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RESEARCH PAPER

Distance decay effects predominantly shape spider but not carabid community composition in crop fields in north-western Europe

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ABSTRACT

Agricultural intensification and expansion are regarded as main drivers of biodiversity loss. This conclusion is mainly based on observed declines of local diversity (α-diversity), while effects on community composition homogenization (decrease of β-diversity) at a larger spatial scale are less well understood. Carabid beetles and spiders represent two widespread guilds and are important predators of pest species. Here we surveyed carabid beetles and spiders in 66 winter wheat fields in four northwestern European countries (Germany, the Netherlands, Sweden and UK) and analyzed how their community composition was related to geographic distance (separation distance between any pairwise fields) and three environmental variables: crop yield (proxy for land-use intensity), percentage cropland (proxy for landscape complexity) and soil organic carbon content (proxy for local soil conditions). We further analyzed whether the relationship between carabid beetle and spider community composition and geographic distance was influenced by environmental variables. We found that, 55 % and 75 % of all observed carabid and spider individuals, respectively, belonged to species that occurred in all four countries. However, individuals of species that were unique to a particular country only accounted for 3 % of all collected individuals for both taxa. Furthermore, we found a negative relationship between distance and similarity of spider communities but not for carabid beetle communities. None of the environmental variables were related to similarity of carabid beetle and spider communities, nor moderated the effects of distance. Our study indicates that across a great part of the European continent, arthropod communities (especially carabid beetles) in agricultural landscapes are composed of very similar species that are robust to current variations in environment and land-use.

Introduction

For centuries, a large proportion of Europe's surface area has been used for agricultural production. Historically, a diversity of low-input farming practices created structurally diverse agricultural landscapes that supported numerous species and high levels of biodiversity (Henle et al., 2008; Vasilescu et al., 2023). However, in response to a combination of the continuously increasing demand for agricultural products and global trade, land-use intensity in agricultural landscapes has increased, with more pesticides and fertilizer being applied to pursue higher yields per unit area and lower costs per unit production. Farming needed to become more efficient, which resulted in larger fields planted with the same crop. This resulted in the loss of semi-natural habitats and has substantially simplified and homogenized agricultural landscapes (Tscharntke et al., 2005). Combined, these changes have resulted in a dramatic loss of biodiversity over recent decades (Kleijn et al., 2009;

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Emmerson et al., 2016; Maxwell et al., 2016), which is not only problematic from a conservation perspective, but can also jeopardize long-term agricultural productivity as many ecosystem services supported by biodiversity are critical for agricultural production (Zhang et al., 2007).

Arthropod predators such as carabid beetles and spiders provide important pest control services in agricultural systems; however, both of these taxa are affected by agricultural intensification. Most research on effects of agricultural intensification and expansion on natural enemy diversity have focused on local-scale diversity (α-diversity). These studies have demonstrated that trends in α-diversity can be driven by a range of on-field agricultural practices like application of fertilizers and insecticides (Hendrickx et al., 2007; Geiger et al., 2010; Li et al., 2018) as well as simplification of the landscapes (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Dainese et al., 2019). Recently, more studies have begun to explore the effects of agricultural intensification and expansion on the variation in species composition of arthropod predators among sites (β-diversity) (e.g., Hendrickx et al., 2007; Diekötter et al., 2010). However, these studies have only examined how community composition of a single taxon responds to a single practice of agricultural intensification or agricultural landscape simplification (Ekroos et al., 2010; Inclán et al., 2015; Rusch et al., 2016a). Although these studies have provided valuable insights, we still know much less about how community composition of different taxa responds to environmental factors at multi-spatial scales. Beta-diversity is an important component of biodiversity that is influenced at larger spatial scales (Socolar et al., 2016), therefore β-diversity is invariably related to separation distance because the distribution of organisms is inherently determined by two processes: the adaptation of species to the local environmental conditions and dispersal limitation (Hubbell, 2001; Tuomisto et al., 2003). With increasing distance, the environmental conditions will in general become less similar from the local environmental conditions (like climate and soil conditions) and these places will be more difficult to disperse to (Keil et al., 2012; Rodriguez-Artigas et al., 2016). This leads to a typical decrease in similarity (or increase in β-diversity) between communities that are located further apart (distance decay effects, Soininen et al., 2007). However, it has been rarely examined whether for natural enemies such patterns will be affected by environmental or management factors. For plant communities, Buhk et al. (2017) found that β-diversity of plants was lower in intensively managed agricultural landscapes than in low-intensity landscapes because in the intensively managed landscapes plant communities from different regions only contained species that were generalists or good dispersers.

The inconsistent response of plants in different landscapes could also apply to natural enemies as dominant and rare species may respond inconsistently to increasing land-use intensity or landscape simplification (Gámez-Virués et al., 2015; Simons et al., 2016). Rare or specialist species are more vulnerable to agricultural intensification and disappear more rapidly (Davies et al., 2004; Öckinger et al., 2010), while generalist species are more robust and persist or even increase (Flohre et al., 2011; Kleijn et al., 2015). This, across large areas, could result in arthropod communities that inhabit intensive agricultural landscapes becoming composed of the same generalist species or species with similar functional traits, thereby driving the biotic homogenization of agricultural farmlands (McKinney & Lockwood, 1999; Gámez-Virués et al., 2015; Ponisio et al., 2016). Furthermore, ground-dwelling natural enemy community composition can also be affected by local soil characteristics. Soil with a higher organic matter content provides resources for a larger soil food web potentially accommodating larger numbers of top predators such as natural enemies (Bulluck et al., 2002; Birkhofer et al., 2008). In theory, this could allow more rare and endemic species to persist in sites with higher soil organic matter content regardless of land use intensity or landscape simplification, resulting in more heterogeneous communities between sites. However, studies that have to date examined the effects of soil organic matter on natural enemy communities have produced contrasting results. It has been found that higher soil organic matter supported more diverse and even carabid and spider communities and such effects were greater on non-dominant species (Gagic et al., 2017; Aldebron et al., 2020; Kolb et al., 2020). In contrast, Hadjicharalampous et al. (2002) found that the abundance of dominant arthropod species groups was positively related with soil organic matter while this relationship was negative for rare and uniquely distributed species groups. In sum, there is still no consensus about how soil organic matter content influences α-diversity of natural enemies and we have only scratched the surface of the relationship between soil organic matter content and β-diversity.

Here we collected data on carabid beetle and spider communities in 66 paired winter wheat fields contrasting in soil organic carbon content in four northwestern European countries (Germany, the Netherlands, Sweden and United Kingdom), and quantified landscape composition, local land-use intensity and soil organic matter content for each site. We aimed to understand how β-diversity of carabid beetles and spiders responds to geographic distance and local and landscape environmental variables. Specifically, we asked (1) whether and how the β-diversity of carabid beetle and spider communities is related to geographic distance, landscape composition, land-use intensity and soil organic carbon content and (2) whether and how the relationship between β-diversity and geographic distance was influenced by any of the considered environmental variables.

Materials and methods

Study design

In 2014, we selected eight pairs of conventionally managed winter wheat fields in the Netherlands, Sweden and the United Kingdom and nine pairs in Germany, resulting in a total of 33 pairs of fields (Appendix A: Fig. S1). These paired fields were a subset of the fields used by Gagic et al. (2017). The two fields within each pair had contrasting soil organic matter content resulting from different management histories such as the application of mineral fertilizers, manure, crop rotation or tillage practices but were otherwise as similar as possible with respect to landscape complexity and soil conditions (e.g., soil pH and texture). In Germany, Sweden and the United Kingdom, each field was always closer to its paired field than to fields in other pairs (Appendix A: Table S1). Due to high soil variability in the Netherlands, it was not always possible to pair nearby fields with matching soil type and local landscape context so that here similar fields were not paired spatially but were all located in a single study region.

To validate whether fields within each pair had contrasting soil organic matter content but the same soil type and similar pH (i.e. a difference of no more than 0.5), we collected five soil samples at each field. These soil samples were collected before the first fertilizer application at a distance of 5–8 m from the crop edge and were pooled and mixed before analysis. Soil organic carbon (SOC) content was measured as the proxy for soil organic matter content. SOC content was assessed via the loss on ignition method (Hoogsteen et al., 2015). Mean SOC content in Germany was 1.63 % (SD ± 1.03) for high sites and 1.20 % (SD ± 0.49) for low sites; the Netherlands, averaged 2.00 % (SD ± 0.23) in high sites and 1.39 % (SD ± 0.30) in low sites; in Sweden, high sites had 4.44 % (SD ± 1.11) SOC and low sites 2.90 % (SD ± 0.42); in the United Kingdom, high sites had 1.48 % (SD ± 0.57) and low sites 1.05 % (SD ± 0.30). This showed that differences between paired high and low SOC content fields turned out to be relatively small and some low SOC fields were found to actually have higher SOC content than a high SOC content field in another pair. We therefore decided to use SOC content as a continuous variable in the statistical analyses instead of a categorical one (high or low). Within each region, field pairs were chosen across a gradient in landscape complexity, which was calculated as the percentage of cropland within a 1-km radius around each study field. The percentage cropland is often used as a proxy for landscape complexity

and is generally negatively related to the proportion of semi-natural area and habitat diversity in the landscape (Rusch et al., 2016b; Martin et al., 2019).

The original study of Gagic et al. (2017) was designed to experimentally examine the impacts of fertilizer and pesticide applications. These experimental treatments are not being used in the current study, but to understand how the data were obtained we briefly describe the experimental design here. In each field, a plot with a minimum size of 56 × 12 m was set up with the longer side adjacent to the field boundary and at least 10 m away from the nearest field corner. The field boundary characteristics were matched as far as possible within each pair. Each plot was divided into four equally sized treatment subplots to which randomly allocated fully crossed insecticide and mineral fertilizer applications (present vs absent) were assigned. The insecticides were locally recommended types of pyrethroids (broad spectrum) and the fertilizers were ammonium nitrate based and both were applied by project members following regionally recommended rates and frequency. Insecticides were applied regardless of pest outbreaks and farmers were allowed to use herbicides and fungicides in the treatment plots.

In each treatment subplot, we selected squares sized 0.25 m^2 (a total of 1 m^2 for each field) and manually harvested the wheat. The harvested wheat ears were air dried to approximately 14 % moisture content, threshed and then weighed (expressed as grain dry weight per hectare: t/ha). We used wheat yield as a proxy for local land-use intensity, which is often done (Winqvist et al., 2011; Dietrich et al., 2012; Gabriel et al., 2013), as it represents the end result of all short- and long-term management practices.

Surveying ground-dwelling arthropods

Pitfall traps (polypropylene beakers 155 mm high and 95 mm across) were used to survey ground-dwelling arthropods during the wheat flowering season (late May to early June). We placed one pitfall trap in the center of each treatment subplot at least 10 m from the field boundary and filled it with 200 mL of a mixed solution of 2/3 water and 1/3 glycol and a drop of detergent to lower surface tension. A square aluminum plate was placed *c*. 10 cm above each pitfall trap to prevent flooding by rain. Pitfall traps were opened for a period of 10 days after which all arthropods were collected and stored in 70 % ethanol solution for later identification. From all arthropods, we selected the two most abundant species groups, carabid beetles (Carabidae) and adult spiders (Araneae) as our bioindicators and they were counted and identified to species level using standard keys (Hackston, 2020; Nentwig et al., 2021).

Data analysis

All statistical analyses were conducted in R version 4.2.0 (Core Team, 2022).

Response variables

Because in this study we were interested in factors explaining similarities in species composition between fields, and not in the subplot-scale effects of the different experimental treatments (which had already been examined by Gagic et al., 2017), we pooled the collected carabid beetles and spiders over the different treatments. Each field had been subjected to the same combination of treatments and earlier analyses showed that the effects of these treatments on carabid beetle and spider abundance were generally not influenced by the environmental variables (Appendix 3 of Gagic et al., 2017). We further conducted RDA analysis as preliminary analysis to check whether different treatments at plot scale affected the community composition. Our results suggested that these effects were not significant for both carabid beetles (fertilizer $F_{(1)}$=0.686, P = 0.461; insecticide $F_{(1)}$=0.148, P = 0.872) and spiders (fertilizer $F_{(1)}$=1.138, P = 0.306; insecticide $F_{(1)}$=0.506, P = 0.736). Abundance-based Morisita-Horn dissimilarity index was calculated (using "vegan" package; Oksanen et al., 2020). Morisita-Horn index incorporates information about the relative abundance of each species in addition to the occurrence of species. Moreover, the Morisita-Horn index is robust to variations in sampling sizes (Chao et al., 2006). Given that our arthropod collections were conducted across four countries with consistent sampling intensities, employing the Morisita-Horn index helps mitigate potential biases arising from differences in community densities among these countries.

The Morisita-Horn index ranges from 0 (two communities with the same species and each species with the same abundance) to 1 (two communities with no species in common). Since using similarity would be more intuitive, we used 1 minus Morisita-Horn index to quantify the community composition similarity for each group and employed it as our response variable.

Explanatory variables

The environmental variables SOC content, wheat yield and percentage cropland in a 1 km buffer were included as explanatory variables (Appendix A: Table S2). For each possible field-pair combination and environmental variable, we calculated and included in the analyses both the difference in environmental variables between pairs of fields and the mean of the two fields that were compared. The difference provides an indication of the contrast in environmental conditions, while the mean gives an indication of the overall conditions in the two fields (Gossner et al., 2016). Additionally, the geographic distances between all possible combinations of pair-wise compared fields were included as an explanatory variable, calculated using the "geodist" package (Padgham & Sumner, 2022). The mean geographic distance between two sites in Germany was 24.76 km (SD ± 12.89), in the Netherlands 16.68 km (SD ± 10.39), in Sweden 31.46 km (SD ± 19.06) and in United Kingdom 18.06 km (SD ± 16.68). The mean geographic distance of two sites between Germany and the Netherlands was 383.13 km (SD ± 18.92), between Germany and Sweden 690.68 km (SD ± 15.16), between Germany and United Kingdom 812.75 km (SD ± 19.18), between the Netherlands and Sweden 673.87 km (SD ± 13.13), between the Netherlands and United Kingdom 469.90 km (SD ± 17.79) and between Sweden and United Kingdom 1074.22 km (SD ± 19.27). Thus, seven variables were included as explanatory variables in our study.

Statistical analysis

Fields with missing data for environmental variables, carabid beetle or spider data were omitted from the analyses resulting in a total of 57 and 56 fields for carabid beetles and spiders, respectively. Simply making all-possible combinations of pairwise comparisons between all fields would result in pseudo-replication. We therefore used a randomization procedure. We first randomly divided fields into two equal subsets of 28 fields each and then randomly paired fields between the two subsets resulting in 28 pairwise community similarity comparisons for both species groups. This randomization procedure was repeated to generate 10,000 datasets that made independent comparisons of carabid beetles and spiders, respectively, which were then used in all following analyses (Chappell et al., 2016).

Distance generally plays an important role in influencing community similarity, but it is less clear what distance function best explains community similarity (Nekola & White, 1999; Tuomisto et al., 2003; Ferenc et al., 2014). We therefore first used linear regression models to examine which of four distance functions (linear distance, ln-transformed distance, square-root transformed distanced and quadratic polynomial transformed distance) best explained the community similarity of carabid beetles and spiders, respectively. Since the sampling sites were distributed in four different countries, we further explored the between-country effects. We used a categorical variable, country

difference, as explanatory variable (for example, if the two sites compared were selected in Germany and Sweden, then the categorical explaining variable would be the absolute value as |GE-SE|, with 0 indicating if the compared sites were selected from the same country). In these analyses, for all distance functions the calculated distances between paired fields from the 10,000 datasets were standardized using the R package "standardize" (Eager, 2021). We compared the output of the models using different distance functions using the Akaike Information Criterion values corrected for small sample size (AICc) using R package MuMIn Bartoń (2020) and then ranked the models based on the mean AICc value across the analyses of the 10,000 datasets. For both carabid beetles and spiders, between-country effects consistently produced the highest mean AICc value and ln-transformed distance was always the best predictor (Appendix A: Table S3), therefore, we discarded between-country effects and used ln-transformed distance in all subsequent analyses.

The core analyses used multiple linear regression models to examine how ln-transformed distance and (combinations of) different environmental variables influence community similarity of carabids and spiders. For each of the 28 pairwise fields in all 10,000 datasets we calculated the difference and mean values of the environmental variables, which were then standardized within each dataset (using the R package "standardize"; Eager, 2021). We constructed one intercept-only model, seven models each with a single explanatory variable (only distance or difference or mean of environmental variables), six models each including distance and one of the difference or mean of environmental variables as explanatory variables, and six models each including interactions of distance and one of the six environmental variables as explanatory variables, thus resulting in a total of 20 models (Appendix A: Table S4). To check for multicollinearity of explanatory variables, we calculated variance inflation factors (VIF; Draper & Smith, 1998) using the R package "car" (of models of all 10,000 datasets. The highest VIF for carabid beetles was 3.55 and for spiders was 4.16 (Appendix A: Table S5), which is well below the threshold of 10 (Dormann et al., 2013). Next, for each model we calculated mean AICc values based on analysis of all the 10,000 datasets, ranked the different models based on the mean AICc values and then calculated full-model averaged parameter estimates and confidence intervals based on all models with Δ mean AICc < 8 (Appendix A: Table S4).

Results

Overall, we collected 3284 carabid beetles belonging to 63 species and 2730 adult spiders belonging to 71 species and 15 families. Five carabid beetle species and eight spider species were observed in all four countries and the relative abundance of these species were 55.4 % and 74.9 % respectively. There were 13 carabid beetle species and 24 spider species only observed in Germany with relative abundance of 1.19 % and 1.79 % respectively. These numbers were 5 and 3 (0.27 % and 0.21 %) for the Netherlands, 16 and 15 (1.47 % and 1.32 %) for Sweden and 8 and 2 (0.37 % and 0.07 %) for the United Kingdom (Fig. 1).

For spiders, distance played an important role in shaping community similarity. The model with only distance as explanatory variable was the most highly ranked model (Appendix A: Table S4) and the confidence interval of the mean coefficient did not overlap zero (Table 1). This suggests that between sites the similarity in community composition for spiders was strongly negatively related with distance (Fig. 2). Although for carabid beetles the model with only distance as explanatory variable was also the most highly ranked model, here the intercept-only model was included in the candidate set of best models (second best model at $\Delta AIC_c = 0.13$; Appendix A: Table S4). This indicates that the model with only distance as an explanatory variable did not perform meaningfully better than a model without any explanatory variable. The difference in relationship between community composition and distance between the two species groups was further highlighted by the mean coefficients which was almost three times steeper for spiders than for carabids (-0.1147 vs -0.0435, Table 1). Interestingly, there was no support for any of the environmental variables being strongly related with between-site similarity in carabid beetle or spider communities: coefficients of all environmental variables were low and confidence intervals overlapped zero without exception (Table 1). Furthermore, we found no support for these variables moderating the relationship with distance as none of the interactions between environmental variables and distance had high mean coefficients and all confidence intervals overlapped zero (Appendix A: Table S4).

Discussion

We found support for a negative relationship between distance and similarity of spider communities but not for carabid beetle communities. Furthermore, we found no support for any of our investigated environmental variables being related to between-field community similarity,

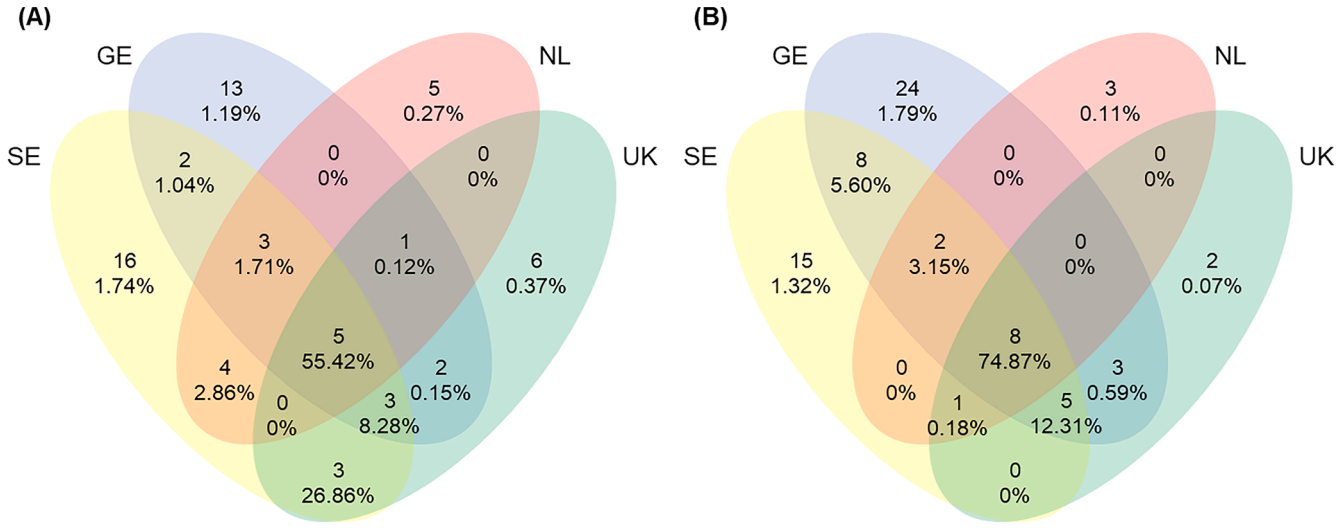

Fig. 1. Venn diagrams of observed (A) carabid beetle and (B) spider species in four countries (GE, Germany; NL, the Netherlands; SE, Sweden; UK, the United Kingdom). Top numbers indicate the species number shared between different countries or unique to each country, bottom numbers with percent sign indicate the relative abundance of the corresponding species.

Table 1
Model averaged results for distance and environmental variables explaining community composition similarity of carabid beetles and spiders. Since ln-transformed distance was found to be the best model than other types of distance for both carabid beetles and spiders (Appendix A: Table S4), "distance" in this table indicates ln-transformed distance. * indicates the interaction between distance and environmental variables. Predictors with a 95 % confidence interval that did not overlap 0 are shown in bold. Models were averaged based on the candidate set of best models (Δ mean AICc < 8 in Appendix A: Table S4). Results are based on 10,000 iterations.

Guild	Predictor	Mean Coefficient	Mean adjusted SE	95 % confidence interval
Carabids	Distance	−0.0435	0.2290	−0.1280 to 0.0413
	Lcrop Mean	−0.0072	0.1621	−0.0672 to 0.0528
	SOC Mean	−0.0015	0.1518	−0.0577 to 0.0547
	Yield Mean	0.0018	0.1541	−0.0553 to 0.0589
	Lcrop Difference	−0.0013	0.1590	−0.0602 to 0.0576
	SOC Difference	−0.0006	0.1565	−0.0586 to 0.0574
	Yield Difference	−0.0059	0.1639	−0.0666 to 0.0548
	Distance * Lcrop Mean	−0.0007	0.1140	−0.0429 to 0.0415
	Distance * SOC Mean	−0.0010	0.1084	−0.0412 to 0.0392
	Distance * Yield Mean	−0.0016	0.1131	−0.0435 to 0.0403
	Distance * Lcrop Difference	0.0019	0.1194	−0.0423 to 0.0461
	Distance * SOC Difference	−0.0012	0.1288	−0.0489 to 0.0465
	Distance * Yield Difference	0.0007	0.1237	−0.0451 to 0.0465
Spiders	**Distance**	**−0.1147**	**0.2344**	**−0.2015 to −0.0279**
	Lcrop Mean	0.0011	0.1375	−0.0498 to 0.0520
	SOC Mean	0.0116	0.1628	−0.0487 to 0.0719
	Yield Mean	0.0121	0.1577	−0.0463 to 0.0705
	Lcrop Difference	−0.0004	0.1418	−0.0565 to 0.0485
	SOC Difference	0.0092	0.1651	−0.0520 to 0.0704
	Yield Difference	0.0064	0.1491	−0.0488 to 0.0616
	Distance * Lcrop Mean	−0.0006	0.1220	−0.0458 to 0.0446
	Distance * SOC Mean	0.0006	0.1227	−0.0448 to 0.0460
	Distance * Yield Mean	0.0004	0.1297	−0.0476 to 0.0484
	Distance * Lcrop Difference	−0.0012	0.1301	−0.0494 to 0.0470
	Distance * SOC Difference	−0.0006	0.1517	−0.0568 to 0.0556
	Distance * Yield Difference	−0.0015	0.1336	−0.0510 to 0.0480

nor for them moderating the relationship with distance. The lack in differentiation in natural enemy communities in response to environmental variables may have been caused by communities from both guilds being dominated by individuals from species that are widespread in northwestern Europe, with 55 % and 75 % of the total number of the observed carabid and spider individuals, respectively, belonging to species that occurred in all four countries (Fig. 1). Although approximately two-thirds of the total number of species of both groups were observed in a single country, the total relative abundance of these species was very low (only 3 % for both groups).

In line with previous studies (Soininen et al., 2007; Keil et al., 2012; Boieiro et al., 2013; Zhang et al., 2013), we found that distance played a predominant role in shaping community β-diversity for spiders. This pattern was not caused by spider communities in nearby sites being consistently similar. Rather, spider communities in fields that were far apart were consistently dissimilar and communities from nearby fields showed the entire range from being similar to dissimilar (Fig. 2). This shows that two communities close to one another are not necessarily similar (Arribas et al., 2021), but on average nearby communities are more similar than communities that are far apart. Furthermore, we found that β-diversity of spiders (and carabid beetles) was best explained by ln-transformed distance. This suggests that the relationship between distance and community similarity was not linear but showed the most pronounced change at smaller distances and changed relatively less at greater distances (Condit et al., 2002; Tuomisto et al., 2003).

Interestingly we found no convincing support for any explanatory variable explaining the similarity of carabid beetles between fields. One reason could be that the level of endemism of the observed species in our study was much lower for carabid beetles than for spiders. While some spider species were found to be exclusively distributed in Germany and Sweden, none of the carabid beetle species were found to be uniquely distributed in any of these four countries (Schuldt & Assmann, 2009 & 2010). This potentially suggests higher species nestedness for spiders than for carabid beetles, which may have resulted in a stronger distance decay effect on spider assemblages. For carabid beetles the lack of any meaningful relation with distance suggests that wheat fields in Sweden harbored essentially the same carabid beetle communities as wheat fields in Germany or the UK which are ~1000 km apart.

In general, the similarity of environmental conditions will decrease with increasing distance between two sites, which is supposed to drive the main effects determining distance decay effects (Tuomisto et al., 2003). However, in arable fields farmers attempt to minimize variation and eliminate factors constraining agricultural production. In northwestern Europe, virtually all arable fields are therefore nutrient-rich, well-drained and mostly free of any plant species that is not the crop. In our study we furthermore only sampled a single crop type making the studied fields even more similar. The increasing contrast in environmental conditions between two sites, that may be expected to occur with increasing distance under natural conditions, may therefore be much less pronounced in the examined arable fields. This could explain why our study, in line with results of earlier studies, did not find land-use intensity, landscape complexity and soil organic carbon content to affect the beta-diversity of both carabid beetles or spiders (Hendrickx et al., 2007; Diekötter et al., 2010; Gossner et al., 2016; Lafage & Pétillon, 2016). The relationship between distance and community similarity for spiders could then be caused by the fact that in this study system, activity density and species richness of spiders are more strongly linked to semi-natural habitats than carabid beetles (Mei et al. 2023). The fact that the collected arthropod communities in our study were dominated by a few species and that these species were found across a significant part of the European continent suggests that these are the species that are well adapted to the conditions of arable fields, these species are robust to environmental differences and that they can persist during environmental change (Desender et al., 2010; Rusch et al., 2013; Gámez-Virués et al., 2015). Therefore, from a utilitarian perspective, our results suggest that similar practices to enhance natural pest control service can be implemented across different countries as these countries share very similar arthropod predator communities.

The results of our study suggest that, while many species may have gone locally extinct because of agricultural intensification and the associated management practices, a few species have most likely been favored by the environmental conditions now available in modern agricultural landscapes, allowing them to dominate communities across large geographical regions. These species can be regarded as "winner species" (McKinney & Lockwood, 1999), which are generally robust to environmental change and human disturbance which can help to

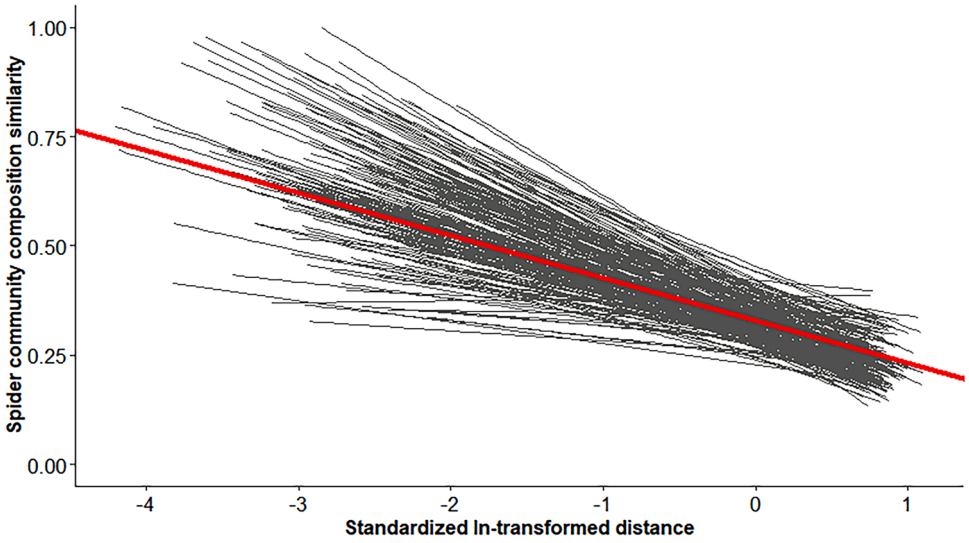

Fig. 2. A visualization of the relationships between distance and community similarity of spiders. Distances were ln-transformed and standardized in each dataset; spider community composition similarity was calculated based on 1 minus Morisita-Horn index. Gray lines indicate regression lines calculated from 200 randomly selected datasets; red line indicates averaged regression line of the overall 10,000 randomized datasets.

guarantee the resilience of natural enemy communities in agricultural landscapes. Furthermore, as the majority of ecosystem services are provided by the wide-spread and dominant species (Kleijn et al., 2015; Winfree et al., 2015), these "winner species" can also provide natural pest control services. However, these "winner species" were estimated to only account for about 1 % of the total number of species (McKinney & Lockwood, 1999). If the trend of agricultural expansion and intensification continues, it will cause severe extinction of specialist and endemic species and drive biotic homogenization in agricultural landscapes (McKinney & Lockwood, 1999; Karp et al., 2012). Since the gain of these "winner species" even may outweigh the loss of the "loser species" and can result in the net increase of species richness (Finderup Nielsen et al., 2019), only focusing on α-diversity may bias the assessment of the status and trends of biodiversity in agricultural landscapes. Our study highlights that biotic homogenization could be a more substantial consequence than local diversity loss under agricultural intensification and expansion. Therefore, the first step of biodiversity conservation should distinguish between the "winner species" and "loser species", followed by more specific conservation measures targeting these "loser species" to create or restore the resources that match the need of these species.

CRediT authorship contribution statement

Zulin Mei: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Jeroen Scheper:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing. **Riccardo Bommarco:** Data curation, Writing – review & editing. **Gerard Arjen de Groot:** Data curation, Writing – review & editing. **Michael P. D. Garratt:** Data curation, Writing – review & editing. **Simon G. Potts:** Data curation, Writing – review & editing. **Sarah Redlich:** Data curation, Writing – review & editing. **Henrik G. Smith:** Data curation, Writing – review & editing. **Wim H. van der Putten:** Data curation, Writing – review & editing. **Stijn van Gils:** Data curation, Writing – review & editing. **David Kleijn:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Supervision, Writing – original draft, Writing – review & editing.

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.

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Supplementary materials

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