



An updated perspective on spiders as generalist predators in biological control

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Abstract

The role of generalist predators in biological control remains controversial as they may not only reduce pest populations but also disrupt biocontrol exerted by other natural enemies. Here, we focus on spiders as a model group of generalist predators. They are among the most abundant and most diverse natural enemies in agroecosystems. We review their functional traits that influence food-web dynamics and pest suppression at organisational levels ranging from individuals to communities. At the individual and population levels, we focus on hunting strategy, body size, life stage, nutritional target, and personality (i.e., consistent inter-individual differences in behaviour). These functional traits determine the spider trophic niches. We also focus on the functional and numerical response to pest densities and on non-consumptive effects of spiders on pests. At the community level, we review multiple-predator effects and effect of alternative prey on pest suppression. Evidence for a key role of spiders in pest suppression is accumulating. Importantly, recent research has highlighted widespread non-consumptive effects and complex intraguild interactions of spiders. A better understanding of these effects is needed to optimize biocontrol services by spiders in agroecosystems.

Keywords Araneae · Agroecosystem · Food-web · Functional trait · Niche · Pest

Introduction

Pest regulation by naturally occurring predators is important for effective crop protection (Furlong et al. 2004; Bommarco et al. 2011). The role of generalist predators such as spiders in pest regulation is debated because they can either significantly contribute to pest suppression (Lang 2003; Schmidt et al. 2004; Birkhofer et al. 2008a; Isaia et al. 2010; Lefebvre et al. 2017) or disrupt it (Lang 2003; Schmidt-Entling and Siegenthaler 2009). Here we review the trophic ecology

of spiders in agroecosystems. Spiders are among the most abundant predators in many agroecosystems and are most diverse generalist predators (Birkhofer et al. 2013). Spiders use a broader range of hunting strategies (Cardoso et al. 2011), occupy wider variety of spatial niches from litter to tree canopies (Marc et al. 1999), and are distributed across more trophic levels (Mestre et al. 2013; Sanders et al. 2015) than other generalist predators, such as carabids and other beetles, earwigs, syrphid flies, and heteropterans. Hence, spiders are excellent model organisms to study the effect of generalist predators on pest suppression.

To improve the pest control potential of spiders, it is necessary not only to investigate the factors that influence their abundance and diversity in agroecosystems (reviewed, e.g., in Birkhofer et al. 2013; Baba and Tanaka 2016; Benamú et al. 2017), but also to understand the trophic ecology of spiders, a subject which has been much less studied. The necessity to combine both approaches arises from the fact that higher abundances and greater diversity of spiders not necessarily translate into more efficient pest control (Hanna et al. 2003; Markó and Keresztes 2014; Tschardt et al. 2016). The mechanistic approach of trophic ecology can help to explain when this occurs. Ideally, it can identify the

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composition of spider communities in agroecosystems that provide the desired pest control outcome (Jonsson et al. 2017).

Our aim with this review was to provide an update of our knowledge on the role of spiders as generalist predators in conservation biological control. There are several excellent reviews on spiders as biocontrol agents each dealing with different aspects of trophic ecology (Riechert and Lockley 1984; Nyffeler and Benz 1987; Hodge 1999; Marc et al. 1999; Riechert 1999; Rypstra et al. 1999; Sunderland 1999; Symondson et al. 2002; Maloney et al. 2003; Wise 2006). However, this field of research has strongly progressed during the past decade. Many perspectives were updated and several basic ecological hypotheses proposed that can be used to improve biocontrol potential of spiders. Examples include the determinants of spider trophic niches, how trophic interactions are influenced by inter- and intraspecific variation in traits, and what role pest control by spiders plays in multi-predator settings. In our review, we focus on the trophic ecology of spiders at levels ranging from individuals to communities. At the individual and population level, we review the determinants and dynamics of spider trophic niches (i.e., intraspecific changes in niche position and/or width), such as hunting strategy, body size, life stage, nutritional target, and personality (i.e., consistent inter-individual differences in behaviour; Bell et al. 2009). We further review the predatory response to pests (i.e., functional and numerical responses), the non-consumptive effects of spiders on pests (i.e., the consequences of predation risk) and the factors that influence them. At the community level, we review multiple-predator effects (i.e., antagonistic, additive, and synergistic effects) on pest populations, the effects of the diversity and composition of spider communities on pest suppression, and the effects of the presence of alternative prey on pest suppression.

Individual and population effects: predator-pest interaction

Bottom-up as well as top-down effects need to be considered to understand how predator–prey interactions affect the biocontrol potential of spiders (Schmitz 2010; Hanley and La Pierre 2015; Fig. 1). The investigation of spider trophic niches and their determinants are essential to elucidate, to the large extent, the bottom-up and top-down interactions. The top-down point of view can help to evaluate the potential of spiders to suppress certain pests or to disrupt the biocontrol by particular natural enemies (Denno et al. 2004; Liu et al. 2015), while the bottom-up point of view can help to identify prey that would sustain abundant spider populations and maintain their high capture rates (Bressendorff and Toft 2011; Tsutsui et al. 2016, 2018). However, it is

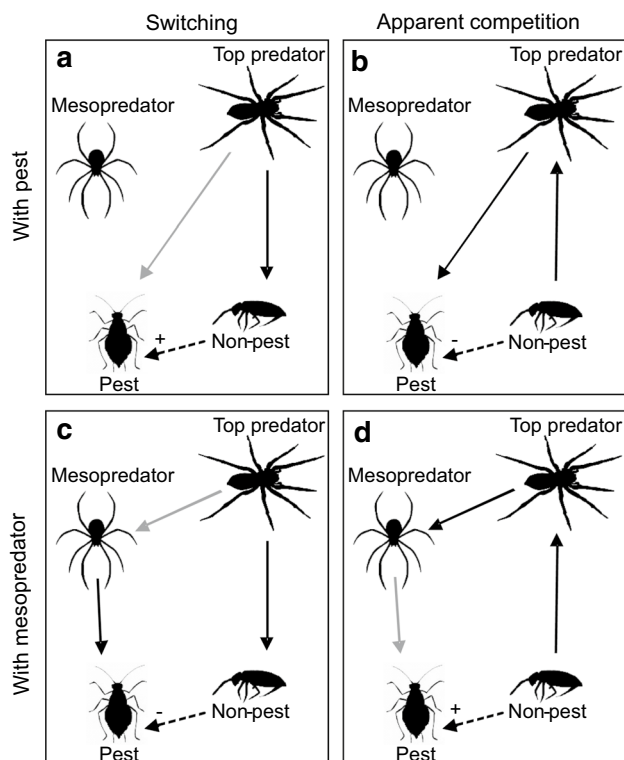


Fig. 1 Effects of alternative prey on pest suppression by a community of generalist predators. Top predators can either switch from the pest (a) or the mesopredator (c) to the non-pest prey. Alternatively, non-pest prey can enhance the density and/or feeding rate of the top predator, thereby inducing apparent competition with the pest (b) or the mesopredator (d). Indirect effects (dashed arrows) of alternative prey on pests can thus be positive (a, d) or negative (b, c). Direct effects are displayed as solid arrows. Effects that are reduced in the presence of alternative prey are displayed in grey

also necessary to consider other effects than prey composition. For example, spider species with low preferences for a pest but a high capture rate can reduce the pest more than other spiders with high preferences for the pest but with a low capture rate (Michalko and Pekár 2017). Alternatively, other spider species can exert a strong non-consumptive effect causing lower fecundity, or a higher emigration rate in the pest, which together can outweigh prey mortality (Werner and Peacor 2003; Schmitz 2010). In this chapter, we review the key aspects that determine the predator pest interactions at the individual and population level, namely the determinants of spider trophic niches (“The determinants of spider trophic niches”), their predatory responses to pest (“Response of predators to pests”), and their non-consumptive effects on pests (“Non-consumptive effects”).

The determinants of spider trophic niches

Generalist spiders are euryphagous predators that prey mostly on arthropods, especially insects and other spiders

(Pekár et al. 2012). Their diets are dominated by Diptera, Hemiptera, Hymenoptera, and Coleoptera (Michalko and Pekár 2016). Generalist spiders have been previously considered as highly opportunistic utilizing their prey proportional to its availability (Riechert and Lockley 1984). However, recent research indicates that many spiders, if not most, show some degree of prey selectivity (e.g., Agustí et al. 2003; Harwood et al. 2004; 2005; 2007; Kuusk and Ekblom 2010, 2012; Kobayashi et al. 2011; Chapman et al. 2013; Schmidt et al. 2012a; Michalko and Pekár 2015; Perkins et al. 2018). The trophic niche of a spider depends on the interplay between traits of the spider (e.g., hunting strategy, body size), of its prey (e.g., body size, movement, defensiveness, nutritional content), and conditions of the environment (e.g., temperature, microhabitat structure, local selection pressures, prey community composition) (Riechert 1991; Kruse et al. 2008; Richardson and Hanks 2009; Schmidt et al. 2012b; Sanders et al. 2015; Michalko and Pekár 2015; Perkins et al. 2018). Given these multiple effects, the realized niches of generalist spiders can exhibit high spatio-temporal dynamics.

Hunting strategy

Spiders employ a wide variety of hunting strategies, which differ in their efficiency in capturing specific prey types (Michalko and Pekár 2016). For example, sit-and-wait spiders are more effective in capturing highly mobile prey, while pursuing spiders are more effective in capturing sedentary prey (e.g., Kuusk and Ekblom 2012; Sweeney et al. 2013). Consequently, spiders with different hunting strategies utilize similar prey types but in different proportions (Birkhofer and Wolters 2012; Michalko and Pekár 2016). This can affect their efficiency in suppressing herbivores.

Relative prey size

Spiders prey on insects of certain body size ranges relative to their own body size (Nentwig and Wissel 1986; Yamanoi and Miyashita 2005; Okuyama 2007; Michalko and Pekár 2014, 2015). Relatively small and large prey is often ignored by spiders because it is unprofitable (Nentwig and Wissel 1986; Stephens et al. 2007). A spider species can be effective in suppressing several pests that fall within its preferred body size range. On the other hand, a spider species may be limited to certain body size cohorts of a pest with a wide range of body sizes, such as caterpillars.

Prey nutritional composition

Generalist spiders need to optimize their nutritional intake while minimizing the intake of toxins in order to maximize their fitness (Wilder 2011; Toft 2013). Different prey

species are of different quality for spiders, which are able to select prey according to its nutritional and toxin content (Toft 1999; Mayntz et al. 2005; Schmidt et al. 2012b). The trophic niche of spiders can, therefore, be determined by the nutritional content of pests and other potential prey in the agroecosystem. Many pests (e.g., aphids) are of sub-optimal quality for spiders (e.g., Toft 2005). Spiders can have an aversion to, and completely ignore low-quality prey (Toft and Wise 1999a). However, due to a generalized search image (e.g., Pekár et al. 2013), generalist spiders can continue to kill low-quality pests but exploit them only for a short time if high-quality prey is present, because spiders may not be able to distinguish between the two prey before attack initiation (Toft and Wise 1999a). In addition, some low-quality prey can be ingested as a nutritional supplement within a mixed diet (Toft 1995).

Trophic niche dynamics

The trophic niche of a spider species can be dynamic in space and time. Niche dynamic means a change in the niche position, width, and internal structure of population niche [i.e., intraspecific niche partitioning (Pearman et al. 2008; Araújo et al. 2011)]. The trophic niche depends on the ontogenetic stage (Bartos 2011; Pekár et al. 2011); body size (Sanders et al. 2015); feeding history [hunger, nutritional state (Riechert 1991; Schmidt et al. 2012a, 2012b)]; environmental factors, such as temperature (Kruse et al. 2008); and on the presence of natural enemies and competitors (Michalko and Pekár 2014). For example, some spiders preferred lipid-rich prey to improve their energy reserves prior to overwintering, but shifted to more protein-rich prey to enhance their growth and development after winter (Bressendorff and Toft 2011).

Ambient temperature can affect the trophic niches of spiders because it influences their ability to catch prey and the ability of the prey to escape (Kruse et al. 2008). Spiders can switch from sit-and-wait to a more active hunting mode with increasing temperature or because temperature affects silk properties (Yang et al. 2005; Kruse et al. 2008). Given the allometric responses of spiders and their prey to changing temperature, the trophic niches of spiders can differ between seasons, years, or regions (Dell et al. 2014).

Feeding preferences of generalist predator are also determined by the relative abundances of alternative prey. Thus, the suitability rank of a pest species changes with its relative availability (Ryabov et al. 2015). For example, the wolf spider *Pardosa milvina* (Hentz) utilizes dipterans more frequently than expected when they are scarce, but less frequently than expected when they are overabundant (Schmidt et al. 2012a).

Spider populations may be exposed to different selection pressures, which can lead to different behavioural

phenotypes (i.e., personalities). Selection pressures that affect spider behaviour include prey availability, predation pressure on spiders, and pesticide application (Riechert and Hedrick 1993; Royauté et al. 2014). The functioning of spiders in an agroecosystem can then largely depend on local selection pressures (Royauté and Pruitt 2015). For example, aggressive individuals have higher capture rates than timid individuals (Pruitt and Riechert 2012). The behavioural types can occupy distinct trophic niches (Riechert 1991; Michalko and Pekár 2014, 2017). Aggressive individuals can then have a wider trophic niche than timid individuals, because they are less prey selective (Riechert 1991; Michalko and Pekár 2014, 2017). Individuals can also differ in their level of activity and, according to the locomotor cross-over hypothesis (Huey and Pianka 1981), more active individuals will more likely catch sedentary pests, while less active individuals will more likely catch mobile pests (Sweeney et al. 2013). The distribution (mean, variance) of behavioural types within a spider population can, therefore, have a profound effect on the abundances of other spiders, and on pest community composition (Bolnick et al. 2011; Royauté and Pruitt 2015; Michalko and Pekár 2017).

Response of predators to pests

The total response of a predator to prey is the product of functional and numerical responses (Solomon 1949). The functional response expresses a relationship between prey density and mean number of prey killed by a single predator (Holling 1965), while the numerical response describes the change in the numbers of predators through aggregation and reproduction (Solomon 1949).

Functional response

There are three basic types (I–III) plus a few rare types, such as the dome-shaped or roller-coaster type of functional response, which are all documented in generalist spiders (Holling 1965; Denno et al. 2003; Vucic-Pestic et al. 2010; Bressendorff and Toft 2011; Schmidt et al. 2012a; Michalko and Košulič 2016).

Type I is characterized by a linear increase in the number of prey killed with prey density to some threshold above which the number of killed prey remains constant (Jeschke et al. 2004; Fig. 2). This type was observed not only in web spiders (e.g., Mansour and Heimbach 1993) but also in actively hunting spiders affected by pesticides that kill but do not consume the prey (Michalko and Košulič 2016).

Spiders have been mainly found to display the type II functional response (e.g., Riechert and Lockley 1984; Fig. 2). The type II functional response implies that predation pressure on the pest is highest at low pest densities (Sinclair et al. 1998). An abundant population or community of

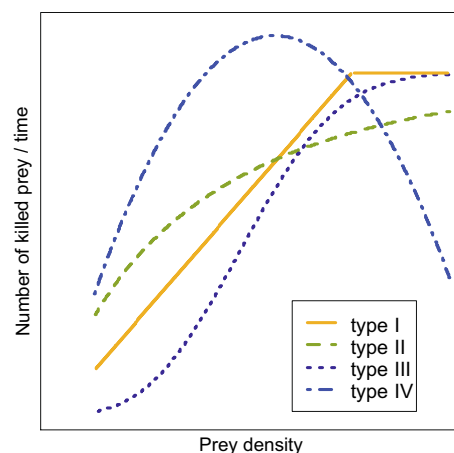


Fig. 2 The four types of predator functional response to prey density

spider predators can, therefore, exert very intense predation pressure on the pest at the beginning of the season when the pest begins to reproduce. This may lead to the local exclusion of a pest and an overall reduction in pest population size, or significantly decelerate the pest's initial population growth (Sinclair et al. 1998). On the other hand, a type II functional response means that once a pest population grows in spite of spider presence, the predatory impact of spiders will diminish.

The type III response (Fig. 2) is characterized by a sigmoid shape with a shifted increase in capture rate from low to intermediate prey densities combined with an asymptotic increase from intermediate to high prey densities (Křivan 2008). The type III response arises due to learning and/or prey switching (Sinclair et al. 1998). It is the only functional response which can by itself stabilize the predator–prey system and by which the predator can keep the pest under control (Sinclair et al. 1998). However, this is only possible if the density of the pest falls within the area of densities in which the killing rate increases more than proportionally to the pest density and the pest does not exceed the release threshold (Křivan 2008). Although the type III response has been observed in spiders, it has previously been considered rare (Riechert and Lockley 1984; Wise 1993). However, the presence of the type III functional response in spiders may be underestimated due to the experimental settings frequently used. The functional responses of spiders have been investigated mostly with only single prey types or in homogenous environments which do not meet the conditions required for a type III to be observed (Křivan 2008). The disproportional predation on various prey types relative to their availability and high behavioural flexibility indicates a high potential for the presence of prey switching in spiders (e.g., Herberstein 2011; Schmidt et al. 2012a). Spiders are able to learn about, and avoid some prey (Toft 1999).

The most common type of functional response among generalist spiders is likely transitional between type II and type III depending on the prey community composition. This arises from imperfect prey selectivity, which means that prey are delimited by their traits such as size, movement, shape, etc. According to the degree of similarity in these traits, predators may or may not be able to distinguish between prey types (Morozov and Petrovskii 2013; Ryabov et al. 2015). Switching will likely be present only in cases where predators are able to distinguish between prey before they kill. Spiders are not able to distinguish between all prey species prior to attack. For example, cursorial *Philodromus* spiders distinguished between a psylla pest and *Dictyna* spiders before they initiated an attack (Petráková et al. 2016). However, cursorial *Pardosa* spiders needed to taste aphids to distinguish between toxic and palatable aphid species (Toft and Wise 1999a).

The type IV functional response is dome-shaped (Fig. 2), which means that the capture rate increases with prey density but sinks above a certain threshold. In spiders, the dome-shaped capture rate can be caused, for example, by a nutritional imbalance induced by overconsumption of prey of low nutritional quality (Bressendorff and Toft 2011; Schmidt et al. 2012b). The absence of high-quality prey or prey with complementary nutritional content (alternative, pest) reduces the conditions of spiders and consequently can reduce their predation rate. Therefore, alternative prey can act as a nutritional balancer that would maintain a high killing rate with respect to the pest (Fig. 1; Mayntz and Toft 2000; Oelbermann and Scheu 2009; von Berg et al. 2009).

Regardless of the type of functional response, spiders have a high asymptote of capture frequency compared to other predators, delaying the saturation of prey capture rates (Wise 1993; Nyffeler and Birkhofer 2017). This is due to partial feeding and overkilling (Riechert and Harp 1987; Samu 1993; Samu and Bíró 1993). The high killing rate predestines spiders to impose high predation pressure on pests.

Numerical response

Aggregation of spiders in prey-rich areas is determined by their movement behaviour. Spiders are able to move through the air by ballooning (Decae 1987; Bell et al. 2001). However, ballooning is passive with little control over the landing location, which limits the ability of spiders to direct themselves to prey-rich locations. Spiders can direct themselves to areas of high prey density by walking, or by a series of ballooning events in which low prey densities enhance their propensity to initiate another flight until an area of high prey density is reached (Mestre and Bonte 2012). Ballooning is thus less suitable for aggregating in areas of high pest infestation compared, for example, to the utilization of prey kairomones by active dispersers such as parasitic wasps

(Schellhorn et al. 2014). In addition, the ballooning ability of spiders is limited to a relatively short period (Decae 1987). The aggregative response of spiders among crop fields is, therefore, ineffective in comparison to that of insect natural enemies with active flight, inasmuch as random dispersal imposes very long lags in the aggregative response (Riechert and Lockley 1984). In contrast to such a slow long-distance aggregative response, the within-field aggregative response in cursorial species can be rapid, as some spiders can be relatively mobile within a crop field and its adjacent habitats (Samu et al. 1999; Birkhofer et al. 2018). Indeed, aggregation in patches with high abundances of their preferred prey has been observed in cursorial spiders as well as in spiders with strong ballooning propensity (Harwood et al. 2003; Schmidt and Rypstra 2010).

Given that most spiders reproduce only once per year while many pest species have several generations, the tracking of pest density through reproduction is impossible for spiders (Riechert and Lockley 1984). The reproductive response of generalist spiders is connected to several rather than to single prey species (Murdoch et al. 2002). In addition, spiders are well adapted to periods of starvation (Riechert and Harp 1987). All this enables spiders to maintain relatively high population densities in agroecosystems throughout the season even when pests are absent. Additional limitations to spiders in biocontrol are their territoriality and their cannibalistic tendencies, which further limit their numerical response to prey availability (Schmidt and Rypstra 2010; Gan et al. 2015; Lesne et al. 2016).

Non-consumptive effects

Spiders, similarly to other predators, exert non-consumptive effects on the prey phenotype (Schmitz 2005; Bucher et al. 2014a). In the short term, pest suppression can be greater due to the non-consumptive than due to the consumptive effect (Cronin et al. 2004; Beleznaï et al. 2017). Spiders can dislodge pests (caterpillars, aphids), which leads to increased mortality as the pests are exposed to other predators and to stressful environmental conditions, or are unable to relocate their host plant and starve (Sunderland 1999). Other non-consumptive effects include behavioural or physiological changes in pests as a response to predation risk (Werner and Peacor 2003). A pest can reduce its movement and foraging activity to lower its detectability by spiders (Rypstra and Buddle 2013; Bucher et al. 2014a; Beleznaï et al. 2015) or can increase its mobility to actively avoid areas of high predation risk (Schmitz et al. 1997; Binz et al. 2014; Bucher et al. 2015a). However, pests can also increase their foraging in the presence of predators to satisfy their increased metabolism due to chronic stress and vigilance, which can lead to increased herbivory and crop damage (Hawlena and Schmitz 2010a, 2010b; Bucher et al. 2014b; Rendon et al.

2016). Behavioural and physiological changes are associated with fitness costs—slower development, lower fecundity, and shorter longevity, which retards pest population growth (Preisser and Bolnick 2008; Hawlena and Schmitz 2010b).

The type and intensity of a pest's behavioural response to predation risk depends on the interplay between the traits of the pest and predator (foraging modes, habitat domains) and can change over the lifetime of the pest (Binz et al. 2014; Miller et al. 2014). A framework for adaptive anti-predator response based on the combination of habitat domains and foraging modes suggests that when the pest has a broad habitat domain relative to the predator, the adaptive anti-predator response is a habitat shift (Schmitz 2005). In contrast, if the pest has a narrow habitat domain, the anti-predator response should always be activity reduction. If both, pest and predator have a broad domain and the predator employs a sit-and-move foraging mode, then the response should be either habitat shift or activity reduction. If the predator hunts actively then the response should be movement out of the zone of immediate danger. The pest can also respond selectively to predators that represent high risk. For example, crickets responded only to the chemo-tactile cues produced by large and common spiders (Binz et al. 2014).

As pests' responses to predation risk are context-dependent, the manner and strength in which non-consumptive effects of spiders cascade down on crops is also context-dependent. Consumptive and non-consumptive effects interact and can act complementarily or antagonistically (Schmitz 2005). In the former case, reduced feeding by a pest and its mortality reduce crop damage or pathogen transmission.

In contrast, increased pest foraging may (over)compensate pest mortality, at least in the short term. The net effect of a spider predator on a crop would then depend on the relative strength of the consumptive and non-consumptive effects and the fitness costs resulting from the non-consumptive effect (Werner and Peacor 2003; Hawlena and Schmitz 2010a). If enhanced per capita feeding by pests exceeds the consumptive effect, then predation pressure could even enhance crop damage. For example, spiders can reduce the numbers of pest caterpillars on cotton by direct consumption but, at the same time, increase their herbivory by increasing feeding activity, which, overall, reduces the cotton yield (Rendon et al. 2016). On the other hand, the stress elicited by predation risk may impose high pest mortality or reduce fecundity (Hawlena and Schmitz 2010b). Especially in the long term, the effects of high mortality and low fecundity among pests likely outweigh the enhanced per capita feeding rate of the pest. As the few investigations on non-consumptive effects of spiders on pests have mostly been short-term and conducted at the individual level, this question about the relative contribution of consumptive and non-consumptive effects on pest suppression remains to be explored.

Theoretically, if the pest response to predation risk is emigration to spider-free patches, the result will be scale-dependent because the pest will cause less damage in the risky patches but more damage in the safe patches where it may aggregate (Schmitz et al. 1997; Bucher et al. 2015b; Fig. 3). The overall damage would then depend on the ratio, juxtaposition, and configuration of risky (high density of predator) and safe (low density of predator) patches, and

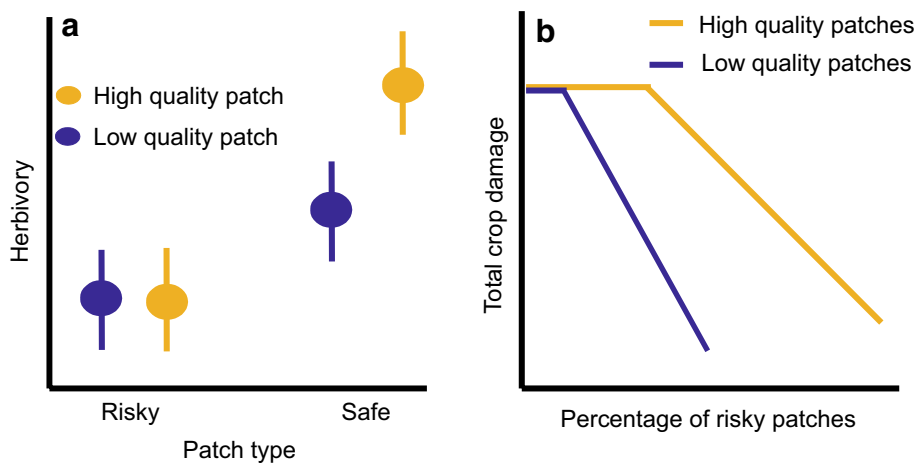


Fig. 3 Theoretical perspective on the long-term non-consumptive effect of spiders on herbivores at various spatial scales. An agroecosystem comprises risky and safe patches for a pest. The pest emigrates from the risky patches to the safe patches as a response to predation. Consequently, there are fewer herbivores in the risky patches but more in the safe patches (a). The number of herbivores in an agroecosystem with low-quality safe patches is lower than in an agroecosystem with high-quality safe patches. On the scale of a

whole agroecosystem (b), there may be no net-effect on herbivores because the high density of herbivores in the safe patches might compensate for the low density in the risky patches. Once the safe patches are unable to compensate for the risky patches, the density of herbivores will start to decline on the scale of the whole agroecosystem. The herbivore density will start to sink sooner and more rapidly in agroecosystems with low-quality safe patches than in agroecosystems with high-quality safe patches

also on the quality of the safe patches (Laundré et al. 2014). For example, in an agroecosystem with a high percentage of risky patches, the relocation of herbivores to safe patches would reduce overall crop damage. The lower the quality of the safe patches for the pest, the faster would overall crop damage decline with increasing percentage of risky patches, because of the increased pest mortality and reduced fecundity (Fig. 3).

The mosaic of risky and safe patches may arise, for example, in the multi-crop agroecosystems with a generalist herbivore where some crops would be unsuitable for spiders. Alternatively, safe patches may be produced by application of pesticides because many pests are more resistant to pesticides than spiders (Pekár 2012). The effect can be long-term if the efficacy of pesticides' residues is long-term or if the pesticides are applied during a period when spiders do not perform long-distance movement (Pekár 2012).

The community effect of multiple predators and alternative prey on pest suppression

In agroecosystems, spiders interact in communities with other natural enemies, pests, and alternative prey. The top-down control exerted by spiders on pest depends on their direct and indirect interactions with other natural enemies and alternative prey. The combined effect of multiple predators on pest suppression can be additive [i.e., the sum of the per capita effects of each predator species in a single population (A) equals the total effect of the diverse predator community (B)], synergistic (i.e., $A < B$), and antagonistic [$A > B$ (Sih et al. 1998; Schmitz 2007)]. Additive and synergistic predation enhances pest mortality while antagonistic predation reduces pest mortality (Sih et al. 1998). The intensity of the top-down control by the predator community is then influenced by the interactions among predators' densities and their traits (Schneider et al. 2012; Klečka and Boukal 2013; Jonsson et al. 2018). Similarly, the effect of alternative prey can affect the pest suppression positively or negatively through various positive or negative and direct and indirect prey–prey, predator–prey, and predator–predator interactions determined by their densities and traits (Klečka and Boukal 2013; Abrams and Cortez 2015; Holt and Bonsall 2017). The mechanisms that enhance and disrupt pest control occur simultaneously, and it depends on community composition, whether the overall effect of diverse community on pest suppression will be positive, negative, or neutral (Letourneau et al. 2009; Griffin et al. 2013).

In this section, we will review the causes of the antagonistic interactions and their impacts on pest suppression (“The causes of antagonistic interactions and their impacts on pest suppression”). We also review the mechanisms that enable the additive and synergistic effects of multiple predators

(“Niche complementarity enables additive and synergistic effects of multiple predators”), and the effect of alternative prey (“Alternative prey and pest suppression”) that can affect the pest suppression directly or through alteration of interactions among predators. We will focus on interactions among spiders and their prey for simplicity and for the sake of space limitation, although spiders interact with many other natural enemies (Traugott et al. 2012; Sitvarin and Rypstra 2014).

The causes of antagonistic interactions and their impacts on pest suppression

Intraguild predation

IGP, i.e., predation among potential competitors, is inevitable among generalist predators (Polis et al. 1989). Spiders prey on diverse spectrum of natural enemies, such as parasitoids, predaceous heteropterans (Whitehouse et al. 2011; Traugott et al. 2012), and other spiders (Wise 1993). Meanwhile, they are themselves exposed to predation from predatory beetles, ants, and birds, etc., (Wise 1993). Spiders represent a substantial proportion of the diet in cursorial spiders (Michalko and Pekár 2016).

IGP among spiders is often body size-dependent (Okuyama 2007; Korenko and Pekár 2010). The probability of a mesopredator (i.e., a predator at lower trophic level) being killed decreases more rapidly with decreasing top predator-to-mesopredator body size ratio in comparison with a top predator-to-herbivore body size ratio (Rypstra and Samu 2005; Michalko and Pekár 2015). This is because spiders are dangerous prey and a mesopredator can seriously harm or even kill a top predator (Foelix 2011; Michalko and Pekár 2017). Furthermore, generalist spider species lack specialized adaptations to overcome IG prey (Pekár and Toft 2015). Other spiders, therefore, represent a low-rank diet item for generalist spiders and the intensity of IGP decreases with the availability of alternative innocuous and palatable prey (Rickers et al. 2006; Oelbermann et al. 2008; Michalko and Pekár 2015; Petráková et al. 2016). However, if the top predator-to-mesopredator body size ratio is sufficiently large, then IGP increases rapidly and small spiders can become more preferable prey for large spiders than pests (Petcharad et al. 2018).

The classical perspective is that IGP reduces pest suppression due to the consumptive and non-consumptive effects of a top predator on a mesopredator (Rosenheim et al. 1995; Müller and Brodeur 2002; Schmidt-Entling and Siegenthaler 2009). The non-consumptive effects are similar as in herbivores described above (“Non-consumptive effects”). The mesopredator can reduce its foraging (Walker and Rypstra 2003), emigrate (Schmidt-Entling and Siegenthaler 2009; Mestre et al. 2014), or change microhabitat (Folz et al.

2006). IGP also reduces the capture rate of the pest by the top predator (Pekár et al. 2015; Michalko and Pekár 2017).

Typically, the consumptive as well as non-consumptive effects of IGP lead to the ecological release of a pest (e.g., Finke and Denno 2006; Schmidt-Entling and Siegenthaler 2009). Several factors determine the extent to which IGP affects pest suppression, such as the relative pest suppression efficiency of the predators, the top predator's prey preferences, and the mesopredator's mobility. If the top predator is more efficient in pest suppression than the mesopredator, then IGP will not have severe consequences for biocontrol. However, if the mesopredator is highly effective against the pest, then IGP can cause the ecological release of the pest (Rosenheim and Harmon 2006; Michalko and Pekár 2017). However, regardless of the differences in suppression efficiency between predators, if the mesopredator's mortality is buffered by immigration, the effect of IGP on pest suppression would probably be minimal.

Most experiments on IGP were conducted at short time-scale whereas at long time-scale the diverse predator community can enhance pest suppression despite strong IGP (Snyder and Ives 2003). If nutritional value of IGP is considered, IGP might, theoretically, have a synergistic effect in the long-term. The general nutritional value of a mesopredator for a top predator is not well known as observations are ambiguous (Toft and Wise 1999b; Oelbermann and Scheu 2002). Mayntz and Toft (2006) concluded that IGP is highly profitable for spiders and that the negative effects found in other studies (Toft and Wise 1999b; Oelbermann and Scheu 2002) were caused by a reluctance to prey on other spiders. In addition, various trophic levels differ systematically in their macronutrient composition (Fagan and Denno 2004; Lease and Wolf 2011). Preying on multiple trophic levels can help spiders to optimize their nutritional demands and IGP can improve their nutritional balance (Matsumura et al. 2004; Mayntz and Toft 2006; Wilder et al. 2013). In addition, IGP can help to overcome periods of alternative prey shortage, prevent starvation, and maintain high abundances of spider top predators in the agroecosystem (Toft and Wise 1999b; Mayntz and Toft 2006).

The high consumption of a pest can cause a nutritional imbalance in a top predator, which would reduce its per capita capture rate and fecundity (Toft 2005; Bressendorff and Toft 2011). As the mesopredator can act as a nutritional balancer, IGP may maintain a high capture rate and high fecundity in the top predator (Mayntz and Toft 2000, 2006; Bressendorff and Toft 2011). The system with a nutritionally balanced top predator might be more efficient than the joint predation of a nutritionally imbalanced top predator and mesopredators. This hypothesis needs to be tested.

Interference competition

Non-consumptive interference among spiders can also reduce their *per capita* capture rate due to lost time in direct interactions, reduced prey acceptance, and/or reduced search efficiency due to reduced activity (Schmidt et al. 2014; Michalko et al. 2017). The *per capita* capture rate decreases with increasing spider density. Interference can be so strong that the enhanced densities of the predators may not be able to compensate for the lower capture rate, which can consequently reduce the overall predation pressure on the pest. For example, overall predation pressure of *Philodromus* spiders on a psyllid pest increased only asymptotically with spider densities (Michalko et al. 2017). This clearly indicates that simply increasing the abundances of spiders does not necessarily lead to increased predation pressure on pests. Non-consumptive interference can also lead to emigration due to reduced consumption, which can further reduce the predation pressure on a pest (Schmidt and Rypstra 2010; Schmidt et al. 2014).

Niche complementarity enables additive and synergistic effects of multiple predators

In synergistic predation, the pest changes its behaviour to avoid one predator but, at the same time, makes itself more vulnerable to other predators. In additive predation, the vulnerability of the pest does not depend on the presence of another predator (Losey and Denno 1999). In both cases, additional predators increase pest mortality. Empirical evidence shows that synergistic effects arise with some type of niche complementarity among natural enemies, which reduces enemy-free space for the pest, and minimizes IGP and interference among spiders (Schmitz 2007). In addition, the utilization of alternative resources reduces exploitative competition and enables larger populations of natural enemies to build up, thus enhancing predation pressure on the pest through numerical responses. The predation pressure is enhanced when niche complementarity occurs within species [due to personality differences and/or individual specialization (Bolnick et al. 2011; Royauté and Pruitt 2015; Pruitt et al. 2016)] as well as between species (Losey and Denno 1999; Finke and Snyder 2008; Knop et al. 2014; Pruitt et al. 2016). Spider niches can be complementary with regards to prey, space, time, and behaviour.

Trophic niche complementarity arises when spiders utilize different prey types and/or body sizes. Apart from reducing exploitation, the utilization of different prey type can also ensure that spiders aggregate in different patches (e.g., Harwood et al. 2003), which may, theoretically, reduce the number of safe patches for the pest (Laundré et al. 2014). With respect to prey body size, spiders can prey on different size cohorts of pests (Nentwig and Wissel 1986), which

reduces the body size-mediated enemy free space for the pest.

Spatial complementarity arises with horizontal and vertical stratification on various scales from habitats to microhabitats. For example, tetragnathid and wolf spiders, these occupying distinct habitat domains, exert synergistic predation on a mirid pest in paddy fields. To avoid predation, mirids shifted from the rice canopy, where they were predated by tetragnathids, to lower plant parts, where they fell prey to wolf spiders (Takada et al. 2013).

Temporal complementarity includes distinct diurnal activity and distinct phenology on the part of predators. For example, the abundance of a dipteran pest in olive orchards was negatively correlated with philodromid spiders at the beginning of season, and negatively correlated with linyphiids later in the season (Picchi et al. 2016).

Spatio-temporal complementarity among spiders may also include condition-dependent efficiency in pest suppression. For example, various spider species are adapted to catch pests at different temperatures. Two syntopic cursorial spider species, *Anyphaena accentuata* (Walckenaer) (Anyphaenidae) and *Philodromus cespitum* (Walckenaer), which occupy a similar trophic niche, differ in their prey capture efficiency at various temperatures (Korenko et al. 2010; Petráková et al. 2016). *Anyphaena* is more efficient in capturing fruit flies at 15 °C while *Philodromus* is more efficient at temperatures above 20 °C (Korenko et al. 2010).

Spiders can be complementary also by means of hunting mode (Schmitz 2005). The adaptive response of a pest to a sit-and-wait spider is reduced activity, but this makes the pest more vulnerable to actively hunting spiders that search for inactive prey. Similarly, the adaptive response of pests to active spiders is enhanced activity as they try to avoid immediate danger and/or emigrate, but this makes the pest more vulnerable to sit-and-wait predators (Schmitz 2005; Sweeney et al. 2013; Miller et al. 2014). Another form of behavioural complementarity may, theoretically, arise if highly body size-structured pests, like caterpillars, reduce their feeding activity due to an anti-predatory response (Schmitz 2005): the slowed growth of the pest may prevent it from reaching a body size-mediated refuge from small predators.

Whether the functional traits of spiders will be complementary or not can be again context-dependent. For niche complementarity to improve the biocontrol efficiency of natural enemies, an environment needs to allow for niche differentiation by means of its spatial, temporal and/or prey heterogeneity (Tylianakis and Romo 2010). For example, body size differences among natural enemies can enable microhabitat niche partitioning in a spatially structured environment, like tree bark, as the small crevices provide enemy free space for the mesopredator by excluding the large top predator (Korenko and Pekár 2010). Increased habitat complexity, which reduces negative predator–predator interactions but

improves niche complementarity, then increases predation pressure on the pest (Riechert and Bishop 1990; Finke and Denno 2006; Michalko et al. 2017). In contrast, in relatively simple environments that do not provide spatial segregations among differently sized generalist predators, body size differences among spiders may enhance IGP and consequently reduce pest suppression efficiency (Finke and Denno 2006; Rusch et al. 2015).

Alternative prey and pest suppression

Spiders also capture alternative prey to pests, which can either reduce, increase, or have no effect on pest suppression by spiders (Madsen et al. 2004; Birkhofer et al. 2008b; Gavish-Regev et al. 2009; Oelbermann and Scheu 2009; Kuusk and Ekbom 2010, 2012; Kobayashi et al. 2011; Samu et al. 2013; Knop et al. 2014; Welch et al. 2016; Roubinet et al. 2017; Fig. 1). Alternative prey can affect pest suppression through a variety of mechanisms and conditions, such as predator switching, apparent competition, prey and pest identity, alternative prey density, and the spatio-temporal overlap between spider, pest and alternative prey.

Predator switching and apparent competition

Through predator switching and apparent competition, alternative prey can affect pest suppression in contrasting ways (Fig. 1). Alternative prey can reduce biocontrol if spiders switch from pest to non-pest prey (Fig. 1a) (Toft 1999; Gavish-Regev et al. 2009; Birkhofer et al. 2008b). Reduced biocontrol can also occur through apparent competition between alternative prey and a mesopredator. If alternative prey increase abundances of a top predator that consequently reduces a mesopredator through IGP, this could benefit the pest (Fig. 1d) (Halaj and Wise 2002; Oelbermann et al. 2008).

On the other hand, alternative prey can enhance biocontrol by spider communities if the top predator switches from the mesopredator to the alternative prey, thus enhancing pest suppression by the mesopredator (Fig. 1c). However, the most commonly observed effect of alternative prey is enhanced biocontrol through apparent competition with the pest (Fig. 1b). Alternative prey can supplement energy and nutrients to spiders and improve their tolerance to toxic prey (Mayntz and Toft 2000; Bressendorff and Toft 2011). Consequently, the subsidy of alternative prey can increase abundances and killing rate of spiders in agroecosystems (Settle et al. 1996; Chen and Wise 1999; Tsutsui et al. 2016, 2018). Alternative prey can further enable niche complementarity between predators (Knop et al. 2014) and reduce IGP (Rickers et al. 2006). Interference among herbivores can increase their vulnerability to spiders (Knop et al. 2014).

Alternative prey and pest identities

The prey selection of spiders can depend on prey community composition (Heong et al. 1991; Schmidt et al. 2012a). The subsidies of different alternative prey types can support or detract from the suppression of certain pest species. For example, the subsidy of prey from an aquatic ecosystem enhanced the suppression of weevils but reduced the suppression of leafhoppers by spiders in a riparian ecosystem (Graf et al. 2017).

Alternative prey density

Alternative prey density can affect the biocontrol efficiency by altering IGP. Theory predicts that a top predator that is superior in interference, and a mesopredator that is superior in exploitation, can coexist only at intermediate abundances of prey unless there is some additional niche partitioning (Janssen et al. 2007; Amarasekare 2008; Fig. 4). At low prey densities, the top predator is excluded by exploitation, while at high prey densities the mesopredator is excluded by interference and exploitation (Holt and Polis 1997; Fig. 4). Therefore, both predators can respond positively to prey density at first, but as the interference intensifies, the top

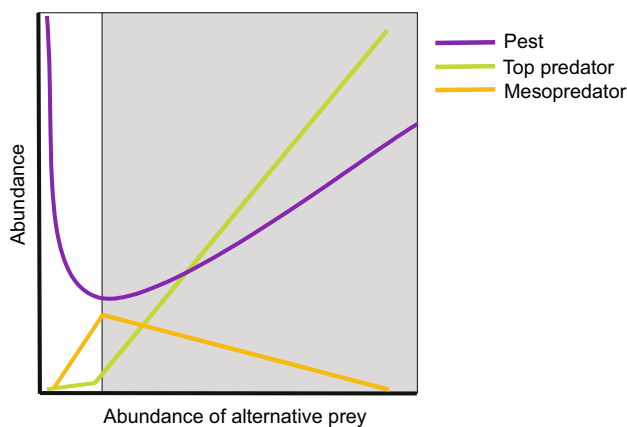


Fig. 4 The hypothetical density-dependent effect of an alternative prey on pest suppression by a community of generalist predators with intraguild predation. Without an alternative prey, the predators are unable to sustain viable populations and the pest that is toxic and/or of poor nutritional quality for the predators thrives. With the increasing density of alternative prey, the abundances of predators also increase, which enhances predation pressure on the pest. However, with the increasing abundances of predators, interference between the predators also intensifies and, at some point, the top predator starts to dominate the mesopredator, which is more efficient in pest exploitation than the top predator. At this point, the predation pressure on the pest starts to sink and pest abundance increases. The area delimited by the white rectangle shows the parameter space in which an alternative prey has a positive effect on pest suppression. The grey rectangle delimits the parameter space in which the alternative prey has a negative effect on pest suppression

predator will start to exclude the mesopredator. For example, *Pardosa milvina* prefers prey-rich patches at first, but it reduces its foraging as other spiders aggregate and consequently emigrates (Schmidt and Rypstra 2010; Schmidt et al. 2014). Therefore, alternative prey might, theoretically, support pest suppression at low to medium densities but reduce it at high densities (Fig. 4).

A change in the density of alternative prey can change the ratio of high-quality prey to low-quality prey. For example, an alternative prey (flies) improved the suppression of the aphid by the wolf spider only at low densities of spiders and flies. At high densities of flies and spiders, the flies disrupted aphid suppression. At low densities, the flies probably improved the condition of spiders and tolerance to the toxicity of aphids, which increased the spiders' capture rate on aphids. At high densities, the flies probably could not improve the condition of spiders anymore and spiders also reached satiation. The higher encounter rate of spiders with flies then buffered the effect of improved condition and reduced the spiders' capture rate on aphids (Oelbermann and Scheu 2009).

Spatio-temporal overlap

The spatio-temporal overlap between spider, pest and alternative prey likely affects pest suppression (Snyder et al. 2005). However, this topic has been little studied. Snyder et al. (2005) hypothesized that alternative prey might support the biocontrol function of spiders especially if the alternative prey and pest are separated spatially or temporally, meaning that the generalist predators are not distracted from predation on the pest. Indeed, alternative prey that supported an abundant community of generalist predators including spiders in rice during the absence of pests and that declined when the pests started to infest rice highly improved biocontrol and prevented the outbreak of the pest (Settle et al. 1996). Spatial segregation between an alternative prey and a pest is, however, not so straightforward. In contrast to the hypothesis provided by Snyder et al. (2005), spatial separation might also decouple the spider–pest association, because spiders might aggregate in the patches of alternative prey without the pest (Harwood et al. 2003). If the alternative prey and pest overlap spatially, spiders might attack the pest (Toft and Wise 1999a, 1999b), and/or suppress the pest by means of non-consumptive effects (Cronin et al. 2004).

Conclusions

Here we reviewed spiders' trophic ecology covering levels from individuals to communities that affect the potential of spiders for pest suppression. At individual and population levels we reviewed how hunting strategy, body size, life

stage, nutritional target, and personality affect the dynamics of spider trophic niche. We further reviewed the functional and numerical responses and the non-consumptive effects of spiders on pests. At the community level, we reviewed multiple-predator effects and the effects of the presence of alternative prey on pest suppression. Generalist spiders are not truly opportunists as they choose their prey. Spiders can reduce pests not only through high consumption but also through non-consumptive effects. Antagonistic intraguild interactions that dampen the pest suppression are ubiquitous in spiders. However, the synergistic and additive effects that enhance pest suppression are evidently present among spiders too and they might be ubiquitous as well given the high diversity in which spiders are present in most agroecosystems. However, intraguild interactions are still understudied. Alternative prey can either reduce predation pressure (switching) or enhance predation pressure (apparent competition) by spiders on the pest or on mesopredators. Thus, alternative prey can not only disrupt pest suppression by spiders, as previously thought, but can also enhance it.

Throughout the review we showed that the effect of spiders on pest is contingent on the phenotype of spiders (e.g., hunting strategy, behavioural type), of pest and alternative prey (e.g., mobility, nutritional content), and environmental conditions (e.g., structurally simple vs. complex). Given the high potential of spiders as pest control agents, future research should identify the conditions under which the generalist predators are most effective, such as suitable composition of hunting strategies and alternative prey. Furthermore, investigations of management options to enhance spiders in agroecosystem (such as pesticide reductions, mulches or wildflower strips) should describe the specific effects on spider communities and their trait composition, because general measures such as species richness or abundance may be poor indicators of pest control potential. As many ecological hypotheses that we outlined are new and some even untested, the investigation of the biocontrol effect of generalist predators remains an exciting research area not only in applied but also in basic ecology. The possible scenarios should be, nevertheless, investigated with the species that naturally occur in agroecosystems rather than with laboratory-reared model species or species living outside the agroecosystems.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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

References

- Abrams PA, Cortez MH (2015) The many potential indirect interactions between predators that share competing prey. *Ecol Monogr* 85:625–641. <https://doi.org/10.1890/14-2025.1>
- Agustí N, Shayler SP, Harwood JD, Vaughan IP, Sunderland KD, Symondson WOC (2003) Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. *Mol Ecol* 12:3467–3475. <https://doi.org/10.1046/j.1365-294X.2003.02014.x>
- Amarasekare P (2008) Coexistence of intraguild predators and prey in resource-rich environments. *Ecology* 89:2786–2797. <https://doi.org/10.1890/07-1508.1>
- Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecol Lett* 14:948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Baba YG, Tanaka K (2016) Environmentally friendly farming and multi-scale environmental factors influence generalist predator community in rice paddy ecosystems of Japan. *NIEAS Ser* 6:171–179
- Bartos M (2011) Partial dietary separation between coexisting cohorts of *Yllenus arenarius* (Araneae: Salticidae). *J Arachnol* 39:230–235. <https://doi.org/10.1636/CP10-63.1>
- Beleznai O, Tholt G, Tóth Z, Horváth V, Marczali Z, Samu F (2015) Cool headed individuals are better survivors: non-consumptive and consumptive effects of a generalist predator on a sap feeding insect. *PLoS One* 10:e0135954. <https://doi.org/10.1371/journal.pone.0135954>
- Beleznai O, Dreyer J, Tóth Z, Samu F (2017) Natural enemies partially compensate for warming induced excess herbivory in an organic growth system. *Sci Rep* 7:7226. <https://doi.org/10.1038/s41598-017-07509-w>
- Bell JR, Wheeler CP, Cullen WR (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *J Zool* 255:377–387. <https://doi.org/10.1017/S0952836901001479>
- Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. *Anim Behav* 77:771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Benamú MA, Lacava M, García LF, Santana M, Viera C (2017) Spiders Associated with Agroecosystems: Roles and Perspectives. In: Viera C, Gonzaga M (eds) *Behaviour and ecology of spiders*. Springer, Cham. https://doi.org/10.1007/978-3-319-65717-2_11
- Binz H, Bucher R, Entling MH, Menzel F (2014) Knowing the risk: crickets distinguish between spider predators of different size and commonness. *Ethology* 120:99–110. <https://doi.org/10.1111/eth.12183>
- Birkhofer K, Wolters V (2012) The global relationship between climate net primary production and the diet of spiders. *Glob Ecol Biogeogr* 21:100–108. <https://doi.org/10.1111/j.1466-8238.2011.00654.x>
- Birkhofer K, Gavish-Regev E, Endlweber K, Lubin YD, von Berg K, Wise DH, Scheu S (2008a) Cursorial spiders retard initial aphid population growth at low densities in winter wheat. *Bull Entomol Res* 98:249–255. <https://doi.org/10.1017/S0007485308006019>

- Birkhofer K, Wise DH, Scheu S (2008b) Subsidy from the detrital food web but not microhabitat complexity affects the role of generalist predators in an aboveground herbivore food web. *Oikos* 117:494–500. <https://doi.org/10.1111/j.0030-1299.2008.16361.x>
- Birkhofer K, Entling MH, Lubin Y (2013) Agroecology: trait composition spatial relationships trophic interactions. In: Penney D (ed) *Spider Research in the 21st Century: Trends and Perspectives*. SIRS Scientific Press, Manchester, pp 220–228
- Birkhofer K, Fevrier V, Heinrich AE, Rink K, Smith HG (2018) The contribution of CAP greening measures to conservation biological control at two spatial scales. *Agric Ecosyst Environ* 255:84–94. <https://doi.org/10.1016/j.agee.2017.12.026>
- Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol* 26:183–192. <https://doi.org/10.1016/j.tree.2011.01.009>
- Bommarco R, Miranda F, Bžund H, Björkman C (2011) Insecticides suppress natural enemies and increase pest damage in cabbage. *J Econ Entomol* 104:782–791. <https://doi.org/10.1603/EC10444>
- Bressendorff BB, Toft S (2011) Dome-shaped functional response induced by nutrient imbalance of the prey. *Biol Lett* 7:517–520. <https://doi.org/10.1098/rsbl.2011.0103>
- Bucher R, Binz H, Menzel F, Entling MH (2014a) Effects of spider chemotactile cues on arthropod behavior. *J Insect Behav* 27:567–580. <https://doi.org/10.1007/s10905-014-9449-1>
- Bucher R, Binz H, Menzel F, Entling MH (2014b) Spider cues stimulate feeding weight gain and survival of crickets. *Ecol Entomol* 39:667–673. <https://doi.org/10.1111/een.12131>
- Bucher R, Heinrich H, Entling MH (2015a) Plant choice herbivory and weight gain of wood crickets under the risk of predation. *Entomol Exp Appl* 155:148–153. <https://doi.org/10.1111/eea.12291>
- Bucher R, Menzel F, Entling MH (2015b) Risk of spider predation alters food web structure and reduces local herbivory in the field. *Oecologia* 178:571–577. <https://doi.org/10.1007/s00442-015-3226-5>
- Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. *PLoS One* 6:e21710. <https://doi.org/10.1371/journal.pone.0021710>
- Chapman EG, Schmidt JM, Welch KD, Harwood JD (2013) Molecular evidence for dietary selectivity and pest suppression potential in an epigeal spider community in winter wheat. *Biol Control* 65:72–86. <https://doi.org/10.1016/j.biocontrol.2012.08.005>
- Chen B, Wise DH (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80:761–772. [https://doi.org/10.1890/0012-9658\(1999\)080%5b0761:BULOPA%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080%5b0761:BULOPA%5d2.0.CO;2)
- Cronin JT, Haynes KJ, Dilleuth F (2004) Spider effects on planthopper mortality dispersal and spatial population dynamics. *Ecology* 85:2134–2143. <https://doi.org/10.1890/03-0591>
- Decae AE (1987) Dispersal: ballooning and other mechanisms. In: Nentwig W (ed) *Ecophysiology of spiders*. Springer-Verlag, Berlin, pp 357–370
- Dell AI, Pawar S, Savage VM (2014) Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J Anim Ecol* 83:70–84. <https://doi.org/10.1111/1365-2656.12081>
- Denno RF, Gratton C, Döbel H, Finke DL (2003) Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology* 84:1032–1044. [https://doi.org/10.1890/0012-9658\(2003\)084%5b1032:PRARS%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084%5b1032:PRARS%5d2.0.CO;2)
- Denno RF, Mitter MS, Langellotto GA, Gratton C, Finke DL (2004) Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression. *Ecol Entomol* 29:566–577. <https://doi.org/10.1111/j.0307-6946.2004.00628.x>
- Fagan WF, Denno RF (2004) Stoichiometry of actual vs. potential predator–prey interactions: insights into nitrogen limitation for arthropod predators. *Ecol Lett* 7:876–883. <https://doi.org/10.1111/j.1461-0248.2004.00641.x>
- Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149:265–275. <https://doi.org/10.1007/s00442-006-0443-y>
- Finke DL, Snyder WE (2008) Niche partitioning increases resource exploitation by diverse communities. *Science* 321:1488–1490. <https://doi.org/10.1126/science.1160854>
- Foelix RF (2011) *Biology of spiders*. Oxford University Press, New York
- Folz HC, Wilder SM, Persons MH, Rypstra AL (2006) Effects of predation risk on vertical habitat use and foraging of *Pardosa milvina*. *Ethology* 112:1152–1158. <https://doi.org/10.1111/j.1439-0310.2006.01276.x>
- Furlong MJ, Zu-Hua S, Yin-Quan L, Shi-Jian G, Yao-Bin L, Shu-Sheng L, Zalucki MP (2004) Experimental analysis of the influence of pest management practice on the efficacy of an endemic arthropod natural enemy complex of the diamondback moth. *J Econ Entomol* 97:1814–1827. <https://doi.org/10.1603/0022-0493-97.6.1814>
- Gan W, Liu S, Yang X, Li D, Lei C (2015) Prey interception drives web invasion and spider size determines successful web takeover in nocturnal orb-webs spiders. *Biol Open* 4:1326–1329. <https://doi.org/10.1242/bio.012799>
- Gavish-Regev E, Rotkopf R, Lubin Y, Coll M (2009) Consumption of aphids by spiders and the effect of additional prey: evidence from microcosm experiments. *Biocontrol* 54:341–350. <https://doi.org/10.1007/s10526-008-9170-0>
- Graf N, Bucher R, Schäfer RB, Entling MH (2017) Contrasting effects of aquatic subsidies on a terrestrial trophic cascade. *Biol Lett* 13:20170129. <https://doi.org/10.1098/rsbl.2017.0129>
- Griffin JN, Byrnes JE, Cardinale BJ (2013) Effects of predator richness on prey suppression: a meta-analysis. *Ecology* 94:2180–2187. <https://doi.org/10.1890/13-0179.1>
- Halaj J, Wise DH (2002) Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* 83:3141–3151. [https://doi.org/10.1890/0012-9658\(2002\)083%5b3141:IOADS%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%5b3141:IOADS%5d2.0.CO;2)
- Hanley TC, La Pierre KJ (2015) *Trophic ecology: bottom-up and top-down interactions across aquatic and terrestrial systems*. Cambridge University Press, Cambridge
- Hanna R, Zalom FG, Roltsch WJ (2003) Relative impact of spider predation and cover crop on population dynamics of *Erythroneura variabilis* in a raisin grape vineyard. *Entomol Exp Appl* 107:177–191. <https://doi.org/10.1046/j.1570-7458.2003.00051.x>
- Harwood JD, Sunderland KD, Symondson WOC (2003) Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. *J Anim Ecol* 72:745–756. <https://doi.org/10.1046/j.1365-2656.2003.00746.x>
- Harwood JD, Sunderland KD, Symondson WOC (2004) Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. *Mol Ecol* 13:3549–3560. <https://doi.org/10.1111/j.1365-294X.2004.02331.x>
- Harwood JD, Sunderland KD, Symondson WOC (2005) Monoclonal antibodies reveal the potential of the tetragnathid spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator. *Bull Entomol Res* 95:161–167. <https://doi.org/10.1079/BER2004346>
- Harwood JD, Bostrom MR, Hladilek EE, Wise DH, Obrycki JJ (2007) An order-specific monoclonal antibody to Diptera reveals the impact of alternative prey on spider feeding behavior in

- a complex food web. *Biol Control* 41:397–407. <https://doi.org/10.1016/j.biocontrol.2007.02.008>
- Hawlena D, Schmitz OJ (2010a) Physiological stress as a fundamental mechanism linking predation to ecosystem functioning. *Am Nat* 176:537–556. <https://doi.org/10.1086/656495>
- Hawlena D, Schmitz OJ (2010b) Herbivore physiological response to predation risk and implications for ecosystem nutrient dynamics. *PNAS* 107:15503–15507. <https://doi.org/10.1073/pnas.1009300107>
- Heong KL, Bleih S, Rubia EG (1991) Prey preference of the wolf spider *Pardosa pseudoannulata* (Boesenberg et Strand). *Popul Ecol* 33:179–186. <https://doi.org/10.1007/BF02513547>
- Herberstein ME (2011) Spider behaviour: flexibility and versatility. Cambridge University Press, Cambridge
- Hodge MA (1999) The implications of intraguild predation for the role of spiders in biological control. *J Arachnol* 27:351–362
- Holling CS (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Mem Entomol Soc Can* 97:5–60. <https://doi.org/10.4039/entm9745fv>
- Holt RD, Bonsall MB (2017) Apparent competition. *Ann Rev Ecol Evol Syst* 48:447–471. <https://doi.org/10.1146/annurev-ecolsys-110316-022628>
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764. <https://doi.org/10.1086/286018>
- Huey RB, Pianka ER (1981) Ecological consequences of foraging mode. *Ecology* 62:991–999. <https://doi.org/10.2307/1936998>
- Isaia M, Beikes S, Paschetta M, Sarvajayakesevalu S, Badino G (2010) Spiders as potential biological controllers in apple orchards infested by *Cydia* spp (Lepidoptera: Tortricidae). In: Nentwig W, Entling M, Kropf C (eds) Proceedings of the 24th European Congress of Arachnology, Bern, pp 25–29
- Janssen A, Sabelis MW, Magalhães S, Montserrat M, van der Hammen T (2007) Habitat structure affects intraguild predation. *Ecology* 88:713–7219. <https://doi.org/10.1890/06-1408.1>
- Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biol Rev* 79:337–349. <https://doi.org/10.1017/S1464793103006286>
- Jonsson M, Kaartinen R, Straub CS (2017) Relationships between natural enemy diversity and biological control. *Curr Opin Insect Sci* 20:1–6. <https://doi.org/10.1016/j.cois.2017.01.001>
- Jonsson T, Kaartinen R, Jonsson M, Bommarco R (2018) Predictive power of food web models based on body size decreases with trophic complexity. *Ecol Lett* 21:702–712. <https://doi.org/10.1111/ele.12938>
- Klečka J, Boukal D (2013) Foraging and vulnerability traits modify predator–prey body mass allometry: freshwater macroinvertebrates as a case study. *J Anim Ecol* 82:1031–1041. <https://doi.org/10.1111/1365-2656.12078>
- Knop E, Zünd J, Sanders D (2014) Interactive prey and predator diversity effects drive consumption rates. *Oikos* 123:1244–1249. <https://doi.org/10.1111/oik.00926>
- Kobayashi T, Takada M, Takagi S, Yoshioka A, Washitani I (2011) Spider predation on a mirid pest in Japanese rice fields. *Basic Appl Ecol* 12:532–539. <https://doi.org/10.1016/j.baae.2011.07.007>
- Korenko S, Pekár S (2010) Is there intraguild predation between winter-active spiders (Araneae) on apple tree bark? *Biol Control* 54:206–212. <https://doi.org/10.1016/j.biocontrol.2010.05.008>
- Korenko S, Pekar S, Honěk A (2010) Predation activity of two winter-active spiders (Araneae: Anyphaenidae Philodromidae). *J Therm Biol* 35:112–116. <https://doi.org/10.1016/j.jtherbio.2009.12.004>
- Křivan V (2008) Prey–predator models. In: Jorgensen SE, Fath BD (eds) Encyclopedia of ecology. Elsevier, Amsterdam, pp 2929–2940
- Kruse PD, Toft S, Sunderland KD (2008) Temperature and prey capture: opposite relationships in two predator taxa. *Ecol Entomol* 33:305–312. <https://doi.org/10.1111/j.1365-2311.2007.00978.x>
- Kuusk AK, Ekbom B (2010) Lycosid spiders and alternative food: feeding behavior and implications for biological control. *Biol Control* 55:20–26. <https://doi.org/10.1016/j.biocontrol.2010.06.009>
- Kuusk AK, Ekbom B (2012) Feeding habits of lycosids spiders in field habitats. *J Pest Sci* 85:253–260. <https://doi.org/10.1007/s10340-012-0431-4>
- Lang A (2003) Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* 134:144–153. <https://doi.org/10.1007/s00442-002-1091-5>
- Laundré JW, Hernández L, Medina PL, Campanella A, López-Portillo J, González-Romero A, Grajales-Tam KM, Burke AM, Gronemeyer P, Browning DM (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95:1141–1152. <https://doi.org/10.1890/13-1083.1>
- Lease HM, Wolf BO (2011) Lipid content of terrestrial arthropods in relation to body size phylogeny ontogeny and sex. *Physiol Entomol* 36:29–38. <https://doi.org/10.1111/j.1365-3032.2010.00767.x>
- Lefebvre M, Franck P, Olivares J, Ricard JM, Mandrin JF, Lavigne C (2017) Spider predation on rosy apple aphid in conventional organic and insecticide-free orchards and its impact on aphid populations. *Biol Control* 104:57–65. <https://doi.org/10.1016/j.biocontrol.2016.10.009>
- Lesne P, Tralalon M, Jeanson R (2016) Cannibalism in spiderlings is not only about starvation. *Behav Ecol Sociobiol* 70:1669–1678. <https://doi.org/10.1007/s00265-016-2172-5>
- Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR (2009) Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial E ecosystems. *Annu Rev Ecol Evol Syst* 40:573–592. <https://doi.org/10.1146/annurev.ecolsys.110308.120320>
- Liu S, Li Z, Sui Y, Schaefer DA, Alele PO, Chen J, Yang X (2015) Spider foraging strategies dominate pest suppression in organic tea plantations. *Biocontrol* 60:839–847. <https://doi.org/10.1007/s10526-015-9691-2>
- Losey JE, Denno RF (1999) Factors facilitating synergistic predation: the central role of synchrony. *Ecol Appl* 9:378–386. [https://doi.org/10.1890/1051-0761\(1999\)009%5b0378:FFSPTC%5d2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009%5b0378:FFSPTC%5d2.0.CO;2)
- Madsen M, Terkildsen S, Toft S (2004) Microcosm studies on control of aphids by generalist arthropod predators: effects of alternative prey. *Biocontrol* 49:483–504. <https://doi.org/10.1023/B:BICO.0000036442.70171.66>
- Maloney D, Drummond FA, Alford R (2003) Spider predation in agroecosystems: can spiders effectively control pest populations? Technical Bulletin 190. University of Maine, Orono
- Mansour F, Heimbach U (1993) Evaluation of Lycosid Micryphantid and Linyphiid spiders as predators of *Rhopalosiphum padi* (Hom: Aphididae) and their functional response to prey density-laboratory experiments. *Biocontrol* 38:79–87. <https://doi.org/10.1007/BF02373142>
- Marc P, Canard A, Ysnel F (1999) Spiders (Araneae) useful for pest limitation and bioindication. *Agric Ecosyst Environ* 74:229–273. [https://doi.org/10.1016/S0167-8809\(99\)00038-9](https://doi.org/10.1016/S0167-8809(99)00038-9)
- Markó V, Keresztes B (2014) Flowers for better pest control? Ground cover plants enhance apple orchard spiders (Araneae) but not necessarily their impact on pests. *Biocontrol Sci Technol* 24:574–596. <https://doi.org/10.1080/09583157.2014.881981>
- Matsumura M, Trafelet-Smith GM, Gratton C, Finke DL, Fagan WF, Denno RF (2004) Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology* 85:2601–2615. <https://doi.org/10.1890/03-0629>
- Mayntz D, Toft S (2000) Effect of nutrient balance on tolerance to low quality prey in a wolf spider (Araneae: Lycosidae). *Ekológia* 19:153–158

- Mayntz D, Toft S (2006) Nutritional value of cannibalism and the role of starvation and nutrient imbalance for cannibalistic tendencies in a generalist predator. *J Anim Ecol* 75:288–297. <https://doi.org/10.1111/j.1365-2656.2006.01046.x>
- Mayntz D, Raubenheimer D, Salomon M, Toft S, Simpson SJ (2005) Nutrient-specific foraging in invertebrate predators. *Science* 307:111–113. <https://doi.org/10.1126/science.1105493>
- Mestre L, Bonte D (2012) Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. *Behav Ecol* 23:759–764. <https://doi.org/10.1093/beheco/ars024>
- Mestre L, Piñol J, Barrientos JA, Espadaler X, Brewitt K, Werner C, Platner C (2013) Trophic structure of the spider community of a Mediterranean citrus grove: a stable isotope analysis. *Basic Appl Ecol* 14:413–422. <https://doi.org/10.1016/j.baae.2013.05.001>
- Mestre L, Bucher R, Entling MH (2014) Trait-mediated effects between predators: ant chemical cues induce spider dispersal. *J Zool* 293:119–125. <https://doi.org/10.1111/jzo.12127>
- Michalko R, Košulič O (2016) Temperature-dependent effect of two neurotoxic insecticides on predatory potential of *Philodromus* spiders. *J Pest Sci* 89:517–527. <https://doi.org/10.1007/s10340-015-0696-5>
- Michalko R, Pekár S (2014) Is different degree of individual specialisation in three closely related spider species caused by different selection pressures? *Basic Appl Ecol* 15:496–506. <https://doi.org/10.1016/j.baae.2014.08.003>
- Michalko R, Pekár S (2015) The biocontrol potential of *Philodromus* (Araneae: Philodromidae) spiders for the suppression of pome fruit orchard pests. *Biol Control* 82:13–20. <https://doi.org/10.1016/j.biocontrol.2014.12.001>
- Michalko R, Pekár S (2016) Different hunting strategies of generalist predators result in functional differences. *Oecologia* 181:1187–1197. <https://doi.org/10.1007/s00442-016-3631-4>
- Michalko R, Pekár S (2017) The behavioral type of a top predator drives the short-term dynamic of intraguild predation. *Am Nat* 189:242–253. <https://doi.org/10.1086/690501>
- Michalko R, Petráková L, Sentenská L, Pekár S (2017) The effect of habitat complexity and density-dependent non-consumptive interference on pest suppression by winter-active spiders. *Agric Ecosyst Environ* 242:26–33. <https://doi.org/10.1016/j.agee.2017.03.025>
- Miller JR, Ament JM, Schmitz OJ (2014) Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *J Anim Ecol* 83:214–222. <https://doi.org/10.1111/1365-2656.12111>
- Morozov A, Petrovskii S (2013) Feeding on multiple sources: towards a universal parameterization of the functional response of a generalist predator allowing for switching. *PloS One* 8:e74586. <https://doi.org/10.1371/journal.pone.0074586>
- Müller CB, Brodeur J (2002) Intraguild predation in biological control and conservation biology. *Biol Control* 25:216–223. [https://doi.org/10.1016/S1049-9644\(02\)00102-0](https://doi.org/10.1016/S1049-9644(02)00102-0)
- Murdoch WW, Kendall BE, Nisbet RM, Briggs CJ, McCauley E, Bolser R (2002) Single-species models for many-species food webs. *Nature* 417:541–543. <https://doi.org/10.1038/417541a>
- Nentwig W, Wissel C (1986) A comparison of prey lengths among spiders. *Oecologia* 68:595–600. <https://doi.org/10.1007/BF00378777>
- Nyffeler M, Benz G (1987) Spiders in natural pest control: a review. *J Appl Entomol* 103:321–339. <https://doi.org/10.1111/j.1439-0418.1987.tb00992.x>
- Nyffeler M, Birkhofer K (2017) An estimated 400–800 million tons of prey are annually killed by the global spider community. *Sci Nat* 104:30. <https://doi.org/10.1007/s00114-017-1440-1>
- Oelbermann K, Scheu S (2002) Effects of prey type and mixed diets on survival growth and development of a generalist predator *Pardosa lugubris* (Araneae: Lycosidae). *Basic Appl Ecol* 3:285–291. <https://doi.org/10.1078/1439-1791-00094>
- Oelbermann K, Scheu S (2009) Control of aphids on wheat by generalist predators: effects of predator density and the presence of alternative prey. *Entomol Exp Appl* 132:225–231. <https://doi.org/10.1111/j.1570-7458.2009.00876.x>
- Oelbermann K, Langel R, Scheu S (2008) Utilization of prey from the decomposer system by generalist predators of grassland. *Oecologia* 155:605–617. <https://doi.org/10.1007/s00442-007-0927-4>
- Okuyama T (2007) Prey of two species of jumping spiders in the field. *Appl Entomol Zool* 42:663–668. <https://doi.org/10.1303/aetz.2007.663>
- Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. *Trends Ecol Evol* 23:149–158. <https://doi.org/10.1016/j.tree.2007.11.005>
- Pekár S (2012) Spiders (Araneae) in the pesticide world: an ecotoxicological review. *Pest Manag Sci* 68:1438–1446. <https://doi.org/10.1002/ps.3397>
- Pekár S, Toft S (2015) Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). *Biol Rev* 90:744–761. <https://doi.org/10.1111/brv.12133>
- Pekár S, Martišová M, Bilde T (2011) Intersexual trophic niche partitioning in an ant-eating spider (Araneae: Zodariidae). *PLoS One* 6:e14603. <https://doi.org/10.1371/journal.pone.0014603>
- Pekár S, Coddington JA, Blackledge TA (2012) Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. *Evolution* 66:776–806. <https://doi.org/10.1111/j.1558-5646.2011.01471.x>
- Pekár S, Michalko R, Korenko S, Šedo O, Líznavá E, Sentenská L, Zdráhal Z (2013) Phenotypic integration in a series of trophic traits: tracing the evolution of myrmecophagy in spiders (Araneae). *Zoology* 116:27–35. <https://doi.org/10.1016/j.zool.2012.05.006>
- Pekár S, Michalko R, Loverre P, Líznavá E, Černecká L (2015) Biological control in winter: novel evidence for the importance of generalist predators. *J Appl Ecol* 52:270–279. <https://doi.org/10.1111/1365-2664.12363>
- Perkins MJ, Inger R, Bearhop S, Sanders D (2018) Multichannel feeding by spider functional groups is driven by feeding strategies and resource availability. *Oikos* 127:23–33. <https://doi.org/10.1111/oik.04500>
- Petcharad B, Košulič O, Michalko R (2018) Insecticides alter prey choice of potential biocontrol agent *Philodromus cespitum* (Araneae, Philodromidae). *Chemosphere* 202:491–497. <https://doi.org/10.1016/j.chemosphere.2018.03.134>
- Petráková L, Michalko R, Loverre P, Sentenská L, Korenko S, Pekár S (2016) Intraguild predation among spiders and their effect on the pear psylla during winter. *Agric Ecosyst Environ* 233:67–74. <https://doi.org/10.1016/j.agee.2016.08.008>
- Picchi MS, Bocci G, Petacchi R, Entling MH (2016) Effects of local and landscape factors on spiders and olive fruit flies. *Agric Ecosyst Environ* 222:138–147. <https://doi.org/10.1016/j.agee.2016.01.045>
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330. <https://doi.org/10.1146/annurev.es.20.110189.001501>
- Preisser EL, Bolnick DI (2008) The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS One* 3:e2465. <https://doi.org/10.1371/journal.pone.0002465>
- Pruitt JN, Riechert JE (2012) The ecological consequences of temperament in spiders. *Curr Zool* 58:589–596. <https://doi.org/10.1093/czoolo/58.4.589>

- Pruitt JN, Bolnick DI, Sih A, DiRienzo N, Pinter-Wollman N (2016) Behavioural hypervolumes of spider communities predict community performance and disbandment. *Proc R Soc B* 283:20161409. <https://doi.org/10.1098/rspb.2016.1409>
- Rendon D, Whitehouse ME, Taylor PW (2016) Consumptive and non-consumptive effects of wolf spiders on cotton bollworms. *Entomol Exp Appl* 158:170–183. <https://doi.org/10.1111/eea.12390>
- Richardson ML, Hanks LM (2009) Partitioning of niches among four species of orb-weaving spiders in a grassland habitat. *Environ Entomol* 38:651–656. <https://doi.org/10.1603/022.038.0316>
- Rickers S, Langel R, Scheu S (2006) Stable isotope analyses document intraguild predation in wolf spiders (Araneae: Lycosidae) and underline beneficial effects of alternative prey and micro-habitat structure on intraguild prey survival. *Oikos* 114:471–478. <https://doi.org/10.1111/j.2006.0030-1299.14421.x>
- Riechert SE (1991) Prey abundance vs diet breadth in a spider test system. *Evol Ecol* 5:327–338. <https://doi.org/10.1007/BF02214236>
- Riechert SE (1999) The hows and whys of successful pest suppression by spiders: insights from case studies. *J Arachnol* 27:387–396
- Riechert SE, Bishop L (1990) Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* 71:1441–1450. <https://doi.org/10.2307/1938281>
- Riechert SE, Harp JM (1987) Nutritional ecology of spiders. In: Rodriguez JG, Slansky F (eds) Nutritional ecology of insects mites and spiders. Wiley, New York, pp 645–672
- Riechert SE, Hedrick AV (1993) A test for correlation among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae Agelenidae). *Anim Behav* 46:669–675. <https://doi.org/10.1006/anbe.1993.1243>
- Riechert SE, Lockley T (1984) Spiders as biological control agents. *Annu Rev Entomol* 29:299–320. <https://doi.org/10.1146/annurev.en.29.010184.001503>
- Rosenheim JA, Harmon JP (2006) The influence of intraguild predation on the suppression of a shared prey population: an empirical reassessment. In: Boivin G, Brodeur J (eds) Trophic and guild in biological interactions control. Springer, Netherlands
- Rosenheim JA, Kaya HK, Ehler LE, Marois JJ, Jaffee BA (1995) Intraguild predation among biological-control agents: theory and evidence. *Biol Control* 5:303–335. <https://doi.org/10.1006/bcon.1995.1038>
- Roubinet E, Birkhofer K, Malsher G, Staudacher K, Ekbom B, Traugott M, Jonsson M (2017) Diet of generalist predators reflects effects of cropping period and farming system on extra- and intraguild prey. *Ecol Appl* 27:1167–1177. <https://doi.org/10.1002/eap.1510>
- Royauté R, Pruitt JN (2015) Varying predator personalities generates contrasting prey communities in an agroecosystem. *Ecology* 96:2902–2911. <https://doi.org/10.1890/14-2424.1>
- Royauté R, Buddle CM, Vincent C (2014) Interpopulation variations in behavioral syndromes of a jumping spider from insecticide-treated and insecticide-free orchards. *Ethology* 120:127–139. <https://doi.org/10.1111/eth.12185>
- Rusch A, Birkhofer K, Bommarco R, Smith HG, Ekbom B (2015) Predator body sizes and habitat preferences predict predation rates in an agroecosystem. *Basic Appl Ecol* 16:250–259. <https://doi.org/10.1016/j.baae.2015.02.003>
- Ryabov AB, Morozov A, Blasius B (2015) Imperfect prey selectivity of predators promotes biodiversity and irregularity in food webs. *Ecol Lett* 18:1262–1269. <https://doi.org/10.1111/ele.12521>
- Rypstra AL, Buddle CM (2013) Spider silk reduces insect herbivory. *Biol Lett* 9:20120948. <https://doi.org/10.1098/rsbl.2012.0948>
- Rypstra AL, Samu F (2005) Size dependent intraguild predation and cannibalism in coexisting wolf spiders (Araneae Lycosidae). *J Arachnol* 33:390–397. <https://doi.org/10.1636/CT05-10.1>
- Rypstra AL, Carter PE, Balfour RA, Marshall SD (1999) Architectural features of agricultural habitats and their impact on the spider inhabitants. *J Arachnol* 27:371–377
- Samu F (1993) Wolf spider feeding strategies: optimality of prey consumption in *Pardosa hortensis*. *Oecologia* 94:139–145. <https://doi.org/10.1007/BF00317315>
- Samu F, Bíró Z (1993) Functional response multiple feeding and wasteful killing in a wolf spider (Araneae: Lycosidae). *Eur J Entomol* 90:471–476
- Samu F, Sunderland KD, Szinétár C (1999) Scale-dependent dispersal and distribution patterns of spiders in agricultural systems: a review. *J Arachnol* 27:325–332
- Samu F, Beleznai O, Tholt G (2013) A potential spider natural enemy against virus vector leafhoppers in agricultural mosaic landscapes—Corroborating ecological and behavioral evidence. *Biol Control* 67:390–396. <https://doi.org/10.1016/j.biocontrol.2013.08.016>
- Sanders D, Vogel E, Knop E (2015) Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. *J Anim Ecol* 84:134–142. <https://doi.org/10.1111/1365-2656.12271>
- Schellhorn NA, Bianchi FJJA, Hsu CL (2014) Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. *Annu Rev Entomol* 59:559–581. <https://doi.org/10.1146/annurev-ento-011613-161952>
- Schmidt JM, Rypstra AL (2010) Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia* 164:899–910. <https://doi.org/10.1007/s00442-010-1785-z>
- Schmidt MH, Lauer A, Purtauf T, Thies C, Schaefer M, Tscharnkte T (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proc R Soc Lond B* 270:1905–1909. <https://doi.org/10.1098/rspb.2003.2469>
- Schmidt MH, Thewes U, Thies C, Tscharnkte T (2004) Aphid suppression by natural enemies in mulched cereals. *Entomol Exp Appl* 113:87–93. <https://doi.org/10.1111/j.0013-8703.2004.00205.x>
- Schmidt JM, Harwood JD, Rypstra AL (2012a) Foraging activity of a dominant epigeal predator: molecular evidence for the effect of prey density on consumption. *Oikos* 121:1715–1724. <https://doi.org/10.1111/j.1600-0706.2011.20366.x>
- Schmidt JM, Sebastian P, Wilder SM, Rypstra AL (2012b) The nutritional content of prey affects the foraging of a generalist arthropod predator. *PLoS One* 7:e49223. <https://doi.org/10.1371/journal.pone.0049223>
- Schmidt JM, Crist TO, Wrinn K, Rypstra AL (2014) Predator interference alters foraging behavior of a generalist predatory arthropod. *Oecologia* 175:501–508. <https://doi.org/10.1007/s00442-014-2922-x>
- Schmidt-Entling MH, Siegenthaler E (2009) Herbivore release through cascading risk effects. *Biol Lett* 5:773–776. <https://doi.org/10.1098/rsbl.2009.0436>
- Schmitz OJ (2005) Behavior of predators and prey and links with population-level processes. In: Barbosa P, Castellanos I (eds) Ecology of predator–prey interactions. Oxford University Press, Oxford
- Schmitz OJ (2007) Predator diversity and trophic interactions. *Ecology* 88:2415–2426. <https://doi.org/10.1890/06-0937.1>
- Schmitz OJ (2010) Resolving Ecosystem Complexity. Princeton University Press, Princeton
- Schmitz OJ, Beckerman AP, O'Brien KM (1997) Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78:1388–1399. [https://doi.org/10.1890/0012-9658\(1997\)078%5b1388:BMTCEO%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078%5b1388:BMTCEO%5d2.0.CO;2)

- Schneider FD, Scheu S, Brose U (2012) Body mass constraints on feeding rates determine the consequences of predator loss. *Ecol Lett* 15:436–443. <https://doi.org/10.1111/j.1461-0248.2012.01750.x>
- Settle WH, Ariawan H, Astuti ET, Cahyana W, Hakim AL, Hindayana D, Lestari AS (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77:1975–1988. <https://doi.org/10.2307/2265694>
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355. [https://doi.org/10.1016/S0169-5347\(98\)01437-2](https://doi.org/10.1016/S0169-5347(98)01437-2)
- Sinclair ARE, Pech RP, Dickman CR, Hik D, Mahon P, Newsome AE (1998) Predicting effects of predation on conservation of endangered prey. *Conserv Biol* 12:564–575. <https://doi.org/10.1111/j.1523-1739.1998.97030.x>
- Sitvarin MI, Rypstra AL (2014) The importance of intraguild predation in predicting emergent multiple predator effects. *Ecology* 95:2936–2945. <https://doi.org/10.1890/13-2347.1>
- Snyder WE, Ives AR (2003) Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84:91–107. [https://doi.org/10.1890/0012-9658\(2003\)084%5b0091:IBSAGN%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084%5b0091:IBSAGN%5d2.0.CO;2)
- Snyder WE, Chang GC, Prasad RP (2005) Conservation biological control. In: Barbosa P, Castellanos I (eds) *Ecology of predator–prey interactions*. Oxford University Press, Oxford
- Solomon ME (1949) The natural control of animal populations. *J Anim Ecol* 18:1–35. <https://doi.org/10.2307/1578>
- Stephens DW, Brown JS, Ydenberg RC (2007) *Foraging: behavior and ecology*. University of Chicago Press, Chicago
- Sunderland K (1999) Mechanisms underlying the effects of spiders on pest populations. *J Arachnol* 27:308–316
- Sweeney K, Cusack B, Armagost F, O'Brien T, Keiser CN, Pruitt JN (2013) Predator and prey activity levels jointly influence the outcome of long-term foraging bouts. *Behav Ecol* 24:1205–1210. <https://doi.org/10.1093/beheco/art052>
- Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? *Annu Rev Entomol* 47:561–594. <https://doi.org/10.1146/annurev.ento.47.091201.145240>
- Takada MB, Kobayashi T, Yoshioka A, Takagi S, Washitani I (2013) Facilitation of ground-dwelling wolf spider predation on mirid bugs by horizontal webs built by *Tetragnatha* spiders in organic paddy fields. *J Arachnol* 41:31–35. <https://doi.org/10.1636/P12-30.1>
- Toft S (1995) Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *J Appl Ecol* 32:552–560. <https://doi.org/10.2307/2404652>
- Toft S (1999) Prey choice and spider fitness. *J Arachnol* 27:301–307
- Toft S (2005) The quality of aphids as food for generalist predators: implications for natural control of aphids. *Eur J Entomol* 102:371
- Toft S (2013) Nutritional aspects of spider feeding. In: Nentwig W (ed) *Spider ecophysiology*. Springer-Verlag, Berlin
- Toft S, Wise DH (1999a) Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. *Oecologia* 119:198–207. <https://doi.org/10.1007/s004420050777>
- Toft S, Wise DH (1999b) Growth development and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia* 119:191–197. <https://doi.org/10.1007/s004420050776>
- Traugott M, Bell JR, Raso L, Sint D, Symondson WOC (2012) Generalist predators disrupt parasitoid aphid control by direct and coincidental intraguild predation. *Bull Entomol Res* 102:239–247. <https://doi.org/10.1017/S0007485311000551>
- Tscharntke T, Karp DS, Chaplin-Kramer R et al (2016) When natural habitat fails to enhance biological pest control—five hypotheses. *Biol Conserv* 204:449–458. <https://doi.org/10.1016/j.bioco.2016.10.001>
- Tsutsui MH, Tanaka K, Baba YG, Miyashita T (2016) Spatio-temporal dynamics of generalist predators (*Tetragnatha* spider) in environmentally friendly paddy fields. *Appl Entomol Zool* 51:631–640. <https://doi.org/10.1007/s13355-016-0440-5>
- Tsutsui MH, Kobayashi K, Miyashita T (2018) Temporal trends in arthropod abundances after the transition to organic farming in paddy fields. *PLoS One* 13:e0190946. <https://doi.org/10.1371/journal.pone.0190946>
- Tylianakis JM, Romo CM (2010) Natural enemy diversity and biological control: making sense of the context-dependency. *Basic Appl Ecol* 11:657–668. <https://doi.org/10.1016/j.baae.2010.08.005>
- von Berg K, Thies C, Tscharntke T, Scheu S (2009) Cereal aphid control by generalist predators in presence of belowground alternative prey: complementary predation as affected by prey density. *Pedobiologia* 53:41–48. <https://doi.org/10.1016/j.pedobi.2009.03.001>
- Vucic-Pestic O, Birkhofer K, Rall BC, Scheu S, Brose U (2010) Habitat structure and prey aggregation determine the functional response in a soil predator–prey interaction. *Pedobiologia* 53:307–312. <https://doi.org/10.1016/j.pedobi.2010.02.003>
- Walker SE, Rypstra AL (2003) Hungry spiders aren't afraid of the big bad wolf spider. *J Arachnol* 31:425–427. <https://doi.org/10.1636/S02-63>
- Welch KD, Whitney TD, Harwood JD (2016) Non-pest prey do not disrupt aphid predation by a web-building spider. *Bull Entomol Res* 106:91–98. <https://doi.org/10.1017/S0007485315000875>
- Werner EE, Peacor SD (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology* 84:1083–1100. [https://doi.org/10.1890/0012-9658\(2003\)084%5b1083:AROTI1%5d2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084%5b1083:AROTI1%5d2.0.CO;2)
- Whitehouse MEA, Mansfield S, Barnett MC, Broughton K (2011) From lynx spiders to cotton: behaviorally mediated predator effects over four trophic levels. *Aus Ecol* 36:687–697. <https://doi.org/10.1111/j.1442-9993.2010.02204.x>
- Wilder SM (2011) Spider nutrition: an integrated perspective. *Adv Insect Physiol* 40:87–136
- Wilder SM, Norris M, Lee RW, Raubenheimer D, Simpson SJ (2013) Arthropod food webs become increasingly lipid-limited at higher trophic levels. *Ecol Lett* 16:895–902. <https://doi.org/10.1111/ele.12116>
- Wise DH (1993) *Spiders in ecological webs*. Cambridge University Press, Cambridge
- Wise DH (2006) Cannibalism food limitation intraspecific competition and the regulation of spider populations. *Annu Rev Entomol* 51:441–465. <https://doi.org/10.1146/annurev.ento.51.110104.150947>
- Yamanoi T, Miyashita T (2005) Foraging strategy of nocturnal orb-web spiders (Araneidae: *Neoscona*) with special reference to the possibility of beetle specialization by *N punctigera*. *Acta Arachnol* 54:13–19. <https://doi.org/10.2476/asjaa.54.13>
- Yang Y, Chen X, Shao Z, Zhou P, Porter D, Knight DP, Vollrath F (2005) Toughness of spider silk at high and low temperatures. *Adv Mater* 17:84–88. <https://doi.org/10.1002/adma.200400344>