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ORIGINAL ARTICLE

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This study presents the first description of a tri-trophic interaction network with crab spiders as predators. Monthly observations of flowering entomophilous plant species were recorded between December 2009 and March 2010 and their flower visitors and predators (crab spiders) were caught, with or without prey. Moreover, flower visitors of different orders were caught to evaluate the amount of pollen transported. In order to analyze changes in the plant species and crab spiders, we evaluated the interaction networks in which we had removed different orders of prey (Hymenoptera, Diptera and Lepidoptera) from the original network. Our results indicate that crab spiders select their preys within the community. Furthermore, the Hymenoptera carried higher pollen loads and were the less frequent prey. When the Diptera preys were removed from the initial interaction network, network changes mainly affected the species richness of crab spiders. Decrease in density of Diptera could increase plant resources useful for flower visitors carrying great pollen loads and could promote pollination. Crab spider prey might be restricted to only the more vulnerable flower visitors (e.g. smaller dimensions, without sting or with delicate cuticula) which consume resources and are inefficient as pollen carriers. The selected predation could not negatively affect the fitness of plants.

Keywords: tri-trophic interaction network; pollinator prey; triple-interaction; crab spiders

Introduction

Networks are useful descriptors of ecological systems that can show their composition and the interactions between multiple elements. The application of networks to ecosystems provides a conceptual framework with which to assess the consequences of perturbations at the community level (Bascompte 2009). Recently, the study of interaction networks of terrestrial organisms has focused on mutualistic interaction, such as plant–pollinator (Biesmeijer et al. 2006; Alarcón et al. 2008) and plant–disperser networks (Carnicer et al. 2009), although there are also examples of antagonistic interaction networks (Henneman & Memmott 2001; Vázquez et al. 2005; Valladares et al. 2006). However, knowledge about interaction networks in terrestrial systems involving more than two trophic levels is still scarce (Memmott et al. 1994, 2000; Melián et al. 2008; Cagnolo et al. 2009).

Although pollination is an important ecosystem service, little is known about the effect that predators of flower visitors might have on the reproduction success of plant species (Dukas 2001; Muñoz & Arroyo 2004). The wide diversity of predators of

flower visitors comprises vertebrates such as birds (Gentry 1978; Ambrose 1990) and lizards (Muñoz & Arroyo 2004) and invertebrates, such as wasps (Dukas 2005), spiders (Morse 2007), predacious bugs (Greco & Kevan 1995) and praying mantids (Caron 1990). These predators may significantly influence the pollination service and may even considerably reduce plant fitness (Dukas 2005; but see Brechbühl, Kropf, et al. 2010). They can modify the pollination service in two different ways: firstly by directly killing flower visitors and thereby decreasing their abundance, and secondly by indirectly altering the foraging behavior of pollinators (Dukas & Morse 2003; Ings & Chittka 2008, 2009; Romero et al. 2011). Pollinator foraging patterns strongly influence selfing rates within and among plant populations. Also, pollinator visitation patterns are thought to influence several important aspects of the plants mating systems, such as variation in male fertility, patterns of mate diversity at the whole-plant level and patterns of multiple paternity within fruits (Mitchell et al. 2009).

Crab spiders (Araneae: Thomisidae and Philodromidae) are the best studied taxa among all predators of flower visitors. Thomisidae are abundant

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sit-and-wait predators, whereas Philodromidae are running predators. Both are widely distributed and recognizable by their behavior of trapping flower visitors while they feed on flowers (Morse 2007). In general, the life cycles of crab spiders are synchronized with their prey and, in some cases, are longer than those of the flower visitors (Romero & Vasconcellos-Neto 2003; González et al. 2009). Some species of Thomisidae are capable of changing the color of their integument according to the substrate on which they are found. They are capable of varying the tone between white and yellow, depending on the species, to reduce the chromatic contrast with the flowers on which they lie in ambush for insect pollinators (Chittka 2001; Théry & Casas 2002; but see Brechbühl, Casas, et al. 2010).

Most studies evaluating the effect of predators on flower visitors focused on only one plant species (Muñoz & Arroyo 2004; Dukas 2005) and/or on a low number of flower visitors (Dukas & Morse 2003). Therefore, by studying this type of interaction at the community level, the effect that predators might exert on flower visitors, and on the plants on which they are searching for prey, might be better understood. The effects of crab spiders on flower visitors and plant fitness are mostly indirect, i.e. pollinators frequently avoid predation risk sites so that they are not caught and consequently the trophic cascade to plant fitness is typically via a trait-mediated indirect effect (Gonçalves-Souza et al. 2008). The capture rate of flower visitors by crab spiders is in fact very low (Dukas & Morse 2003, 2005; Brechbühl, Casas, et al. 2010), suggesting that there is evidence of strong indirect effects of crab spiders on the behavior of flower visitors. Plant–crab spider interaction might be mutualistic in the case when predators mainly catch prey that are inefficient pollinators, transport few pollen grains adhering to the bodies and consume flower resources.

The few studies assessing network interactions in tri-trophic terrestrial systems have been limited to plant, herbivores and parasitoids as the highest trophic level (Henneman & Memmott 2001; Cagnolo et al. 2009; Macfadyen et al. 2009). These previous examples did not show any direct interactions between parasitoids and plants, so the structure of the networks would have differed from the one presented in this paper. The objectives of this study are: (i) to show, for the first time, the structure of a tri-trophic interaction network involving crab spiders (Thomisidae and Philodromidae) at the highest trophic level; (ii) to determine the main prey; and (iii) to analyze the selective prey-capture of the crab spiders. To address these questions, we test the hypothesis that spiders selectively prey on those flower visitors that are (1) poor pollinators (i.e. those transport fewer pollen grains adhering to their body); and (2) most vulnerable (i.e. without sting or with delicate cuticula).

Materials and methods

Study area

The study was carried out in a grassland area (Bilenca & Miñarro 2004) in an agricultural matrix in the centre of the Pampas region (35° 56′ S, 61° 11′ W, Buenos Aires province, Argentina). The temperate climate of the region has an average annual precipitation of $c.1015$ mm, with an average annual minimum temperature of 10°C and a maximum of 21.9°C (data obtained from the National Meteorological Service). The study area was a 2 ha plot in relictual native grassland where no agricultural activity had taken place for more than 20 years (Tognetti et al. 2010) and which contained a great diversity of plants with entomophilous flowers.

Surveys

Four monthly samples were taken, on two consecutive days, between December 2009 and March 2010, the period in which most entomophilous plants are flowering and the flower visitors are active (Marrero 2013). In order to maximize arthropod activity sampling was carried out under similar climatic conditions and favorable weather (temperature above 15° C, null or moderate wind and sunny days) between 10:00 and 17:00 h. The first day, two observers walked the entire study plot and all entomophilous plants in flower were registered and the flower visitors foraging on flowers were caught. Plants were collected and taken to the laboratory for identification. Flower visitors were caught with a net, killed, mounted with entomological pins and identified to the lowest taxonomic level possible. All insects (body size ≥3 mm) foraging on a unit of floral attraction (flowers or inflorescences of Asteraceae, Apiaceae and Dipsacaceae) were considered as flower visitors. Sampling effort was held constant (2 hours/sampling). On the second day, the same two observers caught spiders which were killed and preserved in ethanol. Spiders were only caught when consuming prey. Those seen without prey were not immediately collected, but the plant on which they were found was labeled and observed periodically during that day. At the end of the sampling day, all observed spiders were caught, whether with or without prey. Prey were mounted with entomological pins and identified. Sampling effort was held constant (2 hours/sampling).

This methodology was repeated in each of the four monthly sampling periods. All flower visitors and spiders collected were identified to the lowest taxonomic level possible. The specimens that could not be identified at the species level were assigned to morpho-species.

Analysis

The interaction networks among the flowers, their visitors and the crab spiders were analyzed and graphed using the R statistical software (R Development Core Team 2013) bipartite package (Dormann et al. 2009). All interactions observed between flower visitors and crab spiders were put together in one network. We used two indices to analyze the interactions between the crab spiders and their prey: (1) Strength: S = Σd_{i-j}, where Σd_{i-j} is the sum of the dependences, and dependence represents the proportion of the interactions for each species with its partners $d_i = f_i/T$; f_i is the frequency of interaction of species i and T is the total frequency interaction; and (2) Partner diversity: PD = $-\Sigma\ p_i$ $\log_2 p_i$, where p_i is the frequency of individuals of species i with respect to total individual frequency. Strength (S) provides information on the asymmetry in the interaction networks and partner diversity (PD) takes the diversity of the prey into account. If the values of strength for the species of a trophic level are similar, they indicate symmetry in the interaction network (Bascompte et al. 2006). On the other hand, partner diversity is the Shannon diversity of the interactions of each species.

We also calculated the richness/order of flower visitors and the richness/order of prey. We carried out a paired t-test (ln-transformed) with the InfoStat statistical program (Di Rienzo et al. 2008) to analyze whether there were any differences between the richness/order of prey and flower visitors.

We caught the crab spiders' prey and counted the pollen grains transported on their bodies (35 individuals of 17 species of flower visitors) in order to evaluate the differences in the number of pollen grains transported by flower visitors of different orders. Under a binocular microscope, a cube of glycerine with safranin (~27 mm³) was passed over the bodies of the flower visitors to extract the pollen grains adhering to the bodies (Alarcón 2010). Care was taken to not pass the cube over parts of the bodies where pollen was not available for pollination (e.g. scopae in bees). A temporary pollen preparation on a glass slide was made with this jelly cube and the pollen grains were counted under the microscope at 200 × magnification. We performed an ANOVA (ln-transformed), followed by post-hoc Tukey tests to correct for multiple

comparisons and we estimated the differences in mean numbers of pollen grains carried by all individuals belonging to each order with the InfoStat statistical program (Di Rienzo et al. 2008).

To analyze the possible effect of crab spiders in the community, we evaluated interaction networks in which we had removed one of the three main orders of prey from the original network. The three resulting networks (without Diptera, without Lepidoptera, and without Hymenoptera) were analyzed as bipartite interaction networks (plant–flower visitors and flower visitors–crab spiders) and were compared with the original network. The number of lower and higher trophic levels (trophic levels richness), connectance (realized links/possible links) and the mean number of links per species were calculated for each network. Specifically, we emphasize which species/order recorded as prey can have a greater effect on plants and spiders communities.

Results

Thirty species of entomophilous plants were flowering during the four-month study and arthropod interactions were seen in 28 of them (24 with flower visitors, 17 with crab spiders and 12 with both; Appendix 1). Additionally, 112 species of flower visitors were caught, belonging to 37 families of six orders (Table 1; Appendix 2). Five species of crab spiders were caught, four of which belonged to Thomisidae and one to Philodromidae (Table 2).

Interaction networks

Two spider species (*Misumenops pallidus* and *Misumenops* sp. 2) were present in most (74.3%) of the tri-trophic interactions (Figure 1) and interacted with numerous plant species (14 and 12, respectively). Moreover, they showed the highest values for strength and partner diversity (Table 2). Among flower

Table 1. Number of species of flower visitors to entomophilous plants and number of species that were caught by crab spiders on these flowers in a grassland ecosystem in the Pampean region, Argentina. The differences between the richness of flower visitors and prey were significant ($n = 6$; T = 4.1; $p < 0.05$).

Order	Richness of flower visitors (%)	Richness of prey (%)
Diptera	38 (33.93)	17 (65.39)
Lepidoptera	11 (9.82)	3 (11.53)
Hymenoptera	43 (38.39)	6 (23.08)
Coleoptera	17 (15.19)	–
Hemiptera	2 (1.77)	–
Blattaria	1 (0.90)	–
Total	112	26

Table 2. Values obtained for strength and partner diversity for five crab spiders studied in a tri-trophic interaction network in a grassland ecosystem, Argentina.

Family	Thomisidae				Philodromidae
	Misumenops		Thomisidae		*Paracleocnemis*
Species	*pallidus*	sp. 2	sp. 1	sp. 2	sp. 1
Strength	10.425	11.361	1.403	2.361	0.450
Partner diversity	2.189	2.653	1.330	1.332	0.693

visitors, Hymenoptera were most species rich (38.4% of total flower visitors) and Blattaria were the poorest (0.9%). On the other hand, 65.4% of individuals that fell prey to the spiders were Diptera, 23.1% were Hymenoptera and 11.5% were Lepidoptera. No species of Blattaria, Coleoptera or Hemiptera were caught by crab spiders (Table 1; Appendix 3). The paired t-test showed significant differences between the number of species/orders recorded as flower visitors and the number of species/orders recorded as prey of crab spiders ($n = 6$; $T = 4.1$; $p < 0.05$) (Table 1).

Pollen transport

Number of pollen grains adhering to the bodies of Hymenoptera (mean = 8994.17, SD = 4242.38) was significantly greater than to Diptera (mean = 473.12; SD = 134.79) and Lepidoptera (mean = 34.25; SD = 33.25), and the number of pollen grains transported by Diptera was significantly greater than Lepidoptera ($n = 35$; $F = 13.66$; $p < 0.0001$) (Table 3).

Modeling interaction networks

Plant–flower visitor networks obtained by removing the individuals belonging to taxonomic order recorded as prey varied in different statistics depending on which taxonomic group was removed. This removal is simply an exclusion of data points. When individuals belonging to Diptera were removed from the original network, no great variation occurred in plant richness, connectance or links for species in the plant–flower visitor network (Table 4A). However, the disappearance of Diptera species led to a large decrease in crab spider richness, while it slightly increased the connectance and decreased the links for species in flower visitor–crab spider network (Table 4B). On the other hand, when we removed Hymenoptera or Lepidoptera, statistics were not greatly affected for either the plant–flower

visitor or flower visitor–crab spider networks (Table 4A, B).

Discussion

This study presents the description of a tri-trophic interaction network with crab spiders as predators in a grassland ecosystem. We found that crab spiders are not opportunistic, consuming selectively prey belonging to a subgroup of flower visitors, principally Diptera, in the sampled community. These flower visitors captured by crab spider were inefficient as pollen carriers.

Interaction networks

The richest trophic level of the networks was that of the flower visitors and the poorest one was that of the spiders. The species of *Misumenops* behaved as generalist predators given the great diversity of species recorded as their prey. The values for strength showed asymmetry in the flower visitor–crab spider network, in which *Misumenops pallidus* and *Misumenops* sp. 2 showed higher values. This asymmetry could be generated due to a higher abundance of these two species in the community, or due to specific traits (larger body size, stronger poison) that make them better predators. A network might be highly asymmetric when a crab spider species depends strongly on a prey species. Bascompte et al. (2006) showed that the asymmetry in the interaction networks is generated by the heterogeneous dependences of different species that might be related in coevolutionary adaptations which would lead to an increase in the biodiversity of a community. In our study, these adaptations might be associated with morphological and/or behavioral characteristics of different species of crab spiders (larger and stronger individuals, with the most powerful poisons, larger quantity of poison, mimesis, etc.) that would allow them to catch a wider range of prey.

As already mentioned, it has been reported that spiders can negatively modify the pollination service offered by only a few species of bees and bumblebees (Suttle 2003; Dukas 2005). However, little is known
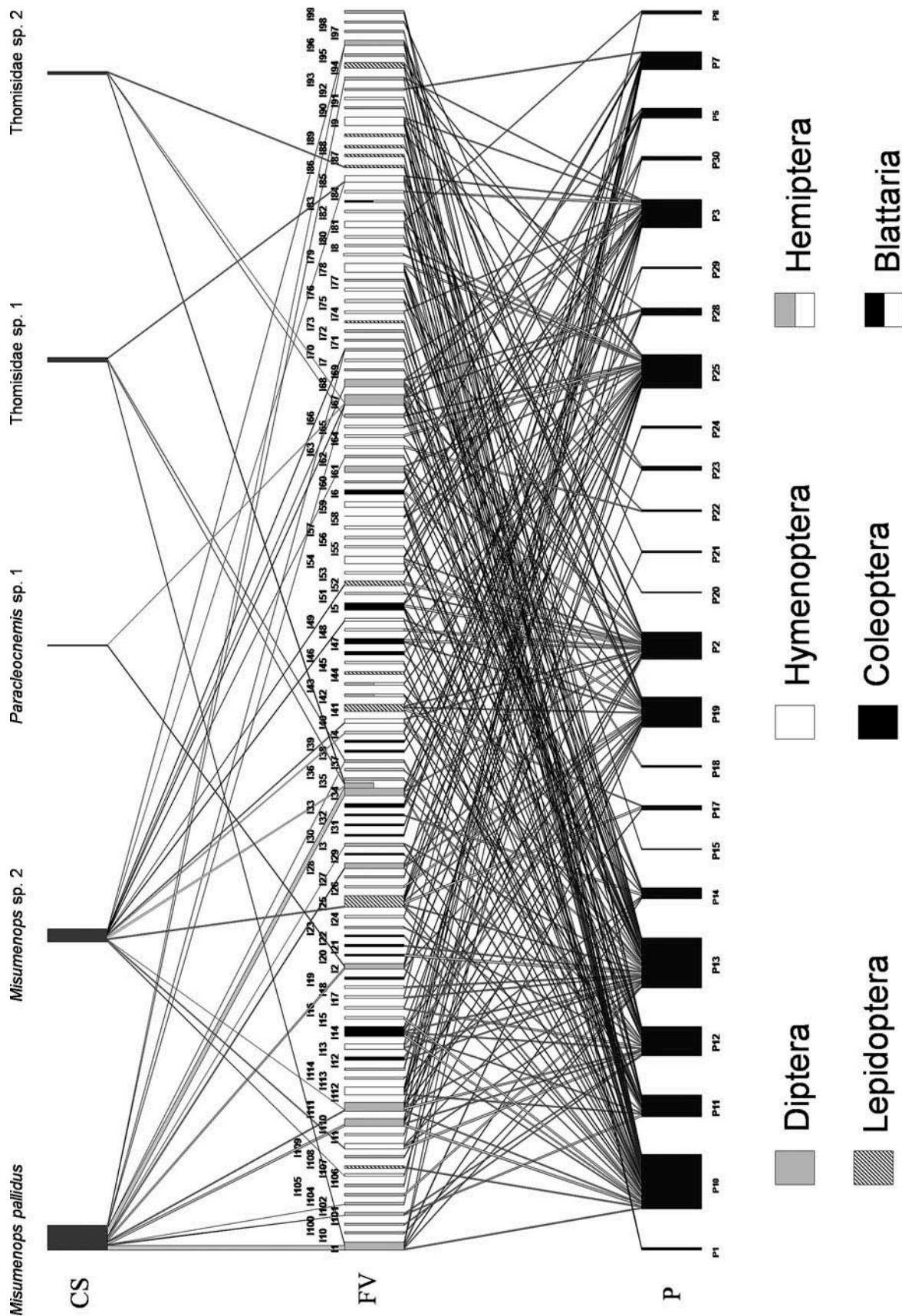
Figure 1. Tripartite interaction network: plants in the lowest trophic level (P); flower visitor in the intermediate trophic level (FV); and crab spiders in the highest trophic level (CS). The bipartite interaction network of the highest level (flower visitor–crab spider) is quantitative and the links represent the frequency with which a particular crab spider caught a prey species. The width of the nodes represents the number of interactions of each species. The insect I34 is represented by a larger node so that the interactions with the crab spiders are shown proportionately.

Table 3. Comparison of the number of pollen grains (mean ± SE) adhering to the bodies of flower visitors (excluding scopae in bees) that had fallen prey of crab spiders collected on entomophilous plants in a grassland ecosystems in the Pampean region, Argentina, showing the number of individuals analyzed and species richness ($n = 35$; F = 13.66; $p < 0.0001$). Means with different letters are significantly different (post-hoc Tukey tests $p < 0.05$).

Order	Number of pollen grains	Individuals analyzed	Species analyzed
Hymenoptera	8994.17 (±4242.38) a	6	4
Diptera	473.12 (±134.79) b	25	12
Lepidoptera	34.25 (±33.25) c	4	3

about the effect of spiders on other groups of flower visitors, such as flies, butterflies, and beetles. For example, although numerous families of flies are recognized flower visitors (Larson et al. 2001), they transport smaller amounts of pollen on their bodies than other insects, such as bees (Table 2; Alarcón 2010), whereas they consume resources offered by the plant, i.e. flies might be wasting pollen and/or nectar of the host plant. Crab spiders in a community might reduce the density of flies which would result in a reduced loss of resources that would then be available to more efficient visitors.

In this work, the hymenopteran flower visitors, the taxon with the highest species richness (and probably the highest visitation frequency and/or abundance), were not proportionally taken as prey by the spiders. In fact, the commonest species of prey were Diptera, perhaps because they are more vulnerable than bees which have the opportunity to defend themselves with their sting. Also, bees learn to recognize and avoid predators on flowers (Dukas & Morse 2003; Ings & Chittka 2008, 2009; Abbott & Dukas 2009). However, Brechbühl, Casas, et al. (2010) found that the most common prey of *Misumena vatia* were bees,

which were the most abundant flower visitors with the highest visitation rate. In this case, the explanation could be linked to the size of the spiders which were all adults with a lot of experience in capturing and with maximal strength and venom reservoir. In contrast, we worked with juveniles and adults. Cheli et al. (2006) mentioned that *Misumenops pallidus* preferred small, highly mobile prey, with soft exoskeletons and without repellents. González et al. (2009) found that *M. pallidus* preferred moth larvae as prey because they have soft cuticula and do not contain defensive substances, as Heteroptera do. We found that crab spiders did not consume hard cuticula (strongly sclerotized) prey, such as Coleoptera, but no larvae were found on flowers, so flies and butterflies were probably the flower visitors with the softest cuticula.

In our study we found differences between the richness of orders of flower visitors and the richness of orders of prey of the crab spiders, which indicates that the crab spiders are selective when catching their prey. Brechbühl, Casas, et al. (2010) found that prey capture success was lower than 10% of total visits for most of the flower visitors, except for non-syrphid flies (less specialized flies) whose success was higher than 20%. Brechbühl et al. (2011) measured the vulnerability of all flower visitors, and indeed flies were the most vulnerable ones, together with some solitary bees. These were also two groups that were strongly avoiding flowers with spiders (see also Brechbühl, Casas, et al. 2010; Brechbühl, Kropf, et al. 2010). Our results indicate that the Hymenoptera carried the largest pollen loads in the community and were one of the less frequent prey types. Furthermore, flies carried few pollen grains and that likely makes them more efficient as pollinators. On the other hand they also consume plant resources such as nectar or pollen. A decrease in density of flies could increase plant resources available for flower visitors carrying great pollen loads and more likely to promote pollination.

Table 4. Statistics calculated for the original interaction network and for the three resultant interaction networks after removing principal prey orders from the original interaction network. The network analysis was carried out as bipartite interaction networks; A: plant–flower visitor and B: flower visitor–crab spider.

	Original network	Without Diptera	Without Lepidoptera	Without Hymenoptera
A. Plant–flower visitor				
Flower visitor richness	112	95	109	106
Plant richness	24	23	24	23
Connectance	0.097	0.091	0.094	0.100
Link for species	1.912	1.678	1.849	1.884
B. Flower visitor–crab spider				
Crab spider richness	5	3	5	5
Flower visitor richness	26	9	23	20
Connectance	0.300	0.370	0.313	0.320
Link for species	1.268	0.833	1.286	1.280

Thus, a reduction in the abundance of these flies might have positive effects on the fitness of some plant species in the community. Moreover, crab spider prey might be restricted to only the more vulnerable (e.g. small and/or defenseless) flower visitors and thereby promote a better pollen flow with larger flower visitors.

Modeling interaction networks

When Diptera prey were removed from the original interaction network, observed changes mainly affected the species richness of crab spiders. Small variations in plant richness were observed in the resulting networks. Only one plant extinction occurred despite the removal of 17 species of Diptera. Moreover, by removing these prey species two crab spider species become extinct, indicating the importance of flies as prey. So, prey consumed by crab spiders may not have a direct effect on the plants they interact with. The structure of mutualistic networks is directly related to the abundance of the species they include (Vázquez et al. 2007), therefore it is important to understand how plant–pollinator interaction networks are modified by the presence of predators. The function of crab spiders might be to model the structure of plant–pollinator networks, decreasing the density or modifying the behavior of flower visitors. In conclusion, we found that spiders selected prey. Furthermore, the prey species were flower visitors with low numbers of pollen grains adhering to their bodies, which could not negatively affect the fitness of plants.

Acknowledgments

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Appendix 1. List of entomophilous plant species collected at the study site, showing the type of visitor observed (flower visitor and/or crab spider). The abbreviations correspond to those used in Figure 1. The two underlined species did not receive any visits.

Abbrev.	Plants	Family	Flower visitors	Crab spiders
P1	*Adesmia bicolor* (Poir.) DC.	Fabaceae	X	
P2	*Baccharis pingraea* DC.	Asteraceae	X	X
P3	*Carduus acanthoides* L.	Asteraceae	X	X
P4	*Centaurium pulchellum* (Sw.) Druce	Gentianaceae		
P5	*Cirsium vulgare* (Savi) Ten.	Asteraceae	X	
P6	*Pluchea sagittalis* (Lam.) Cabrera	Asteraceae		X
P7	*Conium maculatum* L.	Apiaceae	X	X
P8	*Convolvulus hermanniae* L'Her.	Convolvulaceae	X	
P9	*Conyza bonariensis* (L.) Cronquist	Asteraceae		X
P10	*Diplotaxis tenuifolia* (L.) DC	Brassicaceae	X	X
P11	*Dipsacus sativus* (L.) Honck.	Dipsacaceae	X	X
P12	*Eryngium horridum* Malme	Apiaceae	X	X
P13	*Eryngium elegans* Cham. & Schltdl.	Apiaceae	X	X
P14	*Foeniculum vulgare* Mill.	Apiaceae	X	
P15	*Galactia marginalis* Benth.	Fabaceae	X	
P16	*Geranium* sp.	Geraniaceae		X
P17	*Glandularia peruviana* (L.) Small	Verbenaceae	X	
P18	*Hydrocotyle bonariensis* Lam.	Apiaceae	X	X
P19	*Hirschfeldia incana* (L.) Lagr.-Foss.	Brassicaceae	X	X
P20	*Lactuca serriola* L.	Asteraceae	X	
P21	*Medicago lupulina* L.	Fabaceae	X	
P22	*Melilotus albus* Desr.	Fabaceae	X	X
P23	*Solanum pilcomayense* Morong.	Solanaceae	X	
P24	*Solanum sisymbriifolium* Lam.	Solanaceae	X	
P25	*Solidago chilensis* Meyen	Asteraceae	X	X
P26	*Sonchus oleraceus* L.	Asteraceae		
P27	*Trifolium repens* L.	Fabaceae		X
P28	*Verbascum thapsus* L.	Scrophulariaceae	X	X
P29	*Verbena bonariensis* L.	Verbenaceae	X	
P30	*Verbena intermedia* Gillies & Hook. ex Hook.	Verbenaceae	X	X
	Total		24	17

Appendix 2. List of species of flower visitors (order and family) caught in flowers of entomophilous plants. The abbreviations correspond to those used in Figure 1. The underlined species were prey of the crab spiders.

Abbrev.	Flower visitors	Order	Family
I1	*Allograpta exotica* Wiedemann	Diptera	Syrphidae
I2	Anthomyiidae sp. 1	Diptera	Anthomyiidae
I3	Anthomyiidae sp. 2	Diptera	Anthomyiidae
I4	*Apis mellifera* L.	Hymenoptera	Apidae
I5	*Astylus atromaculatus* Blanch.	Coleoptera	Melyridae
I6	*Astylus quadrilineatus* (Germ.)	Coleoptera	Melyridae
I7	*Augochlora iphigenia* Holmberg	Hymenoptera	Halictidae
I8	*Augochlorella ephyra* (Schrottky)	Hymenoptera	Halictidae
I9	*Bombus bellicosus* Smith	Hymenoptera	Apidae
I10	Bombyliidae sp. 2	Diptera	Bombyliidae
I11	*Brachynomada* sp. 1	Hymenoptera	Apidae
I12	*Bruchidius endotubercularis* Arora	Coleoptera	Chrysomelidae
I13	*Ceratina* cf. *montana* Holmberg	Hymenoptera	Apidae
I14	*Chauliognathus scriptus* (Germ.)	Coleoptera	Cantharidae
I15	*Chilicola* sp. 1	Hymenoptera	Colletidae
I16	*Chlorion hemipyrrhum* (Sichel)	Hymenoptera	Sphecidae
I17	Chrysididae sp. 1	Hymenoptera	Chrysididae
I18	Chrysididae sp. 2	Hymenoptera	Chrysididae
I19	Chrysomelidae sp. 1	Coleoptera	Chrysomelidae
I20	Chrysomelidae sp. 2	Coleoptera	Chrysomelidae
I21	Chrysomelidae sp. 3	Coleoptera	Chrysomelidae
I22	Chrysomelidae sp. 4	Coleoptera	Chrysomelidae
I23	*Cochliomyia macellaria* (Fabricius)	Diptera	Calliphoridae
I24	*Coelioxys* sp. 1	Hymenoptera	Megachilidae
I25	*Colias lesbia* (Hübner)	Lepidoptera	Pieridae
I26	*Colletes* sp. 1	Hymenoptera	Colletidae
I27	Conopidae sp. 1	Diptera	Conopidae
I28	Culicidae sp. 1	Diptera	Culicidae
I29	Curculionidae sp. 1	Coleoptera	Curculionidae
I30	Curculionidae sp. 2	Coleoptera	Curculionidae
I31	Curculionidae sp. 3	Coleoptera	Curculionidae
I32	*Cycloneda sanguinea* (L.)	Coleoptera	Coccinellidae
I33	*Diabrotica speciosa* (Germ.)	Coleoptera	Chrysomelidae
I34	*Dilophus* cf. *similis* Rondani	Diptera	Bibionidae
I35	Diptera sp. 1	Diptera	?
I36	Diptera sp. 2	Diptera	?
I37	Diptera sp. 4	Diptera	?
I38	Elateridae sp. 1	Coleoptera	Elateridae
I39	*Eriopis connexa* (Germ.)	Coleoptera	Coccinellidae
I40	*Eucyrtothynnus* cf. *ichneumoneus* (Klug)	Hymenoptera	Tiphiidae
I41	*Euptoieta claudia* (Blanchard)	Lepidoptera	Nymphalidae
I42	Heteroptera sp. 1	Heteroptera	?
I43	Heteroptera sp. 2	Heteroptera	?
I44	*Hylephila phyleus* (Drury)	Lepidoptera	Hesperiidae
I45	Hymenoptera sp. 1	Hymenoptera	?
I46	Lampyridae sp. 1	Coleoptera	Lampyridae
I47	Lampyridae sp. 2	Coleoptera	Lampyridae
I48	*Larra* sp. 1	Hymenoptera	Crabronidae
I49	*Lasioglossum* (*Dialictus*) sp. 1	Hymenoptera	Halictidae
I51	*Lasioglossum* (*Dialictus*) sp. 3	Hymenoptera	Halictidae
I52	*Lerodea eufala* (Edwards)	Lepidoptera	Hesperiidae
I53	*Megachile* (*Acentron*) sp. 1	Hymenoptera	Megachilidae
I54	*Megachile gomphrenae* Holmberg	Hymenoptera	Megachilidae
I55	*Megachile* sp. 1	Hymenoptera	Megachilidae
I56	*Megachile* sp. 2	Hymenoptera	Megachilidae
I57	*Melissodes rufithorax* Brèthes	Hymenoptera	Apidae
I58	*Melissoptila tandilensis* Holmberg	Hymenoptera	Apidae
I59	*Melissodes tintinnans* (Holmberg)	Hymenoptera	Apidae

Appendix 2. (Continued).

Abbrev.	Flower visitors	Order	Family
I60	*Microcerella* sp. 1	Diptera	Sarcophagidae
I61	*Mischocyttarus drewseni* Saussure	Hymenoptera	Vespidae
I62	Muscidae sp. 1	Diptera	Muscidae
I63	*Myzinum* sp. 1	Hymenoptera	Tiphiidae
I64	*Oxybelus* sp. 1	Hymenoptera	Crabronidae
I65	*Oxybelus* sp. 2	Hymenoptera	Crabronidae
I66	*Oxysarcodexia terminalis* (Wiedemann)	Diptera	Sarcophagidae
I67	*Oxysarcodexia varia* (Walker)	Diptera	Sarcophagidae
I68	*Palpada distinguenda* Wiedemann	Diptera	Syrphidae
I69	*Palpada elegans* Blanchard	Diptera	Syrphidae
I70	*Palpada meigenii* Wiedemann	Diptera	Syrphidae
I71	*Palpada rufiventris* (Macquart)	Diptera	Syrphidae
I72	*Pampasatyrus periphas* (Godart)	Lepidoptera	Nymphalidae
I73	*Palpada* sp. 1	Diptera	Syrphidae
I74	*Peponapis fervens* (Smith)	Hymenoptera	Apidae
I75	*Pepsis* sp. 1	Hymenoptera	Pompilidae
I76	*Perilampus* sp. 1	Hymenoptera	Perilampidae
I77	*Poecilognathus* sp. 1	Diptera	Bombyliidae
I78	*Polistes cinerascens* Saussure	Hymenoptera	Vespidae
I79	*Prionyx* sp. 1	Hymenoptera	Sphecidae
I80	*Protandrena* sp. 1	Hymenoptera	Andrenidae
I81	*Psaenythia* sp. 1	Hymenoptera	Andrenidae
I82	*Psaenythia* sp. 2	Hymenoptera	Andrenidae
I83	*Pseudomops neglecta* Shelford	Blattaria	Blattellidae
I84	*Pseudagapostemon puelchanus* (Holmberg)	Hymenoptera	Halictidae
I85	*Pseudagapostemon pampeanus* (Holmberg)	Hymenoptera	Halictidae
I86	Pyralidae sp. 1	Lepidoptera	Pyralidae
I87	Pyralidae sp. 2	Lepidoptera	Pyralidae
I88	*Pyrgus communis* (Grote)	Lepidoptera	Hesperiidae
I89	*Rachiplusia nu* (Guenée)	Lepidoptera	Noctuidae
I90	*Blaesoxipha* sp. 1	Diptera	Sarcophagidae
I91	*Sphecodes* sp. 1	Hymenoptera	Halictidae
I92	Stratiomyidae sp. 1	Diptera	Stratiomyidae
I93	Stratiomyidae sp. 2	Diptera	Stratiomyidae
I94	*Strymon eurytulus* (Hübner)	Lepidoptera	Lycaenidae
I95	*Syritta flaviventris* Macquart	Diptera	Syrphidae
I96	Tachinidae sp. 1	Diptera	Tachinidae
I97	Tachinidae sp. 10	Diptera	Tachinidae
I98	Tachinidae sp. 2	Diptera	Tachinidae
I99	Tachinidae sp. 3	Diptera	Tachinidae
I100	Tachinidae sp. 4	Diptera	Tachinidae
I101	*Limnophora* sp. 1	Diptera	Muscidae
I102	Tachinidae sp. 6	Diptera	Tachinidae
I104	Tachinidae sp. 8	Diptera	Tachinidae
I105	Tachinidae sp. 9	Diptera	Tachinidae
I106	*Tachytes* sp. 1	Hymenoptera	Crabronidae
I107	*Tatochila* sp. 1	Lepidoptera	Pieridae
I108	Asilidae sp. 1	Diptera	Asilidae
I109	*Tiphia andina* Brèthes	Hymenoptera	Tiphiidae
I110	*Toxomerus* sp. 1	Diptera	Syrphidae
I111	*Trichopoda* sp. 1	Diptera	Tachinidae
I112	*Xylocopa ciliata* Burmeister	Hymenoptera	Apidae
I113	*Lasioglossum* (*Dialictus*) sp. 2	Hymenoptera	Halictidae
I114	Bombyliidae sp. 1	Diptera	Bombyliidae

Appendix 3. Matrix of interactions showing the crab spiders (columns) and flower visitors that were prey (rows). The number in each cell shows individuals of prey and is proportional to the width of the links in Figure 1.

	Crab spider				
Prey	*Misumenops pallidus*	*Misumenops* sp. 2	*Paracleocnemis* sp. 1	Thomisidae sp. 1	Thomisidae sp. 2
Allograpta exotica Wiedemann	7			1	
Limnophora sp. 1	1				
Tachinidae sp. 6	1				
Tachytes sp. 1		1			
Tiphia andina Brèthes		1			
Toxomerus sp. 1	3				
Trichopoda sp. 1	1	1			
Anthomyiidae sp. 1	4		1		
Colias lesbia (Hübner)		2			
Culicidae sp. 1	2				
Anthomyiidae sp. 2	1				
Dilophus cf. *similis* Rondani	12	2		2	2
Diptera sp. 4	1			2	
Apis mellifera L.		2			
Eucyrtothynnus cf. *ichneumoneus* (Klug)		2			
Lasioglossum (*Dialictus*) sp. 1		1			
Lerodea eufala (Edwards)		1			
Muscidae sp. 1		1			
Oxysarcodexia terminalis (Wiedemann)					1
Oxysarcodexia varia (Walker)	1	1	1		1
Palpada distinguenda Wiedemann		1			
Palpada meigenii Wiedemann	1	1			
Pseudagapostemon pampeanus (Holmberg)		1		1	
Pyralidae sp. 1					1
Stratiomyidae sp. 2	2				
Tachinidae sp. 1	1	1			