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Legacy of landscape crop diversity enhances carabid beetle species richness and promotes granivores

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ABSTRACT

It is well understood that agricultural expansion and associated loss of semi-natural habitat in the landscape are major drivers for the marked decline in biodiversity. While conserving remaining semi-natural habitat patches is essential to reverse ongoing biodiversity declines, increasing focus has also been put on diversifying cropland itself by increasing landscape crop diversity as a measure of compositional heterogeneity, and reducing field sizes as a measure of configurational heterogeneity. Both these cropland diversification approaches have shown promise to enhance biodiversity in the year of sampling, but it is unknown whether legacies of crop diversity in the landscape promote biodiversity by building up arthropod communities over time. We selected 14 faba bean fields in landscapes dominated by cropland. The fields were chosen along three gradients: landscape crop diversity of the year of sampling (2017), landscape crop diversity of the previous year (2016) and mean field size in landscapes. Using pitfall traps, we show that the carabid beetle species richness is higher in landscapes with higher crop diversity in the previous year. Especially, granivorous carabid beetles benefitted from legacies of crop diversity. Rove beetles were more abundant and genus rich in landscapes with larger field sizes, while spiders were not responding to any of the landscape variables. A diversity of crops in the landscape and their associated weed communities could provide more diverse food resources and shelter habitats, which build populations of carabid beetle species over time. There is a need to explore the effects of agri-environmental schemes across multiple years to better understand legacy effects, and to structure sustainable agricultural landscapes.

1. Introduction

Over the past century, the intensification of crop production has led to the conversion of natural habitats, such as grasslands and forests, into arable fields. Subsequently, agricultural landscapes are increasingly characterised by large arable fields on which monocultures of few high-yielding crops are grown (Landis, 2017). This landscape homogenisation is a main driver of an unprecedented decline in biodiversity (Biesmeijer et al., 2006; IPBES, 2019; Kleijn et al., 2009; Raven and Wagner, 2021). With each species lost, ecological interactions and ecosystem functions are eroded, some of which are essential for crop production, such as pollination, natural pest regulation and nutrient cycling (Losey and Vaughan, 2006).

Farmland diversification has been proposed to balance the trade-offs between achieving high yields and avoiding further loss of biodiversity in agricultural landscapes (Bommarco et al., 2013; Kleijn et al., 2019). Adoption of diversification practices can enhance ecosystem functions and its providers (Gayer et. al, 2019; Kremen and Merenlender, 2018; Tamburini et al., 2020). At landscape scale, heterogeneity effects in terms of arable land versus semi-natural habitats are well understood, with the retention of remnant forest and grassland patches supporting higher insect densities (Billeter et al., 2008; Holland et al., 2016; Landis et al., 2000) and ecosystem services such as crop pollination (Ricketts et al., 2008) and natural insect pest control (Rusch et al., 2016; Tamburini et al., 2020). Heterogeneity effects within the cropland on biodiversity and ecosystem functions remain poorly studied even though cropland occupies 40% of the Earth's land surface (Foley et al., 2005). A more heterogeneous crop mosaic might harbour higher biodiversity and

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strengthen ecosystem services (Vasseur et al., 2013). Both compositional heterogeneity (higher number and evenness of crop types in the landscape) and configurational heterogeneity (smaller field sizes, higher field border densities) have potential to counteract the negative effects of intensive crop production without having to take a large amount of land out of production (Fahrig et al., 2011). Landscape crop diversity can support pollinators and natural enemies of pests by providing more diverse and continuous food resources or shelter habitats within fields (Aguilera et al., 2020; Raderschall et al., 2021; Redlich et al., 2018). Furthermore, different crops are associated with distinct weed communities (Hyvönen and Salonen, 2002). A higher variety of weed species provide more diverse food resources, such as higher and more diverse availability of seeds and pollen, and herbivorous prey (Bretagnolle and Gaba, 2015; Carvalheiro et al., 2011; Diehl et al., 2012) but also a range of habitat structures, which can provide beneficial micro-climates within the fields (Diehl et al., 2012). Likewise, increased field border density in the landscape provides a greater network of undisturbed nesting and shelter habitats and alternative food resources, which benefits pollinators and natural enemies of pests and strengthens ecosystem services (Bosem Baillod et al., 2017; Hass et al., 2018; Martin et al., 2019). Effects of landscape crop diversity on beneficial arthropods have mostly been investigated using landscape crop diversity in the year of sampling (but see: Bertrand et al., 2016). Bertrand and colleagues (2016) investigated the legacy effects of landscape crop diversity over a five-year period on the carabid beetle community, but the proportion of grassland and crop diversity were negatively correlated which made it difficult to disentangle the effects of crop diversity from agricultural land use (annual crops versus perennial grasslands) or management intensity. Legacy effects of crop diversity, such as resource continuity across years, and the legacy effects of certain crops and their associated weeds in the crop rotation on population dynamics across years deserves more attention.

Crop rotations with annual crops result in yearly restructuring of the landscape composition. The relocation of crops from one year to the next is likely to induce redistribution of beneficial arthropods that are either favoured or deterred by a certain crop. For example, a high proportion of oilseed rape in the previous year increased abundances of pollinators and carabid beetles during the sampling year (Marrec et al., 2015; Riedinger et al., 2015). The crop rotational history of a landscape can thus act as an ecological filter of the species pool and modulate the local species assemblage observed in any given field and year (Bertrand et al., 2016). However, the effects of these temporal crop patterns in the landscape on biodiversity metrics are rarely considered (Bertrand et al., 2016; Marrec et al., 2017).

Ground-dwelling generalist predators, such as carabid beetles, rove beetles and ground spiders provide natural pest control services in agricultural landscapes (Aguilera et al., 2021; Dainese et al., 2017; Schmidt et al., 2003; Symondson et al., 2002; Tamburini et al., 2016). In addition to preying on agricultural insect pests, carabid beetles are also important weed seed predators (Bohan et al., 2011; Frei et al., 2019; Honek et al., 2003) capable of regulating weed populations (Daouti et al., 2022). Being active on the ground, these predator groups are favoured by perennial and diverse structural habitats as shelter or microclimatic refuges both while active (Diehl et al., 2012) and during overwintering (Ganser et al., 2019; Schmidt and Tscharntke, 2005; Thomas et al., 1992). Habitat patches without intensive agricultural management such as unmanaged field margins or permanent grasslands are also essential for the survival of eggs and beetle larvae, which are key to the persistence and long-term survival of ground predators (Lövei and Sunderland, 1996). Adults are also susceptible to disturbances of the soil associated with intensive crop management such as tillage due to direct mechanical injury or indirectly by reducing the availability of alternative prey (Carbonne et al., 2021; Ganser et al., 2019; Tamburini et al., 2016). However, some carabid beetles and rove beetles also benefit from high turnover of crops over time (Bertrand et al., 2016) and recently disturbed habitats (Boetzl et al., 2022). Ground-dwelling spiders are highly mobile and able to disperse over larger distances compared with carabid beetles (Halley et al., 1996). Spiders require undisturbed refuge habitats, where they can overwinter and colonise crop fields for foraging (Schmidt and Tscharntke, 2005; Thorbek and Topping, 2005). They benefit from landscapes with more natural habitat patches and a higher number of habitat types (Li et al., 2018; Thorbek and Topping, 2005), but also undisturbed, structurally diverse local patches (Thorbek and Topping, 2005), including sown annual flower strips (Raderschall et al., 2022; Schmidt-Entling and Döbeli, 2009). In order to build up populations in agricultural landscapes, carabid beetles, rove beetles and spiders require favourable habitat types both for overwintering and foraging. Due to differences in diets, overwintering requirements and dispersal distances, responses to landscape features differ within and between the species groups (Martin et al., 2019). For example, plant traits, soil and agricultural management are strong predictors of functional trait compositions of carabid beetle communities (Pakeman and Stockan, 2014). As such, carabid beetles, rove beetles and spiders might respond differently to landscape crop diversity, its legacy effects and mean field size in the landscape.

Here we examined the effects of landscape crop diversity of the year of sampling and the previous year (legacy effect) as a measure of compositional heterogeneity, and of mean field size in the landscape (MFS) as a measure of configurational heterogeneity, on ground-dwelling predator activity density, species richness and Shannon diversity in faba bean fields (*Vicia faba* minor) in southern Sweden. We hypothesise that 1) Carabid and rove beetle communities will have a higher activity density and will be more species rich and diverse in landscapes with higher crop diversity of both the year of sampling and the previous year, because a more diverse composition of crops will provide food resources for more species with different diet traits. 2) Especially granivorous carabid beetle species will benefit from the diverse seed resources from both crops and weeds associated with landscape crop diversity 3) Ground-dwelling spiders will benefit from landscapes with smaller MFS because of their requirement for less disturbed and more structurally diverse habitats provided by the field margins from where they colonise arable fields.

2. Methods

2.1. Experimental design

We estimated the activity densities of ground-dwelling predators in 14 conventional faba bean fields in 2017. Fields were selected along gradients of landscape crop diversity for both the year of sampling (2017) and the previous year (2016) as well as MFS in the landscape within a 1 km radius. Since the focus of this study was to assess the respective roles of landscape crop compositional and configurational heterogeneity for supporting ground-dwelling predators, field sites were chosen in landscapes with high proportions of arable land (mean: 0.87, range: 0.68–0.95). We also measured the proportion of semi-natural habitat (SNH) in the landscape, which included all forest patches and pastures in the landscape. We did not further analyse the effect of SNH in the models. The reasons for this were that the gradient of the proportion of SNH among the landscapes was narrow (mean 0.03, range: 0–0.22) and discontinuous with all but one field having SNH proportion of less than 0.05. The proportion of SNH was uncorrelated to any other landscape variables (Table S1). Adding a fourth explanatory variable would, given the replication of 14 fields, have risked to over-parameterise the model giving spurious results. We focused our analyses on 1 km landscape radii since ground-dwelling predators such as carabid beetles, rove beetles and ground spiders are likely dispersing across such distances between seasons (Bertrand et al., 2016; Den Boer, 1977; Firle et al., 1998; Hibbert and Buddle, 2008; Öberg et al., 2007; Thiele, 1977; Turin and Den Boer, 1988), and because a 1 km landscape radius has been shown statistically to be an appropriate scale to study landscape effects on spider assemblages (Horváth et al., 2019; Schmidt et al., 2008). Field centres were located at least 2.9 km apart such that there was no overlap between landscapes at the 1 km scale (Fig. 1). Field sites were located in southernmost Sweden in the county of Skåne, which spans across approximately 100 by 100 km, and of which approximately 40% is arable land (Statistics Sweden, 2018). The most common crops grown in this region are, in descending order, winter wheat, ley, spring barley and winter oilseed rape, but several other crops including faba bean are also cultivated (Statistics Sweden, 2018). The average size of our experimental fields was 15 ha (range 3–40 ha, Table S2). While each experimental field was sown with a single faba bean cultivar, the cultivar grown differed among experimental fields (Raderschall et al., 2021). Each field contained two sampling areas of 24 m by 50 m situated adjacent to each other along the field edge. One sampling area was assigned to receive no insecticide, while the other sampling area together with the rest of the field was assigned to receive conventional insecticide treatment. However, as insecticide use was uncommon among farmers, only five sampling areas were treated with insecticides and at different times during the sampling period. To exclude samples from sprayed field areas, we excluded data from 15 sampling events belonging to five field areas that were conducted after the field areas had been sprayed from the analysis. We did not analyse the effect of insecticide use.

2.2. Landscape gradients

The land cover in the landscapes surrounding each focal faba bean field was characterised within a radius of 1 km from each experimental field centre. We assessed landscape crop diversity (hereafter crop diversity) in the year of sampling (2017) and the previous year (2016) as a measure of crop compositional heterogeneity. We estimated mean field size in the landscape (MFS) as a proxy for crop configurational heterogeneity. Data for pastures, crops and field sizes were obtained from the Integrated Administration and Control System (IACS), administered by the Swedish Board of Agriculture. To calculate forest cover, we used a digitalised map layer (Terrängkartan, Lantmäteriet, 2018) in ArcMap software version 10.4.1 (ESRI, 2015). Unlike crop compositions, MFS, pasture and forest cover values are more or less stable across seasons, and we used values from 2017. Crop information was missing for 5.9% of the arable land in the landscape buffers for both 2016 and 2017. We complemented part of the missing crop information for 2017 by visually mapping crops in the landscape. This allowed us to prove that crop diversity between corrected and uncorrected landscapes in 2017 were strongly correlated ($r = 0.99$, $p < 0.001$). For consistency, we used the uncorrected values of both years for the analysis.

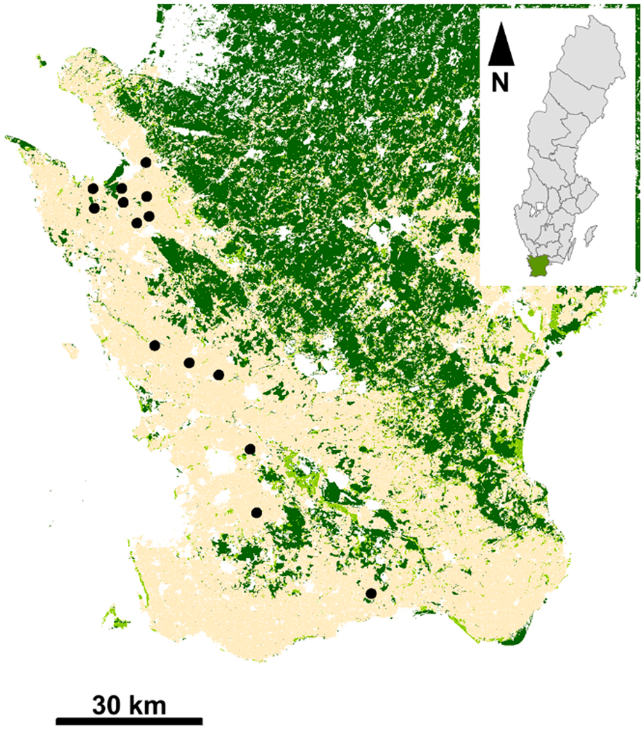

Fig. 1. Locations of our 14 1 km landscape buffers (black dots) centred around the focal faba bean fields in Skåne, southernmost Sweden (inset) with arable land in beige, semi-natural grassland in light green and forest in dark green.

Landscape crop diversity was calculated according to Raderschall et al. (2021). We categorised all crops that contributed to the landscape buffers surrounding focal fields into 14 crop categories: beets, spring sown brassica, winter sown brassica, spring sown cereal, winter sown cereal, clover, corn, fallow, ley, potatoes, pulses, trees, vegetables/-fruits/berries and other. The Shannon index of crop diversity was then calculated for each landscape buffer based on the crop category and crop area information using the “vegan” package in R (Oksanen et al., 2019) and ranged from 1.27 to 1.90 in 2017 (year of sampling) and 0.90–1.68 in 2016 (previous year). The gradients for crop diversity of the year of sampling (2017) and MFS were negatively correlated ($r = -0.44$, $p = 0.025$, Table S1), but all other gradients were uncorrelated, and collinearity was low (variance inflation factor < 2, Table S1).

2.3. Ground-dwelling predators

Ground-dwelling predators including carabid beetles (Carabidae), rove beetles (Staphylinidae) and spiders (Aranae) were sampled using pitfall traps. We set up four pitfall traps in each sampling area (eight per field) 10 m apart from each other and situated 10 m into the field in parallel to the field edge. Pitfall traps were made from polypropylene beakers (12 cm diameter) filled with 200 mL of detergent water. We emptied and refilled traps weekly (every 6–7 days) for four sampling rounds corresponding to early faba bean bloom (BCCH 60, June 14) until early pod set (BCCH 72, July 15). Pitfall contents were stored in 70% ethanol and later identified to species (carabid beetles and spiders) or genus (rove beetles) level.

2.4. Carabid beetle diet traits

To test the hypotheses that landscape crop diversity promotes granivorous carabid beetles, we characterised the carabid beetle species composition using diet traits, differentiating between predominantly carnivorous, omnivorous and granivorous species. Diet traits of carabid species were collected from the literature (Lindroth, 1985) and the online trait database https://carabids.org (Homburg et al., 2014). We further conducted an analysis, where we considered granivorous and omnivorous carabid species as a single diet trait group due to some omnivores (e.g. *Harpalus rufipes* Degeer) having been shown to be effective weed seed predators (Carbonne et al., 2020).

2.5. Statistical analysis

Data was pooled per sampling area for each field across the entire season. The activity densities of carabid beetles, rove beetles and spiders were analysed using a Conway-Maxwell error distribution and a log link to adjust for underdispersion. The activity density of carnivorous carabid beetles was analysed using a negative binomial error distribution with a log link and the activity density of granivorous and omnivorous carabid beetles was analysed using a Poisson error distribution with a log link. We excluded pitfall trap samples from sampling rounds that were conducted after an insecticide was sprayed, which gave uneven sampling efforts among fields. We therefore added log-transformed number of pitfall days as an offset to all models analysing activity density (mean trap days per field area: 100 days, range: 88–112) (Zuur et al., 2009). The species richness of carabid beetles was calculated as the effort-adjusted species richness using the following formula:

Richness *adj* = S/(Q^0.25), whereby S = collected species richness, Q = pitfall days*pitfall perimeter (Saska et al., 2021). Pitfall days was derived by multiplying the number of traps with their exposure time (days). This formula for effort-adjusted richness was shown to be the most effective measure to standardise carabid species richness data from pitfall trapping with differential sampling effort (Saska et al., 2021). We adopted the estimated value of the slope parameter (0.25) from Saska and colleagues (2021). The slope was estimated based on pitfall trap catches from arable fields in Europe and North America that were comparable to our landscapes. The effort-adjusted species richness was analysed using Gaussian error distribution with an identity link. Since there is no method to adjust for uneven sampling effort for rove beetles and spiders, and it might not be adequate to transfer the species accumulation curve developed for carabid beetle species richness to spider species richness and rove beetle genus richness, we used the observed species/genus richness for spiders and rove beetles. Rove beetle genus richness and spider species richness were estimated with a Conway-Maxwell error distribution and a log link to adjust for under-dispersion. We complemented our analyses by calculating the species richness of carabid beetles using observed species richness, and rove beetle genus and spider species richness using the effort-adjusted richness function we used for the carabid beetles. All results remained qualitatively the same between the observed and the effort-adjusted calculations (Table S3). For the effort-adjusted rove beetles species richness, we fitted, however, a model with a quadratic term for MFS to improve model fit (Table S3). The Shannon diversity of ground predators was analysed assuming Gaussian error distribution with an identity link.

All statistical analyses were done using linear mixed-effect models or generalised linear mixed-effect models (package: “glmmTMB”, Brooks et al., 2017) in R version 4.1.1 for Windows (R Core Team, 2021). As response variables we used the activity density, species/genus richness (per unit effort for carabid beetles), and Shannon diversity for carabid beetles, rove beetles and spiders in separate models. For carabid beetles, we also analysed the activity density of carnivorous, omnivorous and granivorous species in three separate models. As explanatory variables we used the three landscape variables: landscape crop diversity 2017, landscape crop diversity 2016 and MFS. As random effects we used field identity. We tested model assumptions and obtained residual diagnostic plots using the testDispersion and the simulateResidual functions (package: “DHARMa”, Hartig, 2022). We computed the marginal and conditional R^2 values of our models using the r2_nakagawa function (package: “performance”, Lüdecke et al., 2021) according to Nakagawa et al. (2017). All models were tested for spatial autocorrelation using the testSpatialAutocorrelation function, which performs a Moran’s I test (package: “DHARMa”, Hartig, 2022), and were found to be spatially uncorrelated. The variance inflation factor (vif) was below 2 in all cases suggesting that collinearity in our models was low (Zuur et al., 2009).

3. Results

Across the entire sampling season, we collected 28,450 carabid beetles belonging to 65 species (Table S4). Carabid beetle activity density and Shannon diversity were not explained by any landscape variables (Table 1). Effort-adjusted carabid beetle species richness was higher in fields surrounded by a high landscape diversity in the previous year (2016) (Fig. 2a), while the landscape crop diversity of the year of sampling (2017) had no effect (Table 1). We collected a total of 3238 rove beetles belonging to 22 genera (Table S4). Both rove beetle activity density and rove beetle genus richness increased with mean field size in the landscape (MFS) (Table 1, Fig. 2b, c). We collected a total of 3462 spiders belonging to 71 species (Table S4). Neither spider activity density, species richness nor Shannon diversity were explained by any of the landscape variables.

For 28,229 (99%) caught individuals belonging to 40 carabid species, we obtained diet information and of those there were 23,582 carnivorous, 4368 omnivorous and 279 granivorous individuals (Table S4). The activity density of granivorous carabid beetles increased with increasing crop diversity in the previous year (2016) (Table 1, Fig. 3). This effect was likely driven by the activity density of the carabid

Table 1

Estimates (*est*), standard errors (*se*) and p-values (*p*) from mixed-effect models for the activity densities, effort-adjusted carabid species richness, observed rove beetle genus and spider species richness, and Shannon diversity of carabid beetles, rove beetles and spiders as well as the activity densities of granivorous, carnivorous and omnivorous carabid beetles. Explanatory variables were landscape crop diversity of the sampling year 2017 (CropDiv17) and the previous year 2016 (CropDiv16), and mean field size (MFS) in the landscape. *P*-values in bold are significant at the 0.05 level. Marginal R-square (Rm) and conditional R-square values (Rc) are given for each model to represent the variance explained by the fixed effects only, and the variance explained by both the fixed and the random effects together, respectively.

	Variables		Intercept	CropDiv17	CropDiv16	MFS	Rm	Rc
Carabid beetles	Activity density	*est*±*se*	0.540 ± 3.87	1.23 ± 1.70	-0.259 ± 1.52	-0.034 ± 1.11	0.063	0.90
		p	0.89	0.47	0.87	0.76		
	Richness *(adj.)*	*est*±*se*	0.043 ± 2.98	0.503 ± 1.33	**4.95 ± 1.31**	-0.0028 ± 0.087	0.40	0.54
		p	0.99	0.70	**< 0.0010**	0.98		
	Shannon diversity	*est*±*se*	1.26 ± 1.18	-0.443 ± 0.518	0.552 ± 0.474	0.023 ± 0.035	0.17	0.86
		p	0.29	0.39	0.25	0.67		
	Granivores	*est*±*se*	**-11.81 ± 3.02**	1.30 ± 1.37	**4.18 ± 1.33**	0.134 ± 0.087	0.17	0.31
		p	**< 0.0010**	0.95	**0.0017**	0.012		
	Carnivores	*est*±*se*	1.12 ± 4.37	0.953 ± 1.91	-0.515 ± 1.75	-0.044 ± 0.129	0.042	0.77
		p	0.78	0.62	0.77	0.74		
	Omnivores	*est*±*se*	-2.76 ± 3.61	1.73 ± 1.57	0.216 ± 1.42	-0.031 ± 0.107	0.083	0.64
		p	0.44	0.27	0.88	0.77		
	Granivores & omnivores	*est*±*se*	-4.20 ± 3.19	2.04 ± 1.39	0.75 ± 1.25	0.0098 ± 0.094	0.11	0.61
		p	0.19	0.39	0.55	0.92		
Rove beetles	Activity density	*est*±*se*	-3.02 ± 2.84	1.87 ± 1.24	-0.930 ± 1.12	**0.168 ± 0.084**	0.15	0.53
		p	0.29	0.13	0.40	**0.045**		
	Richness *(obs.)*	*est*±*se*	**1.75 ± 0.589**	0.030 ± 0.261	0.241 ± 0.247	**0.035 ± 0.017**	0.073	0.20
		p	**0.0030**	0.91	0.33	**0.045**		
	Shannon diversity	*est*±*se*	0.564 ± 0.939	0.312 ± 0.413	-0.0089 ± 0.380	0.047 ± 0.028	0.17	0.81
		p	0.55	0.49	0.98	0.085		
Spiders	Activity density	*est*±*se*	-0.402 ± 2.00	0.249 ± 0.872	0.357 ± 0.789	-0.052 ± 0.059	0.036	0.34
		p	0.84	0.78	0.65	0.38		
	Richness *(obs.)*	*est*±*se*	1.329 ± 0.783	0.461 ± 0.350	0.485 ± 0.333	-0.0064 ± 0.023	0.034	0.089
		p	0.089	0.19	0.15	0.78		
	Shannon diversity	*est*±*se*	-0.020 ± 0.849	0.665 ± 0.378	0.195 ± 0.362	0.022 ± 0.025	0.17	0.50
		p	0.98	0.078	0.59	0.39		

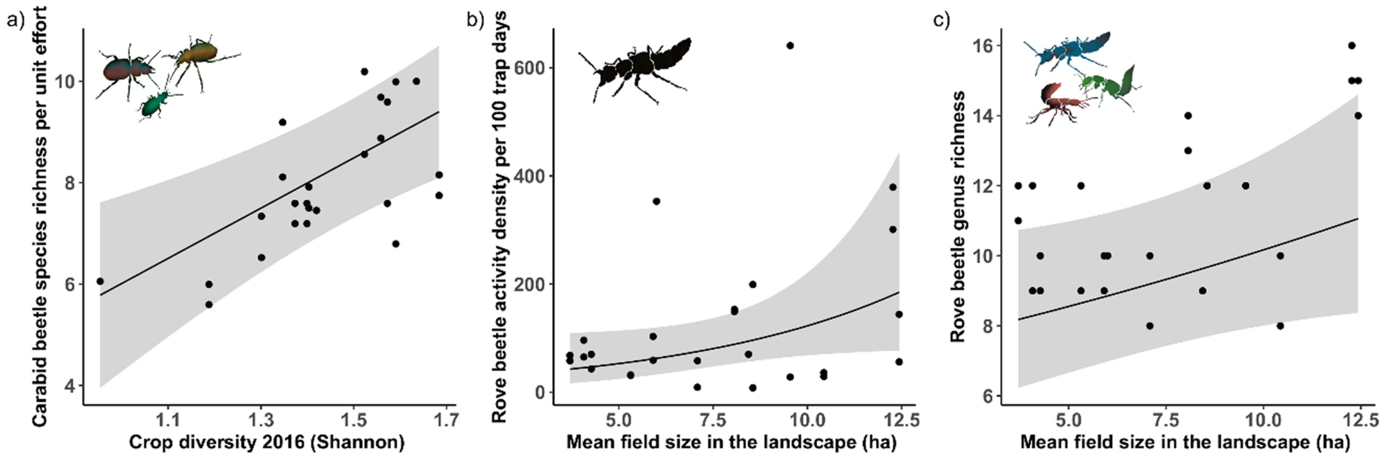

Fig. 2. Effort-adjusted carabid beetle richness increases with crop diversity of the previous year (2016) a), rove beetle activity density b) and observed rove beetle genus richness c) increase with mean field size in the landscape (MFS). Shown are fitted lines with data points (black dots) and shaded areas represent the 95% confidence intervals. Data points in b have been adjusted to reflect equal sampling effort per field area.

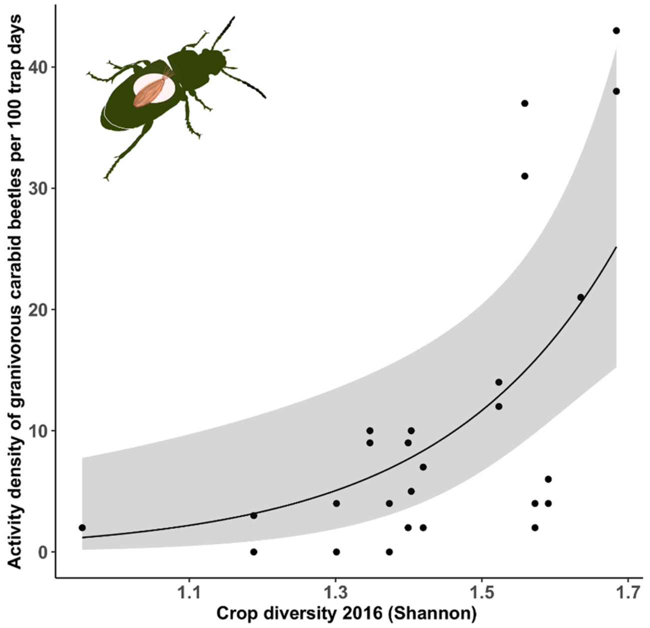

Fig. 3. The activity density of granivorous carabid beetles increases with increasing crop diversity of the previous year (2016). Shown are fitted lines with data points (black dots) and shaded areas represent the 95% confidence intervals. Data points in have been adjusted to reflect equal sampling effort.

beetle *Harpalus affinis* (Schrank), which was the most abundant granivorous carabid species (n = 241, Table S4). When considering omnivores and granivores as a single diet group, we found no effect of landscape characteristics on their activity density (Table 1).

4. Discussion

Landscape crop diversity (compositional heterogeneity) and MFS (configurational heterogeneity) affected the activity densities and species richness of carabid beetles and rove beetles, respectively, while ground-dwelling spiders did not respond to any of the landscape variables tested. Partially in line with our first hypothesis, species richness of carabid beetles increased with crop diversity of the previous year but not in the year of sampling, suggesting that crop diversity has a positive legacy effect on certain carabid beetle species. When characterising carabid beetle communities using diet traits, we could confirm our second hypothesis that crop diversity in the previous year increased the activity density of granivorous carabid beetles. Contrary to our hypotheses for rove beetles and spiders, rove beetle activity density and genus richness was not affected by crop diversity but instead increased with MFS in the landscape, while spiders were not affected by any of the tested landscape variables.

Landscapes with higher crop diversity in the previous year hosted carabid communities with a higher species richness. Positive legacy effects of specific crops on carabid abundances have been found before. Fields previously grown with oilseed rape host higher abundances of carabid species (Marrec et al., 2015). This could be because oilseed rape fields offer more food resources than for example cereal fields, which leads to individuals with a higher nutritional state able to lay more eggs, which increases adult emergence the subsequent year (Labruyere et al., 2016b). A higher cover of oilseed rape and grassland in the landscape in the year of sampling also increase carabid abundance, suggesting that in-field activity densities of carabids are influenced by the spatial distribution of crop types at landscape scale (Labruyere et al., 2016a). However, the proportion of oilseed rape in our landscapes was negatively correlated with crop diversity in the previous year (Table S5), suggesting that factors other than oilseed rape drove the positive legacy effect. It is unlikely that local legacy effects at the field scale (preceding crops) are driving our results, because 12 of our 14 fields were cultivated with either winter-or spring-sown cereals in 2016, and the two fields for which we do not have preceding crop information had intermediate landscape Shannon diversity indices (Table S2). Crops differ in weed community composition (Hyvönen and Salonen, 2002), vegetation architecture, plant density, microclimate and agronomic practices. Hence, it is likely the composite of habitat and food resource diversity, that drives the positive legacy effect on the carabid community. The legacy effects of crop diversity promoted granivorous carabids, to which seeds of grasses, weeds and flowering crops are central for their diet (Talarico et al., 2016; Thiele, 1977). Plant traits, soil and management factors have been shown to influence functional trait compositions of carabid beetle communities (Pakeman and Stockan, 2014).

Landscapes with larger mean field sizes fostered higher rove beetle activity density and genus richness. This result was unexpected given that rove beetles overall are more abundant in landscapes with high edge-density and large proportions of semi-natural habitats (Martin et al., 2019; Méndez-Rojas et al., 2021). Yet, when arthropods are grouped based on trait syndromes rather than overall species groups, a subset of species of ground-dispersing predators, which overwinter in both arable and natural habitats, were most abundant in landscapes with few edges and high cover of arable land (Martin et al., 2019). We identified rove beetles to genus level. Species within and between genera might respond differently to the landscape factors due to their feeding or dispersal traits. Our taxonomic resolution might thereby have masked trait-specific effects of landscape characteristics on rove beetle communities. Given that all our field sites were located in landscapes with primarily arable land cover, it is possible that the majority of the rove beetle species found in our landscapes are specialised to crop habitats and therefore benefit from agricultural resources.

Spiders did not respond to any of the tested landscape variables. This was against our hypothesis, in which we predicted that spiders would benefit from smaller field sizes in the landscapes as a proxy for a denser network of undisturbed and structurally diverse field border shelter habitats. However, our result is in line with earlier observations, where landscape configuration had no effect on spider abundances and species richness (Martin et al., 2016) nor spider functional diversity (Gallé et al., 2019). It is possible that the benefit of field borders for spiders depends on their quality, and that borders in our landscapes were of poor quality. For example, if field borders are still under agricultural management such as cutting, which has a negative impact on spider communities (Baines et al., 1998) positive border effects might be lost. Alternatively, spiders in field margins might have not dispersed into the arable fields, leading to distinct communities between arable fields and grassy field margins. Indeed, spiders in agricultural landscapes are relatively specialised for their specific habitats, with neither landscape configuration nor composition influencing their level of habitat specialisation (Lami et al., 2021; Nardi et al., 2019). Likewise, spider communities in grassy field margins were observed to be distinct from adjacent arable fields (Kromp and Steinberger, 1992). Since we only sampled spiders within the field, we might have missed potential benefits of MFS on communities restricted to field margins. As we did not analyse any trait-specific responses of spiders, we cannot exclude that certain trait groups of species respond to the landscape characteristics tested.

Species rich communities are essential to support ecosystem services such a natural pest control (Dainese et al., 2019). As such, legacy effects of crop diversity are likely not only valuable in providing favourable habitat resources for a more diverse carabid community, but also facilitate more efficient ecosystem services delivery to boost crop production. Crop diversity, in particular holds great potential to enhance weed seed predation in arable fields, by enhancing granivorous carabids. Weed seed removal is an important ecosystem service for agriculture, whose strength was shown to be strongly related to the Shannon diversity of granivorous carabids (Trichard et al., 2013). Similarly, abundant and diverse weed seed predator communities consisting of carabids, ants and crickets generally boosted weed seed predation intensity and stability, except for predator communities dominated by large species, where an increase in their abundance led to partial suppression of seed predation possibly due to intra-guild predation (Lami et al., 2020). To test whether or not carabid communities supported by legacies of crop diversity enhance weed seed predation, a next step would be to directly test the effect of crop diversity on weed seed removal.

For agriculture to become more sustainable, crop management needs to be developed that reduces the reliance on external inputs such as pesticides and fertilisers. Interactions between above-ground and below-ground organisms are important drivers of plant health and crop productivity. Making better use of such interactions by using ecological principles when designing agricultural landscapes holds great potential in making crop production more sustainable (Doré et al., 2011). Legacy effects – be it related to the crop species per se, its associated management regime, or its associated weeds, have the potential to shape above- and below-ground ecosystem functions that can be used to harness ecosystem services. Yet, our understanding of legacy effects related to crop diversification schemes at both field and landscape scale is still poor. Our challenge will be to redesign our agricultural systems with beneficial crop combinations both spatially using intercropping or landscape-wide crop diversity, and over time by crop rotations that create legacies that build beneficial communities and strengthen ecosystem services in the long term (Veen et al., 2019).

CRediT authorship contribution statement

Chloé Raderschall: Conceptualization (equal), Methodology (equal), Investigation (lead), Formal analysis (lead), Visualization (lead), Writing – original draft (lead), Writing – review & editing (equal). **Ola Lundin**: Methodology (equal), Investigation (support), Formal analysis (equal), Writing – review & editing (equal). **Guillermo Aguilera**: Formal analysis (equal), Writing – review & editing (equal). **Sandra Lindström**: Methodology (equal), Investigation (support), Writing – review & editing (support). **Riccardo Bommarco**: Conceptualization (equal), Methodology (equal), Investigation (support), Writing – review & editing (equal), Funding acquisition (lead).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2022.108191.

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