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Variations in trophic niches of generalist predators with plant community composition as indicated by stable isotopes and fatty acids

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Abstract

Arthropods are a dominant component of biodiversity in terrestrial ecosystems. They are considered pest control agents and drive important ecosystem processes like nutrient cycling. However, such ecosystem effects of arthropods may depend on the environmental context influencing nutrition and behaviour. In the framework of a grassland plant diversity experiment (Jena Experiment), we used stable isotope and fatty acid analysis to investigate intraspecific variations in the diet of two of the most abundant predatory arthropods in grasslands: the ground beetle *Harpalus rufipes* and the wolf spider *Trochosa ruricola*. The results show that the diet of *H. rufipes* varied significantly with plant species diversity, consuming more plant material, probably seeds, at high diversity plots, and in the presence of grasses and small herbs. By contrast, in presence of legumes *H. rufipes* consumed more animal prey, presumably aphids and/or collembolans. Compared to *H. rufipes*, the diet of *T. ruricola* consisted of animal prey only and varied mainly with body size, with larger individuals occupying higher trophic position in the food web. Moreover, the diet of *T. ruricola* changed in response to summer flooding two months before sampling. Presumably, the availability of secondary decomposer prey as well as intraguild prey was increased in severely flooded plots. As both species are considered pest control agents, the results underline the importance of plant diversity and the composition of plant communities for biological pest control.

Keywords spider | Lycosidae | beetle | Carabidae | grassland | diet

Introduction

Knowledge of the diet of consumers is essential for understanding ecological and trophic interactions, such as niche relationships, competition, coexistence and predation (Cantor et al. 2010, García et al. 2009, Vieira & Port 2007). In particular for improving biological pest control, knowledge of predator–prey interrelationships is essential (Kromp 1999, Wilby & Thomas 2002). This applies to the level of species but also of individuals as individual variation in the diet is a significant component of niche variation (Bolnick et al. 2003, Roeder & Behmer 2014, Sih et al. 2004). Thus, intraspecific variation and plasticity may provide a key mechanism promoting species coexistence (Clark et al. 2007) and plays an important role in intra- and

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interspecific interactions that shape population and community dynamics (Agrawal et al. 2007, McGill et al. 2006).

Generalist predators are important control agents of lower trophic level consumers such as herbivores (Romero & Harwood 2010, Wise 1993). In terrestrial ecosystems, spiders and predatory beetles are among the most important antagonists of insect herbivore species and play a major role in insect pest control (Kulkarni et al. 2015, Symondson et al. 2002). Notably, spiders and carabid beetles typically occupy different niches and complement each other in prey population control. Carabids are considered opportunistic generalist predators (Gallandt et al. 2005, Lee et al. 2001), with some of them consuming substantial amounts of plant seeds (Harrison et al. 2003, Lund & Turpin 1977). Thereby, they not only act as antagonists of insect pest species, but also may contribute to plant community composition and act as antagonists of weeds (Gallandt et al. 2005, Kulkarni et al. 2015, Menalled et al. 2006). With feeding on seeds they are likely to benefit from diverse plant communities because of the higher amount of seeds produced by diverse plant communities. Indeed, it has been shown that higher plant diversity in organic farming systems increases resource supply for seed feeding carabid beetles (Diehl et al. 2012, Graziani et al. 2012). Such increased food availability increase their potential to control weeds as well as insect pest species (Bàrberi et al. 2010).

Similar to carabid beetles, spiders have been shown to effectively control insect herbivore pest species (Griffin et al. 2013, Sunderland 1999). Their wide prey spectrum allows them to occupy a variety of niches (Wise 1993). Besides prey availability, physical habitat characteristics, such as plant architecture, determine spider species diversity and composition of spider communities (Langellotto & Denno 2004, Uetz 1991). In addition to providing structure for web building, the composition of plant species also affects spider assemblages indirectly via driving the abundance and composition of herbivore prey (Dennis et al. 2001). Thereby, plant species composition may indirectly alter the control of invertebrate herbivores by spiders and in turn, top-down control of insect herbivores by spiders may alter plant community composition and e.g., enhance plant diversity (Haddad et al. 2009, Schmitz 2003, Snyder et al. 2006).

For our study, we chose two of the most abundant predatory arthropods in central European grasslands, the ground beetle *Harpalus rufipes* (De Geer, 1774) (Coleoptera; Carabidae) and the wolf spider *Trochosa ruricola* (De Geer, 1778) (Araneae; Lycosidae). Both species are geographically widespread, locally abundant and present in many natural and agricultural ecosystems (Clough et al. 2005, Freude et al. 2004, Öberg & Ekbom 2006). *H. rufipes* forms part of a group of large sized carabid beetles (10–17 mm) characterized by a life cycle lasting two years, autumnal breeding, nocturnal activity and good dispersal by moving on the ground but also by flying (Purtauf et al. 2004, Zhang et al. 1997). Notably, *H. rufipes* not only feeds on animal prey but also on seeds of plants as both larvae and adults (Hartke et al. 1998, Harrison & Gallandt 2012, Shearin et al. 2008). By contrast, *T. ruricola* is a generalist predator feeding exclusively on living animal prey hunted during the day. As most lycosid spiders, their prey is identified by optical and tactile cues (Ford 1977) attacking virtually all mobile prey species entering their reach, however, following the attack they may reject distasteful prey (Ford 1977, Toft & Wise 1999b). Feeding on a variety of prey differing in food quality has been shown to beneficially affect lycosid spiders (Oelbermann & Scheu 2002, Toft 1995, Toft & Wise 1999a). However, the food spectrum is assumed to be determined predominantly by prey availability (Riechert & Harp 1987, Wise 1993) and includes small soft-bodied arthropods, such as flies, springtails, bugs and spiders (Chen & Wise 1999, Kajak 1995).

Stable isotope analysis is an important and widely used tool for studying the trophic structure of animal communities and ecosystem functions (Martinez del Rio & Wolf 2005, Post 2002, Potapov et al. 2019). Although used predominantly for investigating interspecific differences in trophic niches, it allows investigating both intra- and interspecific variability in trophic relationships (Layman et al. 2012, Michener & Lajtha 2007, Oelbermann & Scheu 2002). The nitrogen isotope ratio ($^{15}N/^{14}N$, usually expressed as $\delta^{15}N$) increases in insects by about 2.5 ‰ ± 1.8 ‰ (mean ± 1 SD) per trophic level (Ikeda et al. 2010) thereby reflecting the trophic position of species in food webs. The carbon isotope ratio ($^{12}C/^{13}C$, usually expressed as $\delta^{13}C$) changes little (about +1 ‰; France & Peters 1997, Potapov et al. 2019), and it is commonly used to evaluate the source of carbon, often to distinguish between the flux of carbon fixed by C_3 plants from that fixed by C_4 plants (Tiunov 2007, Potapov et al. 2019). The comparison of $\delta^{13}C$ and $\delta^{15}N$ values within and among species allows assessing the degree of trophic overlap between species and among individuals of the same species (Gratton & Forbes 2006, Halaj et al. 2005, Wise et al. 2006). However, this discrimination may vary depending on a consumer's nutritional status, diet quality, body size, age, dietary ontogeny and tissue and elemental composition (Ben-David & Schell 2001, Vanderklift & Ponsard 2003).

Another approach to investigate the diet of the animals is the analysis of fatty acids (FAs) as FAs can be traced

from one trophic level to another, uncovering the diet of consumers and consequently food web links (Ruess et al. 2002, Ruess & Chamberlain 2010). In consumers, most of the assimilated FAs are converted into neutral lipid FAs (NLFAs) and incorporated into the fat body which may comprise a large fraction of their body mass. Since it is energetically more efficient to incorporate FAs without modification ('dietary routing', Blem 1976, Pond 1981), NLFAs of the fat body reflect the FA composition of the food sources to a significant extent (Ruess et al. 2004) and therefore allow tracing food relationships. In addition, phospholipid fatty acid (PLFA) offers information about the microbial community composition in the soil (Ramsey et al. 2006). This information can be used to study consumer – resource interrelationships. The combination of stable isotope and FA analysis allows detailed insight into trophic niches of species but also individuals and their changes in time and between ecosystems (Ferlian & Scheu 2014, Lau et al. 2008).

We analysed variations in the diet of two of the most abundant arthropod predators in central European grasslands, i.e., the carabid beetle *H. rufipes* and the lycosid spider *T. ruricola* using natural stable isotopes and fatty acids analysis. We expected *T. ruricola* to occupy a higher trophic position than *H. rufipes* due to its strictly carnivorous diet. Further, we hypothesized the diet of *H. rufipes* to vary more with plant community composition than that of *T. ruricola* due to the omnivorous diet of the former also feeding on plant seeds.

Material and Methods

Study site and experimental design

The study site is a semi-natural temperate grassland in the Saale River floodplain near to the city of Jena (Thuringia, Germany). The site had been used as arable field for more than 40 years before the plant diversity experiment was established in 2002 (Jena Experiment, see Roscher et al. 2004). The experiment comprises 80 plots of 5 × 6 m arranged in four blocks to control for changes in soil texture with increasing distance to the river. A gradient of plant species richness (1, 2, 4, 8, 16 and 60) and plant functional group richness (1–4 functional groups: grasses, small herbs, tall herbs, and legumes) was established to represent a typical hay meadow in the region. Plots are mown twice a year and weeded three times per year (for details see Roscher et al. 2004).

In May 2013, rainfall in Germany was exceptionally high; in Jena, precipitation amounted 150 mm resulting in the experimental field being flooded for 24 days (30 May to 24 June). This led to anaerobic soil conditions, as shown by redox potentials ranging from -121 to 193 mV in the soil (Wright et al. 2015). Water coverage was measured for each plot daily from 31 May to 24 June and ascribed to five levels: 0, 25, 50, 75, and 100 %. Flooding severity was evaluated using a continuous flooding index (sum of the percentage water coverage per day over the flooding period, Wright et al. 2015). Flooding index was used as explanatory covariable to inspect for potential effects of flooding intensity.

Sampling

H. rufipes and *T. ruricola* were collected using pitfall traps in August 2013. Two 4.5 cm diameter pitfall traps containing 3 % formalin were placed in each plot. Animals were collected every two weeks, stored in 70 % ethanol (for details see Ebeling et al. 2014) and identified to species (Engelhardt 1964, Schaefer 2010). Because of a high variability body size of *T. ruricola,* individuals were divided into small (from 0.1 to 0.4 cm) and large (from 0.5 to 1.0 cm) ones. *H. rufipes* individuals were highly homogenous in their body size.

Stable isotope analysis

Prior to analysis of natural variations in $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios, *T. ruricola* and *H. rufipes* specimens were dried at 105°C for 48 h and then ground using a mortar and pestle. Ground animal tissue was transferred into tin capsules (one individual per sample), weighed and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios measured using an elemental analyser (NA 1500, Carlo Erba, Milano, Italy) coupled with a mass spectrometer (MAT 251, Finnigan, Bremen, Germany; Langel & Dyckmans 2014, Reineking et al. 1993). PD belemnite and atmospheric nitrogen served as primary standard for ^{13}C and ^{15}N, respectively. Acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) was used for internal calibration. Isotope natural abundance was expressed by the delta notation with $\delta^{13}C$ or $\delta^{15}N$ [‰] = $(R_{sample} - R_{standard})/(R_{standard} \times 1000)$, where R is the ratio of the heavier isotope to the lighter isotope.

Inorganic carbon typically is isotopically heavy as compared to organic carbon and positively skews $\delta^{13}C$ values of animals if they contain carbonate-rich skeletons (Fry 1988, Haines & Montague 1979). In order to remove inorganic carbon, prior to stable isotope analysis, *H. rufipes* samples were also analysed after adding 0.1 N HCl (Hobson et al. 2002).

Stable isotope values of plants of the Jena Experiment have been studied in detail by Gubsch et al. (2011) and

Roscher et al. (2010). $\delta^{15}N$ values were close to 0‰ in legumes and varied between 2–4‰ in other plant functional groups; generally, they decreased slightly with plant species richness with the decrease largely being due to species specific responses (Gubsch et al. 2011). $\delta^{13}C$ values of plants in the Jena Experiment vary between -30 and -32‰ reflecting typical C_3 vegetation with some assimilation of soil borne CO_2 (Roscher et al. 2010). As we focused on comparing variations in stable isotope ratios between the two predator species studied, we did not consider variations in stable isotope ratios between plant functional groups in our statistical analyses.

The data were checked for normality and homoscedasticity using Shapiro – Wilk and Fligner – Killeen tests. Linear models (ANOVA, type I sum of squares) were used to analyse the effect of Block (categorical variable, four blocks), body size of the animal (small, large; only in *T. ruricola*), flooding index (ranging from 1 to 23), plant diversity (ranging from 1 to 60; log-transformed, Hooper et al. 2005), and presence/absence of legumes, grasses, small herbs, and tall herbs including interactions. The Akaike Information Criterion (AIC) was used to select the best model by dropping non-significant variables from the full model in a step wise manner (Faraway 2014, Zuur et al. 2007). Variables were fitted in the following order: Block and flooding index were fitted first followed by body size and plant species richness; thereafter, presence/absence of grasses, legumes, tall herbs, and short herbs were fitted. *F*-values given in text and tables refer to models in which the respective factor was fitted first (Schmid et al. 2002). Statistical analyses were performed using R 3.2.1 (R Development Core Team 2014, http://www.R-project.org).

Fatty acid analysis

T. ruricola and *H. rufipes* specimens were cleaned to remove particles attached to the body surface before extraction of total lipids from each individual, which were then extracted and fractionated into neutral lipids as described in Haubert et al. (2004). The neutral lipid fraction was dried in a rotation vacuum concentrator (50°C), and the lipids saponified, methylated and washed following the protocol for the Sherlock Microbial Identification System (MIDI Inc., Newark, USA). Fatty acid methyl esters (FAMEs) were transferred into small vials, capped and analysed by gas chromatography (CLARUS 500, Perkin Elmer, Waltham, USA). The analysis system used was equipped with a flame ionization detector (PE-5 capillary column, 30 m × 0.32 mm i.d., 0.25 mm film thickness, Perkin Elmer, Waltham, USA); helium was used as carrier gas. FAMEs were identified by comparing retention times of samples and standard mixtures comprising unbranched and branched (bacterial) FAMEs. The following fatty acids served as biomarkers for bacteria: the methyl-branched FAs i15:0, a15:0, i16:0, and i17:0 (Gram-positive) and the cyclic FAs cy17:0 and cy19:0 (Gram-negative). The unsaturated FAs 18:1ω9 and 18:2ω6,9 served as relative plant and fungal markers, respectively (Ruess & Chamberlain, 2010). Moreover, 16:2ω6,9 and 16:3ω3,6,9 were used as biomarkers of green algae (Chlorophyceae) (Buse et al., 2013). Monoenic C20 FAs were used as indicator of a eukaryote diet (Ruess et al. 2004). All other markers, such as 10:00 and 12:00, cannot be assigned to specific taxa and were used as unspecific markers.

PLFAs were extracted from soil taken in September 2013 (93 days after the natural flood). Three soil cores of 2 cm diameter were taken from 0–10 cm soil depth and were pooled to form one composite sample. Afterwards soil was sieved with 2 mm mesh size to remove stones and animals. PLFA extraction followed the protocol by Frostegård et. al. (1991) with modifications as mentioned by Wagner et. al. (2015) using 5 g of fresh soil. The analysis system used (GC 17A, Shimadzu, Kyoto, Japan) was equipped with column DB 225MS (60 m × 0.25 mm i.d., 0.25 µm) and an autosampler (AOC 5000, Shimadzu). Hydrogen was used as carrier gas. The software GC Lab Solution (Shimadzu) were used to assign peaks to fatty acids by comparing FAMEs to retention times of samples and standard mixtures comprising unbranched and branched (bacterial) FAMEs. The same biomarker FAs as described for NLFAs were used.

Percentage values of NLFAs and PLFAs were logit-transformed and non-metric multidimensional scaling (NMDS) was used to compress the data. MANOVA was performed using the scores of the NMDS axes. Thereafter, if significant, differences within individual FAs were inspected by single factor analysis of variance (ANOVA). Principal components analyses (PCAs) of logit-transformed mole percentage values were performed using Canoco 5 (Ter Braak & Smilauer 2012). Flooding index, plant functional group, plant species richness and the presence of legumes, grasses, tall herbs and small herbs were included as supplementary variables. Pearson correlations were used to evaluate the relationship between logit-transformed marker FA concentrations [sum of bacterial markers, fungal marker (18:2ω6,9) and plant marker (18:1ω9)] in soil microorganisms (PLFAs) and those in *H. rufipes* and *T. ruricola* (NLFAs).

Results

Harpalus rufipes

The $\delta^{15}N$ signature of *H. rufipes* was on average 5.88 ‰, but the values were highly variable and ranged from 3.52 to 8.63 ‰ spanning 5.11 δ units (Fig. 1). ^{15}N signatures decreased significantly with increasing plant species richness (Fig. 2), whereas they were slightly increased in the presence of legumes (Table 1). The $\delta^{15}N$ signatures did not vary significantly with the flooding index. Average $\delta^{13}C$ signature of *H. rufipes* was -23.92 ‰, but again values were highly variable, ranging from -18.28 to -29.21 ‰, i.e. spanning over 10.93 δ units (Fig. 1). $\delta^{13}C$ signatures significantly increased in the presence of grasses and small herbs, but were not significantly affected by other plant community properties and flooding index (Table 1).

The FA composition of *H. rufipes* was significantly affected by the presence of legumes and marginally by the presence of grasses (Table 2). Concentrations of the plant marker 18:1ω9 increased significantly with the presence of grasses and marginally with the presence of legumes (Table 3). Similarly, the unspecific FA marker 18:00 increased significantly in the presence of legumes. The eukaryote FA markers 20:4ω6 and 20:1ω9 significantly increased in the presence of legumes. The unspecific marker FAs 16:00 (significantly) and 18:1ω7 (marginally) increased in the presence of grasses, whereas the unspecific FA 23:00 decreased significantly (Table 3).

Bacterial marker FAs in *H. rufipes* were negatively correlated with the bacterial marker PLFAs in soil (Table 4). By contrast, the plant FA marker in *H. rufipes* (18:1ω9) was positively correlated with the plant PLFA

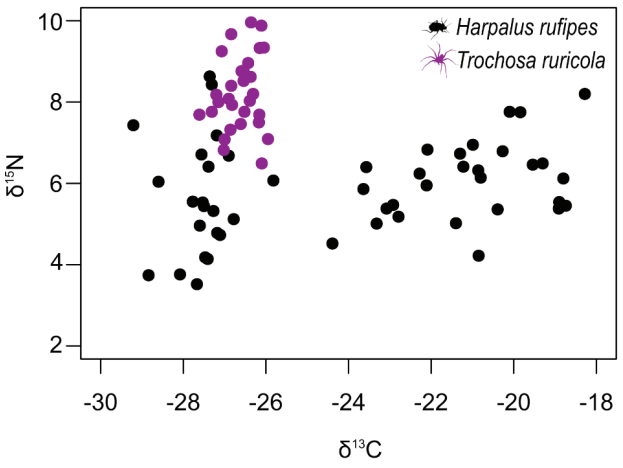

Figure 1. Variations in $\delta^{15}N$ and $\delta^{13}C$ signatures of *Harpalus rufipes* (black) and *Trochosa ruricola* (pink) across the study site of the Jena Experiment.

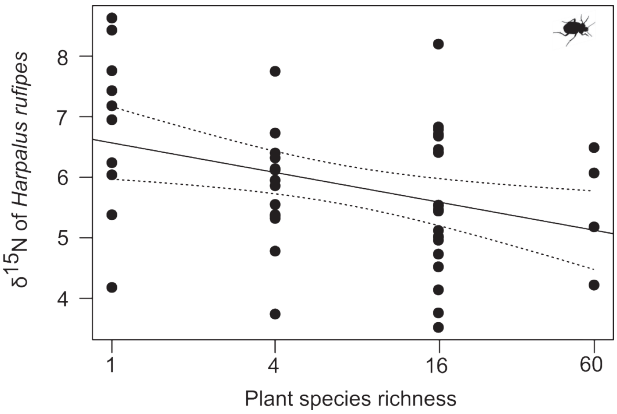

Figure 2. Variations in $\delta^{15}N$ signatures of *Harpalus rufipes* ($P < 0.01$, $R^2 = 0.11$) as affected by plant species richness (log-transformed).

Table 1. ANOVA table of *F*-values on the effect of block, body size, flooding index (FI), plant species richness (SR), presence of grasses (Gr), legumes (Leg), small herbs (SH) and tall herbs (TH) on the $\delta^{15}N$ and $\delta^{13}C$ signatures of *Harpalus rufipes* and *Trochosa ruricola*. Significant effects ($P < 0.05$) are given in bold and marginally significant effects ($P < 0.10$) in italics. ↑ Increase, respectively ↓ decrease with increasing plant species richness, body size, flooding index, or in presence of the respective plant functional group.

	Harpalus rufipes				*Trochosa ruricola*			
	$\delta^{15}N$		$\delta^{13}C$		$\delta^{15}N$		$\delta^{13}C$	
Factors	df	*F*	df	*F*	df	*F*	df	*F*
Block	-		3,49	**4.37**	-		*3,29*	*2.32*
Size	-		-		1,29	↑**31.66**	-	
FI	-		-		1,29	↑**3.70**	-	
SR	1,50	↓**7.73**	-		-		-	
Gr	-		1,49	↑**5.18**	-		-	
Leg	1,50	↑*3.44*	-		-		-	
SH	-		1,49	↑ **4.33**	-		-	
TH	-		-		-		-	

Table 2. MANOVA table of *F*-values on the effect of block, body size (*Trochosa ruricola* only), flooding index (FI), presence of grasses (Gr), legumes (Leg), small herbs (Sh) and tall herbs (Th) on the neutral fatty acid composition of *Harpalus rufipes* and *T. ruricola*, as well as the phospholipid fatty acid (PLFA) composition of soil microorganisms (based on NMDS axes; see Methods). Significant effects ($P < 0.05$) are given in bold and marginally significant effects ($P < 0.10$) in italics. ↑ Increase, respectively ↓ decrease with increasing plant species richness, body size, flooding index, or in presence of the respective plant functional group.

	H. rufipes		*T. ruricola*		PLFA	
	df	*F*	df	*F*	df	*F*
Block	3,45	**2.17**	-		3,45	**2.82**
Size	-		1,46	**5.31**	-	
FI	-		-		1,45	*2.51*
Sh	-		1, 46	*2.32*	-	
Th	-		1, 46	*2.27*	1,45	*2.61*
Leg	1,45	**3.28**	-		-	
Gr	1,45	*2.47*	-		-	

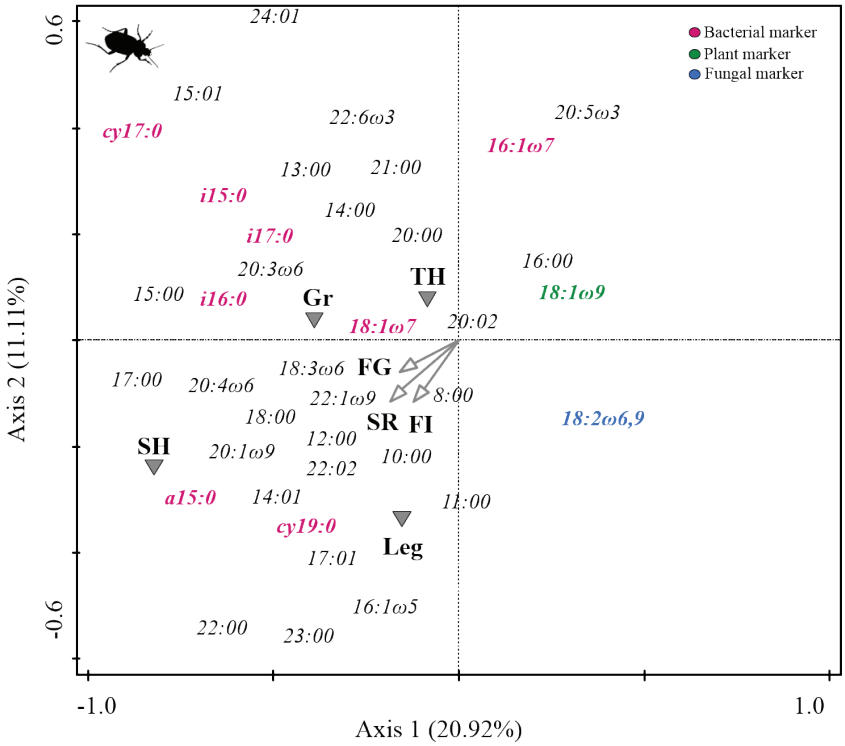

Figure 3. Principal components analysis of the relative abundance (mol%, logit-transformed) of individual NLFAs of *Harpalus rufipes* using flooding index (FI), plant species richness (SR), plant functional group richness (FG), presence of grasses (Gr), legumes (Leg), small herbs (SH) and tall herbs (TH) as supplementary variables.

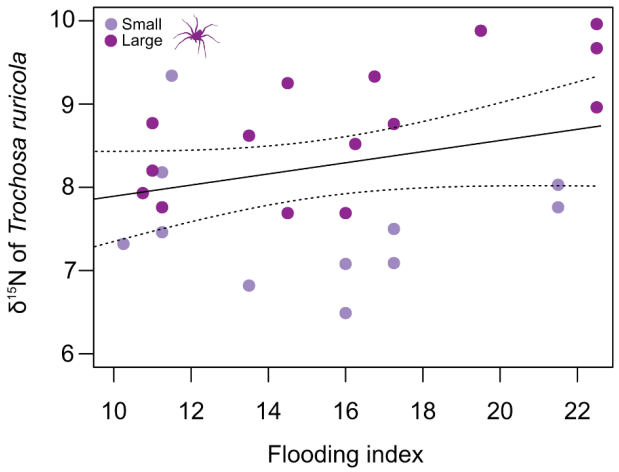

Figure 4. Variations in $\delta^{15}N$ signatures of *Trochosa ruricola* as affected by flooding index ($P = 0.04$, $R^2 = 0.12$) and body size (small, large; $P < 0.01$).

marker in soil. There was no correlation with the fungal FA marker in *H. rufipes* and the plant PLFA marker in soil.

The first four PCA axes explained 51.8% of the total variation in the FA composition of *H. rufipes*, with the first axis accounting for 20.9% and the second axis for 11.1% (Fig. 3). The first axis was separated by bacterial markers *vs*. fungal and plant markers. Further, the plant marker seems to correlate negatively with flooding index, plant functional group and species richness. The first axis was related to the presence of small herbs, whereas the second axis was associated with the presence of legumes. Concentrations of the bacterial markers cy17:0 and a15:0, and the unspecific markers 15:00 and 17:00 increased in the presence of small herbs. Concentrations of unspecific FA markers such as 16:1ω5 and 22:00 were higher in presence of legumes.

Trochosa ruricola

The $\delta^{15}N$ signature of *T. ruricola* was on average 8.22‰, but the values were variable and ranged from 6.49 to 9.96‰ (Fig. 1). However, the range (3.47 δ units) was considerably lower than that in *H. rufipes*. The $\delta^{15}N$ signatures of *T. ruricola* significantly increased with flooding index and body size (Fig. 4, Table 1).

Average $\delta^{13}C$ signature of *T. ruricola* was -26.60‰. Contrasting *H. rufipes*, $\delta^{13}C$ signatures of *T. ruricola* only varied over 1.66 δ units, i.e., from -25.95 to -27.61‰ (Fig. 2). None of the factors studied significantly affected the $\delta^{13}C$ signatures of *T. ruricola* (Table 1).

The FA composition of *T. ruricola* varied significantly with body size (Table 2). The eukaryote marker FAs

Table 3. ANOVA table of *F*-values (with degrees of freedom) on the effects of legumes (Leg), grasses (Gr) and body size (*Trochosa ruricola* only) on neutral fatty acids of *Harpalus rufipes* and *T. ruricola* as well as on phospholipid fatty acids (PLFAs) of soil microorganisms. Significant effects ($P < 0.05$) are given in bold and marginally significant effects ($P < 0.10$) in italics. ↑ Increase, respectively ↓ decrease with presence of legumes or grasses.

	H. rufipes		*T. ruricola*			*PLFA*	
FA	Leg $F_{1,45}$	Gr $F_{1,45}$	Size $F_{1,46}$	Sh $F_{1,46}$	Th $F_{1,46}$	FI $F_{1,45}$	Th $F_{1,45}$
8:00	-	-	-	↓*3.93*	-	-	-
10:00	↑*3.33*	-	↓**12.91**	↓**5.34**	-	-	-
12:00	-	-	↓**17.22**	-	-	-	-
i16:0	-	-	-	-	-	↑**5.31**	-
16:00	-	↑**4.10**	-	↓*3.28*	↓**4.59**	-	↑**5.31**
16:1ω7	-	-	-	-	↓*3.45*	-	-
i17:0	-	-	-	-	-	-	↓*3.54*
17:01	-	-	-	-	-	↑*3.05*	↓*3.16*
cy17:0	-	-	-	-	-	↑*4.05*	-
17:00	-	-	-	-	-	↑**6.49**	-
18:3ω6	↑*3.52*	-	-	-	-	-	-
18:2ω6,9	-	-	↑*3.97*	-	-	↓**4.14**	↑*3.69*
18:1ω9	↑*3.20*	↑**6.28**	-	-	-	↑**4.63**	-
18:1ω7	-	↑*3.35*	↑**5.45**	-	-	-	-
18:00	↑**6.04**	-	-	↓**4.68**	-	↓**6.44**	-
cy19:0	-	-	-	-	-	-	↑**5.22**
20:4ω6	↑**4.41**	-	↑**11.11**	↑*3.10*	-	-	-
20:5ω3	-	-	↑**24.70**	-	-	-	-
20:1ω9	↑**5.39**	-	-	-	-	-	-
21:00	-	-	-	-	-	↓**6.10**	↑4.05
23:00	-	↓**4.39**	-	-	-	-	-

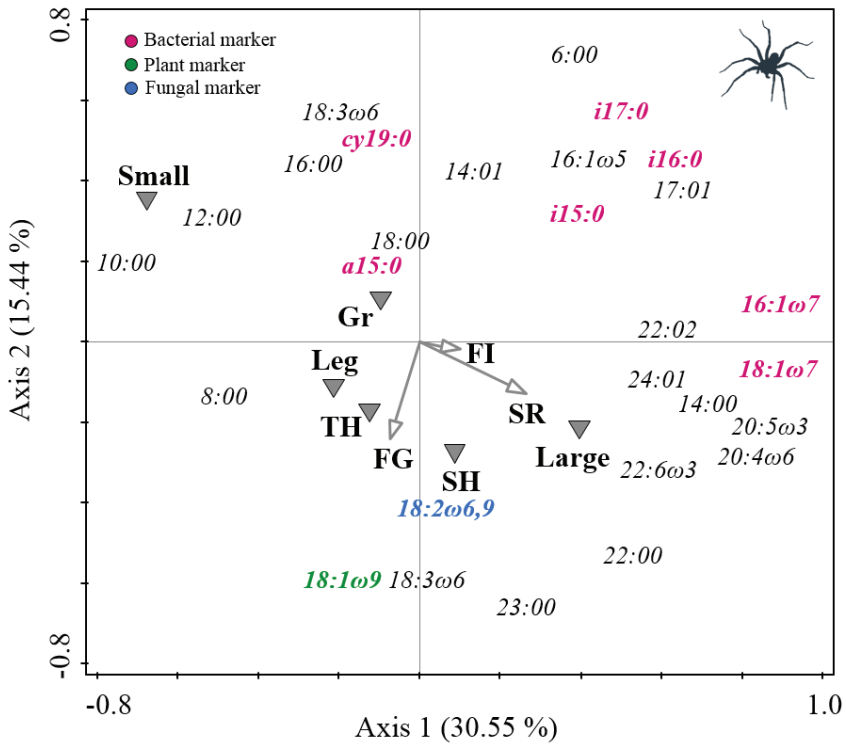

Figure 5. Principal components analysis of the relative abundance (mol%, logit- transformed) of individual NLFAs of *Trochosa ruricola* using body size (small, large), flooding index (FI), plant species richness (SR), plant functional group richness (FG), presence of grasses (Gr), legumes (Leg), small herbs (SH) and tall herbs (TH) as supplementary variables.

20:4ω6 and 20:5ω3 significantly increased with body size (Table 3). Further, the fungal marker FA 18:2ω6,9 increased marginally with body size. Unspecific marker FAs 10:00 and 12:00 decreased significantly, while the bacterial marker FA 18:1ω7 increased significantly with body size (Table 3). The FAs 10:00 and 16:00 decreased in the presence of small herbs. Further, the unspecific FAs 16:00 (significantly) and the bacterial marker FA 16:1ω7 (marginally) decreased in presence of tall herbs. FAs of *T. ruricola* were not correlated significantly with any microbial PLFA markers in soil (Table 4).

The first four PCA axes explained 67.4% of the total variation in the dataset, with axis 1 accounting for 30.5% and axis 2 for 15.4% (Fig. 5). The first axis of the PCA reflected variations in FAs of *T. ruricola* with body size (small, large), with the concentration of eukaryote markers 20:4ω6 and 20:5ω3 increasing in larger individuals. By contrast, small individuals contained higher concentrations of unspecific FAs such as 10:00 and 12:00. The second axis of the PCA was related to the number of plant functional groups and the presence of small herbs, but the effect was small. Concentrations of the FAs 18:2ω6,9 and 18:3ω6 increased at sites with higher number of plant functional groups and in the presence of small herbs.

Microbial PLFAs in soil

MANOVA results based on NMDS scores indicated Block (significantly), flooding index (marginally) and tall herbs (marginally) to affect the composition of microbial PLFAs in soil (Table 2). The bacterial marker i16:0 and the plant marker 18:1ω9 increased significantly in heavily flooded plots (Table 3). By contrast, concentrations of the fungal marker 18:2ω6,9 significantly decreased with

Table 4. Pearson correlation coefficients of regressions between logit-transformed marker phospholipid fatty acid (PLFA) concentrations [sum of bacterial markers (see Methods), fungal marker (18:2ω6,9), and plant marker (18:1ω9)] of soil microorganisms and the respective neutral fatty acids in *Harpalus rufipes* and *Trochosa ruricola*. Significant effects ($P < 0.05$) are given in bold.

		PLFA markers		
		Bacterial	Plant	Fungal
H. rufipes markers	Bacterial	**-0.45**	**0.48**	0.01
	Plant	0.07	-0.03	-0.15
	Fungal	-0.06	0.02	0.16
T. ruricola markers	Bacterial	-0.03	0.04	0.03
	Plant	0.10	-0.11	0.03
	Fungal	0.07	-0.05	-0.10

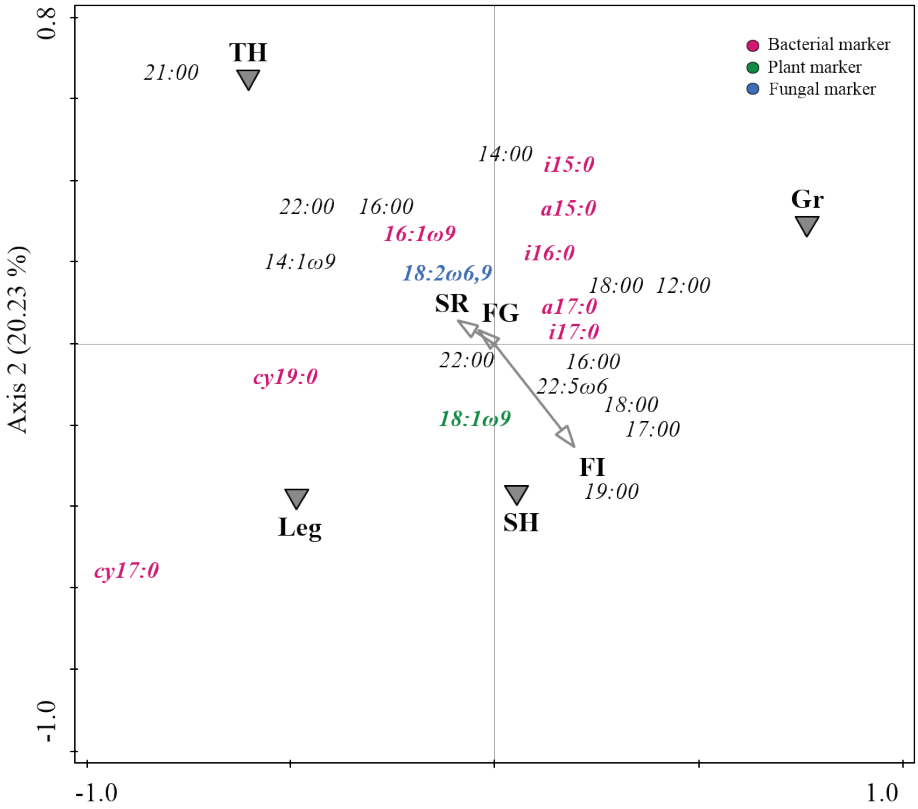

Figure 6. Principal components analysis of the relative abundance (mol%, logit- transformed) of individual PLFAs of soil microorganisms using flooding index (FI), plant species richness (SR), plant functional group richness (FG), presence of grasses (Gr), legumes (Leg), small herbs (SH) and tall herbs (TH) as supplementary variables.

increasing flooding index. The unspecific marker FAs 17:00 increased significantly at higher flooding index, whereas FAs 18:00 and 21:00 significantly decreased. The bacterial marker cy19:0 and the unspecific FA marker 16:00 increased significantly in the presence of tall herbs (Table 3).

The first four PCA axes explained 83.0% of the total variation in PLFAs. The first axis accounted for 39.2% and the second axis for 20.2% (Fig. 6). The distribution of the FAs varied with plant functional groups. The first axis represented the presence of grasses and legumes, whereas the second axis represented the presence of tall herbs and small herbs. In presence of tall herbs concentrations of the eukaryote marker FA 21:00 and the bacterial marker cy17:0 increased, whereas in the presence of small herbs the bacterial FA marker 19:00 increased.

Discussion

As we expected, stable isotope analysis suggests that *T. ruricola* occupies a higher trophic position than *H. rufipes*. As indicated by fatty acid analysis, the diet of *H. rufipes* includes plant seeds. The more variable diet of *H. rufipes* also is reflected by the wider range of stable isotope values as compared to *T. ruricola*, which is only feeding on animal prey, pointing to an omnivorous diet with substantial contribution of plant seeds. The variation in the relative contribution of plant and animal dietary components in *H. rufipes* is reflected in particular in the wide range of $\delta^{15}N$ values spanning > 5 δ units which exceeds considerably the commonly assumed 3.4‰ per trophic level suggesting that some individuals live on a rather pure plant (seed) diet, whereas others exclusively feed on animal prey including intraguild predators.

As we hypothesized, the diet of *H. rufipes* varied significantly with plant community composition. Its diet markedly depended on the available plant resources, as indicated by the close correlation between the FA plant marker in the soil and in body tissues. *H. rufipes* consumed more plant resources in more complex and species-rich plant communities as also indicated by the decrease in $\delta^{15}N$ values with plant species diversity. Seed predation by insects has been shown to increase with increasing plant species richness (Preukschas et al. 2014, Vockenhuber et al. 2013). The phenology of plants differs among species, and therefore more diverse communities provide seeds over a longer period of time, presumably benefiting *H. rufipes*. In fact, beetles of the genera *Harpalus* were shown to become more abundant in the presence of higher numbers of weed plants in agricultural fields (de Snoo et al. 1995, Kokta 1988). Also, *H. rufipes* has been shown to benefit from a diet comprising a diversity of seeds rather than only seeds of one plant species (Bilde & Toft 1994, Brygadyrenko & Reshetniak 2014), and seeds generally have been shown to be of high food quality for granivorous carabid beetles (Fawki & Toft 2005).

In the present study, the presence of grasses and small herbs increased the $\delta^{13}C$ signatures of *H. rufipes*. In the Jena Experiment, grasses produce their seeds earlier during the vegetation period than most tall herbs and legumes, and generate larger amounts of seeds than herbaceous plants (C. Roscher, pers. comm.). This may explain the increased contribution of plants (seeds) to the diet of *H. rufipes*. Besides, fatty acid analyses indicated that in the presence of legumes the diet of *H. rufipes* shifted towards more animal prey, presumably including aphids and collembolans (Kielty et al. 1999). Legumes are considered key plant species (Milcu et al. 2008), which suffer more from herbivore attack than other plant functional groups (Loranger et al. 2014). Further, legumes favour detritivore soil invertebrates by providing nitrogen-rich litter material (Spehn et al. 2002). Indeed, in the Jena Experiment the density and diversity of Collembola increased in the presence of legumes (Sabais et al. 2011) and Collembola are important prey of carabid beetles, in particular of juveniles (Eitzinger & Traugott 2011, Mundy et al. 2000).

The $\delta^{13}C$ values of *H. rufipes* spanned a markedly wide range including values considerably higher than those of C_3 plants suggesting that its body carbon originated from food sources other than the C_3 plants dominating at the study site. Primary producers characterized by high $\delta^{13}C$ values include algae (Akamatsu et al. 2004, Ruess et al. 2004), and potentially *H. rufipes* may have fed on algivore prey species such as soil surface dwelling Collembola (Potapov et al. 2018), but no algae FA markers were detected in *H. rufipes*. Further, high $\delta^{13}C$ values may have been due to *H. rufipes* feeding on seeds of C_4 plants or on herbivores feeding on C_4 plants. Although not included in our sampling regime, there are two plots of 10 × 20 m with a C_4 plant species (*Amaranthus retroflexus* L.) in the Jena Experiment. For identifying if seeds or herbivores of these plants may have contributed to the diet of *H. rufipes* we investigated if the enrichment in $\delta^{13}C$ values in *H. rufipes* was more pronounced close to the two *A. retroflexus* plots. In fact, however, distance to the *A. retroflexus* plots did not significantly correlate with $\delta^{13}C$ values in *H. rufipes* arguing against this explanation. Nevertheless, this does not rule out this explanation as carabid beetles such as *H. rufipes* are able to fly long distances (Zhang et al. 1997) and also move fast on the soil surface in a random way (Galis & Jong 1988). Although *A. retroflexus* produces small seeds, feeding efficiency (i.e., seeds eaten per distance travelled) in *H. rufipes* is particularly high for seeds of this species (Harrison & Gallandt 2012).

Moreover, seed production of *A. retroflexus* is excessive with 5000 to 300,000 seeds per plant (Costea et al. 2003), suggesting that the observed high $\delta^{13}C$ values in *H. rufipes* may have been due to feeding on plants of this species. Irrespective of the exact source responsible for the high $\delta^{13}C$ values in *H. rufipes*, the marked variations in $\delta^{13}C$ values reflect that this species acquired a substantial fraction of its body carbon from other locations than the plots they were captured. In fact, carabid beetles such as *H. rufipes* are characterized by larger home ranges than the size of our plots of 5 × 6 m; however, variations in stable isotope ratios and fatty acid composition in *H. rufipes* with plot specific plant characteristics also reflect that they used local resources from the plots they were caught.

In contrast to *H. rufipes*, the diet of *T. ruricola* did not vary with plant species richness, being more independent of the diversity and structure of plant communities than *H. rufipes*, suggesting that it may be independent of variations in environmental factors and plant associated prey communities (Ebeling et al. 2017). However, the lack in variations in the diet of *T. ruricola* with plant community composition may also have been due to the small size of the plots of 5 × 6 m and reflect that *T. ruricola* acquired most of its prey from larger areas of the Jena Experiment field site. Rather than with plot specific plant characteristics, it changed markedly with body size, indicating dietary changes during developmental stages, from first towards secondary predators (i.e., decomposers and predators with higher $\delta^{15}N$ values). The fact that larger juveniles and adults of *T. ruricola* occupy higher trophic positions in the food web than smaller individuals suggests that with increasing body size intraguild predation and/or cannibalism becomes more important (König et al. 2011, Schneider et al. 2012). Indeed, spiders are known to be voracious intraguild predators (Denno et al. 2004, Lensing & Wise 2004) and the larger the top predator the more it is feeding on larger other predator species (Riede et al. 2011, Schneider et al. 2012). As a consequence, larger predators may switch from exploitative competition with similar sized predators over intraguild predation to occupying higher trophic level with the largest predator at the top. High $\delta^{15}N$ values in *T. ruricola* adults therefore may reflect its position as second order predator. Notably, in severely flooded plots, the $\delta^{15}N$ values of *T. ruricola* were higher than in plots little affected by the flood. Earlier studies showed that flooding decreased bacterial biomass, whereas it increased fungal biomass, reflecting the elevated availability of dead plant biomass in severely flooded plots (Wagner et al. 2015, Wright et al. 2015), which probably increased the abundance of detritivore prey to *T. ruricola*. Overall, therefore, the diet of *T. ruricola* may have consisted mainly of secondary decomposers such as Collembola in severely flooded plots.

Conclusions

Carabid beetles and spiders are among the most abundant and important predators in grasslands. Stable isotope and fatty acid analysis of *H. rufipes* and *T. ruricola* yielded novel insights into factors driving trophic interrelationships of these species and their role in controlling herbivores. Notably, the study allowed investigating the role of variations in plant species richness, plant functional group richness and presence/absence of functional groups of plants on intraspecific dietary variation of these predator species. The results indicate that the diet of *H. rufipes* varied with the availability of plant resources and increased with increasing plant diversity as well as in the presence of grasses and small herbs. By contrast, presence of legumes increased the consumption of animal prey, presumably aphids and collembolans. In contrast to *H. rufipes*, the diet of *T. ruricola* comprised only animal prey and was independent of plant species richness. Interestingly, however, it varied markedly with body size with larger individuals occupying higher trophic positions as second order predators highlighting the importance of IGP. Moreover, the diet of *T. ruricola* changed due to flooding, presumably by increased availability of secondary decomposers as well as intraguild prey in severely flooded plots. Our results reinforce the view that there are feedback loops between plant and invertebrate predator communities with more effective control of pest species in more diverse plant communities. Notably, generalist predators of different taxonomic and functional groups, such as carabid beetles with a wide diet including also seeds and wolf spiders with animal prey only, are likely to complement each other in controlling insect herbivore species and thereby herbivore–plant interactions.

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References

Agrawal, A. A., D. D. Ackerly, F. Adler, A. E. Arnold, C. Cáceres, D. F. Doak, E. Post, P. J. Hudson, J. L. Maron, K. A. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. G. Turner & E. Werner (2007): Filling key gaps in population and community ecology. – The Ecological Society of America **5**: 145–152.

Akamatsu, F., H. Toda & T. Okino (2004): Food source of riparian spiders analyzed by using stable isotope ratios. Ecological Research **19**, 655–662 [doi:10.1111/j.1440-1703.2004.00680.x].

Bàrberi, P., G. Burgio, G. Dinelli, A. C. Moonen, S. Otto, C. Vazzana & G. Zanin (2010): Functional biodiversity in the agricultural landscape: Relationships between weeds and arthropod fauna. – Weed Research **50**: 388–401 [doi:10.1111/j.1365-3180.2010.00798.x].

Ben-David, M., D. M. Schell (2001): Mixing models in analyses of diet using multiple stable isotopes: A response. Oecologia **127**: 180–184 [doi:10.1007/s004420000570].

Bilde, T. & S. Toft (1994). Prey preference and egg production of the carabid beetle Agonum dorsale. – Entomologia Experimentalis et Applicata **73**: 151–156 [doi:10.1111/j.1570-7458.1994.tb01850.x].

Blem, C. R. (1976): Patterns of Lipid Storage and Utilization in Birds. – Integrative and Comparative Biology **16**: 671–684 [doi:10.1093/icb/16.4.671].

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey & M. L. Forister (2003): The ecology of individuals: incidence and implications of individual specialization. – American Naturalist **161**: 1–28 [doi:10.1086/343878].

Brygadyrenko, V. V. & D. Y. Reshetniak (2014): Trophic preferences of *Harpalus rufipes* (Coleoptera, Carabidae) with regard to seeds of agricultural crops in conditions of laboratory experiment. – Baltic Journal of Coleopterology **14**: 179–190.

Buse, T., L. Ruess & J. Filser (2013): New trophic biomarkers for Collembola reared on algal diets. – Pedobiologia **56** [doi:10.1016/j.pedobi.2013.03.005].

Cantor, M., L. A. Ferreira, W. R. Silva & E. Z. F. Setz (2010): Potential seed dispersal by *Didelphis albiventris* (Marsupialia, Didelphidae) in highly disturbed environment. – Biota Neotropica **10** [doi:10.1590/S1676-06032010000200004].

Chen, B. & D. H. Wise (1999): Bottom-Up Limitation of Predaceous Arthropods in a Detritus-Based Terrestrial Food Web. – Ecology **80**: 761–772.

Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau & M. Wolosin (2007): Resolving the biodiversity paradox. – Ecology Letters **10**: 647–659 [doi:10.1111/j.1461-0248.2007.01041.x].

Clough, Y., A. Kruess, D. Kleijn & T. Tscharntke (2005): Spider diversity in cereal fields: Comparing factors at local, landscape and regional scales. – Journal of Biogeography **32**: 2007–2014 [doi:10.1111/j.1365-2699.2005.01367.x].

Costea, M., S. E. Weaver & F. J. Tardif (2003): The biology of Canadian weeds. 130. *Amaranthus retroflexus* L., *A.powellii*, S. Watson and *A. hybridus* L. – Anadian Journal of Plant Science **83**: 1039–1066.

de Snoo, G. R., R.J. van der Poll & J. de Leeuw (1995): Carabids in sprayed and unsprayed crop edges of winter wheat, sugar beet and potatoes. – In: Riedel, S. T. & W. (Ed.): Arthropod Natural Enemies in Arable Land. I. Density, Spatial Heterogeneity and Dispersal. – Århus, Denmark: 199–211.

Dennis, P., M. R. Young & C. Bentley (2001): The effects of varied grazing management on epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland Scotland. – Agriculture, Ecosystems and Environment **86**, 39–57 [doi:10.1016/S0167-8809(00)00263-2].

Denno, R. F., M. S. Mitter, G. A. Langellotto, C. Gratton & D. L. Finke (2004): Interactions between a hunting spider and a web-builder: Consequences of intraguild predation and cannibalism for prey suppression. – Ecological Entomology **29**: 566–577 [doi:10.1111/j.0307-6946.2004.00628.x].

Diehl, E., V. Wolters & K. Birkhofer (2012): Arable weeds in organically managed wheat fields foster carabid beetles by resource- and structure-mediated effects. – Arthropod-Plant Interactions **6**: 75–82 [doi:10.1007/s11829-011-9153-4].

Ebeling, A., J. Hines, L. R. Hertzog, M. Lange, S. T. Meyer, N. K. Simons & W. W. Weisser (2017): Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. – Basic and Applied Ecology **26**: 50–63 [doi:10.1016/J.BAAE.2017.09.014].

Ebeling, A., S. T. Meyer, M. Abbas, N. Eisenhauer, H. Hillebrand, M. Lange, C. Scherber, A. Vogel, A. Weigelt & W. W. Weisser (2014): Plant diversity impacts decomposition and herbivory via changes in aboveground arthropods. – PLoS ONE **9**: e106529 [doi:10.1371/journal.pone.0106529].

Eitzinger, B. & M. Traugott (2011): Which prey sustains cold-adapted invertebrate generalist predators in arable land? – Examining prey choices by molecular gut-content analysis 591–599 [doi:10.1111/j.1365-2664.2010.01947.x].

Engelhardt, W. (1964): Die mitteleuropäischen arten der gattung Trochosa C. L. Koch, 1848 (araneae, lycosidae). Morphologie, chemotaxonomie, biologie, autökologie. – Zeitschrift für Morphologie und Ökologie der Tiere **54**: 219–392 [doi:https://doi.org/10.1007/BF00390678].

Faraway, J. J. (2014): Linear models with R. – CRC Press: 286 p.

Fawki, S. & S. Toft (2005): Food preferences and the value of animal food for the carabid beetle Amara similata (Gyll.)

(Col., Carabidae). – Journal of Applied Entomology **129**: 551–556 [doi:10.1111/j.1439-0418.2005.00992.551-556].

Ferlian, O. & S. Scheu (2014): Shifts in trophic interactions with forest type in soil generalist predators as indicated by complementary analyses of fatty acids and stable isotopes. – Oikos **123**: 1182–1191 [doi:10.1111/j.1600-0706.2013.00848.x].

Ford, M. (1977): Metabolic costs of the predation strategy of the spider *Pardosa amentata* (Clerck)(Lycosidae). – Oecologia **28**: 333–340.

France, R. L. & R. H. Peters (1997). Ecosystem differences in the trophic enrichment of 13C in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences **54**: 1255–1258.

Freude, H., K. W. Harde, G. A. Lohse & B. Klausnitzer (2004): Die Käfer Mitteleuropas, Band 2 Adephaga 1: Carabidae (Laufkäfer) – Spektrum Akademischer Verlag: 521 p.

Frostegård, A., A. Tunlid & E. Baath (1991): Microbial biomass measured as total lipid phosphate in soils of different organic content. – Journal of Microbiological Methods **14**: 151–163 [doi:10.1016/0167-7012(91)90018-l].

Fry, B. (1988): Food web structure on Georges Bank from stable C, N, and S isotopic compositions. – Limnology and Oceanography **33**: 1182–1190.

Galis, F. & P. W. De Jong (1988): Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. – Water 175–184.

Gallandt, E. R., T. Molloy, R. P. Lynch & F. A. Drummond (2005): Effect of cover-cropping systems on invertebrate seed predation. Weed Science **53**: 69–76 [doi:10.1614/ws-04-095r

García, D., M. A. Rodríguez-Cabal, G. C. Amico (2009): Seed dispersal by a frugivorous marsupial shapes the spatial scale of a mistletoe population. – Journal of Ecology **97**: 217–229 [doi:10.1111/j.1365-2745.2008.01470.x].

Gratton, C. & A. E. Forbes (2006): Changes in $\delta^{13}C$ stable isotopes in multiple tissues of insect predators fed isotopically distinct prey. – Oecologia **147**: 615–624 [doi:10.1007/s00442-005-0322-y].

Graziani, F., A. Onofri, E. Pannacci, F. Tei & M. Guiducci (2012): Size and composition of weed seedbank in long-term organic and conventional low-input cropping systems. – European Journal of Agronomy **39**: 52–61 [doi:https://doi.org/10.1016/j.eja.2012.01.008].

Griffin, J. N., J. E. K. Byrnes & B. J. Cardinale (2013): Effects of predator richness on prey suppression: A meta-analysis. – Ecology **94**: 2180–2187 [doi:10.1890/13-0179.1].

Gubsch M, C. Roscher, G. Gleixner, M. Habekost, A. Lipowsky, B. Schmid, E.-D. Schulze, S. Steinbeiss & N. Buchmann (2011): Foliar and soil $\delta^{15}N$ values reveal increased nitrogen partitioning among species in diverse grassland communities. – Plant, Cell and Environment **34**: 895–908 [doi: 10.1111/j.1365-3040.2011.02287.x].

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, J. M. H. Knops & D. Tilman (2009): Plant species loss decreases arthropod diversity and shifts trophic structure. – Ecology Letters **12**: 1029–1039 [doi:10.1111/j.1461-0248.2009.01356.x].

Haines, E. B. & C. L. Montague (1979): Food sources of estuarine invertebrates analyzed using $^{13}C/^{12}C$ ratios. – Ecology **60**: 48–56.

Halaj, J., R. W. Peck & C. G. Niwa (2005): Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: A stable isotope analysis with $\delta^{15}N$ and $\delta^{13}C$. – Pedobiologia **49**: 109–118 [doi:10.1016/j.pedobi.2004.09.002].

Harrison, S. & E. R. Gallandt (2012). Behavioural studies of *Harpalus rufipes* de geer: An important weed seed predator in northeastern US agroecosystems. – International Journal of Ecology **2012** [doi:10.1155/2012/846546].

Harrison, S. K., E. E. Regnier & J. T. Schmoll (2003): Postdispersal predation of giant ragweed (*Ambrosia trifida*) seed in no-tillage corn. Weed Science **51**: 955–964 [doi:10.1614/P2002-110].

Hartke, A., F. A. Drummond & M. Liebman (1998): Seed feeding, seed caching, and burrowing behaviors of *Harpalus rufipes* De Geer Larvae (Coleoptera: Carabidae) in the Maine potato agroecosystem. – Biological Control **13**: 91–100 [doi:10.1006/bcon.1998.0645].

Haubert, D., M. M. Häggblom, S. Scheu & L. Ruess, (2004): Effects of fungal food quality and starvation on the fatty acid composition of *Protaphorura fimata* (Collembola). Comparative Biochemistry and Physiology – B Biochemistry and Molecular Biology **138**: 41–52 [doi:10.1016/j.cbpc.2004.02.009].

Hobson, K. A., A. Fisk, N. Karnovsky, M. Holst, J. M. Gagnon & M. Fortier (2002): A stable isotope ($\delta^{13}C$, $\delta^{15}N$) model for the North Water food web: Implications for evaluating trophodynamics and the flow of energy and contaminants. – Deep-Sea Research Part II: Topical Studies in Oceanography **49**: 5131–5150 [doi:10.1016/S0967-0645(02)00182-0].

Hooper, D. U., F. S. I. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle (2005): Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. – Ecological Monographs **75**: 3–35 [doi:10.1890/04-0922].

Ikeda, H., K. Kubota, A. Kagawa & T. Sota (2010): Diverse diet compositions among harpaline ground beetle species revealed by mixing model analyses of stable isotope ratios. Ecological Entomology **35**: 307–316 [doi:10.1111/j.1365-2311.2010.01182.x].

Kajak, A. (1995): The role of soil predators in decomposition processes. – European Journal of Entomology [doi:10.14411/eje.1995.073].

Kielty, J. P., L. J. Allen-Williams & N. Underwood (1999): Prey preferences of six species of Carabidae (Coleoptera) and one Lycosidae (Araneae) commonly found in UK arable crop fields. – Journal of Applied Entomology **123**: 193–200 [doi:10.1046/j.1439-0418.1999.00355.x].

Kokta, C. (1988): Beziehungen zwischen der Verunkrautung und phytophagen Laufkäfern der Gattung Amara. – Mitteilungen der biologischen Bundesanstalt für Land- und Forstwirtschaft **247**: 139–145.

König, T., R. Kaufmann & S. Scheu (2011): The formation of terrestrial food webs in glacier foreland: Evidence for the pivotal role of decomposer prey and intraguild predation. – Pedobiologia **54**: 147–152 [doi:10.1016/j.pedobi.2010.12.004].

Kromp, B. (1999): Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. – In: Paoletti, M. G. (Ed.): Agriculture, ecosystems and environment. – Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes **74**: 187–228.

Kulkarni, S. S., L. M. Dosdall & C. J. Willenborg (2015): The Role of Ground Beetles (Coleoptera: Carabidae) in Weed Seed Consumption: A Review. – Weed Science **63**: 355–376 [doi:10.1614/WS-D-14-00067.1].

Langel, R. & J. Dyckmans (2014): Combined ^{13}C and ^{15}N isotope analysis on small samples using a near-conventional elemental analyzer/isotope ratio mass spectrometer setup. – Rapid Communications in Mass Spectrometry **28**: 1019–1022 [doi:10.1002/rcm.6878].

Langellotto, G. A., & R. F. Denno (2004): Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. – Oecologia **139**: 1–10 [doi:10.1007/s00442-004-1497-3].

Lau, D. C. P., K. M. Y. Leung & D. Dudgeon (2008): Experimental dietary manipulations for determining the relative importance of allochthonous and autochthonous food resources in tropical streams. – Freshwater Biology **53**: 139–147 [doi:10.1111/j.1365-2427.2007.01873.x].

Layman, C.A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop (2012):. Applying stable isotopes to examine food-web structure: An overview of analytical tools. – Biological Reviews **87**, 545–562 [doi:10.1111/j.1469-185X.2011.00208.x].

Lee, J. C., F. D. Menalled & D. A. Landis (2001): Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. – Journal of Applied Ecology **38**: 472–483 [doi:10.1046/j.1365-2664.2001.00602.x].

Lensing, J. R. & D. H. Wise (2004). A test of the hypothesis that a pathway of intraguild predation limits densities of a wolf spider. – Ecological Entomology **29**: 294–299 [doi:10.1111/j.0307-6946.2004.00601.x].

Loranger, H., W. W. Weisser, A. Ebeling, T. Eggers, E. De Luca, J. Loranger, C. Roscher & S. T. Meyer (2014): Invertebrate herbivory increases along an experimental gradient of grassland plant diversity. – Oecologia 174: 183–193 [doi:10.1007/s00442-013-2741-5].

Lund, R.D. & F. T. Turpin (1977):. Carabid Damage to Weed Seeds Found in Indiana Cornfields. – Environmental Entomology **6**: 695–698 [doi:10.1093/ee/6.5.695].

Martinez del Rio, C. & B. O. Wolf (2005): Mass balance models for animal isotopic ecology. – Physiological and Ecological Adaptations to Feeding in Vertebrates 141–174.

McGill, B. J., B. J. Enquist, E. Weiher & M. Westoby (2006): Rebuilding community ecology from functional traits. – Trends in Ecology and Evolution **21**: 178–185 [doi:10.1016/j.tree.2006.02.002].

Menalled, F. D., M. Liebman, K. A. Renner, H. P. Singh, D. R. Batish & R. Kohli (2006): The ecology of weed seed predation in herbaceous crop systems. – Handbook of Sustainable Weed Management: 297–327.

Michener, R. H. & K. Lajtha (2007): Stable isotopes in ecology and environmental science, Ecological methods and concepts series. – Blackwell Publishing: 594 p [doi:10.1899/0887-3593-028.002.0516].

Milcu, A., S. Partsch, C. Scherber, W. W. Weisser & S. Scheu (2008): Earthworms and legumes control litter decomposition in a plant diversity gradient. – Ecology **89**: 1872–1882 [doi:10.1890/07-1377.1].

Mundy, C. A., L. J. Allen-Williams, N. Underwood & S. Warrington (2000): Prey selection and foraging behaviour by *Pterostichus cupreus* L . (Col ., Carabidae) under laboratory conditions. – Journal of Applied Entomology **124**: 349–358.

Öberg, S. & B. Ekbom (2006): Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. – Annals of Applied Biology **149**: 203–211 [doi:10.1111/j.1744-7348.2006.00088.x].

Oelbermann, K. & S. Scheu (2002): Stable isotope enrichment ($\delta^{15}N$ and $\delta^{13}C$) in a generalist predator (*Pardosa lugubris*, Araneae: Lycosidae): Effects of prey quality. – Oecologia **130**: 337–344 [doi:10.1007/s004420100813].

Pond, C. M. (1981): Storage. – In: Townsend, C. R., P. Calow (Eds): Physiological Ecology: An Evolutionary Approach to Resource Use. – Blackwell, London: 190–219.

Post, D. M. (2002): Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions **83**: 703–718.

Potapov, A. M., A. Y. Korotkevich & A. V. Tiunov (2018): Non-vascular plants as a food source for litter-dwelling Collembola: Field evidence. – Pedobiologia **66**: 11–17 [doi:10.1016/j.pedobi.2017.12.005].

Potapov, A.M., A. V. Tiunov & S. Scheu (2019): Uncovering the structure of soil food webs using bulk natural stable isotope composition. – Biological Reviews **94**: 37–59.

Preukschas, J., M. Zeiter, M. Fischer & A. Stampfli (2014): Biotic resistance to plant invasion in grassland: Does seed predation increase with resident plant diversity? – Basic and Applied Ecology **15**: 133–141 [doi:10.1016/j.baae.2014.01.004].

Purtauf, T., J. Dauber & V. Wolters (2004): Carabid communities in the spatio-temporal mosaic of a rural landscape. – Landscape and Urban Planning **67**: 185–193 [doi:10.1016/S0169-2046(03)00038-0].

R Development Core Team (2012): R: A language and environment for statistical computing.

Ramsey, P. W., M. C. Rillig, K. P. Feris, W. E. Holben, J. E. Gannon (2006): Choice of methods for soil microbial community analysis: PLFA maximizes power compared to CLPP and PCR-based approaches. – Pedobiologia **50**: 275–280 [doi:10.1016/j.pedobi.2006.03.003].

Reineking, A., R. Langel & J. Schikowski (1993): ^{15}N, ^{13}C-Online Measurements with an Elemental Analyser (Carlo Erba, NA 1500), a Modified Trapping Box and a Gas Isotope Mass Spectrometer (Finnigan, MAT 251). – Isotopenpraxis Isotopes in Environmental and Health Studies **29**: 169–174 [doi:10.1080/10256019308046151].

Riechert, S. & J. Harp (1987): Nutritional ecology of spiders. In: Slansky, F. J. & J. Rodriguez (Eds.): Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. – Wiley, New York: 645–672.

Riede, J. O., U. Brose, B. Ebenman, U. Jacob, R. Thompson, C. R. Townsend & T. Jonsson (2011): Stepping in Elton's footprints: A general scaling model for body masses and trophic levels across ecosystems. – Ecology Letters **14**: 169–178 [doi:10.1111/j.1461-0248.2010.01568.x].

Roeder, K. A. & S. T. Behmer (2014): Lifetime consequences of food protein-carbohydrate content for an insect herbivore. Functional. – Ecology **28**: 1135–1143 [doi:10.1111/1365-2435.12262].

Romero, S. A. & J. D. Harwood (2010): Diel and seasonal patterns of prey available to epigeal predators: Evidence for food limitation in a linyphiid spider community. – Biological Control **52**: 84–90 [doi:10.1016/J.BIOCONTROL.2009.09.013

Roscher, C., W. L. Kutsch & E. D. Schulze (2010): Light and nitrogen competition limit *Lolium perenne* in experimental grasslands of increasing plant diversity. – Plant Biology **13**: 134–144 [doi:10.1111/j.1438-8677.2010.00338.x].

Roscher, C., J. Schumacher, J. Baade, W. Wilcke, G. Gleixner, W. W. Weisser, B. Schmid & E. Schulze (2004): The role of biodiversity for element cycling and trophic interactions : an experimental approach in a grassland community. – Basic and Applied Ecologyasic **5**: 107–121.

Ruess, L. & P. M. Chamberlain (2010): The fat that matters: Soil food web analysis using fatty acids and their carbon stable isotope signature. – Soil Biology and Biochemistry **42**: 1898–1910 [doi:10.1016/j.soilbio.2010.07.020].

Ruess, L., M. M. Häggblom, E. J. García Zapata & J. Dighton (2002): Fatty acids of fungi and nematodes—possible biomarkers in the soil food chain? – Soil Biology and Biochemistry **34**: 745–756 [doi:10.1016/S0038-0717(01)00231-0].

Ruess, L., M. M. Häggblom, R. Langel & S. Scheu (2004): Nitrogen isotope ratios and fatty acid composition as indicators of animal diets in belowground systems. – Oecologia **139**: 336–46 [doi:10.1007/s00442-004-1514-6].

Sabais, A. C. W., S. Scheu & N. Eisenhauer (2011): Plant species richness drives the density and diversity of Collembola in temperate grassland. – Acta Oecologica **37**: 195–202 [doi:10.1016/j.actao.2011.02.002].

Schaefer, M. (2010): Brohmer – Fauna von Deutschland, 23rd ed. – Wiebelsheim, Quelle & Meyer.

Schmid, B., A. Hector, M. Huston, P. Inchausti, I. Nijs, P. Leadley & D. Tilman (2002): The design and analysis of biodiversity experiments. – In: Press, O. U. (Ed.): Biodiversity and Ecosystem Functioning: Synthesis and Perspectives: 61–78.

Schmitz, O. J. (2003): Top predator control of plant biodiversity and productivity in an old-field ecosystem. – Ecology Letters **6**: 156–163 [doi:10.1046/j.1461-0248.2003.00412.x].

Schneider, F. D., S. Scheu & U. Brose (2012): Body mass constraints on feeding rates determine the consequences of predator loss. – Ecology Letters **15**: 436–443 [doi:10.1111/j.1461-0248.2012.01750.x].

Shearin, A. F., S. Chris Reberg-Horton, E. R. Gallandt (2008): Cover Crop Effects on the Activity-Density of the Weed Seed Predator *Harpalus rufipes* (Coleoptera: Carabidae). – Weed Science **56**: 442–450 [doi:10.1614/WS-07-137.1].

Sih, A., A. Bell & J. C. Johnson (2004): Behavioral syndromes: An ecological and evolutionary overview. – Trends in Ecology and Evolution **19**: 372–378 [doi:10.1016/j.tree.2004.04.009

Snyder, W. E., G. B. Snyder, D. L. Finke & C. S. Straub (2006): Predator biodiversity strengthens herbivore suppression. – Ecology Letters **9**: 789–796 [doi:10.1111/j.1461-0248.2006.00922.x]

Spehn, E. M., M. Scherer-Lorenzen, B. Schmid, A. Hector, M. C.Caldeira, P. G. Dimitrakopoulos, J. A. Finn, A. Jumpponen, G. O'Donnovan, J. S. Pereira, E. D. Schulze, A. Y. Troumbis & C. Körner (2002): The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. – Oikos **98**: 205–218 [doi:10.1034/j.1600-0706.2002.980203.x].

Sunderland, K. (1999): Mechanisms Underlying the Effects of Spiders on Pest Populations. – The Journal of Arachnology **27**: 308–316 [doi:10.2307/3706002].

Symondson, W. O. C., K. D. Sunderland & M. H. Greenstone, (2002): D Iffusion of E Ffective B Ehavioral. – Annual Review Entomology **47**: 561–594 [doi:10.1146/annurev.ento.47.091201.145240].

Ter Braak, C. J. F. & P. Smilauer (2012): Canoco Reference Manual and User's Guide: Software for Ordination (version 5.0). – Microcomputer Power, Ithaca, USA.

Tiunov, A. V. (2007): Stable isotopes of carbon and nitrogen in soil ecological studies. – Biology Bulletin **34**: 395–407 [doi:10.1134/S1062359007040127].

Toft, S. (1995): Value of the Aphid Rhopalosiphum padi as Food for Cereal Spiders. – Journal of Applied Ecology **32**: 552–560 [doi:10.2307/2404652].

Toft, S. & D. H. Wise (1999b) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. – Oecologia **119**: 191–197 [doi:10.1007/s004420050776].

Toft, S. & D. H. Wise (1999a): Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. – Oecologia **119**: 198–207 [doi:10.1007/s004420050777].

Uetz, G. W. (1991): Habitat structure and spider foraging. – In: McCoy, E. D., S. S. Bell & H. R. Mushinsky (Ed.): Habitat Structure: The Physical Arrangement of Objects in Space. – Chapman and Hall, London: 325–348.

Vanderklift, M. A. & S. Ponsard (2003): Sources of variation in consumer-diet $\delta^{15}N$ enrichment: A meta-analysis. – Oecologia **136**: 169–182 [doi:10.1007/s00442-003-1270-z

Vieira, E. M. & D. Port (2007): Niche overlap and resource partitioning between two sympatric fox species in southern Brazil. – Journal of Zoology **272**: 57–63 [doi:10.1111/j.1469-7998.2006.00237.x].

Vockenhuber, E., P. Kabouw, T. Tscharntke & C. Scherber (2013): Plant–animal interactions in two forest herbs along a tree and herb diversity gradient. – Plant Ecology & Diversity **6**: 205–216 [doi:10.1080/17550874.2013.782368].

Wagner, D., N. Eisenhauer & S. Cesarz (2015): Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event. – Soil Biology and Biochemistry **89**: 135–149 [doi:10.1016/j.soilbio.2015.07.001].

Wilby, A. & M. B. Thomas (2002): Natural enemy diversity and pest control: patters of pest emergence with agricultural intensification. – Ecology Letters **5**: 353–360 [doi:10.1046/j.1461-0248.2002.00331.x].

Wise, D. H. (1993): Spiders in ecological webs. – Cambridge University Press, Cambridge: 328 p.

Wise, D. H., D. M. Moldenhauer & J. Halaj (2006): Using Stable Isotopes to Reveal Shifts in Prey Consumption by Generalist Predators. – Ecological Applications **16**: 865–876.

Wright, A. J., A. Ebeling, H. de Kroon, C. Roscher, A. Weigelt, N. Buchmann, T. Buchmann, C. Fischer, N. Hacker, A. Hildebrandt, S. Leimer, L. Mommer, Y. Oelmann, S. Scheu, K. Steinauer, T. Strecker, W. Weisser, W. Wilcke & N. Eisenhauer (2015): Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. – Nature Communications **6**: 6092 [doi:10.1038/ncomms7092].

Zhang, J. X., F. A. Drummond, M. Liebman & A. Hartke (1997): Phenology and dispersal of *Harpalus rufipes* DeGeer (Coleoptera: Carabidae) in agroecosystems in Maine. – Journal of Agricultural Entomology **14**: 171–186.

Zuur, A., E. N. Ieno & G. M. Smith (2007): Analysing Ecological Data. – Springer-Verlag New York: 672 p [doi:10.1007/978-0-387-45972-1].