Functional diversity measures and community-weighted mean values for every sampling site and year were used as responses and were Tukey-transformed prior to statistical analyses to meet model assumptions on normal distribution. Year and distance entered the models as continuous variables and were included as fixed effects in the models, while transect identity was treated as random effect (to account for sampling the same transects in consecutive years). Differences between habitat types were analysed by adjusting the reference level of the model. To test for differences in temporal development between different habitat types (OG, NG, CN and CF), we tested for differences in the slopes by introducing an interaction between year and habitat type. To test if FD-diversity measures and CWM change with distance from OG, we tested if the slope of the interaction of habitat type (only NG, CN, CF) and distance to OG was significantly different from zero. Changes in species richness and abundance compared to and in increasing distance from OG were also tested

using linear mixed effect models with sampling sites as random factor. The results are visualized in boxplots with significance levels based on lmer results and Tukey post hoc tests. The models were fitted with the lmer function in R and Maximum Likelihood.

3 | RESULTS

3.1 | Species richness and abundance

In the 3 years of the study, we recorded 15,085 carabid beetles (74 species), 11,337 spiders (89 species), 2,112 bees (91 species) and 2,072 hoverflies (63 species). Details on abundant species are reported in Appendix S4. Compared to the OG, different patterns for predator and pollinator species richness and abundance were observed (Appendix S5). For carabids and spiders, species richness and abundance were significantly different in all other habitat types, except for spider richness and abundance between OG and NG (Appendix S6). While species richness and abundance of carabids increased across the habitat gradient, spider species richness and abundance decreased from OG to NG, CN and CF. For bees and hoverflies, species richness and abundance (Appendix S6) increased significantly from OG to NG, and significantly decreased between OG and the two cereal field transects CN and CF; with the only exception of bee species richness, where the decline from OG to cereal fields was not significant (only eight species with 14 individuals recorded in total).

Similar results were observed along spatial distances from the old grasslands. While species richness and abundance of carabids increased significantly with increasing distance from OG ($p = 0.008$ and <0.001, respectively), spider richness and abundance tended to decrease, but not significantly ($p = 0.08$ and $= 0.35$ respectively). With increasing distance to old grasslands, bee abundance increased ($p = 0.02$) while bee species richness remained unchanged ($p = 0.08$). For hoverflies, species richness and abundance slightly decreased with distance from OG, but only marginally or not significant ($p = 0.05$ and 0.12 respectively).

3.2 | Functional richness and evenness

Carabids and spiders showed mixed and considerably different patterns of functional diversity (FDRic) and functional evenness (FDEve) comparing habitat types (Figure 2), year effects and distance to OG (Appendices S7 and S8). While FDRic of carabids, representing the volume of occupied niche space, was only significantly smaller in CN, it significantly increased over 3 years and with increasing distance to OG—but with less even exploitation of functional niches and respective resources (FDEve). Contrary, responses of the spider species community were more pronounced for FDEve than for FDRic, showing that spider species populated their niche space more evenly at increasing distances outside OG, but more unevenly between years (Appendices S7 and S8). For bees and hoverflies, FDric and FDEve did not differ significantly between habitat types (Figure 2) or years, but both their occupied niche space and exploitation of resources increased significantly with increasing distance from OG (Appendices S9 and S10).
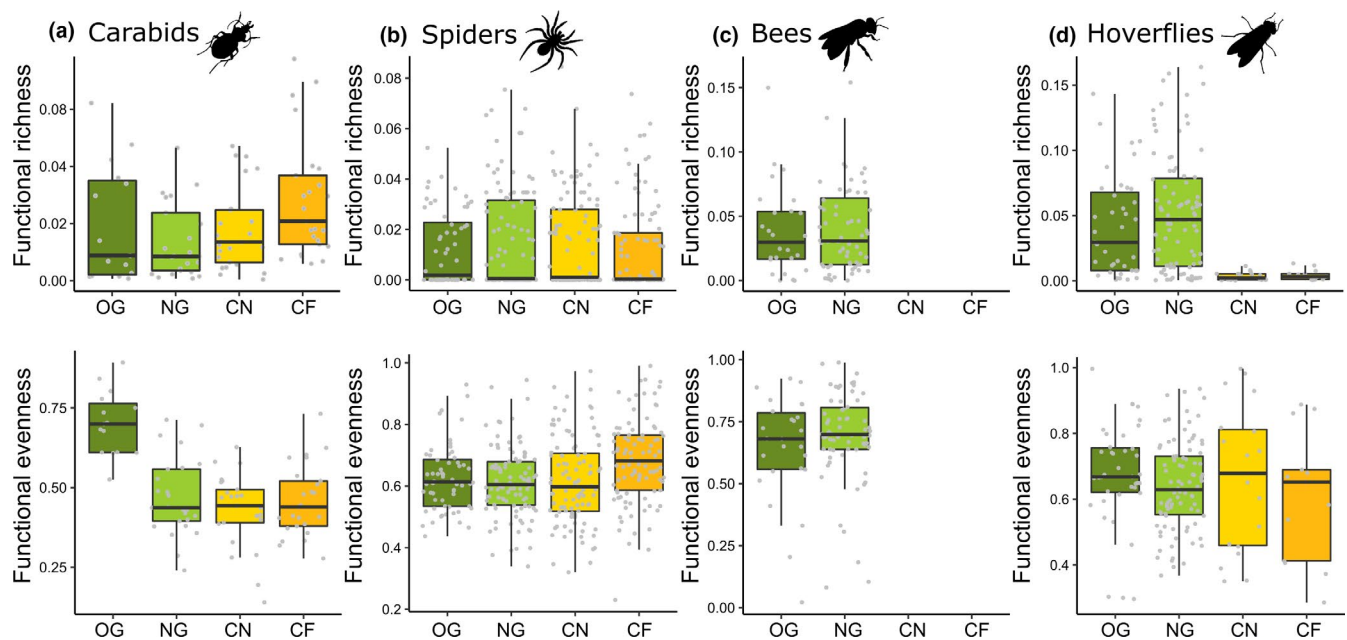

FIGURE 2 Effects of habitat types on functional richness and functional evenness of (a) carabids, (b) spiders, (c) bees and (d) hoverflies in old grasslands (OG), newly established grasslands (NG), nearby cereal fields (CN) and far distanced cereal fields (CF). Original data points are indicated by grey circles and significance levels due not differ between groups according to lmer and Tukey post hoc tests

3.3 | Functional traits

The analysis of functional key traits revealed further intra- and interspecific differences between predator and pollinator communities. While smaller carabids increased in habitats outside and further away from OG (Figure 3), larger species significantly increased over 3 years, especially in NG (Appendix S11). Smaller spiders also increased outside and further away from OG (Figure 3), but without significant year-effects (Appendix S12). The density of zoophagous

carabids significantly increased in cereal fields CN and CF, while the density of spider hunting activity significantly decreased across all habitat types compared to OG (Figure 3). A significant increase of large zoophagous carabids and ambush hunting spiders was observed with increasing distance to OG, but not over 3 years (Appendices S11 and S12).

While arable carabids and spiders were significantly more represented in all habitat types outside OG (Figure 3), they decreased significantly in NG over years (Appendices S13 and S14). While arable carabids significantly decreased in CF over 3 years, arable spiders increased significantly. Similarly, forest species in the spider species community of CF increased, while carabids showed significant decreases of forest species in NG and CN. With increasing distance to OG, arable species in both communities increased significantly and forest species decreased significantly (Appendices S13 and S14).

Compared to OG, the proportion of large bees and hoverflies was significantly higher in NG, but not significantly different from CN and CF (Figure 4). Bees in CN were significantly smaller. Simultaneously, the number of hoverflies with zoophagous larvae and the number of polylectic bees were significantly lower in NG than in OG across 3 years, and increased for hoverflies in remote CF sites (Appendices S15 and S16). All pollinator groups with these characteristic dispersal
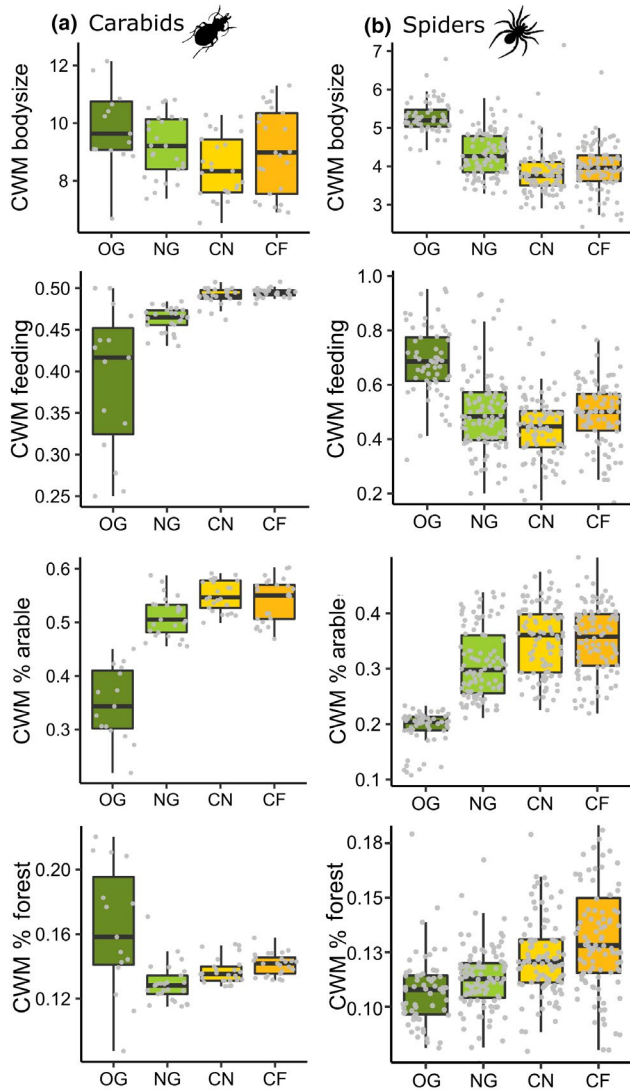

FIGURE 3 Community-weighted means of selected traits of carabids (left column) and spiders (right column) across the four habitat types (OG: old grassland; NG: new grassland; CN: cereal field adjacent to NG; CF: cereal field far from NG). Response variables represent community-weighted means (CWM) of body size (continuous ranged between 0 and 1); feeding preference of carabids (phytophagous: 0; polyphagous: 0.5; and zoophagous: 1) and spider´s hunting mode (weavers: 0; ground hunters: 0.5; and ambush hunters: 1); as well as the relative occurrence of carabid or spider species in arable lands or forests in Austria (continuous in %). Grey circles indicate original data points. Significance levels due not differ between groups (lmer and Tukey post hoc tests)
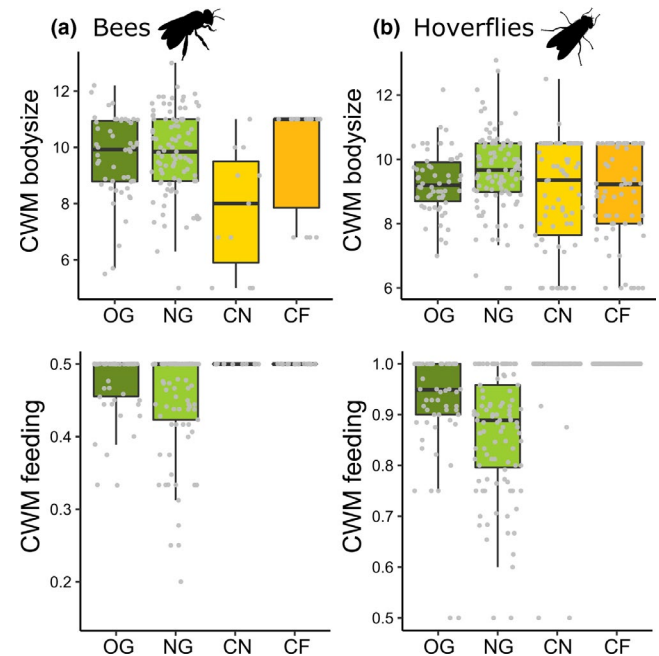

FIGURE 4 Community-weighted means of selected traits of bees (left column) and hoverflies (right column) across the four habitat types (OG: old grassland; NG: new grassland; CN: cereal field adjacent to NG; CF: cereal field far from NG). Response variables represent community-weighted means (CWM) of body size (continuous ranged between 0 and 1); and feeding preference of bees (oligolectic: 0 and polylectic: 0.5) or hoverfly larvae (phytophagous: 0; saprophagous: 0.5; and predatory: 1). Grey circles indicate original data points. Significance levels due not differ between groups (lmer and Tukey post hoc tests)

and ecosystem service-related traits increased significantly with increasing distance to OG.

4 | DISCUSSION

In line with our hypotheses, we show that predators and pollinators disperse to new grasslands in the agricultural matrix quite differently in space and time (H1), and that spatio-temporal dispersal is driven by species-specific functional traits (H2). Our findings on trait-specific responses to new grasslands demonstrate the potential of high-diversity grassland strips as an effective measure to promote multifunctionality and counteract biodiversity decline in agricultural landscapes that are currently failing to deliver necessary resources for pollinators and predators at sufficient quantities (Boetzl et al., 2020; Cole et al., 2020).

4.1 | Distance and time effects

Spatio-temporal dispersal patterns differed considerably between species groups, where spatial effects such as distance to old semi-natural grasslands appeared to have a strong direct influence on the dispersal and related colonization ability of predators and pollinators, while temporal effects such as duration of newly established grasslands did not show a clear trend. After 3 years, the species composition of newly established grassland strips became increasingly similar to the old semi-natural grasslands, but with remaining significant differences in the functional composition of predators and pollinator species. According to the observed trends after 3 years, pollinators such as solitary wild bees, bumblebees and honey bees, as well as hoverflies to some extent, appear to benefit from the introduction of new grasslands while effects on epigeic predators remain unclear, indicating that it takes longer than 3 years for carabids and spiders to adapt to new grasslands (Alignier & Aviron, 2017; Holland et al., 2017). Moreover, it seems likely that generalist predator species benefit from higher prey availability and lower intraguild predation in crop fields and thus use new grasslands more, when resources in crop fields become limited, for example, during harvesting (Rusch et al., 2015). Our results also confirm that protecting old grasslands in the agricultural matrix presents an urgently needed measure to preserve source habitats for species dispersal and colonization, as well as for associated ecological functions (Winfree et al., 2018; Wintermantel et al., 2019). This has been found not only for arthropod communities in intensified agricultural landscapes (Garrido et al., 2019), but for other forms of agrobiodiversity such as plants (Melts et al., 2018), birds (Cannon et al., 2019), mammals (Fischer et al., 2018) and their interactions (Perović et al., 2018). Because the number of old semi-natural grasslands continuously declines in European agricultural landscapes (Pe'er et al., 2014), newly established grasslands could contribute to the re-enhancement of beneficial agrobiodiversity and associated functions if they provide suitable and sufficiently stable

habitats and resources over longer periods (Boetzl et al., 2020; Cole et al., 2020).

The establishment of high-diversity grassland strips therefore appears to be a suitable long-term measure to compensate for the loss of semi-permanent set-aside land in the agricultural landscape. The technical and time effort in establishing grassland strips (or transects as described in this study) is comparable to efforts needed to establish less diverse conservation schemes or AES (Grandl et al., 2016; Hülber et al., 2017). However, the current high cost and limited availability of more diverse seed material is a potential constraint to large-scale implementation, which would be facilitated through implementation in AES and related promotion of seed production networks. The ecological enhancement of agricultural landscapes through highly diverse grassland strips would promote the continuity of resources that are particularly important for increasingly threatened pollinators and predators with high resource requirements (Boetzl et al., 2020; Cole et al., 2020; Willmer & Finlayson, 2014; Wintermantel et al., 2019).

4.2 | Trait-specific effects

The dispersal of different species groups depended, as expected, mainly on their body size, species-specific feeding or habitat preferences (as a surrogate for dispersal ability and resource demand). These findings are in line with studies on different grasslands arthropod communities in Europe (Ekroos et al., 2013; Garrido et al., 2019; Holland et al., 2016; Öckinger et al., 2018), complementing the existing evidence by new insights on the potential of newly established grasslands to serve as temporary feeding habitat and dispersal corridor for arthropods in increasingly intensified agricultural landscapes.

After 3 years, the functional diversity of predators (except large and actively hunting spiders) and pollinators became increasingly similar between new and old grasslands. This finding highlights the potential of establishing more diverse grasslands in agricultural landscapes to the benefit of associated ecosystem services, especially when old grasslands are declining or rare (Cadotte et al., 2011; Finney & Kaye, 2017; Gallé et al., 2019). The suitability of newly established grasslands as a dispersal corridor for carabids is demonstrated by our results, while distance had rather neutral or mixed effects on the occurrence of spiders, and pollinators tended to decrease with increasing distance from the old grassland habitat. While the body size of carabids and spiders outside and at increasing distance from the old grassland decreased, larger bees and hoverflies increased with increasing distance to old grasslands. These findings indicate that potential corridor effects of new grasslands are related to species-specific dispersal capacity, environmental factors such as vegetation density and resource availability (Holzschuh et al., 2007). Our results on spiders and bees with different feeding preferences indicate that actively hunting or oligolectic species may prefer more open or mono-dominant habitats than orb-weaving spiders or polylectic bees. Large carabids are often wingless and therefore limited in their dispersal, emphasizing the importance of

older habitats for the survival and functionality of these species in the agricultural matrix (Boetzl et al., 2020). Previous studies have demonstrated a negative relationship between predation rates of aphids and the community averaged body size of carabids and spiders, pointing to increased intraguild predation among these groups, which may also affect their dispersal and contribution to pest control services (Rusch et al., 2015). For bees and nectarivorous hoverflies, a positive correlation between body size and pollination effectiveness has been demonstrated (Willmer & Finlayson, 2014). Furthermore, spatial effects become increasingly important in the assessment of habitat specialists of the open agricultural landscape (Winfree et al., 2018), demonstrating the relevance of considering species-specific functional traits in the management of agricultural landscapes and beneficial ecosystem services such as pollination and biological pest control (Öckinger et al., 2018; Wood et al., 2015).

The study of species-specific traits improves our understanding of the multiple linkages between agrobiodiversity, ecosystem services and their targeted management in agricultural landscapes (Cole et al., 2020; Wood et al., 2015). Trait-based approaches allow scientists and practitioners to understand why common predators such as carabids and spiders respond very differently to agri-environment schemes (Boetzl et al., 2020; Gallé et al., 2019), and how the management of ecological functions can be optimized. It also helps to better understand what influences the dispersal ecology of pollinators to counteract their rapid decline in European agricultural landscapes, as well as the decline of threatened habitat or feeding specialists (Ekroos et al., 2013). Through ongoing efforts to address species traits, compiling data on local management practices and developing infrastructure to continue adding new studies that focus on different crops and landscape management factors, trait-based ecological research approaches like the ones used in this study will play a key role in our understanding and ability of ecosystem service management (Gallé et al., 2019). We thus suggest that the multiple and complex interactions of biotic and abiotic factors should be given more consideration in future agro-ecological research and agricultural management.

5 | CONCLUSIONS

Widespread expansion and intensification of agricultural practices combined with landscape simplification decrease the amount of semi-permanent and semi-natural habitats in the agricultural matrix and threaten agricultural biodiversity (Ekroos et al., 2014; Pe'er et al., 2014). Over 3 years, the newly established grasslands in our study developed similar plant species composition to old semi-natural grasslands and thus supported more large-sized and actively foraging and hunting species in the agricultural landscape. Adjacent crop fields are likely to benefit from such measures through enhanced predation and pollination services, if the established new grassland habitats provide suitable habitat for dispersal, colonization and survival of pollinators and predators. Pollinators appear to adopt newly established grasslands, at least as feeding habitat,

more rapidly than predators, probably due to their higher mobility (Öckinger et al., 2018), but their dispersal may also depend on environmental factors such as local vegetation density and resource availability that deserves further investigation (but see Holzschuh et al., 2007 and Holland et al., 2016). However, our results also suggest that a 3-year period is too short to enhance functional diversity and related ecosystem services through newly established grasslands. Short-term measures thus need to be complemented by long-living compensation areas and, importantly, by the conservation of permanent semi-natural habitats to effectively maintain species and functional diversity. Our findings should be acknowledged by European policy and agricultural decision makers for the design of more effective agri-environment schemes, taking into account trait-related responses of agricultural biodiversity to ongoing land use expansion and intensification, as well as concurrent effects on ecosystem functions and services.

AUTHORS' CONTRIBUTIONS

T.F., D.M. acquired the funding for this study, conceived ideas and, together with B.M., designed the methodology; B.M. led the data collection and analysis as well as the writing and revision of the manuscript; M.B., R.I.H., D.R. and R.W. supported data collection. All authors contributed critically to manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The entire dataset that supports the findings of this study is available via a permanent open access data repository of the University of Vienna http://phaidra.univie.ac.at/o:1168756 (Maas et al., 2021). Most of the data supporting the findings of this study at the journal level are available within the paper (and its Supporting Information files). Extended data are available on request from the authors.

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