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RESEARCH ARTICLE

Small-scale agricultural landscapes promote spider and ground beetle densities by offering suitable overwintering sites

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Abstract

Context Intensive agricultural management practices and landscape homogenisation are the main drivers of biodiversity loss in agricultural landscapes. Agricultural fields are regularly disturbed and provide unstable habitats due to crop management regimes. This may lead to movement of arthropods into neighbouring non-arable habitats, as natural and semi-natural habitats provide suitable overwintering sites.

Objectives Here we assessed the effect of landscape composition and configuration on the overwintering spider and carabid fauna of grassy field margins and hedgerows.

Methods We sampled ground-dwelling arthropods at field edges of different types (grassy field margin and hedgerows), landscape composition (diverse and simple) and configuration (mosaic and large-scale agricultural landscapes).

Results We detected larger spiders in hedgerows than in grassy field margins and in complex landscapes rather than in simple landscapes. We found a significant effect of interaction between landscape composition and edge type on ballooning propensity of

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spiders. Agrobiont carabids were more abundant in field edges of compositionally simple and large-scale agricultural landscapes. Furthermore, we showed an effect of interaction between landscape composition and edge type on agrobiont spiders. We collected larger carabids in grassy field margins than in hedgerows and carabids were smaller in simple landscapes than in diverse landscapes. The spider community was affected by edge type, and landscape composition had a significant effect on the carabid community.

Conclusions Small-scale agricultural landscapes may have higher overall densities of ground-dwelling spiders and carabids than large scale landscapes due to the relatively high edge density and the higher quantity of available overwintering sites.

Keywords Grassy field margin · Overwintering arthropods · Landscape composition · Landscape configuration · Hedgerow

Introduction

Agricultural intensification and the associated fragmentation of natural and semi-natural habitats is a major threat to global biodiversity (Sala et al. 2000) and can negatively affect ecosystem services such as biological control (Bianchi et al. 2006). Generalist invertebrate predators, such as spiders and predatory carabid beetles, display a wide range of foraging methods and play a major role in biological control by reducing crop pest numbers significantly (Symondson et al. 2002; Nyffeler and Sunderland 2003).

In agricultural areas, the landscape structure has a major effect on the biota (Chaplin-Kramer et al. 2011). The two components of landscape structure are (1) composition (the diversity and abundance of different land use or land cover types), and (2) configuration (the size of land cover patches and their spatial arrangement) (Concepción et al. 2008; Fahrig et al. 2011). The effect of landscape scale parameters on predatory invertebrates in arable fields is well documented (Drapela et al. 2008; Pluess et al. 2010; Tscharntke et al. 2012). The increasing quantity of non-crop habitats has a positive effect on invertebrate diversity (Rundlöf et al. 2008; Batáry et al. 2012). Complex agricultural landscapes with high quantity of non-arable habitats (for example, grasslands, forests and hedgerow stripes) have extended arable and non-arable boundaries and a relatively large proportion of the arable land near to non-arable habitats, allowing effective colonisation by predatory invertebrates in the arable fields (Bianchi and van der Werf 2003; Bianchi et al. 2006).

In landscapes dominated by arable fields, agricultural management practices have major effects on species, which in turn are mediated by species traits (Hendrickx et al. 2007), and may change community structure and ecosystem functioning (Batáry et al. 2012). Agrobiont species are indicators of arable habitats, adapted to regular disturbances due to crop management and reach high densities in agricultural fields, although several agrobiont species are rare in natural habitats (Samu and Cs 2002).

Grassy field margins are usually narrow linear landscape elements with herbaceous vegetation, and hedgerows are wider linear semi-natural habitats composed of shrubs and trees (Baudry et al. 2000). The role of such landscape elements in the conservation of biodiversity has long been recognised (Way 1977). Linear landscape elements may counteract the negative effect of agricultural intensification on a landscape scale on biodiversity (Martin and Major 2001; Holland et al. 2016) by increasing habitat connectivity and providing source habitats and overwintering sites for several predatory invertebrate species (Schaffers et al. 2012). Agricultural fields provide unstable and ephemeral habitats due to crop management regimes. Harvest and tilling directly cause mortality of agrobiont organisms and induce abrupt and substantial change in habitat structure, reducing the diversity of feeding and shelter microhabitats (Thorbek and Bilde 2004). This may lead to movement of invertebrates into neighboring non-arable habitats (Opatovsky and Lubin 2012). Spillover dispersal of predatory invertebrates from harvested fields to adjacent habitats and early season spillover from semi-natural habitats to arable fields have been reported (Tscharntke et al. 2012, González et al. 2016). However, the impact of spillover dispersal on the local assemblage and food web remain underestimated (Blitzer et al. 2012; Madeira et al. 2016). After crop harvest, semi-natural habitats provide suitable overwintering microhabitats and alternative prey species that are important to sustain predatory invertebrate populations in agricultural landscapes (Landis et al. 2000) and early season colonization of arable fields from overwintering habitats may prevent pest outbreaks (Landis et al. 2000; Rand et al. 2006).

In this study, we examined the overwintering spider and carabid fauna of grassy field margins and hedgerows in different landscape contexts. We hypothesised that: (1) hedgerows support both habitat specialist and agrobiont overwintering arthropod species, whereas grassy field margins mainly support agrobiont species and edge type has an effect on the species composition of spider and carabid assemblages; (2) higher proportion of non-arable habitats in the local landscape will enhance the species richness of spiders and carabids, and this effect is mediated by species dispersal traits; (3) mosaic landscape configuration (i.e. small arable field sizes and high edge density in the local landscape) will increase the abundance of agrobiont species by enhancing the amount of suitable overwintering sites.

Materials and methods

Study area

We selected 32 sampling sites in the southern part of the Great Hungarian Plain. The study area is situated in a temperate climate zone with a mean winter temperature of 2.3 °C and an annual precipitation range between 203 and 838 mm (Makra et al. 2012). The landform of the study region is a plain at altitudes of between 75 and 90 m a.s.l., and the soil of the area is composed mainly of Chernozem and Fluvial soils. Due to the very fertile Chernozems, with high organic matter and low salt content, conventional arable fields (mainly cereals and maize) dominate the landscape with insignificant share of organically managed fields. Intensive grassland management does not occur in the region. Forest patches, hedgerows, extensive pastures and meadows are the main semi-natural elements of landscapes (Lóczy 2015; Szilassi et al. 2017). The map of the study area is provided in Online Appendix 1.

Sampling design

The land cover patches and the linear landscape elements (roads, tree lines and grassland margins) of the study areas were digitalised based on the visual interpretation of Google Earth (2016) satellite images using ArcGIS 10.1 software. The minimum widths of the mapped landscape units were 5 m in case of the linear elements and 0.1 ha in case of the land cover patches or arable land parcels. We measured the percentage cover of arable lands and semi-natural habitats areas to characterise landscape composition. We described the landscape configuration using area-weighted mean patch size (AWMPS) of land cover patches (i.e. the average area of the land cover patches), arable fields and with edge density (ED), which describes the total length of edges divided by the area of the local landscape (m/ha) (Turner and Gardner 2015). We calculated these landscape metrics for each local landscape (n = 32) based on land cover patches, in which centroids were less than 1000 m from the study sites, using V-LATE and Hawth's Analysis Tools for ArcGIS extensions of the Arc GIS 10.1 software (Lang and Tiede 2003; ESRI 2012).

The distance between the nearest sampling sites was set to at least 2 km (the average Euclidean distance of the sample points is 3615 m) to enhance the spatial independency of sampling sites.

We applied a cross-sampling design with three independent variables: (1) edge type—hedgerow versus grassy margin; (2) landscape composition—diverse (mean value 12.6 ± 5.3% of semi-natural habitat) versus simple landscape structure (mean value 1.9 ± 1.3% of semi-natural habitat), and (3) landscape configuration—mosaic (mean AWMPS 12.2 ± 7.8 ha, mean ED 317 ± 68 m/ha) versus large scale landscapes (mean AWMP 31.7 ± 19.6 ha, mean ED 188 ± 63 m/ha) (Fig. 1). Our sampling design involved 4 replicates of all parameter combination (Fig. 2).

Arthropod sampling

We sampled arthropods (spiders and carabids) using pitfall traps (500-ml white plastic cups, 8.5 cm in diameter). Traps were fitted with transparent plastic funnels and a 20 × 20 cm metal roof to reduce vertebrate bycatches and dilution of the preservative. The traps were filled with 50% ethylene–glycol and water solution containing a few drops of odourless detergent. At each sampling site, four pitfall traps were employed, spaced 8 m apart, along a transect running parallel with the field edge. Sampling was conducted during two periods, 5th–26th November 2016, after autumn management of crop fields and after migration of spiders and carabids to overwintering habitats, and

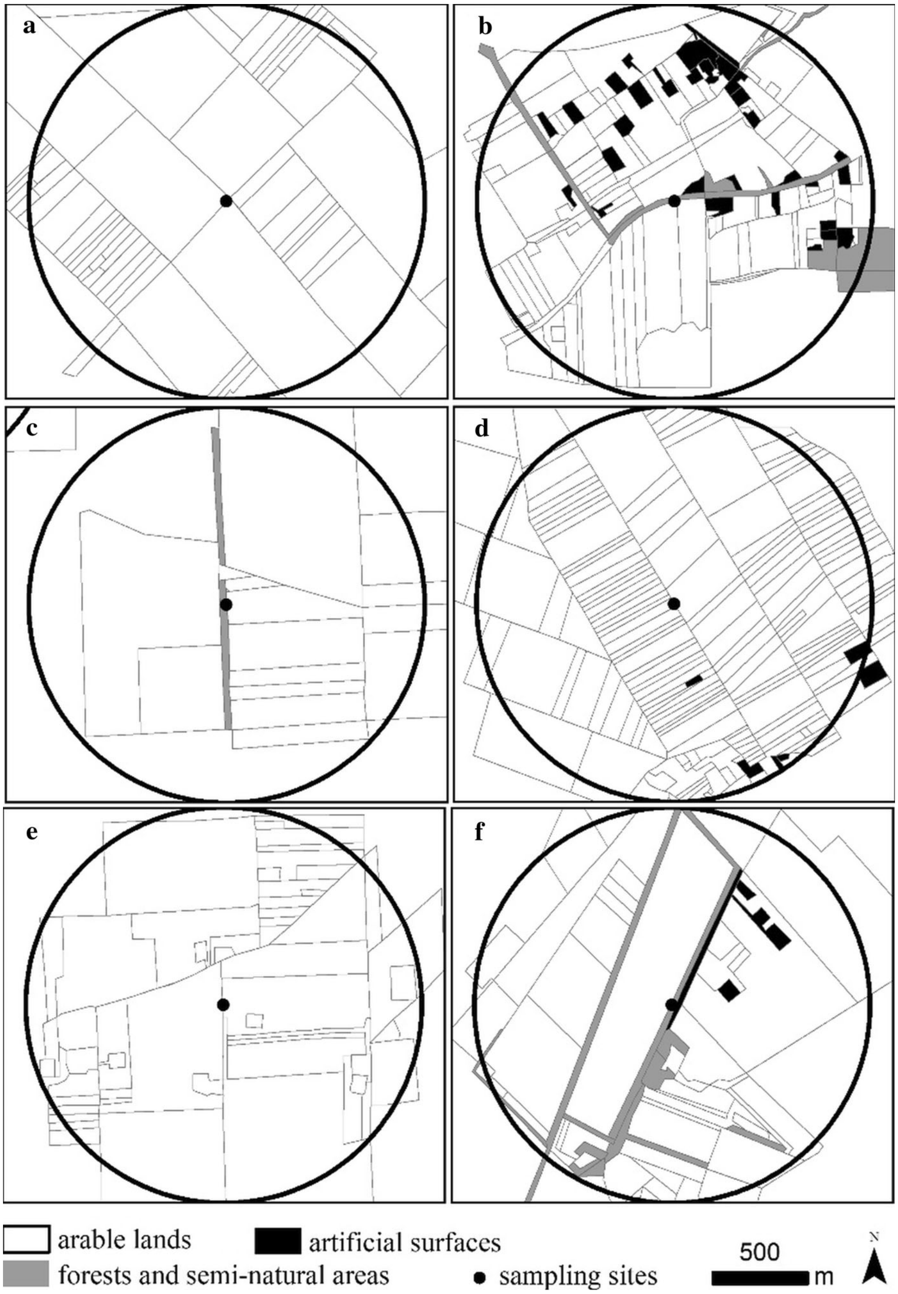

Fig. 1 The effect of landscape parameters and edge type on spider dispersal and size. **a** community weighted mean values of ballooning propensity; **b** community weighted mean values spider size (mm)

10th–31st March 2017, before spring agricultural activities started, and before spiders and carabids are leaving overwintering sites.

Data analysis

Species were classified on the basis of dispersal traits. Spider ballooning dispersal was classified using three categories, according to Bell et al. (2005) and Blandenier (2009): (1) species known to balloon (species included in lists of ballooning spiders), (2) species likely to balloon (other species of the genus included in lists), and (3) species unlikely to balloon (not included in lists). We characterised carabid flying ability according to the wing morphology of the species (Hendrickx et al. 2009). Carabid wing systems were classified as: (1) marcopterous, (2) species with polymorphic wings, and (3) apterous/brachypterous species. Ground-dwelling dispersal ability of arthropod species is linked to the size of the species (Homburg et al. 2014), thus we used size as a proxy for ground surface dispersal ability. Size of the spiders and carabids was given as a continuous variable, with the average body size being recorded in mm (Homburg et al. 2014; Nentwig et al. 2017). Species were classified into agrobiont species, according to Samu and Cs (2002) and Birkhofer et al. (2013) for spiders, and Hurka (1996), Freude et al. (2004) and Homburg et al. (2014) for carabids.

For each sampling site (n = 32), we pooled the data from the two collection periods and four traps. We calculated community weighted mean (CWM) values for airborne and surface active dispersal traits in each sampling site (Ricotta and Moretti 2011).

We used GLMs to determine the effect of edge type landscape composition, configuration and their second order interaction on species richness, abundance of agrobiont species and dispersal traits of spiders and carabids. We used the Poisson model for species richness, negative binomial model for agrobiont abundance data to account over-dispersion of the data and Gaussian error term for CWM values. We generated candidate models with all possible combinations of explanatory variables and their interaction and ranked them using Akaike's information criterion, corrected for small sample sizes (AICc), using the 'dredge' function from the 'MuMIn' package (Bartón 2015). Model averaging was performed for competitive models (ΔAICc $\leq$ 10) to include the uncertainty arising from the high number of candidate models (Burham and Anderson 2003). For each explanatory variable and their interaction, we estimated AIC-weighted importance values, and we also estimated the significance of the variables with the 'LmerTest' package (Kuznetsova et al. 2015).

To explore and visualise the effect of landscape characteristics and edge type on the species composition of spiders and carabids, we used constrained redundancy analysis (RDA) of the species-abundance matrix and the environmental variables (edge type, landscape composition and configuration). We applied the Hellinger transformation on the species-abundance data prior to the RDA (Legendre and Gallagher 2001). The marginal effects of the variables were tested by Monte Carlo permutation tests with 5000 permutations. To detect characteristic species for the levels of the influential variables according to the RDA, we calculated indicator values (IndVal; Dufrene and Legendre 1997) with the 'labdsv' package (Roberts 2012).

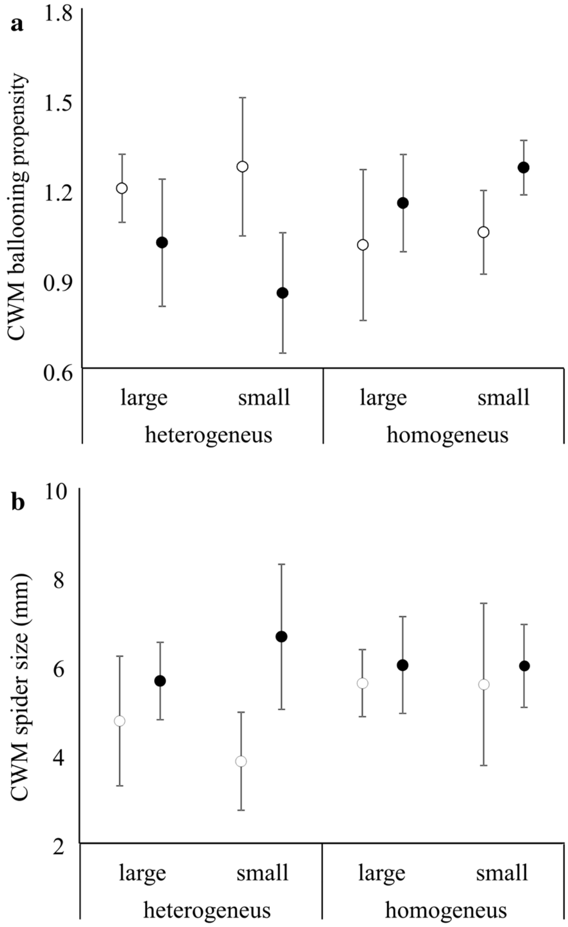

Fig. 2 Sampling design according to different investigated agricultural landscape structures of **a** homogeneous agricultural landscape; **b** heterogeneous agricultural landscape **c** Large scale agricultural landscape with large AWMPS and small ED values **d** Small-scale agricultural landscape with small AWMPS and large ED values **d** Agricultural landscape with small grassland margins **e** Agricultural landscape with large tree line, or bush margins

Results

Spiders

During the two sampling periods, we recorded a total of 2502 adult spiders belonging to 72 species (Table S1). The most abundant species were *Trochosa terricola* Thorell, (557 individuals, 22% of the total catch) and *Pachygnatha degeeri* Sundevall, (438 individuals, 17% of the total catch).

We detected a significant interaction between the effects of landscape composition and edge type on the CWM value of ballooning spiders ($z = 2.440$, $p = 0.014$), indicating that landscape composition had different effect on spider communities of hedgerows and grassy field margins (Table 1, Fig. 3a). We collected larger species in complex landscapes than in simple landscapes ($z = 2.347$, $p = 0.018$), and spiders in hedgerows were larger than spiders in grassy field margins ($z = 2.433$, $p = 0.015$, Table 1, Fig. 3b). However, we did not find any significant effect of edge type and landscape scale parameters on the species richness of spiders or on the abundance of agrobiont species. The Akaike weights of candidate models are given in Online Appendix 2.

The RDA model (constrained inertia 16.5%, $F = 1.851$, $p = 0.005$) indicated the significant effect of edge type on species composition of spiders ($F = 3.677$, $p < 0.001$). *T. terricola* (IndVal = 0.763, $p = 0.002$) and *Zelotes apricorum* (L. Koch) (IndVal = 0.546, $p = 0.026$) were associated with hedgerows. *Syedra apetlonensis* Wunderlich, (IndVal = 0.511, $p = 0.011$) and *Trichoncoides piscator* (Simon) (IndVal = 0.343, $p = 0.04$) were associated with grassy field margins (Fig. 4a).

Carabids

We collected 3004 carabids belonging to 66 species (Table S2). The most abundant carabids, *Anchomenus dorsalis* (Pontoppidan) (830 individuals, 27% of the total catch) and *Trechus quadristriatus* (Schrank) (384 individuals, 12% of the total catch), were relatively good dispersers and occurred in arable fields.

Agrobiont carabid abundance was significantly affected by the interaction of landscape composition and configuration ($z = 0.597$, $p = 0.009$), higher in field edges of simple and large-scale agricultural landscapes than edges of complex and small scale landscapes. Furthermore, we found a significant interaction effect between landscape composition and edge type ($z = 2.055$, $p = 0.039$); diverse landscapes had a more pronounced negative effect on the abundance of agrobiont spiders in grassy field margins than in hedgerows (Table 2, Fig. 4a). The Akaike weights of candidate models are given in Online Appendix 2.

We collected larger carabids in grassy field margins than in hedgerows, and carabids were smaller in simple landscapes than in diverse landscapes (Table 2, Fig. 4b). The interaction effect of edge type and landscape composition was indicated by carabids that

Table 1 The effect of landscape variables and edge type on spiders according to GLMs and model averaging

Model	Variable	Relative importance, (z values)	Multimodel estimate
Species richness[b]	Edge type	50%, (1.461)	− 0.136 ± 0.198
	Configuration	19%, (0.241)	− 0.022 ± 0.185
	Composition	19%, (0.105)	− 0.009 ± 0.104
Agrobiont abundance[c]	Edge type	40%, (1.438)	− 0.412 ± 0.561
	Composition	19%, (0.008)	− 0.002 ± 0.583
	Configuration	11%, (0.256)	− 0.075 ± 0.581
CWM ballooning[a]	Edge type	43%, (0.884)	− 0.179 ± 0.251
	Composition	39%, (1.397)	− 0.111 ± 0.247
	Comp:type	28%, (2.440)	0.359 ± 0.285*
	Configuration	11%, (0.201)	0.016 ± 0.145
CWM size[a]	Composition	100%, (2.347)	1.162 ± 0.971*
	Edge type	100%, (2.433)	1.205 ± 0.971*
	Comp:type	22%, (0.767)	− 0.662 ± 1.692
	Configuration	15%, (0.025)	0.011 ± 0.750

Relative importance and multimodel estimate ± CI are given

[a] Models were fitted with normal distribution

[b] Models were fitted with Poisson distribution

[c] Models were fitted with negative binomial distribution

*P < 0.05, **P < 0.01, ***P < 0.001

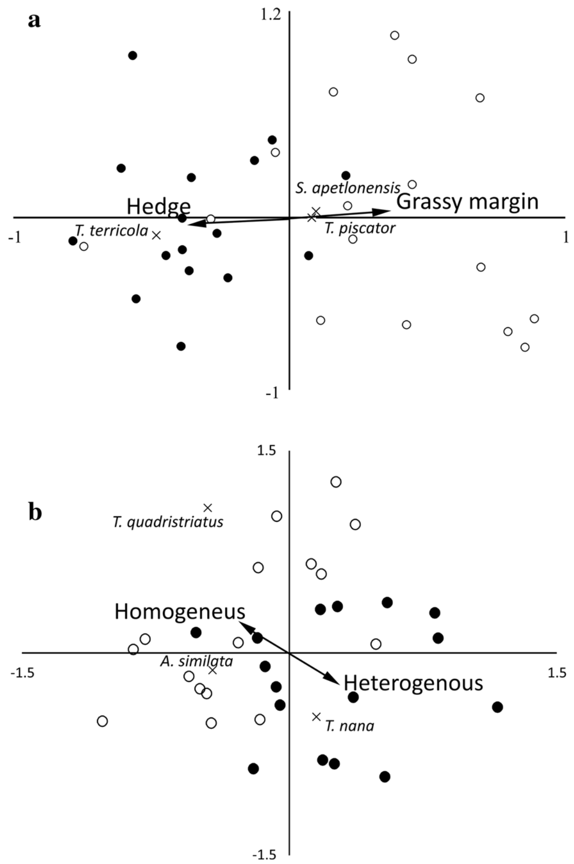

Fig. 3 RDA ordination plots of sampling site (dots), significant landscape and edge descriptors (arrows) and significant indicator species (crosses) along the first and second RDA axes, for **a** spiders, black dots: hedgerows, open circles: grassy field margins and **b** carabids, black dots: heterogeneous landscapes, open circles: homogenous landscapes

were larger in grassy field margins than in hedgerows in diverse landscapes, whereas they were smaller in simple landscapes. The Akaike weights of candidate models are given in Online Appendix 3.

Assemblage composition of carabids was influenced by landscape composition (F = 1.666, p = 0.049) according to the significant RDA model (constrained inertia 14.3%, F = 1.569, p = 0.016). *Tachyta nana* (Gyllenhal) (IndVal = 0.312, p = 0.049) was associated with heterogeneous landscapes, and *T. quadristriatus* (IndVal = 0.698, p = 0.015) and *Amara similata* (Gyllenhal) (IndVal = 0.634, p = 0.020) were associated with homogenous landscapes (Fig. 3b).

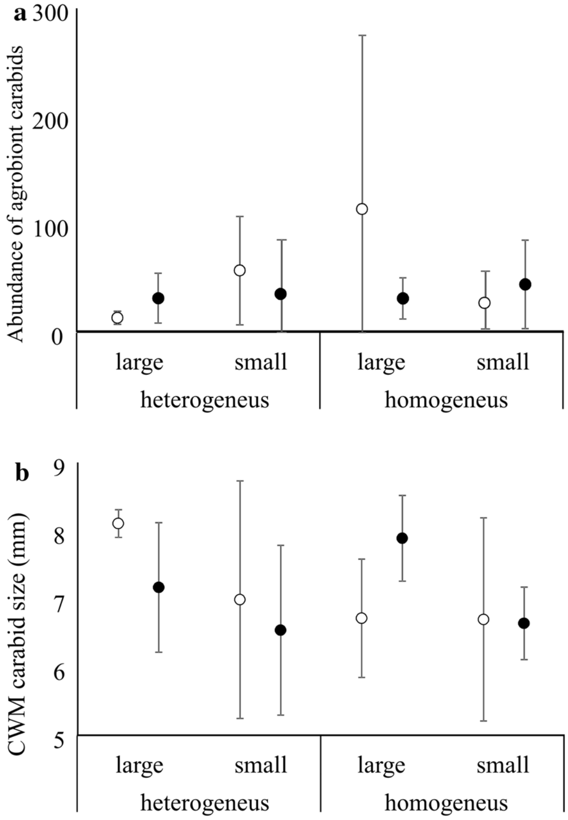

Fig. 4 The effect of landscape parameters and edge type on agrobiont carabids and size of carabids **a** abundance of agrobiont carabids; **b** community weighted mean values carabid size (mm)

Discussion

Our findings confirm that in simple agricultural landscapes with large field sizes under intensive agricultural use, non-arable linear landscape elements provide important and relatively stable habitats for various organisms (Le Viol et al. 2008; Noordijk et al. 2009; Schaffers et al. 2012). Furthermore, they provide important overwintering habitats and refuges from disturbance (Pfiffner and Luka 2000; Sarthou et al. 2014). In this study, we detected high species richness of overwintering spiders and carabids in field edges. We found no difference between the species richness of overwintering spiders and carabids between grassy field margins and hedgerows, however, edge type had a significant effect on the species composition of spiders. Landscape composition had a significant effect on the CWM value for spider and carabid dispersal traits. However, landscape

Table 2 The effect of landscape variables and edge type on carabids according to GLMs and model averaging

Model	Variable	Relative importance	Multimodel estimate
Species richness[b]	Configuration	21%, (0.861)	− 0.090 ± 0.124
	Composition	18%, (0.234)	0.067 ± 0.205
	Edge type	15% (0.131)	− 0.036 ± 0.204
Agrobiont abundance[c]	Composition	63%, (0.455)	0.296 ± 1.252
	Configuration	63%, (1.915)	0.908 ± 929
	Comp:config	47%, 2.584	− 1.543 ± 1.171**
	Edge type	10%, (1.562)	0.606 ± 0.760
	Comp:type	10%,(2.055)	− 1.156 ± 1.103*
CWM flying[a]	Configuration	77%, (0.521)	− 0.066 ± 0.250
	Composition	75%, (0.325)	− 0.041 ± 0.241
	Comp:config	45%, (1.890)	− 0.304 ± 0.315
	Edge type	26%, (0.427)	0.046 ± 0.211
	Config:type	9% (1.498)	0.235 ± 0.307
CWM size[a]	Composition	100%, (3.328)	− 1.722 ± 1.015***
	Configuration	100%, (0.974)	− 0.439 ± 0.894
	Edge type	100%, (3.011)	− 1.242 ± 0. 809**
	Comp:config	63%, (1.880)	− 1.075 ± 1.53
	Comp:type	100%, (4.121)	2.406 ± 1.144***

Relative importance and multimodel estimate ± CI are given

[a] Models were fitted with normal distribution

[b] Models were fitted with poisson distribution

[c] Models were fitted with negative binomial distribution

*P < 0.05, **P < 0.01, ***P < 0.001

composition did not affect species richness. Finally agrobiont carabid abundance was highest in the field edges of large-scale agricultural landscapes with a simple landscape composition.

Edge type effect

Grassy field margins are common in agricultural landscapes worldwide (Cordeau et al. 2012; Ramsden et al. 2015), and their positive effect on farmland carabids and spiders is well known (Marshall et al. 2006; Öberg et al. 2007). Hedgerows also play an important role in maintaining the abundance and diversity of agrobiont natural enemies. However, they may also have different species composition because hedgerows are important landscape elements for forest and woody habitat species (Buddle et al. 2004; Fisher et al. 2013). The majority of collected species occur in a variety of habitats, only 17 out of the 72 spider species were agrobiont, and we collected 31 agrobiont carabid species out of the 66 carabid species, also underpinning that hedgerows and grassy margins are important in conserving habitat specialist, as well as habitat generalist species.

In this study, we demonstrated that the edge type had an effect on species composition and functional diversity of overwintering natural enemies. We collected larger spiders but smaller carabids in hedgerows than in grassy field margins. Schirmel et al. (2012, 2016) also reported an opposing pattern in body size distribution of carabids and spiders. The underlying mechanism may be different for the two species, as body size is correlated with many life cycle events, such as resource use (i.e. larger species prey on larger food), starvation and desiccation resistance (increasing body size leading to low prey availability and dry, hot conditions favouring large-bodied species) and competitive abilities (large species may be better competitors) (Entling et al. 2010; Moretti et al. 2017). Furthermore, body size pattern was altered by landscape composition; carabids in hedgerows were smaller than in grassy field margins in diverse landscapes, but were larger in hedgerows than in grassy field margins in simple landscapes (Fig. 4b).

Spider assemblages markedly differed between edge types according to the RDA and we identified four species with significant indicator values, suggesting different species pools in grassy field margins and hedgerows. *T. terricola* and *Z. apricorum* were associated with hedgerows. Both ground dwelling, active hunter species are abundant in open forests and on forest edges (Buchar and Ruzicka 2002). Further two species, namely *S. apetlonensis* and *T. piscator* were associated with grassy field margins and both are typical inhabitants of open habitats, including agricultural fields (Kalushkov et al. 2008). Sarthou et al. (2014) also found that habitat type determines predatory invertebrate assemblages in overwintering habitats. Leaf litter in hedgerows may provide a suitable microhabitat for forest spiders. Furthermore, woody vegetation plays an important role as a windbreak and can alter winter microclimate (Marshall and Moonen 2002). However, the numerically dominant species were the agrobiont spiders in both types of edges, indicating that both hedgerows and grassy field margins are important overwintering habitats and make a significant contribution to biological control potential (Mansion-Vaquié et al. 2017).

The propensity for spider ballooning was lower in hedgerows than in grassy field margins in diverse landscapes. However, it was higher in hedgerows than in grassy field margins in simple landscapes (Fig. 3a). Undirected passive flying is common in several wingless invertebrate taxa and is particularly common in a large variety of spider families (Bonte et al. 2003; Bell et al. 2005). Ballooning is a strategy for exploiting ephemeral habitats (Schellhorn et al. 2014), such as arable fields where habitats do not persist all year round. In diverse landscapes, the lower propensity for ballooning in hedgerow spiders compared to grassy field margin spiders is in agreement with studies of Southwood (1977) and Entling et al. (2011). The higher extinction risk in severely disturbed habitats, such as regularly managed grassy field margins in this study, favour species with high dispersal ability. In homogenous landscapes, however, the low amount of woody vegetation and the large distance between (semi) natural forests and hedgerows may favour spiders with higher propensity for ballooning.

Landscape structure

We collected a higher number of agrobiont carabids in hedgerows than in grassy field margins in diverse landscapes. However, agrobiont abundance was higher in grassy field margins than in hedgerows in simple landscapes, indicating a negative effect of the increasing proportion of non-arable habitats on agrobiont carabids in grassy field margins (Fig. 4a). Schmidt et al. (2008) also showed that agrobiont species were negatively influenced by a high proportion of semi-natural and natural habitats in the surrounding landscape. Similarly, Ferrante et al. (2017) found that chewing insects predation rate decreases in proximity of natural habitats. This apparent negative effect is presumably due to the low availability of overwintering sites in homogenous landscapes, which may lead to higher densities of overwintering carabids in the semi-natural herbaceous vegetation of grassy field margins.

Autumn breeding carabids overwinter as larvae in the soil of arable fields and these species are influenced by landscape composition less than spring breeders. (Holland et al. 2009). We collected predominantly spring breeding carabids. These overwinter in the adult stage and migrate into the fields from surrounding overwintering sites during spring and, therefore, are particularly affected by the spatial distribution and availability of non-arable habitats (Purtauf et al. 2005). The initial colonisation of spring breeding carabids may be a key factor in determining community structure and biological control potential (Wamser et al. 2011).

Carabid assemblages markedly differed between compositionally diverse and simple landscapes according to the RDA. The forest and forest edge specialist species, *T. nana*, was associated with heterogeneous landscapes, and two very common open habitat species, *Amara similata* (Gyllenhal) and *T. quadristriatus*, were associated with homogenous landscapes. Grassland and forest species had time to colonise the relatively stable field margins and hedgerows from non-crop habitats in diverse landscapes (Werling and Gratton 2008). In simple landscapes, the low proportion and small size of natural and semi-natural habitats are unable to maintain source populations of specialist carabids. However, the most abundant species reported in this study were agrobiont carabids in both diverse and simple landscapes. We found no effect of landscape composition on species richness of carabids, presumably due to a relatively small increase in the proportion of semi-natural habitats (Duflot et al. 2015).

In compositionally heterogeneous landscapes, small-scale agriculture had a positive effect on abundances of overwintering agrobiont carabids. The average edge density in the small-scale landscapes was 1.6 times higher than in large-scale landscapes; this may have fostered overall densities of agrobiont carabids in small-scale landscapes. Small field sizes and high carabid abundance may indicate rapid early season colonisation of arable fields and high biological control potential (Batáry et al. 2017). In simple landscapes, however, we collected more agrobiont carabids in the edges of large fields (Fig. 4a). The lower density of non-arable habitats may have resulted in a high concentration of overwintering predators in the few field edges present (Greiger et al. 2009).

Conclusions

The most important finding of this study was that overwintering spiders and carabids were affected by edge type and landscape composition, and this effect was mediated by landscape configuration for carabid beetles. We found relatively high spider and carabid abundances in all sampled edges. This suggests that higher overall densities of ground dwelling predatory arthropods in agricultural landscape mosaics are due to the relatively high edge density of these landscapes. These findings suggest that agricultural landscape mosaics of small arable fields promote biological control potential of ground-dwelling predatory arthropods, as a higher density of edges provides more suitable overwintering sites.

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