FalloWS and permanent grasslands conserve the species composition and functional diversity of carabid beetles and linyphiid spiders in agricultural landscapes

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Abstract. 1. The European Union reformed the Common Agricultural Policy (CAP 2013) to include greening measures with the aim to decrease negative impacts of farming on the environment and biodiversity. The degree to which greening measures such as permanent grassland or fallows of different ages enhance biodiversity is still debated.
2. We investigate the effect of fallows in two different age classes and permanent grassland in the surrounding landscape on the taxonomic and functional diversity of two numerically dominant groups of natural enemies in cereal fields: soil-emerging carabid beetles (Family Carabidae, Order Coleoptera) and ground-active linyphiid spiders (Family Linyphiidae, Order Araneae).
3. The species richness, abundance and Hill–Shannon diversity of carabids and linyphiids did not differ significantly between fallows and cereal fields and was not significantly related to the proportion of permanent grassland in the surrounding landscape. The species composition of both communities differed significantly between cereal fields and fallows. The functional distinctness, as an index reflecting the similarity among species in terms of functional traits, of linyphiids was significantly higher in fallows than in cereal fields. The trait composition of carabids was significantly related to the proportion of permanent grassland depending on field type (cereal or fallow). Our results document considerable species turnover in natural enemy communities of adjacent cereal fields and fallows, and support the assumption that older fallows (>8 years) produce functionally more diverse natural enemy communities. Maintaining fallows for a long period is an important measure to promote the functional diversity in predaceous arthropod communities.

Key words. Biodiversity, Carabidae, conservation, fallow, functional trait, greening measures, Linyphiidae, permanent grassland.

Introduction

In 2013, the European Union (EU) commission reformed the Common Agricultural Policy (CAP) and introduced greening measures in order to reduce negative effects of agriculture on the environment and biodiversity. The CAP2013 created incentives for European farmers to maintain permanent grassland and dedicate at least 5% of their productive land to the so-called ecological focus areas (EFA). This policy was implemented on 69% of the total arable land in the EU by 2016 (European Commission, 2017). EFA are semi-natural habitats such as fallows, nitrogen-fixing crops or buffer strips with the aim to improve the sustainability of agriculture. Population sizes and the diversity of arthropods in agricultural landscapes benefit from the presence...
of semi-natural habitats (Woodcock et al., 2005), such as grassy field margins (Labruyere et al., 2016), flower fields (Mader et al., 2017) or fallows (Van Buskirk & Willi, 2004).

Among all EFA habitat types, fallows and other non-crop options are generally reported to have the greatest potential to benefit biodiversity (Underwood & Tucker, 2016). Fallows may promote the biodiversity of invertebrate natural enemies by providing additional ecological niches, alternative prey and refuge for breeding or hibernation (Wamser et al., 2011; Mader et al., 2018). The effect of these habitats on biodiversity conservation depends on the focal taxonomic group (European Commission, 2017) and age of the habitat. Older fallows, for example, often have a stronger positive effect on biodiversity than newly established fallows (Frank & Reichhart, 2004; Van Buskirk & Willi, 2004; Tscharntke et al., 2011). However, local land-use decisions should not ignore the landscape context, as the efficiency of agri-environmental schemes for species conservation varies in landscapes with high proportions of semi-natural habitats, such as permanent grasslands (Tscharntke et al., 2016).

The majority of studies focusing on the effects of fallows on arthropods quantified the activity density and species richness in local communities (Frank & Künzle, 2006; Marshall et al., 2006; Holland et al., 2016). The community inhabiting an area is the sum of colonising and locally emerging individuals (minus emigration and mortality), but studies usually do not address the local emergence of species with soil-living stages. It remains unknown if arthropod predator species with soil-living larvae colonise fallows from the surrounding landscape or if individuals emerge locally from fallow soils. Recent studies, using emergence tents highlighted that overall emergence numbers for different beetle families and functional groups differed significantly between arable fields and semi-natural habitats such as permanent grasslands and fallows (Hanson et al., 2016, 2017; Birkhofer et al., 2018). Based on this information, it is important to understand how fallows and permanent grassland affect the emergence of generalist predator species with soil living life stages, and ultimately the contribution of these habitats to species conservation of predator communities.

Taxonomic diversity is an important metric used to evaluate the conservation success of land-use decisions, but may not reflect the consequences on the functional properties of local communities. Analyses of traits are a powerful approach to identify effects of local land-use decisions and surrounding landscapes on functional differences and trait composition of local communities. For generalist predators such as carabids and spiders, several studies indicated that agricultural land-use decisions affect traits. Ribera et al. (2001), for example, concluded that in intensively managed landscapes, carabids have lower variability of morphological traits. Grassy field margins have higher abundances of omnivorous and granivorous carabids than cereal fields (Birkhofer, Wolters, et al., 2014). In spiders, communities of web-building spiders are characterised by larger species in landscapes with a higher proportion of arable land (Mader et al., 2017). Larger (Birkhofer et al., 2015) and less mobile (Birkhofer et al., 2017) species are more sensitive to disturbance than smaller species, and the ability to recolonise disturbed areas is faster with smaller species (Bonte et al., 2002; Schmidt & Tscharntke, 2005b). Spiders from the family Linyphiidae, for example, are considered very mobile as their small size permits ballooning throughout the whole life cycle (Sikes et al., 2013). Many linyphiid species are characteristic for intensively managed arable fields (called agrobiont species, Birkhofer et al., 2013) and some species even benefit from more intense farming practices (Birkhofer, Ekroos, et al., 2014). Recent studies also highlighted the importance of distinguishing between effects of local land-use decisions on arthropod numbers (Hanson et al., 2017) and trait composition (Hanson et al., 2016) in local communities. Carabid communities that inhabited (sampled by pitfall traps) or emerged from (sampled in emergence tents) the same permanent grassland had comparable body sizes in a previous study (Hanson et al., 2016). In contrast, arable fields (winter wheat and sugar beet) were characterised by communities with species of larger body sizes compared to communities that emerged from soils in the same arable fields (Hanson et al., 2016). This discrepancy highlights the need to also understand local emergence of arthropods with soil-living stages by different habitat types to judge the conservation value of semi-natural habitats and, based on trait analyses, to evaluate their potential contribution to ecosystem services.

Spiders from the family Linyphiidae and beetles from the family Carabidae are widespread and abundant as natural enemies of pests in agricultural ecosystems (Kromp, 1999; Birkhofer et al., 2013). To assess effects on these two families of natural enemies, we selected two appropriate sampling methods: for carabids with soil-living larvae, we used pitfall traps inside emergence tents, as this method provides area-based estimates of the emergence of adult beetles from local soils. Linyphiids do not necessarily emerge from soils as egg sac deposition and hatching occurs above the soil surface in most species (Samu et al., 1996). Hence, to also sample sufficient numbers of individuals for our analyses, we used pitfall traps outside emergence tents to provide estimates of community composition based on their activity density.

We investigated the potential of fallows from two distinct age classes (newly established vs. more than 8 years old) compared to cereal fields to locally produce ground beetle species (Coleoptera, Carabidae) and support sheet weaver spider species (Araneae, Linyphiidae) considering both the conservation value for species and individual traits. The field sites were selected to include a gradient addressing the effect of the proportion of permanent grasslands surrounding each site. We hypothesise that at the local scale, older fallows (>8 years) produce the highest number, taxonomic richness and trait diversity for carabids, but do not support a taxonomically and functionally more diverse linyphiid community compared to new fallows or cereal fields. At larger spatial scales, we hypothesise that high proportions of permanent grassland promote the abundance, taxonomic richness and trait diversity of carabids and linyphiids.

Material and methods

Sampling

The field study was conducted in the province Scania, which is a region in southern Sweden dominated by agriculture. We selected 6 replicated study locations for each of three field types...
(cereal fields, old and new fallows) and each of the 18 locations had an adjacent control cereal field. Fallow were either new (established in 0–3 years ago; N = 6) or old (established at least 8 years ago; N = 6) each with an adjacent cereal field (N = 12). Focal cereal fields (N = 6) also had an adjacent cereal field (N = 6). Cereal fields (focal and adjacent, N = 24), new and old fallows (N = 12) are hereafter referred to as field types. Cereal fields (6 focal and 18 control) were 14 spring barley, 8 autumn wheat, 1 rye and 1 oat field under conventional management. The six locations per field type were selected along a gradient of permanent grassland covering the area in a radius of 1 km. The range of permanent grassland cover was 0.89–44.34% (new fallow: mean ± SD = 15.47%, range = 3.82–22.85%; old fallow: mean = 22.95%, range = 5.06–43.45%; cereal field: mean = 17.92%, range = 0.89–44.34%). Grassland cover was calculated using land-use cover data from the Swedish Board of Agriculture’s Integrated Administrative and Control System database (Blockdatabasen).

In each field, study plots were 20 m away from the boundary between the two fields and at least 20 m away from any other field edge. To study the emergence rate of Carabidae, commercially available emergence tents (MegaView Science™) were setup in each study plot during the sampling period. The emergence tents covered an area of 0.6 × 0.6 m was 0.6 m high and was built from a synthetic fabric with a mesh opening of 0.5 mm. A bottle was attached on top of the tent and a pitfall trap (11.5-cm diameter, 12-cm depth) was placed inside. To prevent catching vertebrates, a metal grid with a mesh size of 12.7 × 12.7 mm was attached to the top of all pitfall traps. The base of the tent had flaps that were inserted 10 cm deep into the soil in order to constrain the emerging arthropods from entering or escaping the tent. To study the activity density of Linyphiidae, a single pitfall trap was established 10 m away from each emergence tent in all study plots. These pitfall traps were identical to those used in the emergence tents and were additionally protected from rainfall by a roof. For all pitfall traps, 70% propylene glycol was used to collect arthropods with a few drops of odourless detergent to reduce surface tension.

The 24 cereal fields and 12 fallows were sampled every 14 days to quantify emergence rates of Carabidae and activity densities of Linyphiidae over four sampling periods during the cereal growing season (18–22 May, 1–5 June, 15–19 June and 29 June–3 July 2015). The collected specimens were determined to species level with Lindroth (1985) and Trautner and Geigenmüller (1987) for Carabidae and Nentwig et al. (2020) for Linyphiidae. In total, 978 carabids from 62 species emerged from local soils and 1735 ground-active linyphiids from 50 species were collected.

### Statistical analyses

For carabid and linyphiid communities, the total number of individuals, species richness and Hill–Shannon diversity (Roswell et al., 2021) were calculated. The Hill–Shannon diversity is identical to the true diversity as the number of equally common species would be required to give the value of the Shannon index observed at each study plot (Jost, 2006). The average functional distinctness, as an index reflecting the similarity among species in terms of functional traits, was calculated from a binary-coded matrix of trait variables grouped into trait categories (Table 1) for each species (traits × species matrix) and a site × species matrix with the number of individuals for all species in the respective community (Somerfield et al., 2008; Birkhofer et al., 2015). The average functional distinctness of a community represents the expected distance in trait space between two individuals chosen at random from the sample, provided those two individuals were not from the same species. The trait composition was analysed based on a site × trait variable matrix weighted by the number of species observed at each site that represent each trait variable. Trait space was defined by a resemblance matrix derived from the traits × species matrix based on the simple matching coefficient (Somerfield et al., 2008). In this resemblance matrix, two species are 100% similar if they share the identical set of traits and are 0% similar if all traits are exclusively occurring in one of the species with no overlap in trait presence or absence.

### Table 1. Trait categories with individual trait variables for soil-emerging Carabidae and ground-active Linyphiidae communities. The number in parentheses for each trait variable shows the number of levels in each variable.

| Trait category   | Trait variables                               | Carabidae                                                                 | Linyphiida                                                                 |
|------------------|-----------------------------------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------------|
| Trait size       | Size as 1–4, 4–7, 7–10, 10–13, 13–16, 16–18 and >18 mm (7) | Size as 1–2, 2–3, 3–4, 4–5, 5–6 and 6–7 mm (6)                           |
| Phenology        | Spring, summer or autumn breeder (3)          |                                                                           |                                                                          |
| Trophic mode     | Carnivorous, phytophagous (2)                 |                                                                           |                                                                           |
| Stratum preference| Soil surface, on vegetation (2)               |                                                                           |                                                                           |
| Habitat preference| Wetland, grassland, forest, pioneer vegetation, arable (5) |                                                                           |                                                                           |
| Humidity preference| Stenocous xerophilous, xerophilous, mesophilous, hygrophilous, stenocous hygrophilous (5) |                                                                           |                                                                           |

Sources for carabid traits: Löbl and Smetana (2003), Marggi (1992), Luka et al. (2009). Sources for linyphiid traits: Nentwig et al. (2020), Maurer and Hänggi (1990), Uetz et al. (1999). Arachnologische Gesellschaft (2020).

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absence to another species. To analyse these community properties further, resemblance matrices were created for each variable based on Euclidean distances, as an appropriate resemblance measure for variables without zero values.

Species composition was analysed based on a multivariate matrix of square root-transformed numbers of individuals for each species at each study plot transformed to a resemblance matrix based on Bray–Curtis similarities. Bray–Curtis similarities are a standard resemblance measure for count-based community data, with the advantage that joint absences of a species at two sites are not incorporated into calculations of resemblance (thereby avoiding the double-zero problem). Square root transformation was performed prior to analyses to reduce the impact of very common species compared to less common species on the outcome of the analyses (Clarke & Green, 1988).

We generally used permutational analyses of variance (PERMANOVA) as a suitable method to test for effects on univariate (species composition) data (Anderson et al., 2008). PERMANOVA has the advantage of not assuming normality of residuals or homoscedasticity. All models used the fixed factor Field type (3 levels: cereal field, new fallow or old fallow), the random factor Field pair (18 paired Field type locations with a cereal field and either another cereal field, a new or old fallow adjacent to it) and the covariable Permanent grassland (proportion of unimproved grasslands not receiving synthetic fertilisers in 1 km radius). All models further included interaction terms between the fixed factor and the covariable and a planned contrast based on the design of the study (cereal field vs fallows (combined new and old)). As an analysis of a hierarchical model with a covariable, models are based on type I (sequential) sums of square (fitting terms in the sequence Permanent grassland, Field pair and Field type) as recommended for unbalanced designs with covariates (Anderson et al., 2008).

The sequential fit was motivated by the aim to identify local effects on emergence and activity after accounting for effect of larger spatial scales (permanent grassland at landscape scale and field pair location). Models were performed based on 9999 permutations of residuals under a reduced model as recommended in Anderson et al. (2008).

We also tested for homogeneity of multivariate dispersion in case of a significant PERMANOVA result for the fixed factor as recommended by Anderson and Walsh (2013). PERMDISP (Anderson, 2006) is a distance-based test for homogeneity of multivariate dispersions on the basis of a resemblance measure as a dissimilarity-based multivariate extension of Levene’s test (Levene, 1960). In case of a significant main effect for the fixed factor, differences between the three levels of the fixed factor were tested with pair-wise post hoc PERMANOVA. In case of a significant interaction between the covariable and the fixed factor or contrast, data were further analysed with Spearman correlations between the covariable and individual dependent variables within each level of the fixed factor or contrast respectively. Significant effects of the fixed factor or contrast on species composition data were illustrated with canonical analysis of principal coordinates (Anderson & Walsh, 2003) and then tested for effects on individual species with similarity percentage analyses (SIMPER; Clarke & Gorley, 2015). Venn diagrams were created to visualise the number of exclusive carabid and Linyphiidae communities.

### Table 2. Effects of the proportion of permanent grasslands (1 km radius, covariable), field pair (random factor) and field type (fixed factor: cereal field, new or old fallow) including the planned contrast between fallows (old and new) and cereal fields based on permutational analyses of variance for abundance (soil-emerging Carabidae) or activity density (ground-active Linyphiidae), species richness, Hill–Shannon diversity and species composition of (a) soil-emerging Carabidae and (b) ground-active Linyphiidae communities.

| Source                        | (a) Carabidae | (b) Linyphiidae |
|-------------------------------|---------------|-----------------|
|                               | Abundance     | Species richness | Hill–Shannon diversity | Species composition |
|                               | Pseudo-F | P(perm) | Pseudo-F | P(perm) | Pseudo-F | P(perm) | Pseudo-F | P(perm) |
| Permanent grassland           | 1 | 0.04 | 0.846 | 0.18 | 0.679 | 0.76 | 0.396 | 1.23 | 0.288 |
| Field pair                    | 16 | 2.42 | 0.056 | 3.31 | 0.013 | 2.86 | 0.025 | 1.98 | <0.001 |
| Field type                    | 2 | 1.15 | 0.346 | 0.99 | 0.396 | 1.00 | 0.388 | 2.35 | 0.002 |
| Fallow vs. cereal             | 1 | 0.13 | 0.728 | 0.79 | 0.385 | 2.01 | 0.180 | 2.18 | 0.015 |
| Permanent grassland × field type | 2 | 0.29 | 0.753 | 1.16 | 0.337 | 2.01 | 0.167 | 2.63 | 0.001 |
| Permanent grassland × fallow vs. cereal | 1 | 0.03 | 0.857 | 2.91 | 0.108 | 4.00 | 0.064 | 3.12 | 0.002 |
| Residuals                     | 14 |             |             |             |             |             |             |             |
| Total                         | 35 |             |             |             |             |             |             |             |

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linyphiid species in each field type. To create a balanced number of plots in each field type for this graphical comparison, the communities from six new and old fallows were compared to the six focal cereal fields. We performed all statistical analyses with PRIMER version 7 and the PERMANOVA add-on (PRIMER-e, Quest Research Limited, Auckland, New Zealand).

**Results**

**Carabidae**

The abundance, species richness and Hill–Shannon diversity of emerging carabids did not differ significantly between field types and were not significantly related to the proportion of permanent grassland in the landscape or the interaction between both terms (Table 2). The species composition of emerging carabids significantly differed between field types and between cereal fields and fallows in general (Table 2). The multivariate dispersion of species composition data did not differ significantly between field types (\( P = 0.958 \)). Communities of emerging carabids in new fallows were dominated by a single species (Bembidion tetracolum) contributing 35.7% of all emerging individuals (Fig. 1a). The dominance of the most abundant emerging species in old fallows (Acupalpus exiguous, 23.3%) and cereal fields (Pterostichus melanarius, 16.0%) was lower. The four most dominant species emerging from soils in cereal fields (>10%) have habitat preferences for arable fields, a pattern also observed for 2 out of the 3 most dominant emerging species in new fallows. The only species with more than 10% contribution to emerging individuals in old fallows (A. exiguous) does not have a preference for arable fields but rather for wetland.

Comparing field types, 18 carabid species were found exclusively in old fallows, with 6 exclusive species in new fallows and 10 exclusive species in focal cereal fields (Fig. 2a).

The species composition of old fallows differed significantly from new fallows (pairwise post hoc PERMANOVA: \( P = 0.029 \)) and cereal fields (\( P = 0.002 \)), but communities in cereal fields did not differ significantly from communities in new fallows (\( P = 0.353 \); Fig. 3a). The significant difference between old and new fallows (Bray–Curtis dissimilarity 88.2%) was based on the following three most discriminating species: B. tetracolum (SIMPER; old 0.0 vs. new 8.8 average individuals per site, species contribution to observed dissimilarity 8.6%), Bembidion lampros (0.3 vs. 3.8 individuals per site, contribution 7.4%) and Clivina fossor (1.8 vs. 3.2 individuals per site, contribution 6.8%). Carabid communities in old fallows differed from cereal fields (dissimilarity 88.2%) based on the following three most discriminating species: B. lampros (old fallow 0.3 vs. cereal field 4.0 individuals per site, contribution 6.5%), Pterostichus melanarius (1.0 vs. 4.6 individuals per site, contribution 5.1%) and Harpalus ruflipes (1.7 vs. 2.3 individuals per site, contribution 5.9%). The proportion of permanent grassland affected B. lampros in fallows (Spearman correlation, \( N = 12, R = -0.58, P = 0.047 \)) and Bembidion obtusum in cereal fields (\( N = 24, R = -0.55, P = 0.005 \)) negatively. Two Swedish red list species emerged with one individual each: Clivina collaris (endangered, emerged from a wheat field) and Harpalus luteicornis (vulnerable, emerged from an old fallow).

The average functional distinctness of communities of emerging carabids did not differ significantly between field types and was not related to the proportion of permanent grassland (Table 3). The proportion of permanent grassland affected the functional distinctness significantly depending on the planned
contrast between cereal fields and fallows in the model. The functional distinctness declined significantly with an increasing proportion of permanent grassland in fallows ($N = 12, R = -0.75, P = 0.005$), but not in cereal fields ($N = 18, R = 0.00, P = 0.987$). Trait composition was also significantly related to the proportion of permanent grassland depending on the contrast between cereal fields and fallows (Table 3). The number of summer breeding species was generally very low in all fields (0–2 species), but increased significantly with the proportion of permanent grassland in cereal fields ($N = 18, R = 0.49, P = 0.040$), but not in fallows ($N = 12, R = 0.00, P = 0.987$). The number of species with preferences for wetland habitats ranged between 0–5 species and tended to increase with the proportion of permanent grassland in fallows ($N = 12, R = 0.54, P = 0.073$), but not in cereal fields ($N = 12, R = 0.14, P = 0.515$).

**Linyphiidae**

The activity density, species richness and Hill–Shannon diversity of linyphiids did not differ significantly between field types and were not significantly related to the proportion of permanent grassland in the landscape or the interaction between both terms (Table 2). The species composition of linyphiids differed significantly between field types and between cereal fields and fallows in general (Table 2). The multivariate dispersion of community data (species composition) differed significantly between field types ($P < 0.001$), with significant differences in dispersion between cereal fields and old ($P < 0.001$) or new ($P < 0.001$) fallows, but not between old and new fallows ($P = 0.080$). Linyphiid communities in cereal fields were taxonomically significantly more homogeneous than in fallows (Fig. 3b). Linyphiid communities in new fallows and cereal fields were dominated by a single species (*Erigone atra*) contributing 41.6% or 33.6% respectively of all trapped individuals (Fig. 1b). The dominance of the most abundant species in old fallows was lower (*Pocadicnemis juncea*, 19.8%). The three most dominant species in cereal fields and new fallows (>10%) all show habitat preferences for arable fields. The two most dominant species in old fallows with more than 10% contribution do not show preferences for arable fields, but rather prefer humid grassland and bog habitats (*P. juncea*) or are habitat generalists (*Gongylidiellum latebricola*). Comparing field types, 16 linyphiid species were found exclusively in old fallows, with 5 exclusive species in new fallows and 4 exclusive species in focal cereal fields (Fig. 2b).

The species composition of cereal fields differed significantly from old ($P < 0.001$) and new fallows ($P = 0.020$) and community composition in old and new fallows also differed significantly ($P = 0.002$; Fig. 3b). Linyphiid communities in cereal fields
differed from old fallows (dissimilarity 91.2%) based on the following three most discriminating species: *E. atra* (SIMPER; cereal 18.1 vs. old 0.3 average individuals per site, contribution 13.00%), *Oedothorax apicatus* (9.9 vs. 0.0 individuals per site, contribution 10.4%) and *Erigone dentipalpis* (7.2 vs. 0.0 individuals per site, contribution 9.2%). Linyphiid communities in cereal fields differed from new fallows (dissimilarity 61.8%) based on the following three most discriminating species: *E. atra* (18.1 vs. 23.2 individuals per site, contribution 30.8%), *O. apicatus* (9.9 vs. 7.3 individuals per site, contribution 17.8%) and *E. dentipalpis* (7.2 vs. 10.2 individuals per site, contribution 12.6%). Linyphiid communities in old and new fallows differed (dissimilarity 74.5%) based on the following three most discriminating species: *E. atra* (0.3 vs. 23.2 individuals per site, contribution 8.7%), *E. dentipalpis* (0.0 vs. 10.2 individuals per site, contribution 7.6%) and *Pocadicnemis juncetra* (3.5 vs. 0.0 individuals per site, contribution 6.6%). The proportion of permanent grassland affected *Porrhomma microphthalmum* (Spearman correlation, \(N = 24\), Table 3. Effects of the proportion of permanent grasslands (1 km radius, covariable), field pair (random factor) and field type (fixed factor: cereal field, new or old fallow) including the planned contrast between fallows (old and new) and cereal fields based on permutational analyses of variance of the functional distinctness and trait composition of (a) soil-emerging Carabidae and (b) ground-active Linyphiidae communities.

| (a) Carabidae | Functional distinctness | Trait composition |
|---------------|-------------------------|------------------|
|               | d.f. | Pseudo-\(F\) | \(P(\text{perm})\) | Pseudo-\(F\) | \(P(\text{perm})\) |
| Permanent grassland | 1 | 0.73 | 0.406 | 0.54 | 0.578 |
| Field pair | 16 | 1.17 | 0.341 | 3.06 | 0.005 |
| Field type | 2 | 1.57 | 0.246 | 1.83 | 0.137 |
| Fallow vs. cereal | 1 | 2.80 | 0.112 | 1.80 | 0.163 |
| Permanent grassland \(\times\) field type | 2 | 3.21 | 0.076 | 2.19 | 0.094 |
| Permanent grassland \(\times\) fallow vs. cereal | 1 | 4.90 | 0.043 | 4.61 | 0.023 |
| Residuals | 14 |
| Total | 35 |

| (b) Linyphiidae | Functional distinctness | Trait composition |
|---------------|-------------------------|------------------|
|               | d.f. | Pseudo-\(F\) | \(P(\text{perm})\) | Pseudo-\(F\) | \(P(\text{perm})\) |
| Permanent grassland | 1 | 0.00 | 0.978 | 0.23 | 0.804 |
| Field pair | 16 | 1.69 | 0.157 | 2.08 | 0.057 |
| Field type | 2 | 11.92 | 0.001 | 2.17 | 0.115 |
| Fallow vs. cereal | 1 | 17.30 | <0.001 | 1.16 | 0.300 |
| Permanent grassland \(\times\) field type | 2 | 3.41 | 0.062 | 1.16 | 0.332 |
| Permanent grassland \(\times\) fallow vs. cereal | 1 | 0.92 | 0.361 | 0.52 | 0.537 |
| Residuals | 14 |
| Total | 35 |

Fig 4. Median, 25th and 75th percentile, minimum and maximum and outliers of the average functional distinctness of carabid beetle communities in cereal fields, old and new fallows.

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The average functional distinctness of linyphiid communities differed significantly between field types (Table 3) and cereal fields and fallows in general, with significantly lower functional distinctness in cereal fields compared to old (P < 0.001) and new fallows (P = 0.005; Fig. 4). The average functional distinctness did not differ significantly between old and new fallows (P = 0.198). The composition of traits did not differ between field types and was not significantly related to the proportion of permanent grassland.

Discussion

The number, species richness and Hill–Shannon diversity of emerging carabids and ground-active linyphiids did not differ significantly between field types and was not significantly related to the proportion of permanent grassland in the landscape. In contrast, taxonomic composition and trait-based metrics differed significantly between field types, but often only differed between old fallows on one side and cereal fields and new fallows on the other. The number of exclusive species in both predator groups showed the same pattern. These results highlight the importance to consider compositional and functional metrics in biodiversity studies in addition to traditional diversity measures, as species turnover seems to be an important mechanism during succession of arable fields to fallow land. Effects of falls on communities of predaceous arthropods often only manifested at least 8 years after conversion.

Soil-emerging Carabidae

In contrast to our hypothesis, the abundance, species richness and Hill–Shannon diversity of emerging carabids were not significantly related to the field type or the proportion of permanent grassland. Previous studies primarily focused on carabid beetles collected by pitfall traps in local habitats, but not on locally emerging beetles. Mader et al. (2017) for example, showed that carabid species richness in flowering fields was significantly higher than in adjacent cereal fields. Carabid numbers in grassy margins were lower than in conventionally managed arable fields (Hof & Bright, 2010), which was also observed for organically managed cereal fields and adjacent grassy margins (Birkhofer, Wolters, et al., 2014). Lys and Nentwig (1992) showed that the activity density of carabids in winter wheat fields and adjacent strips did not differ significantly, while the species richness and diversity were significantly higher in adjacent strips. The results of the present study suggest that the previously reported significant differences in activity density or richness between arable fields and adjacent semi-natural habitats are not a consequence of differences in local emergence, but rather result from different colonisation patterns between field types and active habitat selection due to specific preferences. In particular, semi-natural habitats, such as fallows, that persist after harvest can act as important refugia and overwintering areas for adult carabids (Honěk & Kocian, 2003; Wamser et al., 2011).

The composition of communities of emerging carabids in old falls differed significantly from cereal fields and new falls. It takes time to establish a semi-natural area that promotes the carabid community (Günter, 2000). New falls in this study were at most 3 years old, and at this stage, carabid species may not prefer falls over surrounding cereal fields (Frank et al., 2007). Our results suggest that the age of falls is an important factor to consider when deciding on local greening measures, which may not determine the number or richness of emerging carabid beetles but will affect the identity of species emerging from local soils. The most discriminant species between field types (B. tetracolum, B. lampros, P. melanarius and P. rufipes) are more abundant in cereal fields or new falls compared to old falls. Bembidion lampros, B. tetracolum and P. melanarius are common species in cereal fields (Kromp, 1999) with carnivorous diets and important roles in pest control (Lindroth, 1985; Den Boer & van Dijk, 1996). Pterostichus melanarius is omnivorous and the larvae of this species are known to feed on cereal grains (Burmeister, 1939; Thomas et al., 1997). The known preference for agricultural fields of adults in these species might be the major reason for the observed high emergence numbers in cereal fields compared to old falls. At the landscape scale, cereal fields provide food resources for carnivorous carabid species (Tscharntke et al., 2016). Negative relationships between the abundance of natural enemies and the amount of semi-natural habitat in the landscape are observed if the dominant carabid species prefer open habitats and hibernate in arable fields (Rusch et al., 2016). These previous results could explain the observed decrease in the number of emerging individuals of B. tetracolum and B. lampros with an increasing proportion of permanent grassland in this study. To fully understand the effect of landscape composition on the emergence of carabids, future studies should include a larger number of falls on an even more pronounced landscape composition gradient.

The average functional distinctness, as an index reflecting the similarity among species in terms of functional traits, tended to be higher in old falls compared to cereal fields. This result indicates that cereal fields, as an intensively managed habitat, provide a narrower range of resources and environmental conditions, which could only be utilised by species with certain traits compared to falls (for similar patterns comparing permanent grasslands and cereal fields: Birkhofer et al., 2015). Summer breeders in cereal fields, that is, late spring breeders that usually hibernate as adults benefit from the availability of permanent grassland. Puttauf et al. (2005) concluded that a high complexity of landscapes benefits carabid species that prefer a wider range of habitats.

Ground-active Linyphiidae

Field type and the proportion of permanent grassland in the surrounding did not significantly affect the activity density, species richness and Hill–Shannon diversity of linyphiids. This result could partly be a consequence of the relatively late sampling in linyphiid phenology (end of May to the beginning of July) and migration into all field types from the surrounding
areas prior to sampling. Overwintering habitats close to the study plots facilitate quicker colonisation (especially ground-based immigration) into cereal fields and these dispersal patterns have an important role in the population dynamics of dominant species (Lemke & Poehling, 2002). Schmidt and Tscharntke (2005a) for example showed that the abundance of linyphiids was positively correlated to the availability of non-crop areas in May, but not in June. The ongoing immigration of linyphiids into cereal fields at this time had levelled out the differences between crop and non-crop habitats and many of the species of linyphiids had also reproduced by then (see also Topping & Sunderland, 1994; Thorbek et al., 2003). The fact that most linyphiid species are excellent at dispersing by ballooning (Duffey, 1998) could further reduce the differences between arable fields and nearby overwintering sites in number of individuals and species later in the season.

Pest control in agriculture can be enhanced by the proximity of natural habitats (Tscharntke et al., 2016), but this may not always be the case (Karp et al., 2018). Fallows have been proposed to be major source habitats for pests and their close proximity to arable fields could facilitate colonisation of crops (Baur, 2014). In the current study, two of the most dominant linyphiid species in cereal fields, E. atra and E. dentipalpis, are excellent aerial dispersers, while the third, O. apicatus, relies more on ground-based migration (Thomas et al., 1990; Lemke & Poehling, 2002), or may persist in arable fields throughout the year (Mestre et al., 2018). All three species are known to prey on cereal aphis (Alderweireldt, 1994). Clough et al. (2005) and Öberg et al. (2008) found that the number of E. atra and O. apicatus individuals in agricultural fields was not influenced by the surrounding landscape. However, the immigration of spiders from habitats in the surrounding landscape may still have an important impact on the local species richness of spiders (Schmidt, Thies, et al., 2008). So-called mass effects, where species less well-adapted to one habitat continually immigrate from a more favourable source habitat, may enable ecologically similar species to coexist in a habitat and could mask more pronounced differences in species richness or abundance (Amarasekare & Nisbet, 2001; Mouquet & Loreau, 2002).

The old fallows in the current study had higher vegetation cover and plant height than the cereal fields (Amarasekare & Nisbet, 2001; Thorbek et al., 2003). The fact that most linyphiid species are excellent at dispersing by ballooning (Duffey, 1998) could further reduce the differences between arable and nearby fallows in number of individuals and species later in the season.

Conclusions

Our results indicate that fallows do not generally produce a higher taxonomic diversity of soil-emerging carabids or ground-active linyphiids in Southern Sweden. The species composition of communities was significantly different between field types, primarily due to a small number of abundant species that were characteristic for arable fields and young fallows. Older fallows in particular altered communities, as they provided more complex and diverse structure and were inhabited by functionally more diverse carabid and linyphiid communities. Our results suggest that maintaining a combination of agricultural and fallow fields is of high value, not primarily to promote species richness in local habitats, but to conserve taxonomic and functional diversity at larger spatial scales. Fallows aiming at the conservation of predaceous arthropods should be established and maintained over considerable time periods to maximise their benefits for conservation.

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Conflict of interest
The authors declare that there is no conflict of interest.

Data availability statement
Data available on request from the authors.

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