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Different hunting strategies of generalist predators result in functional differences

Radek Michalko[1,2] · Stano Pekár[1]

Abstract The morphological, physiological, and behavioural traits of organisms are often used as surrogates for actual ecological functions. However, differences in these traits do not necessarily lead to functional differences and/or can be context–dependent. Therefore, it is necessary to explicitly test whether the surrogates have general ecological relevance. To investigate the relationship between the hunting strategies of predators (i.e., how, where, and when they hunt) and their function, we used euryphagous spiders as a model group. We used published data on the diet composition of 76 spider species based on natural prey and laboratory prey acceptance experiments. We computed differences in the position and width of trophic niches among pairs of sympatrically occurring species. Pairs were made at different classification levels, ranked according to the dissimilarity in their hunting strategies: congeners, confamiliars (as phylogenetic proxies for similarity in hunting strategy), species from the same main class of hunting strategy, from the same supra-class, and from different supra-classes. As for niche position computed from the natural prey analyses, species from the same class differed less than species from different classes. A similar pattern was obtained from the laboratory studies, but the congeners differed less than the species from the same classes. Niche widths were most similar among congeners and dissimilar among species from different supra-classes. Functional differences among euryphagous spiders increased continuously with increasing difference in their hunting strategy. The relative frequency of hunting strategies within spider assemblages can, therefore, influence the food webs through hunting strategy-specific predator–prey interactions.

Keywords Functional diversity · Guilds · Euryphagy · Niche · Spiders · Araneae

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Introduction

The function of an organism in an environment is determined by utilized resources, tolerances to environmental stress, competitive abilities, and other functionally important traits (Chase and Leibold 2003). However, these characteristics or so-called "hard" functional traits (sensu Lepš et al. 2006) are often difficult to measure. Therefore, surrogates or so-called "soft" functional traits are used instead. These soft functional traits can be various physiological, morphological, and behavioural traits (Lepš et al. 2006; Petchey and Gaston 2006; Mlambo 2014). Although differences in these traits often lead to different niche occupancy (e.g., Almeida Jácomo et al. 2004; Greiner et al. 2007; Michalko and Pekár 2015a), they do not necessarily translate into different niches. This is because there can be more ways to perform a certain role and/or the resources do not allow niche differentiation (Young et al. 2007; Jennings et al. 2010). On the other hand, species with similar

soft functional traits can occupy quite distinct niches due to plastic or flexible traits, such as behaviour, which enables their niche differentiation (Husar 1976; Gutman and Dayan 2005).

The great majority of studies that investigate functional diversity of predators have used soft functional traits without assessing their actual ecological importance. The actual functional similarity among generalist predators has been studied using various soft functional traits (e.g., Chalcraft and Resetarits 2003a, b; Young et al. 2007; Palkovacs and Post 2009; Miller et al. 2014; Sanders et al. 2015). However, most of such studies were limited in the number of investigated predator and/or prey species or had local implications, as the transcription of soft functional traits to actual ecological function can be context-dependent (e.g., Husar 1976; Liu et al. 2015a). In order to assess the general ecological relevance of the soft functional traits across contexts it is necessary to perform meta-analyses on large species numbers across various situations. To our knowledge, this has not yet been done on the hunting strategies of generalist predators.

The various hunting strategies employed by generalist predators can differ in their effectiveness for different prey types. Predators with different strategies may either utilize different prey types or they may also utilize similar prey types but in different proportions. Predators with similar strategies may utilize similar prey types and with similar proportions (Nyffeler and Sterling 1994; Butt and Tahir 2010; Lovari et al. 2015; Michalko and Pekár 2015a). Thus, there should be a positive relationship between similarity in hunting strategies and similarity in trophic niches.

Many predators are food limited (Wise 1993; Hayward and Kerley 2008) and there can be frequent intensive interspecific competition (intraguild interference, exploitation) among those employing a similar hunting strategy (Spiller 1984; Griffen and Byers 2006; Odden et al. 2010). Thus, predators with a similar hunting strategy may orient on different resources to avoid competition (Griffen and Byers 2006; Ingram et al. 2012). On the other hand, complex morphological traits (Young et al. 2010) can perform a similar function and more strategies can be optimal for the same prey type. For example, a specific venom or wrapping by silk can both serve to immobilize large and dangerous prey (Lubin et al. 1978; Pekár et al. 2014). Moreover, the different hunting strategies might provide trade-offs that would enable competitive coexistence on the same resource types (Kneitel and Chase 2004). Therefore, outcomes aside from a positive relationship between similarity in hunting strategies and similarity in trophic niche can arise.

To investigate the relationship between the similarity in hunting strategy and trophic niche in generalists predators, we selected euryphagous spiders as a model group. Spiders belong to the most abundant predators in many terrestrial ecosystems, they are highly diversified in their hunting strategies, and the diet is known for quite a few species (Wise 1993; Cardoso et al. 2011; Pekár et al. 2012). The predation of spiders significantly influences processes within ecosystems through cascade effects (Carter and Rypstra 1995; Schmitz 2008). For example, Schmitz (2008) found that spiders could alter productivity, mineralization, and plant diversity in a grassland ecosystem by predation on grasshoppers. Moreover, the way in which the plant community was altered depended on the hunting strategy of the spiders. The ambush hunter increased plant evenness but reduced the aboveground net primary production and mineralization whereas in an active hunter it was the opposite (Schmitz 2008).

Spiders employ a wide array of hunting strategies but these were classified into eight main classes (Cardoso et al. 2011). Most spiders are euryphagous and generalists, and their diets consist mainly of insects and other arthropods. In addition, their behaviour is largely opportunistic (Wise 1993; Nyffeler 1999; Pekár et al. 2012). This suggests that many spiders might be more or less functionally redundant with respect to their diet composition.

Here, we investigated the relationship between similarity in hunting strategies of generalist spiders and similarity among their trophic niches using data from the published literature. We expected that the niche differences would increase with differences in the hunting strategies. The prey types can be seen as axes of a multidimensional trophic niche and their relative utilization as coordinates on the axes (Chase and Leibold 2003). Therefore, we also compared the relative utilization of prey types by the main classes of hunting strategies in euryphagous spiders (Cardoso et al. 2011) in order to determine in which prey types the hunting strategies differ.

Materials and methods

Hunting strategies of spiders

The classification of hunting strategies of spiders is based on how (e.g. by web, active hunting), when (diurnal, nocturnal), and where (vegetation, ground) they hunt (Nyffeler 1999; Cardoso et al. 2011). As such, we used hunting strategies in a different concept than the "hunting mode" proposed by Schmitz (2005). We use the concept of guilds where species utilize a similar resource in a similar way and so they are expected to interact more intensely with guild members than other species (Root 1967). Hunting strategies of spiders can be classified in two "supraclasses", i.e., web-weavers and cursorial spiders. Each can be further split into several classes to yield eight in total (Cardoso et al. 2011): specialists, sensing-web weavers,

sheet-web weavers, orb-web weavers, space-web weavers, ground hunters, ambush hunters, and other hunters. These classes of spiders' hunting strategies are often grouped at the level of families because congeneric species employ similar hunting strategies, while genera from different families often have different hunting strategies. We therefore distinguished five hierarchical classification levels in this study: congeners—confamiliars—same class—same supra-class—different supra-classes. We then analyzed how the niche properties differ according to the classification level. In some cases, however, confamiliar genera employ quite different hunting strategies. For example, *Pisaura mirabilis* (Clerck 1757) (Pisauridae) is a cursorial hunter (Roberts 1998), while tropical genera of this family are web-builders (Cerveira and Jackson 2002). The hunting strategies used by each genus are shown in Supplementary Material, Appendix 1 Table A1. Spiders considered as specialists by Cardoso et al. (2011) were excluded from the analysis as we were interested only in euryphagous species.

Data survey

We used published as well as unpublished data on the natural diet composition of spiders (Supplementary Material, Appendix 1 Table A1). We used the studies that are listed in Pekár et al. (2012). In addition, we looked for the more recent studies with Google Scholar, using keywords: prey AND spiders; diet AND spiders; trophic niche AND spiders. We searched Google Scholar on 03-Dec-2014. As we looked for the general pattern, and included studies from all ecoregions. We extracted the taxonomic placement and the raw or relative number of each prey category.

We investigated two topics, namely differences in niche properties among various hunting strategies of spiders and the prey types utilized by the various hunting strategies. For both topics, different criteria for data inclusion were employed. To investigate the differences in niche properties, a study was included when it met the following two criteria: (1) It investigated the trophic niche of at least two sympatric species because the trophic niche of euryphagous spiders is partly determined by the availability of potential prey, as the realized niches of two populations of a spider species can differ substantially (Ludy 2007; Líznarová et al. 2013). Consequently, we computed the differences in niche properties among each species within, but not among, studies. If a study contained sympatric as well as allopatric species, we used only the sympatric species. (2) The diet of the two included species was made up of at least 19 prey items, in order to achieve a reasonable statistical inference (range = 19–5030; median = 99). The analyses were based on 25 studies that yielded data for 76 species and 161 species pairs, out of which 15 were congeneric, 32 confamiliar,

31 from the same class, 49 from the same supra-class, and 34 from different supra-classes.

We also compared differences in niche positions (see later for definition of niche position) using data from three experimental studies on prey acceptance (Supplementary Material, Appendix 1 Table A1) to test whether the niche differences were only a side effect of a different microhabitat distribution (Sanders et al. 2015). We computed the differences in niche position between each pair of species using only the prey types that were offered to both species in the pair. In addition, we used only such prey types for which $N > 10$. We obtained 64 species pairs from the experiments on prey acceptance in the laboratory: three congeneric, one confamiliar, 16 from the same class, 17 from the same supra-class, and 27 from different supra-classes. Because there was only one species pair at the level of confamiliar, we clumped this level with congeners, as they all belong to the family Philodromidae.

To investigate the second topic, prey utilization by the main classes of hunting strategies of spiders, we also included studies that recorded prey for a single species or genus. We included only studies where the diet of a species was known from at least 19 prey items. If more studies investigated the diet of the same spider species, we clumped the data together so that each species was represented only once in the final data set. There were five, two, and four such species in Orb-web weavers, Sheet-web weavers, and Space-web weavers, respectively. We obtained diets for 20 species of other hunters, 16 species of ground hunters, seven species of ambush hunters, 14 species of sheet-web weavers, 42 species of orb-web weavers, and 13 species of space-web weavers. We did not analyze sensing-web weavers, as the diet (with at least 19 prey items) was known for only a single species.

Differences in niche properties

The ecological niches have their positions and widths. Here, we consider the niche position of a species as a topology of the species in a multidimensional space. The prey categories represent the axes and the relative utilization of the prey types are coordinates on the axes. We then consider the niche width as diversity of the prey types that a spider species utilizes.

We analyzed differences in niche positions and widths in order to quantify the differences in niche properties among the five levels of similarity in hunting strategy (i.e., congeners—confamiliars—same class—same supra-class—different supra-classes). We used quantitative as well as presence-absence data to discover whether the differences in niche properties were caused by the utilization of different prey types or by the different proportional utilization of similar prey types.

The prey categories, from which the differences in niche properties were computed, depended on the results of particular studies but they were mostly orders and sub-orders. For example, the order Hemiptera was divided into Sternorrhyncha, Auchenorrhyncha, and Heteroptera in some studies, while only Hemiptera could be distinguished in other studies. We also considered larvae of Holometabolan insects as separate categories whenever possible (e.g., Lepidoptera imagoes vs. caterpillars). We also separated Formicidae from Hymenoptera when possible.

In the case of laboratory studies on prey acceptance, the differences in niche positions were computed from the relative acceptance rates (accepted/offered), as the number of offered prey differed among prey types and/or studies and because it also contained the active prey choice. We computed the niche difference for the congeneric level from a study on three *Philodromus* species (Michalko and Pekár 2015b). However, we then used only the acceptance rates of *P. cespitum* to compute the differences among further levels, as otherwise the calculation would involve a pseudoreplication.

Differences in niche position

Statistical analyses were performed within the R environment (R Core Team 2014). Niche overlap can be seen as a measure of the proximity of the positions of niches (Saergant 2007). We used the Czekanowski index for niche overlap (*NO*) (Geange et al. 2011). We computed the differences in niche positions as 1-*NO* (i.e., Bray-Curtis measure of distance) because it is a good distance measure often used for computation of the functional diversity index (Lepš et al. 2006; Geange et al. 2011).

We analyzed the differences in niche position among the five levels of classifications of hunting strategies by Generalized Estimating Equations (GEE). GEE is an extension of Generalized Linear Models (GLM) for data with pseudoreplications (Pekár and Brabec 2012). We used GEE with gamma error structure and log link (GEE-g), as the distance measure can reach values between 0 and 1 and because the data were heteroscedastic (Pekár and Brabec 2009, 2012). To compare niche positions based on presence/absence data, we used GEE with binomial error structure and logit link (GEE-b), as we investigated the proportions of the uniquely utilized prey categories from all categories utilized by both species (Pekár and Brabec 2009). We used an "exchangeable" correlation structure in both GEE-g and GEE-b, as the relationships among the species pairs in a cluster were blocked (Pekár and Brabec 2012). We compared the differences in niche position with GLM with gamma error structure and log link (GLM-g) from the laboratory studies on prey acceptance. In all models, the differences in niche properties and

classification level acted as a response and an explanatory variable, respectively.

Differences in niche width

We refer to niche width based on quantitative data and presence-absence data as niche diversity and niche richness, respectively, as these were computed in the same way as taxonomical diversity and richness. We used the Shannon index as a measure of niche diversity. As the Shannon index can be influenced by differences in sampling effort, we used rarefied values of the index (Lande 1996; Colwell 2013). We computed absolute values of differences between the rarefied Shannon indices to compare differences in niche width. We computed the absolute value of the difference between numbers of prey types to compare differences between niche richness. The number of prey items differed considerably. A relationship exists between the number of individuals in a sample and taxa richness (Gotelli and Colwell 2001). Therefore, we employed the rarefaction procedure. We rounded the rarefied numbers to integers. The rarefaction was performed using EstimateS 9.1 (Colwell 2013). The differences in niche diversity among the levels of classifications were compared with Generalized Least Squares (GLS), as the absolute differences between Shannon indices can take values from 0 to infinity. We used the "varIdent" variance function, when the data were heteroscedastic (Pekár and Brabec 2012). We compared the differences in niche richness by GEE with Poisson error structure and log link (GEE-p), as the data were counts. We used an exchangeable correlation structure for GLS and GEE-p, as the relationships among the species pairs in a cluster were blocked (Pekár and Brabec 2012). The differences in niche width acted as a response variable and the classification level was an explanatory variable.

Prey utilization by particular hunting strategies

We analyzed prey utilization by the eight classes of hunting strategies (Cardoso et al. 2011) only at the level of prey orders, as it was the smallest distinguishable taxonomic level in many studies. We included only such prey types that occurred in the diet at a frequency higher than 5 % of the analyzed spider species. Then, we included only such prey types that reached over 1 % in the diet connected with a particular hunting strategy to compare the proportions of prey types in the diet.

We compared the proportions with GEE-b where species represented the statistical cluster. Where an exact number of prey items could not be determined, the average number of prey for the given hunting strategy was used. We used an exchangeable correlation structure, as the relationships among the prey types in a cluster were blocked.

Where GEE-b did not converge, GLM with quasibinomial structure (GLM-qb) was used to test the significance of the explanatory variable (Pekár and Brabec 2009); the level of significance was set to $\alpha = 0.001$. The proportion in diet and prey type acted as a response and an explanatory variable, respectively.

To distinguish which prey types could characterize particular classes of hunting strategies we conducted redundancy analysis (RDA) following detrended correspondence analysis that revealed the gradient is short (length of the first axis = 2.6) (Šmilauer and Lepš 2014). The data were arcsine transformed as they were proportions. RDA was performed in the program CANOCO 5 (Ter Braak and Šmilauer 2012). The significance was tested by Monte Carlo permutation test with 1000 iterations.

Results

Differences in niche properties

On the basis of natural diets, the distances of niche positions differed significantly among the levels of classification (GEE-g, $X_4^2 = 53.9$, $P < 0.001$, Fig. 1a). All pairs from the same class of hunting strategy were less distant than pairs from different classes (contrasts, $P < 0.03$) regardless of the classification within the class or supra-class membership (contrasts, $P > 0.85$). If only the presence-absence of utilized prey types was considered, the levels of classification did not differ significantly among one another (GEE-b, $X_4^2 = 8.6$, $P = 0.07$). The distances of trophic niches in acceptance experiments also differed among the levels of classification (GLM-g, $F_{4,59} = 3.8$, $P = 0.009$, Fig. 1b). Pairs within the same class were less distant than pairs from different classes (contrasts, $P < 0.028$) regardless of supra-class membership (contrasts, $P = 0.65$). The congeners that included confamiliars were marginally less distant than the spiders from the same class (contrasts, $P = 0.052$).

Differences in niche diversity also varied significantly among the levels of classification (GLS, $F_{4,156} = 6.4$, $P < 0.001$, Fig. 1c). Congeners differed significantly less than other levels of classification (contrasts, $P < 0.002$). The most different were spiders from different supra-classes (contrasts, $P \leq 0.05$). Other levels of classification, i.e., confamiliars, same class, and same supra-class did not differ significantly (contrasts, $P > 0.25$). The differences in niche diversity between web-builders (H' = 1.3, $CI_{95} = 1.2–1.4$) and hunters (H' = 1.6, $CI_{95} = 1.4–1.8$) were caused by the significantly wider niche of cursorial spiders compared to web spiders (GLS, $F_{1,85} = 6.98$, $P = 0.0098$). There was no significant difference in niche richness among the levels of classification (GEE-p, $X_4^2 = 6.6$, $P = 0.16$).

Fig. 1 Comparison of differences in trophic niche properties of generalist spiders employing various distinct hunting strategies at five hierarchical levels of classification: *1* congeners, *2* confamiliars, *3* same main class of hunting strategy, *4* same supra-class, and *5* different supra-classes **a** Difference in niche position from data on natural prey. **b** Difference in niche position from data on prey acceptance in the laboratory. **c** Difference in trophic niche widths from data on natural diet. The *black points* show means, vertical lines are 95 % confidence intervals, and the *grey points* show actual measured values of niche differences
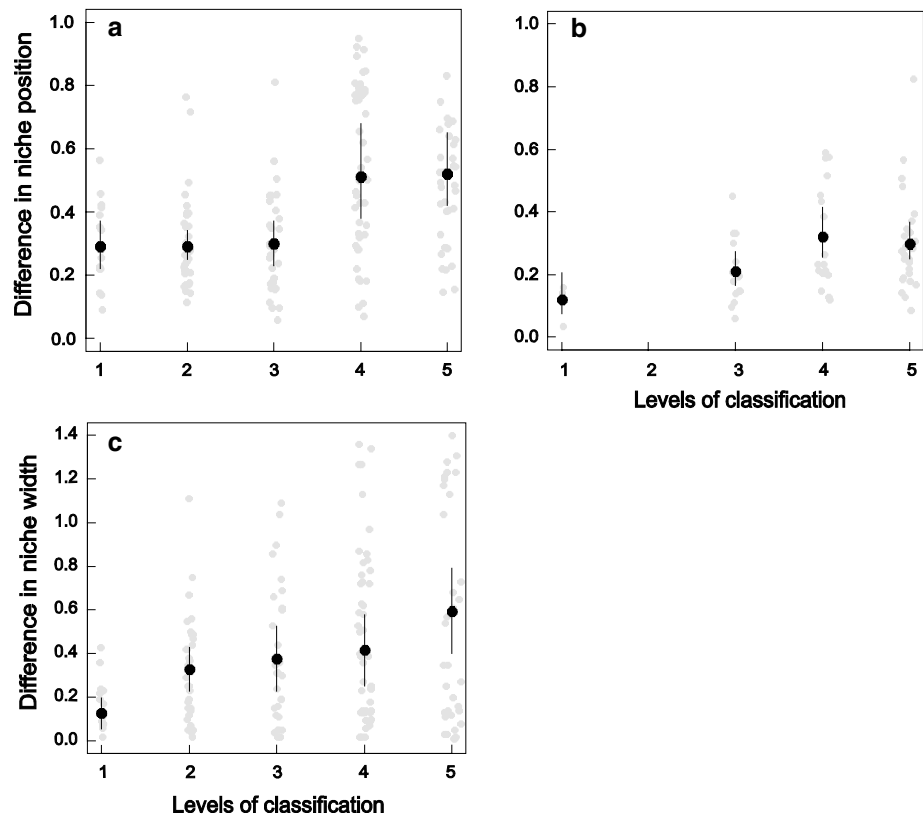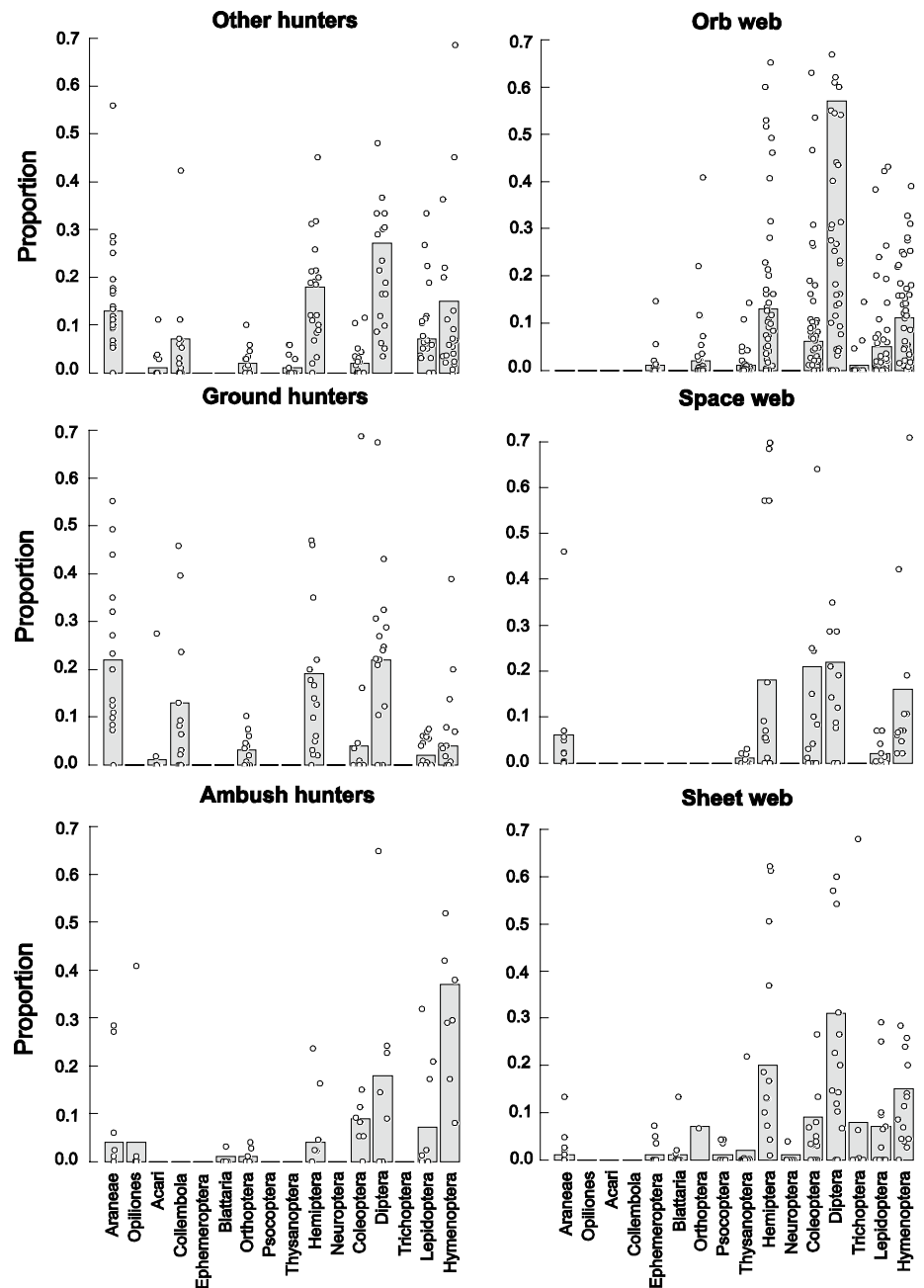
Prey type utilization by particular hunting strategies

Within each hunting strategy the proportions of prey types caught differed significantly (Other hunters: GEE-b, $X_9^2 = 346$, $P < 0.0001$; ground hunters: GEE-b, $X_8^2 = 418$, $P < 0.0001$; ambush hunters: GLM-qb, $F_{8,54} = 6$, $P < 0.0001$; orb-web weavers GEE-b, $X_8^2 = 877$, $P < 0.0001$; space-web weavers: GEE-b, $X_6^2 = 645$, $P < 0.0001$; sheet-web weavers: GEE-b, $X_{12}^2 = 745,967$, $P < 0.0001$, Fig. 2). The most frequently caught prey type by other hunters was Diptera followed by Hemiptera, Hymenoptera, and Araneae. The most frequently caught

prey by ground hunters was Diptera followed by Araneae, Hemiptera, and Collembola. The most frequently caught prey type by ambush hunters was Hymenoptera followed by Diptera. Orb-web weavers captured mostly Diptera. Space-web weavers caught most frequently Diptera followed by Coleoptera, Hemiptera, and Hymenoptera. Sheet-web weavers caught most frequently Diptera followed by Hemiptera and Hymenoptera.

The main classes of hunting strategies had distinct prey composition (RDA, pseudo-$F_{1,5} = 4.7$, $P = 0.001$, Fig. 3). Prey of other and ground hunters had higher proportions of Araneae, Acari, and Collembola than all other hunting

Fig. 2 Relative utilization of prey taxa by main classes of hunting strategies of generalist spiders. The *bars* show means and points show relative utilization by species belonging to the class of hunting strategy
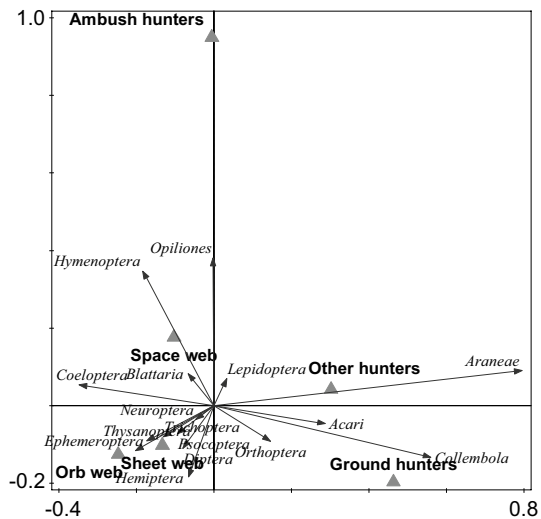
Fig. 3 RDA diagram (first two axes) summarizing the effect of hunting strategy (*triangles*) on prey composition (*arrows*) of spiders. The first two eigenvalues were 0.13 and 0.03, respectively

niches when quantitative data were used, but by a non-significant relationship when only presence-absence data were used. The latter non-significant relationship does not mean that spiders with distinct hunting strategies do not utilize different prey types. Instead, it indicates that the pattern in which similar prey types are utilized in different proportions predominates. It can also indicate a situation in which a spider species employing one hunting strategy utilizes a certain prey type (or prey types) only marginally, while other species with a different strategy do not utilize this prey type (or these prey types) at all.

We were not able to find differences in functional similarity among classifications below the same class from the data on natural diets. This was probably caused by several reasons. First, differences in hunting strategies among the classifications (i.e., congeners, confamiliars, and the same class of hunting strategy) are not large enough to ensure the different utilization of prey. Second, there can be intense competition between spiders with similar hunting strategies that leads to niche segregation due to behavioural plasticity (Herberstein 2011). This segregation may be achieved by an orientation on different prey resources occurring in sympatry (Husar 1976). However, the segregation of trophic niches of species with a similar hunting strategy can also be achieved by microhabitat preference resulting from competition (interference or exploitative) and/or from the different requirements of environmental conditions. Microhabitats can then host distinct prey (Uetz 1977; Herberstein 1998; Folz et al. 2006; Schmidt and Rypstra 2010; Sanders et al. 2015). The scenario in which trophic niche differences are caused by the microhabitat separation of congeners can be supported by the results from the acceptance experiments. The congeners were more similar than any other levels. However, only four species pairs were used to compute the functional difference among congeners (out of which one was confamiliar) in the acceptance experiments. To obtain more reliable results, more species should be analyzed in the future once the data are available.

The third reason could also be competition between spiders with a similar hunting strategy, but the mechanism behind the increased similarity among the levels of classifications below the same class is different. The selection pressures of competition among functionally similar species can lead to an increase in their niche widths. The niche width can be increased by population heterogenization or by increasing width of individuals' niches as the individuals are forced to take sub-optimal resources (Araújo et al. 2011). Interspecific interference has been suggested to heterogenize the trophic niche of a population, e.g., in *Philodromus* spiders (Michalko and Pekár 2014). The increase in niche width can then increase the overlap among species with less similar hunting strategies (Bolnick et al. 2011).

strategies. Nevertheless, the average proportions of Araneae was higher in other hunters while proportions of Collembola and Acari were higher in ground hunters. Average proportions of Orthoptera were higher in ground hunters. Orb-web and sheet-web weavers had higher proportions of various flying insects. Space-web builders had higher proportions of Hymenoptera and Blattaria. Proportions of Hymenoptera and Opiliones were higher in ambush hunters.

Discussion

Differences in niche properties

In general, with respect to the diet composition, generalist spiders employing different hunting strategies occupy more distinct trophic niches than spiders employing similar strategies. Therefore, the hunting strategy of euryphagous spiders can be used as a soft functional trophic trait similarly to, for example, tooth shape in mammals (Davies et al. 2007; Calandra et al. 2008) or intestine length in fishes (Kramer and Bryant 1995; Elliott and Bellwood 2003). Thus, results of this study show that diversity of spider hunting strategies can be used as proxy for the functional diversity. The main hunting strategies can be also considered as guilds because spiders with similar hunting strategies utilize similar resources in a similar way (Root 1967).

Our analysis revealed that euryphagous spiders with different hunting strategies mostly utilize similar prey types but with different frequencies. This was supported by significant differences among levels of classification in trophic

The fourth reason probably influenced the results the most. Prey utilization should be taken as resource electivity, as there is passive as well as active prey choice in spiders (Toft 1999; Geange et al. 2011). Therefore, resource availability should be taken into account (Geange et al. 2011). If these factors are not taken into account, the niche differences can be underestimated (Gotelli and Graves 1996). Unfortunately, most of the studies used did not investigate the availability of potential prey. Therefore, we had to compute the differences in niche position not as for electivity data but only as for categorical data (Geange et al. 2011). In addition, the distinguishable levels of prey categories differed among the studies, which could also be another source of the reduction of niche distances among distant hunting strategies (Greene and Jaksić 1983). Nevertheless, resource selectivity was used in laboratory studies that produced qualitatively very similar results to the natural prey analysis. However, congeners were more similar than any other level of classifications. It is likely that if the sources of bias listed above were reduced, more levels of functional similarities could be distinguished and more accurate results would be obtained.

Differences in niche widths show a slightly different pattern than the differences in niche positions. Congeners were the most similar while cursorial spiders and web-weavers differed significantly. Other classifications differed moderately. The differences in niche widths between web-weavers and cursorial spiders can be explained by the fact that the web-weavers basically wait for a prey to come and these are mainly highly mobile prey types while cursorial spiders encounter mainly with less mobile prey (Nyffeler 1999). Differences in niche widths are important in various ecological contexts. The coexistence of species can be mediated by the trade-off between the ability to obtain prey and the efficiency of processing prey (Wilson and Yoshimura 1994; Straub et al. 2011). With respect to the influence of spiders on prey, a wider niche provides quantitatively more, but weaker, connections in food chains than a narrow niche (Sanders et al. 2015).

Similarly to niche overlap, the relative resource availabilities should be incorporated into the computation of niche width (Smith 1982). Therefore, the results on niche width may be biased due to identical weights applied to rare and common resources as in the niche positions mentioned above.

The functional differences among euryphagous spiders are not discrete but continuous, and this should be taken into account when the functional diversity of spiders is studied. However, even though congeners employing the most similar hunting strategies are functionally the most similar, they are still not functionally equivalent. This means that each spider species in an ecosystem may occupy a unique niche region and contribute to the functional diversity. However, one should be careful to interpret these results as suggesting that each species loss would lead to the loss of a function in an ecosystem. Assemblages of spiders are usually quite diverse even in agroecosystems (Birkhofer et al. 2013). Two (or more) complementary species may together fill up the niche space after the loss of a species. Alternatively, the loss of one species could cause ecological release and niche expansion in another species.

It should be mentioned here that body size of spiders also significantly influence their diet composition (e.g., Sanders et al. 2015). However, here we did not include body size for several reasons. Firstly, we grouped the prey types mostly at the order level and the body size of insects within order is strongly variable. Second, the observation of spider diets come from various ontogenetic stages, which differ in size and consequently in their trophic niches (e.g., Richardson and Hanks 2009; Sanders et al. 2015; Michalko and Pekár 2015b).

Prey types utilized by the main classes of hunting strategies

The hunting strategies differ in their effectiveness in capturing certain prey types, but for other types the effectiveness is similar. Nevertheless, it seems that euryphagous spiders, as a whole, prey mostly on soft bodied, harmless, and abundant prey such as Diptera and Hemiptera. Each hunting strategy is characterized by feeding on certain prey types. We could not draw any conclusions about the capture efficiency of particular hunting strategies with respect to prey categories that made up low proportions in the diet. This is because we were unable to investigate the prey selection of particular spider species that were members of the six analyzed classes of hunting strategies. Therefore, the same weights were applied to the dominant and rare prey types. The low proportion of a prey type in the diet can then either arise from the fact(s) that the prey was negatively selected and/or it was scarce in the environment (Herberstein and Elgar 1994; Ludy 2007; Michalko and Pekár 2015b). However, theoretically, spiders might still be effective in lowering the abundances of prey types that made up the largest proportion in their diets. A large proportion of a particular prey type in the diet could have resulted from the fact that the prey type was highly selected or it was abundant in the environment. The prey could also have been selected negatively, i.e., its proportion in spiders' diets was significantly lower than its availability in a habitat, but still preyed on in high numbers (Michalko and Pekár 2015b). Therefore, some hunting strategies may lower the abundances of certain prey types more effectively than others. This, however, does not mean that the others would not be effective at all. The results support the studies that found that different hunting strategies of spiders have different impacts on the

functioning of various ecosystems (Schmitz 2008; Liu et al. 2015a, b). The relative composition of hunting strategies in the spider assemblage can have, therefore, a large influence on the overall composition of a community through predator–prey interactions and cascade effects. This has implications for biological control, as one may employ management practices that enhance the abundances of particular hunting strategies that are most effective in controlling a certain pest. In addition, species employing few hunting strategies (e.g., other and ground hunters) have quite a high potential to disrupt the biological control of other spiders. Thus, one could employ a management practice that would decrease intraguild predation (Schmidt and Rypstra 2010; Birkhofer et al. 2013).

Conclusions

We found that the different hunting strategies of euryphagous spiders result in functional differences in the trophic niche. Generalist spiders with different hunting strategies utilized similar prey types but in different proportions. The functional differences were not discrete but continuous, and this should be taken into account when computing, for example, indices of functional diversity. The functional differences among the hunting strategies imply that spiders with different hunting strategies differ in their efficiency to suppress different prey types. The relative composition of hunting strategies in spider assemblages can, therefore, influence the composition of the whole community through strategy-specific predator–prey interactions and cascade effects.

Author contribution statement　RM conceived and designed the study. RM performed the data survey. RM analyzed the data. RM and SP wrote the manuscript.

Compliance with ethical standards

Conflict of interest　The authors declare no conflicts of interest.

Ethical approval　This article does not contain any studies with human participants or animals performed by any of the authors.

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