Trait composition and functional diversity of spiders and carabids in linear landscape elements

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ABSTRACT

Agricultural intensification is a cause of global biodiversity decline. Seminatural linear landscape elements (LLE) within agricultural landscapes can considerably mitigate these declines, but their effects on functional properties of biodiversity are poorly known. We analyzed trait composition and functional diversity (functional dispersion) of spiders and carabids in woody and herbaceous LLE. We expected that species assemblages of woody LLE are more diverse and K-selected compared to herbaceous LLE, and that effects of environmental parameters vary between LLE types. We selected 58 LLE in an agricultural landscape in Northwest Germany. We sampled carabids and spiders by pitfall trapping and measured landscape connectivity, landscape-wide land-use diversity, local land-use diversity, and local plant richness as explanatory variables. The trait composition of arthropods in woody LLE was more K-selected (lower dispersal ability, a higher food specialization or trophic level) than in herbaceous LLE. Moreover, spider functional diversity was higher in woody LLE. Spider functional diversity and proportion of predatory carabids in woody LLE increased with increasing connectivity of the habitats. In contrast, in herbaceous LLE local plant richness and landscape-wide land-use diversity were most important drivers for spider and carabid diversity and traits. Our results show that species richness and functional diversity of spiders and carabids were differently affected by landscape and local factors. Therefore, the importance of landscape connectivity was higher in woody LLE, suggesting that their inhabitants are more sensitive to habitat fragmentation than the highly mobile generalist species living in herbaceous habitats.

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1. Introduction

Agricultural intensification is a major reason for global biodiversity decline (Sala et al., 2000). Intensive agriculture is correlated with increased fragmentation and decreased connectivity of natural and seminatural habitats (Fahrig, 2003; Fischer and Lindenmayer, 2007). Since the second half of the twentieth century, this has resulted in simplified landscapes in many agricultural regions worldwide (Stoate et al., 2001; Tscharntke et al., 2005) often associated with biodiversity loss and biotic homogenization (Norris, 2008; Gámez-Virués et al., 2015). Seminatural habitats are important for many species in agricultural landscapes and, therefore, essential for biodiversity

conservation (Marshall and Moonen, 2002; Merckx et al., 2012; Dainese et al., 2015).

In European agricultural landscapes, seminatural habitats are commonly situated along the border between crops. Such linear landscape elements (LLE) can generally be divided into woody elements like hedgerows and tree lines and herbaceous elements like field margins and grass strips (Holland et al., 2016; Marshall and Moonen, 2002; Robinson and Sutherland, 2002). Compared to crop fields they are less disturbed habitats and provide shelter, overwintering sites, reproduction habitats, a favorable microclimate and alternative food sources (Bianchi et al., 2006). Furthermore, LLE can act as dispersal corridors for many organisms and reduce habitat fragmentation (Haddad and Tweksbury, 2005; Holzschuh et al., 2010; Marshall and Moonen, 2002; Thiele et al., 2008). LLE can therefore provide wide-ranging ecological benefits (biodiversity conservation, habitat for beneficials, corridors, etc.) even while occupying little area, through their large perimeter-to-

area ratio, thus reducing the opportunity cost for taking land out of production (Grashof-Bokdam and Langevelde, 2005).

Diversity and species distribution patterns in agricultural landscapes depend on the spatial arrangements and connectivity of seminatural habitats (Fahrig et al., 2011; Tscharntke et al., 2012). Additionally, the agricultural matrix is often not completely hostile to many organisms and may provide important resources (Fahrig et al., 2011; Tscharntke et al., 2012). Species in agricultural landscape react to their environment at different spatial scales. In general, structurally complex landscapes (i.e. landscapes with a large variety of different cover types) often contain more diverse species assemblages than simple landscapes (e.g., Schmidt et al., 2008; Tscharntke et al., 2012; Weibull et al., 2003; Weibull and Östman, 2003). In the same way, connectivity is known to have positive effects on diversity of multiple taxa (e.g. Holzschuh et al., 2009, 2010). In addition to these landscape effects, the local environment shapes species assemblages of seminatural habitats. Thereby, plant species richness, vegetation composition and habitat diversity explain community structure and diversity of many arthropods (Hendrickx et al., 2007; Liu et al., 2015; Schaffers et al., 2008; Thomas and Marshall, 1999).

The habitat templet theory (Southwood, 1977) assumes that the local habitat templets act as filters that sort species according to their traits. According to this, a species can only be part of the local community if it features appropriate traits to pass through the filters defined by habitat properties. Important environmental constraints acting on species and their traits are related to disturbance and stress (Grime, 1977; Southwood, 1977; Whittaker and Wilson, 1967). We expect more r-strategists occurring in herbaceous linear elements, because they are generally more disturbed than woody ones due to regular mowing and the absence of a protecting shrub or tree layer. Traits associated with r-strategists are often a small body size, high dispersal ability and lower specialization. Consequently, we expect more K-strategists in less disturbed woody linear elements.

Little is known about the functional diversity of arthropods in seminatural habitats and the importance of landscape and local effects in fragmented agricultural landscapes (but see Woodcock et al., 2010). This is a drawback since functional diversity provides insights into interactions of organisms with their environment (Petchey et al., 2009; Violle et al., 2007) and is often more sensitive to environmental changes than taxonomic diversity (Cadotte et al., 2009; Schirmel et al., 2012; Woodcock et al., 2014). In agricultural landscapes, investigations of functional diversity of beneficial organisms such as natural enemies allow us to better understand their potential for providing ecosystem services. In particular, functionally diverse predator communities may exert stronger top-down control on a wider range of prey than functionally more uniform predator communities (Hooper et al., 2005; Schuldt et al., 2014).

We analyzed landscape and local effects on ground-dwelling arthropods in woody and herbaceous linear landscape elements in an agricultural landscape in Northwest Germany. We used spiders and carabids because they are proven indicators for landscape and local effects in agricultural landscapes (Aviron et al., 2005; Liu et al., 2015; Purtauf et al., 2005; Schmidt et al., 2008) and are important components of natural enemy assemblages of crop pests (spiders: Marc et al., 1999; Schmidt et al., 2005; carabids: Sunderland et al., 1987; Kromp, 1999).

In a first step, we compared species and functional diversity of both taxa between woody and herbaceous LLE. In a second step, we disentangled the effects of landscape (i.e. landscape connectivity and landscape-wide land-use diversity) and local parameters (i.e. local land-use diversity and local plant richness) on functional diversity separately for woody and herbaceous elements. We hypothesized that: (i) Trait composition in woody LLE will be more

K-selected, i.e. lower dispersal ability, larger body size, higher food specialization and higher trophic level compared to more r-selected trait composition in herbaceous LLE. (ii) Species richness and functional diversity will be higher in less disturbed woody LLE than in herbaceous LLE. Furthermore, we expected that effects will vary between LLE types: (iii) Due to more K-selected communities, effects of landscape connectivity will be stronger in woody compared to herbaceous LLE. (iv) Oppositely, due to higher mobility, effects of landscape-wide land-use diversity will be stronger in herbaceous than in woody LLE.

2. Methods

2.1. Study region and site selection

The study was completed in 2012 in the region "Westfälische Bucht" in Northwest Germany (Fig. 1). The regional climate is temperate oceanic with an annual mean temperature of around $10\,°C$ and annual precipitation around 800 mm (period 1981–2000; Klimaatlas Nordrhein-Westfalen, http://www.klimaatlas.nrw.de). The region is characterized by intensive agriculture and a relatively high proportion of LLE (hedgerows, tree lines, field margins).

Within the study region we selected eight study areas, each 1 km², selected by random points which were stratified by four natural regions (West-, Kern-, Ostmünsterland, and Hellwegbörden) using GIS (Supplementary data Table S1). We wanted to study areas that represent the prevailing agricultural landscapes of the region and, hence, excluded larger settlements, extensive forests, lakes, rivers, and areas of markedly different geology from random sampling based on Corine Land Cover and general soil maps ("Bodenübersichtskarte 1:200.000"). The landform of the study areas is mostly plain at altitudes between 40 and 80 m a.s.l., but slightly hilly in the southernmost area ("Herringser Höfe") at 200–220 m a.s.l. Soils of the study areas are sandy in the western and northeastern part of the study region (West-, Ostmünsterland), loamy in the central part (Kernmünsterland) and loess dominated in the southern part (Hellwegbörden), but always lime-free. In the study areas, land use is dominated by intensive arable farming which occupied on average 70% of the area in 2009. Main crops in the study areas were cereals and maize. All farming in the study areas was conventional. The proportion of LLE in the study areas varied between 2.5 and 10%.

In each study area, we selected 6 or 8 plots (N_{total} = 58 plots) that were randomly located in LLE using random points in GIS. Half of the LLE was herbaceous (field margins, grass strips) while the other half were woody (hedgerows, tree lines). All LLE that were at least 2 m wide and adjacent to arable fields were considered for random sampling, whereas narrower ones were excluded. Plots were 1×25 m in size and at least 100 m apart from each other.

2.2. Landscape and local parameters

We mapped the land-cover of the study areas through visual interpretation from aerial images (20 cm ground resolution) of 2008 or 2009 in a Geographic Information System (GIS) discerning, e.g., arable fields, grasslands, forests, housing, and different types of linear landscape elements, such as tree rows and herbaceous field margins. Delineation of land parcels and landscape elements was unproblematic because of clear land-use boundaries and marked contrasts between adjacent land-uses and seminatural landscape elements in the study areas. Landscape-wide land-use diversity was analyzed in buffers of 500 m around the plot centers based on the land-cover maps. Landscape scales of 500 m radius are known to be relevant for spiders (Clough et al., 2005; Schmidt et al., 2005; Schmidt and Tscharntke, 2005) and carabids (Aviron
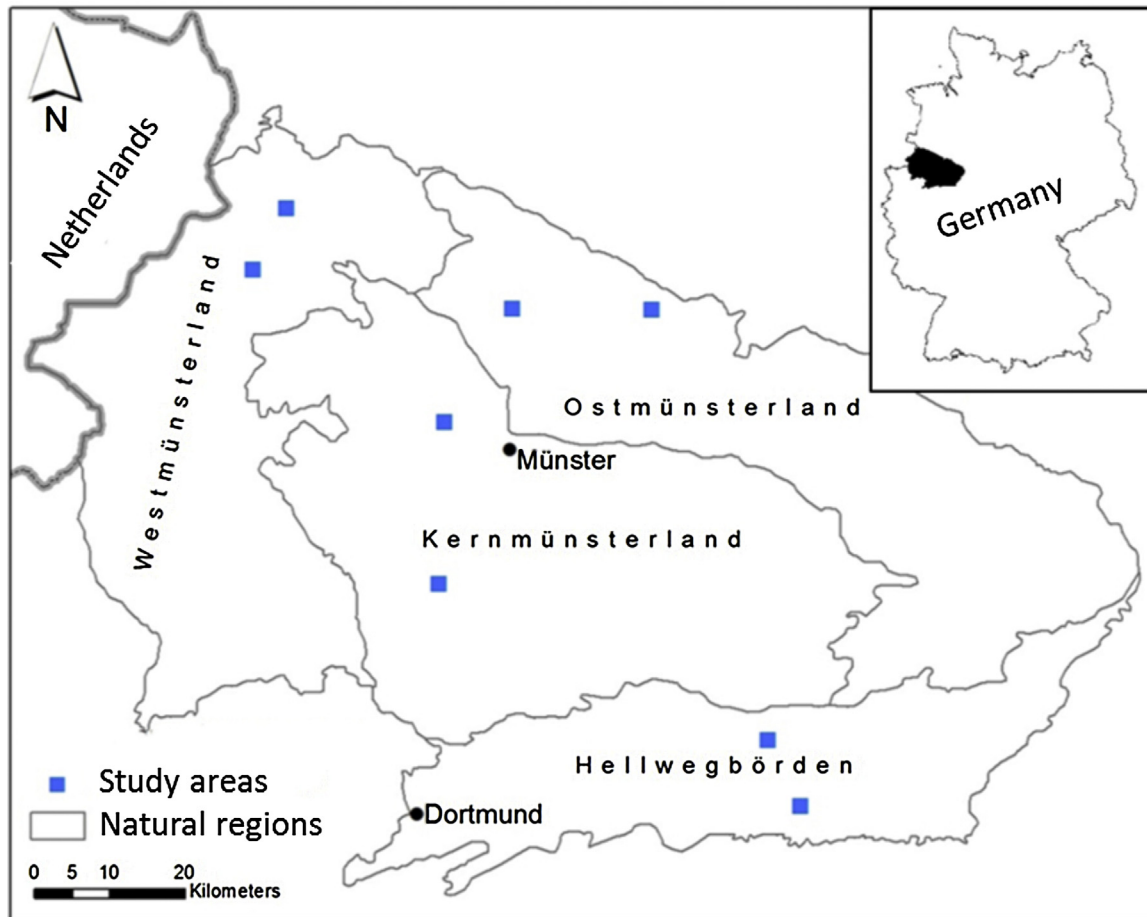
Fig. 1. Map of the region "Westfälische Bucht" in Northwest Germany with the eight study areas.

et al., 2005; Weibull and Östman, 2003; Weibull et al., 2003). In each buffer we calculated the proportional area of land-cover types and based on this the landscape-wide land-use diversity using the Shannon index (Nagendra, 2002) (Table S2). Within the 500 m buffers we also calculated the resistance of the LLE network around the plots using the software Circuitscape 4.0.5. Resistance based on circuit theory, also called 'resistance distance', 'isolation by resistance' or 'effective resistance", is a measure of isolation that considers both multiple connections and variable suitability of land-cover for dispersal (McRae, 2006). For the calculations of resistances, the vector maps of plots, buffer circles and LLE were converted into rasters with 1 m cell size. Then, the plot and the buffer-circle rasters were defined as source and ground ("patches" in Circuitscape), while the LLE raster represented conductors. We used different LLE rasters for herbaceous and woody plots. The rasters used for woody plots contained only woody LLE and forests assuming that herbaceous habitats would not facilitate dispersal of species occurring in shaded habitats. In contrast, the rasters used for herbaceous plots comprised all LLE (both herbaceous and woody) and, additionally, the edges of grasslands, fields and forests. Thus, edges of both herbaceous and woody habitats were considered to be additional dispersal corridors for species occurring in herbaceous habitats. As we hypothesized that LLE and forests (regarding woody plots) or LLE and edges (regarding herbaceous plots) would facilitate dispersal or migration of species, whereas the landscape matrix would impede such movements, we set the conductance of raster cells located in LLE and forests or edges, respectively, to 100 (arbitrary value, not affecting the relative size of connectivity values), whereas all other

cells, representing the matrix, were set to zero conductance. We are aware that even the most intensive agricultural habitats are used by some carabid and spider species, and thus do not completely impede their movements. However, because we were interested if LLE and edges function as a habitat network, we calculated resistance based on the maximal contrast between these structures and the agricultural matrix.

Local land-use diversity of the immediate plot surroundings was expressed as the Shannon diversity of land-cover types in 50 m buffers of the plot centers (analogously to landscape-wide land-use diversity, Table S2). Vegetation sampling was conducted according to the Braun-Blanquet method once per plot (1 × 25 m). We recorded all vascular plant species of the herb, shrub and tree layer and calculated the local plant richness.

2.3. Sampling and identification of spiders and carabids

Spiders and carabids were sampled using pitfall traps. Pitfall traps were 6.5 cm in diameter and 7 cm deep and were filled to one third with a 4% formalin solution with a detergent added to reduce surface tension. Per plot, four pitfall traps (one as a backup) were installed in a row with a distance of 5 m to each other. Traps were exposed for 21 days between 15 May and 8 June 2012.

All adult spider and carabid individuals were identified to species level using the identification keys of Roberts (1998) for spiders and Müller-Motzfeld (2006) for carabids. Due to loss and damage of some pitfall traps, we analyzed a standardized number of three traps per LLE (N_{total} = 174 traps). The three traps per plot were treated as a unit for statistical analyses. We characterized

spiders and carabids according to their body size, hunting mode (spiders) or trophic level (carabids) and dispersal ability (Table 1).

2.4. Calculation of functional diversity of spiders and carabids

We used functional dispersion (FDis) as an index for functional diversity. FDis is a measure of functional richness, which considers species relative abundances by estimating their dispersion in a multidimensional trait space (Laliberté and Legendre, 2010). Trait data for body sizes were continuous while dispersal and hunting mode/trophic level were coded categorically for calculating FDis. The index is distance-based and can be computed for categorical variables (Laliberté and Legendre, 2010). We computed FDis using the R package "FD" (Laliberté and Shipley, 2011).

2.5. Data analysis

We performed two types of analyses: (1) Comparisons of species richness, functional diversity, and trait proportions between woody and herbaceous LLE. (2) Analysis of the effect of environmental parameters on species richness, functional diversity, and trait proportions separately for woody and herbaceous LLE. All statistical analyses were done in R 3.1.2 (R Core Team, 2014).

1. Species richness, functional diversity (FDis), and traits (community weighted mean for body size, otherwise trait proportions as % species with a given trait value of all species) of spiders and carabids between woody and herbaceous linear landscape elements were compared with linear mixed effects models. We used 'LLE type' (woody or herbaceous) as a fixed effect and 'study area' as a random effect (command 'lmer' in R package lme4; Bates et al., 2014). Model residuals were checked graphically for normality and homogeneity of variances using diagnostic plots (Zuur et al., 2009).

2. We analyzed the effect of environmental parameters on species richness, functional diversity (FDis), and traits of spiders and carabids separately for woody and herbaceous LLE with linear mixed effects models ('lmer'). For model simplification and in order to increase the robustness of the parameter estimates we used an information-theoretic approach to multi-model inference (Burnham and Anderson, 2002; Stephenson et al., 2015). Predictor variables in all full models were 'landscape-wide land-use diversity', 'landscape connectivity', 'local land-use diversity', and 'local plant richness' as fixed effects and 'study area' as a random effect. We standardized the regression predictors using the 'standardize' function (R package arm, Gelman and Su, 2015). Collinearity in the predictor variables was assessed calculating variation inflation factors (VIF). In all models predictor variables had VIF values <2.8 indicating low collinearity. For automated model selection we used the 'dredge' function (R package MuMln, Bartón, 2013) and selected those top-ranked models within Δ AICc < 3. We used the AICc for small sample sizes. We then produced averaged parameter estimates from this top set of models using the 'model.avg' function.

3. Results

3.1. Comparisons between woody and herbaceous linear landscape elements

3.1.1. Species compositions

In the 58 LLE we recorded 129 species and 8744 individuals of spiders and 74 species and 2179 individuals of carabids. In woody LLE we found 111 spider species (3859 individuals) and 58 carabid species (977 individuals). In herbaceous LLE 107 spider species (4885 individuals) and 65 carabid species (1202 individuals) were found (Table S3).

Spiders and carabids showed distinct species assemblages between woody and herbaceous LLE. LLE type had a significant effect on spider and carabid species composition, respectively (for methods and statistics see Table S4). In contrast, landscape-wide land-use diversity, landscape connectivity, local land-use diversity, and local plant richness had no significant influence on the taxonomic composition of spider and carabid assemblages (Table S4, Fig. S5).

3.1.2. Species traits

The spider assemblage of woody LLE was characterized by smaller species than those of herbaceous LLE (community weighed mean of body size, t = −4.214, P < 0.001). Spiders in woody LLE showed lower dispersal power than in herbaceous LLE, i.e. the proportion of species with less common (t = 3.749, P < 0.001) and uncommon ballooning behavior (t = 3.307, P < 0.001) was higher in woody LLE while, accordingly, the proportion of commonly ballooning spider species was higher in herbaceous LLE (t = −5.690, P < 0.001). Regarding hunting strategy, ground hunters were more common in herbaceous LLE (t = −3.803, P < 0.001) and sheet-web hunters more common in woody LLE (t = 2.022, P = 0.043) (Fig. 2a).

Opposite to spiders, the community weighted mean body size of carabids was larger in woody than in herbaceous LLE (t = 3.424, P < 0.001). Carabids in herbaceous LLE showed higher dispersal ability than in woody LLE, i.e. the proportion of winged species was higher in herbaceous LLE (t = −2.505, P = 0.012) while the proportion of short-winged/wingless species was higher in woody LLE (t$_{49}$ = 2.113, P = 0.035) (no effect for dimorphic species: t = 1.338, P = 0.181). Herbivore carabids were more common in herbaceous LLE (t = −2.458, P = 0.014) while predators were more common in woody LLE (t = 2.504, P = 0.012) (Fig. 2b).

3.1.3. Species richness and functional diversity

Woody and herbaceous LLE did not differ in their species richness of spiders. In contrast, the spider assemblage of woody LLE was functionally more diverse (FDis) than of herbaceous LLE

Table 1
Trait data of spiders and carabids.

| Trait	Specification	Reference
Spiders		
Mean body size	mm (continuous)	Nentwig et al. (2015)
Hunting mode	ambush, ground-hunter, orb-web, sheet-web, space-web, specialist, other (categorical)	Cardoso et al. (2011)
Dispersal	ballooning common, ballooning less common, ballooning uncommon (categorical)	Bell et al. (2005)
Carabids		
Mean body size	mm (continuous)	Homburg et al. (2014)
Trophic level	herbivore, omnivore, predator (categorical)	Homburg et al. (2014)
Dispersal	winged, dimorphic, short-winged/wingless (categorical)	Homburg et al. (2014)

a) Spiders
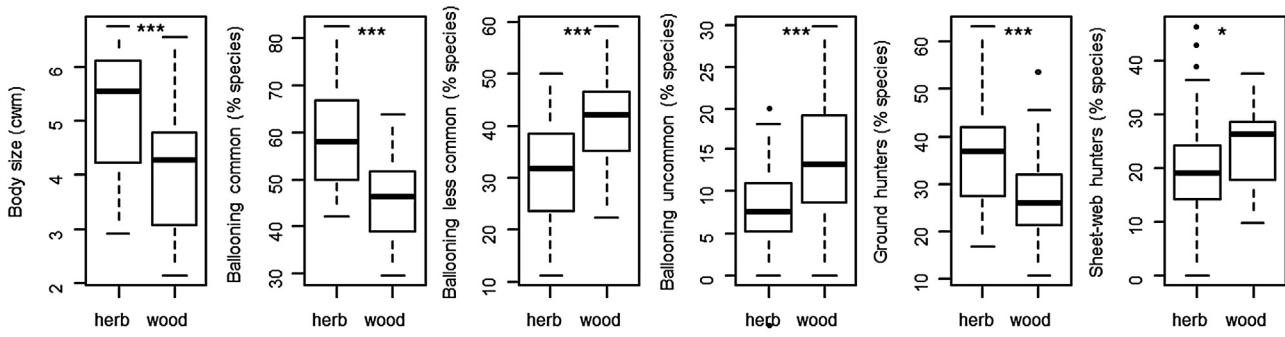
b) Carabids
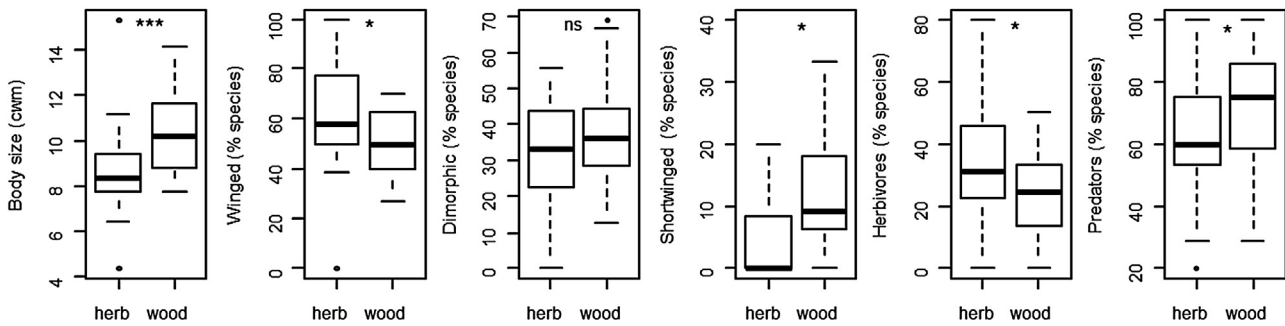
Fig. 2. Comparison of the functional traits of a) spiders and b) carabids between woody and herbaceous linear landscape elements. Shown are boxplots where the box represents the interquartile range (25–75%) and the band inside the median. Whiskers represent the 1.5 of the lower or upper interquartile range and outliers are indicated as points. Differences were tested with linear mixed models. n.s. = not significant, * P < 0.05, ** P < 0.01, *** P < 0.001.

(Table 2). Both LLE types did not significantly differ in carabid species richness and FDis (Table 2).

3.2. Drivers of spider and carabid diversity and trait distribution in LLE

3.2.1. Woody linear landscape elements

Model-averaging results of the top-ranked models showed a significant positive effect of landscape connectivity on spider functional diversity (FDis) in woody LLE (z = 1.967, P = 0.049; Table 3, Fig. 3a). In contrast, we found no significant relations between spider species richness and the predictor variables (Table 3). The community weighted mean body size of spiders significantly increased with increasing landscape-wide land-use diversity (z = 2.206, P = 0.027; Table 3, Fig. 3b). All other spider traits were not significantly related to the predictor variables (Table 3).

We found no effect of any landscape or local parameter on the species richness and functional diversity of carabids in woody LLE (Table 4). However, the proportion of predatory carabid species significantly increased with increasing connectivity of woody LLE and the three woody LLE sites with the highest connectivity value contained solely predatory carabids (z = 3.193, P = 0.001; Table 4, Fig. 3c). Accordingly, the proportion of herbivores was lower in better connected woody LLE (z = −2.593, P = 0.009; Table 4). All other traits of carabids were not related to the predictor variables (Table 4).

3.2.2. Herbaceous linear landscape elements

Model-averaging results of the top-ranked models showed a significant positive effect of local plant richness (z = 2.634, P = 0.008) and landscape-wide land-use diversity (z = 2.192, P = 0.028) on the species richness of spiders in herbaceous LLE (Table 5, Fig. 4a and b). In contrast, functional diversity (FDis) of spiders in herbaceous LLE was unaffected by the predictor variables (Table 5). Interestingly, the proportion of spider species with uncommon ballooning behavior (= less mobile species) significantly increased with increasing local plant richness of herbaceous LLE (z = 2.254, P = 0.024; Table 5, Fig. 4c). None of the other spider trait proportions were related to any parameters in herbaceous LLE (Table 5).

We found no significant effect of any landscape or local parameter on the species richness and functional diversity of carabids in herbaceous LLE (Table 6). Local plant richness had a significant positive effect on the proportion of winged carabids (z = 3.198, P = 0.001; Table 6, Fig. 4d) and a significant negative effect on the proportion of dimorphic carabids (z = 2.423, P = 0.015, Table 6, Fig. 4e). Local plant richness had also a significant positive effect on the proportion of herbivore carabids (z = 2.280, P = 0.023;

Table 2
Comparison of spider and carabid species richness and functional diversity (FDis) between herbaceous and woody linear landscape elements. Differences were tested with linear mixed models. Significant results are shown in bold.

	Linear landscape element			
	Woody	Herbaceous	t	P
Spiders				
Species richness	21.5 ± 0.9	20.4 ± 0.8	1.028	0.309
FDis	0.85 ± 0.02	0.79 ± 0.2	2.010	**0.049**
Carabids				
Species richness	11.0 ± 0.7	11.6 ± 0.9	−0.644	0.522
FDis	0.24 ± 0.01	0.24 ± 0.01	0.380	0.705

Table 3

Model-averaging results of the top-ranked models (delta AICc < 3) for spiders in woody linear landscape elements. Predictor variables in initial models were landscape-wide land-use diversity (landscape), landscape connectivity (connectivity), local land-use diversity (local land-use), and local plant richness (plant richness). Significant results are shown in bold.

Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Connectivity	3.333	1.740	1.916	0.055
	Plant richness	2.062	1.788	1.153	0.249
	Local land-use	0.422	1.737	0.243	0.808
	Landscape	1.180	2.085	0.566	0.571
FDis	Connectivity	0.061	0.031	1.967	**0.049**
	Local land-use	−0.034	0.030	1.133	0.257
	Plant richness	0.040	0.031	1.270	0.204
	Landscape	−0.003	0.035	0.092	0.927
Body size	Local land-use	−0.742	0.416	1.783	0.075
	Landscape	0.918	0.416	2.206	**0.027**
	Plant richness	−0.258	0.380	0.679	0.497
Ballooning common	Connectivity	−0.027	0.034	0.805	0.421
	Local land-use	0.027	0.034	0.785	0.432
	Landscape	0.017	0.034	0.505	0.614
	Plant richness	−0.012	0.034	0.340	0.734
Ballooning less common	Plant richness	−0.025	0.034	0.738	0.460
	Connectivity	−0.012	0.034	0.339	0.735
	Local land-use	−0.010	0.034	0.302	0.763
	Landscape	−0.006	0.034	0.181	0.856
Ballooning uncommon	Connectivity	0.046	0.032	1.436	0.151
	Plant richness	0.034	0.029	1.167	0.243
	Landscape	−0.034	0.036	0.946	0.344
	Local land-use	−0.023	0.030	0.782	0.434
Ground hunters	Local land-use	−0.028	0.038	0.731	0.465
	Landscape	0.028	0.044	0.633	0.527
	Connectivity	−0.027	0.043	0.616	0.538
	Plant richness	0.004	0.041	0.090	0.928
Sheet-web hunters	Plant richness	−0.043	0.028	1.525	0.127
	Local land-use	0.009	0.029	0.318	0.750
	Connectivity	−0.008	0.029	0.294	0.769
	Landscape	0.001	0.029	0.029	0.977

Table 6, Fig. 4f) and, consequently, a negative effect on the proportion of predatory carabids (z = 2.056, P = 0.039; Table 6).

4. Discussion

4.1. Differences in trait composition and (functional) diversity between woody and herbaceous LLE

In accordance with our hypotheses, the trait composition of spiders and carabids in woody LLE was mostly K-selected, i.e. spiders and carabids showed lower dispersal ability and a higher food specialization (spider sheet-web hunters) or trophic level (carabid predators). Lower dispersal ability in less disturbed sites is in agreement with the habitat templet theory (Southwood, 1977), which predicts a higher risk of local extinction in highly disturbed sites favouring species with high dispersal ability that can frequently colonize habitat patches (see also Entling et al., 2011; Ribera et al., 2001). An increase of sheet-web-hunters with increasing habitat stability and woody vegetation was also found by Schirmel et al. (2012). This can be explained by more suitable structures for attaching their webs and that webs are likely less exposed to meteorological conditions (rain, wind, etc.) than in herbaceous habitats. Also in line with our findings, Fußer et al. (2016) found a higher proportion of predatory carabids in woody seminatural habitats compared to herbaceous ones. One explanation can be the often higher vegetation cover (especially of grasses
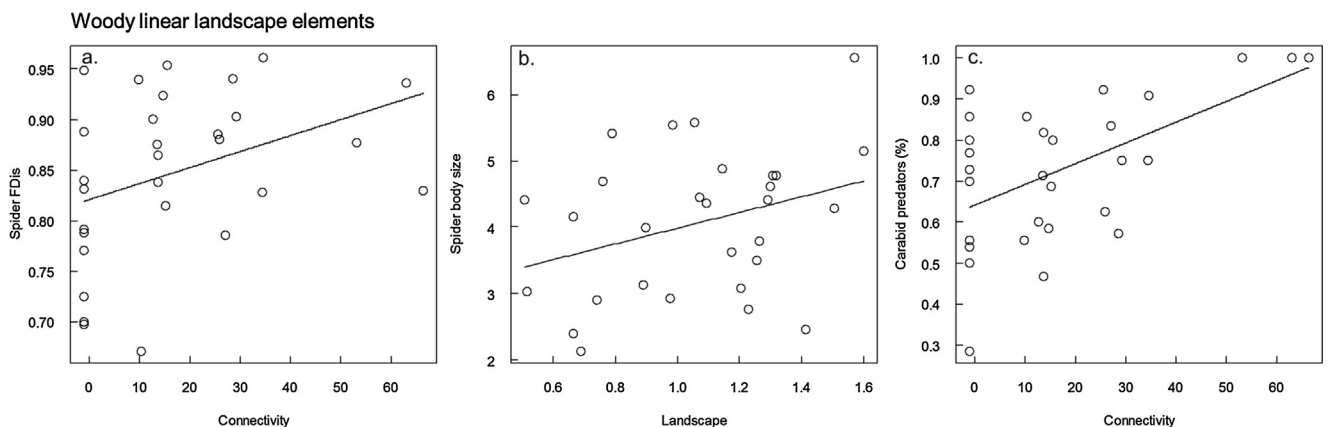

Fig. 3. Effects of a) landscape connectivity (connectivity) on spider functional diversity (FDis), b) landscape-wide land-use diversity (landscape) on spider body size (community weighted mean), and c) landscape connectivity (connectivity) on the proportion of predatory carabids in woody landscape linear elements. For statistics see Tab 3 and 4.

Table 4
Model-averaging results of the top-ranked models (delta AICc < 3) for carabids in woody linear landscape elements. For further details see caption of Table 3 and the text. Significant results are shown in bold.

Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Local land-use	2.174	1.351	1.609	0.108
	Landscape	2.049	1.749	1.171	0.241
	Plant richness	1.540	1.425	1.081	0.280
	Connectivity	−0.304	1.687	0.180	0.857
FDis	Local land-use	−0.022	0.029	0.744	0.457
	Connectivity	−0.015	0.032	0.467	0.641
	Plant richness	0.009	0.031	0.287	0.774
	Landscape	0.002	0.039	0.069	0.945
Body size	Local land-use	−0.711	0.710	1.002	0.316
	Plant richness	0.188	0.722	0.260	0.795
	Connectivity	−0.155	0.722	0.214	0.830
	Landscape	−0.105	0.723	0.145	0.885
Winged	Connectivity	−0.070	0.052	1.348	0.178
	Local land-use	−0.048	0.053	0.910	0.636
Dimorphic	Local land-use	0.064	0.055	1.165	0.244
	Connectivity	0.035	0.056	0.625	0.532
	Plant richness	0.030	0.056	0.546	0.584
	Landscape	0.023	0.056	0.413	0.679
Short-winged/wingless	Connectivity	0.036	0.040	0.897	0.370
	Local land-use	−0.016	0.040	0.405	0.686
	Plant richness	0.009	0.040	0.227	0.821
	Landscape	0.007	0.040	0.176	0.860
Herbivore	Connectivity	−0.154	0.059	2.593	**0.009**
	Landscape	0.076	0.063	1.209	0.227
	Plant richness	0.049	0.056	0.878	0.380
	Local land-use	−0.033	0.056	0.593	0.553
Predator	Connectivity	0.216	0.068	3.193	**0.001**
	Plant richness	−0.097	0.058	1.673	0.094
	Landscape	−0.076	0.066	1.146	0.252
	Local land-use	0.040	0.059	0.671	0.502

and herbs) close to the ground in herbaceous LLE offering food supply for herbivore carabids. As expected, we found larger carabids in woody LLE than in herbaceous ones, which supports findings of prior studies (Ribera et al., 2001; Schirmel et al., 2012).

In contrast, spider body size was smaller in woody LLE. Schirmel et al. (2012) also found more small spiders in woody habitats compared to open and more disturbed habitats. One explanation might be the higher desiccation resistance of large-bodied spiders

Table 5
Model-averaging results of the top-ranked models (delta AICc < 3) for spiders in herbaceous linear landscape elements. For further details see caption of Table 3 and the text. Significant results are shown in bold.

| Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Plant richness	3.900	1.481	2.634	**0.008**
	Landscape	2.993	1.366	2.192	**0.028**
	Local land-use	1.228	1.393	0.881	0.378
FDis	Plant richness	0.035	0.047	0.736	0.462
	Connectivity	0.018	0.049	0.362	0.717
	Local land-use	0.012	0.048	0.246	0.806
	Landscape	−0.011	0.049	0.224	0.823
Body size	Landscape	0.590	0.501	1.177	0.239
	Local land-use	−0.412	0.413	0.998	0.318
	Plant richness	0.256	0.433	0.590	0.555
	Connectivity	−0.045	0.464	0.096	0.923
Ballooning common	Connectivity	−0.083	0.046	1.799	0.072
	Plant richness	−0.040	0.048	0.840	0.401
	Landscape	0.016	0.052	0.301	0.764
	Local land-use	0.014	0.052	0.262	0.793
Ballooning less common	Connectivity	0.069	0.044	1.580	0.114
	Local land-use	0.014	0.049	0.284	0.776
	Landscape	−0.001	0.051	0.023	0.981
	Plant richness	−0.007	0.047	0.152	0.879
Ballooning uncommon	Plant richness	0.046	0.020	2.254	**0.024**
	Local land-use	−0.007	0.021	0.320	0.749
	Landscape	0.006	0.022	0.285	0.776
	Connectivity	0.003	0.022	0.143	0.887
Ground hunters	Plant richness	0.084	0.052	1.638	0.101
	Local land-use	−0.076	0.052	1.459	0.145
	Landscape	0.051	0.050	1.028	0.304
	Connectivity	0.021	0.049	0.428	0.669
Sheet-web hunters	Landscape	−0.071	0.051	1.404	0.160
	Plant richness	−0.050	0.043	1.152	0.249
	Local land-use	0.023	0.043	0.522	0.602
	Connectivity	0.039	0.054	0.719	0.472
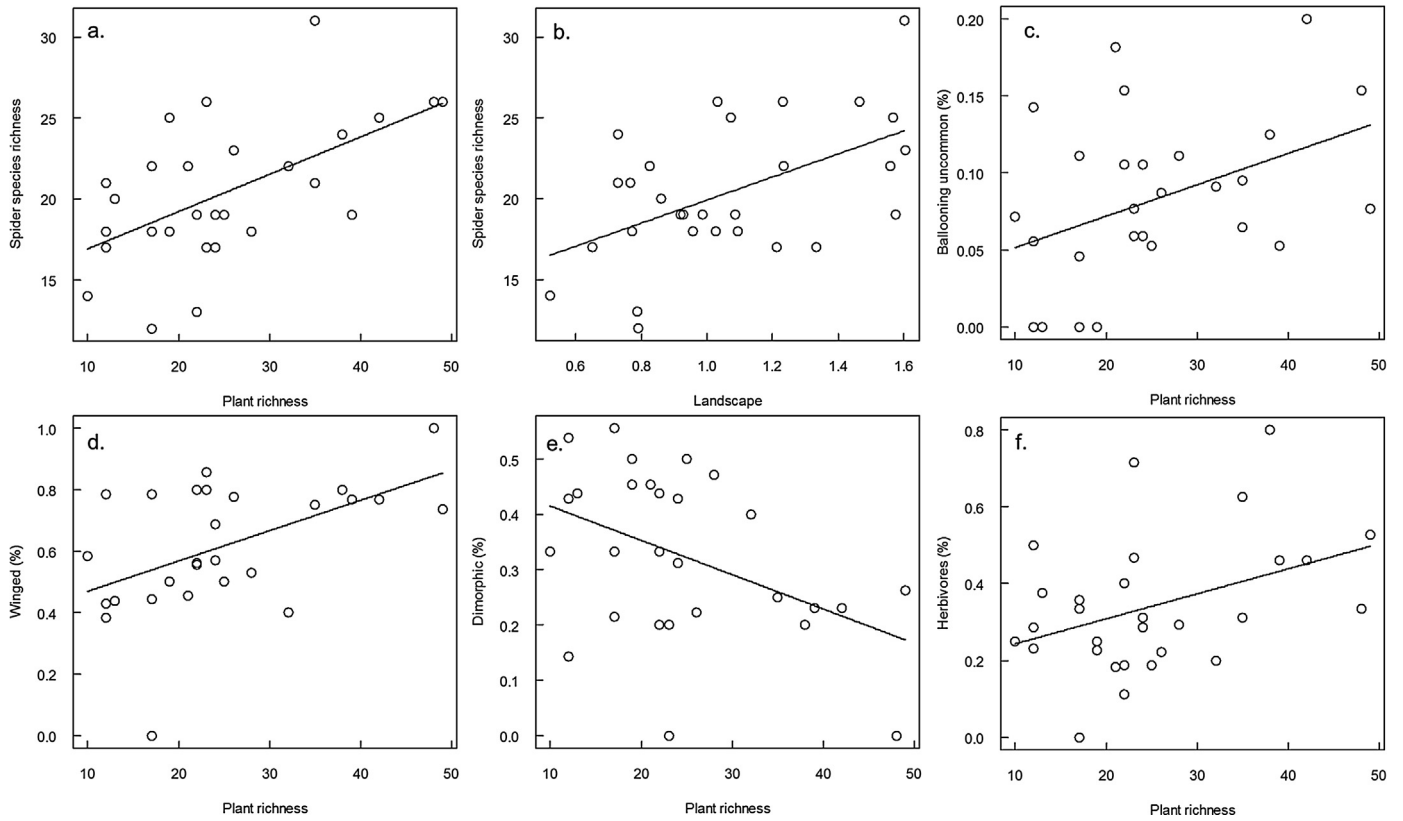
Fig. 4. Effects of a) local plant richness on spider species richness, b) landscape-wide land-use diversity (landscape) on spider species richness, c) local plant richness on the proportion of spiders with uncommon ballooning, d) plant richness on the proportion of winged carabids, e) plant richness on the proportion of dimorphic carabids, and f) plant richness on the proportion of herbivore carabids. For statistics see Tab 5 and 6.

Table 6
Model-averaging results of the top-ranked models (delta AICc < 3) for carabids in herbaceous linear landscape elements. For further details see caption of Table 3 and the text. Significant results are shown in bold.

Dependent variable	Predictor(s)	Estimate	Adjusted SE	z	P
Species richness	Connectivity	−3.377	2.088	1.617	0.106
	Local land-use	−1.496	2.042	0.732	0.464
	Landscape	1.207	2.650	0.455	0.649
	Plant richness	0.772	1.990	0.388	0.698
FDis	Landscape	−0.030	0.025	1.226	0.220
	Plant richness	−0.009	0.025	0.383	0.702
	Connectivity	−0.004	0.025	0.160	0.873
	Local land-use	−0.000	0.025	0.016	0.987
Body size	Connectivity	1.398	0.824	1.696	0.090
	Plant richness	−0.957	0.850	1.125	0.261
	Local land-use	0.663	0.838	0.792	0.428
	Landscape	−0.119	0.948	0.125	0.900
Winged	Plant richness	0.248	0.074	3.198	**0.001**
	Connectivity	−0.132	0.069	1.822	0.069
Dimorphic	Plant richness	−0.135	0.056	2.423	**0.015**
	Connectivity	0.053	0.058	0.914	0.361
	Local land-use	−0.040	0.057	0.703	0.482
	Landscape	0.008	0.056	0.134	0.893
Short-winged/wingless	Plant richness	−0.104	0.055	1.873	0.061
	Connectivity	0.062	0.059	1.056	0.291
	Local land-use	0.064	0.058	1.115	0.265
	Landscape	−0.005	0.054	0.091	0.928
Herbivore	Plant richness	0.157	0.069	2.280	**0.023**
	Connectivity	−0.088	0.070	1.252	0.210
	Landscape	−0.077	0.067	1.145	0.252
	Local land-use	−0.021	0.070	0.306	0.759
Predator	Plant richness	−0.145	0.070	2.056	**0.039**
	Connectivity	0.104	0.070	1.488	0.137
	Landscape	0.060	0.068	0.880	0.379
	Local land-use	0.027	0.070	0.387	0.699

to the comparably drier and hotter microclimate in open habitats (Entling et al., 2010).

In contrast to the trait composition, species richness of spiders and carabids did not differ between the two LLE types. Species richness often remains relatively stable regardless of the dominant vegetation type or plant species composition changes (Brown et al., 2001; Schirmel et al., 2012). Functional diversity has been found to be more sensitive to these changes (Schirmel et al., 2012) and might therefore be a better indicator for environmental effects. For spiders, we found a functionally more diverse assemblage in woody LLE than in herbaceous LLE. This difference was only just significant, but it seems plausible that functional diversity may be higher in the more complex and structurally stable woody LLE that likely provide more niches (e.g. due to decaying wood, more vegetation strata, roots forming holes in the soil) (Birkhofer et al., 2014). However, for carabids we did not find significant differences in functional diversity between the two LLE types. One reason might be that almost all carabids move and prey on the ground and, thus, the three dimensional habitat structure is not as important as for spiders.

Higher functional diversity is expected to improve the potential for prey control (Hooper et al., 2005; Schuldt et al., 2014). Based on our findings, top-down control by spiders may be higher in woody than in herbaceous LLE, which could reduce the survival of crop pests in these habitats. Additionally, small sheet-web-hunters like linyphiids in woody LLE are primary carnivores, and therefore effective pest control species, while large-bodied lycosids dominant in herbaceous LLE more commonly prey on other predators (Sanders and Platner, 2007). However, due to limited dispersal and the preference for shady habitats, spiders of woody LLE might migrate into adjacent crop fields and contribute to pest suppression there less commonly than the mobile generalist species inhabiting herbaceous LLE (Gallé et al., 2014; Martin and Major, 2001; Pajunen et al., 1995). Although herbaceous LLE were less functionally diverse, they also harbor species with a high potential for pest control such as wolf and crab spiders, mostly due to their higher tolerance of the simplified habitat structure and higher disturbance of crop environments.

4.2. Differential importance of landscape and local parameters in woody and herbaceous LLE

Effects of landscape and local parameters on diversity and traits of spiders and carabids varied between LLE types. As expected, we found effects of landscape connectivity on species in woody LLE. We found a marked positive effect of connectivity on the proportion of predatory carabids in woody LLE. Further, functional diversity of spiders was positively associated with increased landscape connectivity in woody LLE even though the p-value was just below the critical level. Increasing connectivity can boost diversity across several taxa (Bailey et al., 2010), which can be explained by metapopulation theory, where immigration of dispersing individuals is higher in connected fragments than in isolated ones (Hanski, 1999). Positive effects of connectivity on insect species richness in agricultural landscapes have often been found (e.g. Kormann et al., 2015; Öckinger et al., 2010). However, our results expand this knowledge, as not only alpha-diversity but also functional diversity can increase with increasing connectivity. In agricultural landscapes, connectivity is assumed to be relevant especially for shade-loving (forest) species of woody habitats, because the surrounding matrix is assumed to be hostile. These species therefore depend on well-connected hedges or bushes as dispersal corridors (Baudry et al., 2000), which can also enhance biological pest control in adjacent agricultural crops (Niemelä, 2001). In contrast, open habitat species mainly occurring in herbaceous elements are less affected by connectivity (see below).

Conversely to woody LLE, spider species richness in herbaceous LLE was positively influenced by landscape-wide land-use diversity. This was hypothesized, and might be explained by the high prevalence of mobile species (see above) in such habitats, which may respond at larger scales. However, spider species richness was also positively related to local plant richness, which can mitigate adverse impacts that arise from habitat patchiness (Jonsson et al., 2009; Knapp and Rezac, 2015). In fact, local plant richness was found to be the only influencing factor for the trait composition of spiders and carabids in herbaceous LLE. High plant diversity is often linked with a heterogeneous habitat structure and provides a broad variety of food resources (Diekötter and Crist, 2013; Zurbrügg and Frank, 2006). This can explain the positive response of herbivore carabids to plant richness. This may also explain the positive effect of plant richness on the dispersal ability of carabids, because herbivore carabids are often able to fly ($\rho_{spearman}$ between % winged and herbivore species = 0.7). The response of herbivore carabids to local habitat conditions such as plant species richness rather than to landscape parameters was also shown by Purtauf et al. (2005) and Woodcock et al. (2010). In contrast, increasing local plant richness was related to a high proportion of spiders with low dispersal ability. One explanation may be that higher plant diversity indicates slightly more complex and stable habitats thereby favouring less mobile species (see above).

Of course, as in any field observational study, we cannot exclude that additional unmeasured management (e.g. current adjacent crop type) or environmental parameters (e.g. soil texture) are important drivers for diversity patterns of spiders and carabids in LLE.

4.3. Conclusion

Species richness and functional diversity of spiders and carabids in woody and herbaceous LLE were affected differently by local and landscape factors. The importance of landscape connectivity appeared to be higher in woody LLE, suggesting that their inhabitants (more K-selected) are more sensitive to habitat fragmentation than the highly mobile generalist species living in herbaceous habitats (more r-selected). The protection and re-establishment of well-connected woody seminatural habitats is crucial for functionally diverse spider assemblages and carabid assemblages with a high proportion of predators. Regarding herbaceous elements, enhancement of landscape-wide land-use diversity and local plant richness can be an efficient way to enhance spider diversity. This may promote functional diversity of ecosystem service providers in adjacent agricultural fields (Woodcock et al., 2014) and may lead to enhanced pest suppression (Snyder and Straub, 2005).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.10.028.

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