Plant, Pollinator... Predator? Ecologies of Tritrophic Interactions, and the Proposed Effects of Flower-Dwelling Thomisids on Host-Plant Fitness

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Writer's Comment: In EVE 149, "Evolution of Ecological Systems," our term paper prompt was to write about a topic relating to community ecology and/or evolution. Ecosystem structuring and symbioses in particular are sustained interests of mine, and thus my project became an exciting opportunity to delve deeper into how we study, classify, and communicate about these fundamentally dynamic aspects of nature. Specifically, I opted to review research regarding the impacts of crab spiders on their host plants' fitness, within the framework of relationships between flowering plants and their associated pollinators. Sit-and-wait arachnid predators can benefit plants by preying on herbivores or nectar thieves, for example, but may also interfere with plant reproduction by consuming or otherwise deterring potentially beneficial floral visitors. Highlights of current literature on these multitrophic interactions (plant-pollinator-predator) include not only nuances of specific triads' developmental patterns and net fitness outcomes, but also emphasis on the importance of considering context dependency—such as spatiotemporal variation of participant species' richness, abundances, and behaviours—in analysis of ecological networks more broadly.

Instructor's Comment: Remote instruction during the Covid-19 pandemic created problems for everyone. My comment on Shannon Reilly's "Prized Writing" essay will be very brief because, unlike under *normal circumstances, I didn't really get to know my remote students very well. Shannon took my course EVE 149, "Evolution of Ecological Systems," in fall 2021. This is an advanced course on the community concept in ecology, viewed from an evolutionary standpoint. It demands a great deal of reading ranging across several fields, from philosophy of science to physiological ecology to paleobiology. The final grade is based on three items, equally weighted: a midterm exam and a final, both long-essay, and a term paper. The term paper must be on a topic chosen by the student and approved by me, dealing with some aspect of interspecific interaction or synecology. It is normally a literature review, with emphasis on the primary literature. Shannon received A+ grades on both exams and an A for this paper. (She didn't get an A+ because she missed a critical reference. To coin a cliché, I was shocked, shocked, shocked given her outstanding overall performance!) Several term papers from this course have won a place in "Prized Writing" and a few have been published. I would not be surprised if Shannon joins the latter, highly exclusive, club.*

—Arthur M. Shapiro, Department of Evolution and Ecology

Abstract

Contemporary flowering-plants' immense diversity is commonly associated with millions of years of hypothesized coevolution with a variety of pollinating animals, particularly flying insects. It is thus unsurprising that much of modern ecological study regarding angiosperm-animal interactions is centered on the various relationships of these taxa and their associated pollinators. Nonetheless, such interactions do not exist in an ecological vacuum, and are naturally subject to several spectra of abiotic and biotic influences which themselves play a role in those plants' fitness determinations and evolution more generally. In this regard, one notable area of ongoing research interest is in the ecological roles of flower-dwelling predators within plant-pollinator associations. This literature review will describe the structures and implications of such tritrophic interactions, primarily focused on the ecological roles of crab spiders (Thomisidae) relative to their host plants and those floras' own insect visitors. In addition, relevant contextual research on extended ecological webs—such as around herbivore consumption, volatile plant signals, and spider crypsis—will also be discussed and evaluated. Examination of the development and consequences of multi-trophic systems like the above-described triads may reveal themes potentially applicable to community ecology and evolution more broadly, such as the context-dependency of categorizing symbiotic relationships (i.e., commensalism versus mutualism or antagonism) or the potentiality of frequency-dependent selection on predators by their prey (in opposition to the perhaps classic model).

Keywords: Thomisidae, plant-pollinator, tritrophic interactions, fitness, selection, symbiosis

Introduction

Plant-pollinator associations frequently function as keystone mutualisms in natural ecosystems, as well as in humans' agricultural systems and broader economies (Benoit & Kalisz 2020). In fact, these often-charismatic examples of interspecific interactions can be critical for the persistence of those relationships' involved species and/or the stability of their surrounding ecological communities (Fründ et al. 2010). As collections of autotrophic producers, terrestrial vegetations form a base layer of productivity and structure for many different organic systems, at a variety of scales; the presence and formations of these organisms in an environment shape much of how other macrobiota move through and interact with that space, over time. And in turn, the respective members of each subsequent layer of herbivore, meso-consumer, or other trophic classes influence the development and composition of the vegetation, as well as each other, both directly and indirectly. Such cascades of interacting effects can profoundly impact the growth and persistence of a species; for flowering plants, these interactions are now being increasingly examined at the scale of primary and secondary associations (Benoit and Kalisz 2020)—exploring how not just pollinator traits, but also factors like herbivory and arthropod predation on floral visitors, play into positive and negative fitness determinations.

As typically generalist predators, spiders are commonly considered important meso-consumers in their respective ecosystems (Silva et al. 2020). Sit-and-wait crab spiders (Thomisidae), as well as actively-hunting lynx spiders (Oxyopidae) are two cosmopolitan arachnid clades notably associated with floral-dwelling and the consumption of plant-associated invertebrates (Kersch-Becker et al. 2018, Romero et al. 2008), though there is also some emerging research on arboreal tarantulas (Theraphosidae) opportunistically attacking tropical hummingbirds that visit flowers (Alcantara Viana et al. 2021). Thomisids are popular study subjects for examining the effects of predation on pollinators and host plants because of their broad geographic distribution, generalist foraging (typically from a plant-associated hideout), and curious capabilities for crypsis or aggressive mimicry (in some genera) (Knauer et al. 2018).

Yet within this growing subfield of community ecology and evolution research, one major point of contention centers around how these flower-dwelling spiders, through their direct influence on pollinator and herbivore traits and behaviors, may indirectly benefit or detract from the survival and fecundity of their host plants. Some authors take a firm stance arguing for either net positive or negative fitness effects (e.g., Cuny et al. 2020, Antiquiera and Romero 2016), while others claim a more nuanced position focused on context-dependency and the dynamicity of biological communities (e.g., Telles et al. 2018, Gavini et al. 2019a, Benoit and Kalisz 2020). This paper will review and synthesize relevant literature attempting to conceptualize and evaluate the tritrophic interactions of spiders, plants, and pollinators, with an emphasis on the ecological role of thomisids relative to their host plants and associated floral visitors, and a secondary focus on contextual concepts including hymenopteran behaviour and crab spiders' evolution and exploitation of both visual and olfactory signals.

Baseline: plant-pollinator interactions

Plant-pollinator associations are commonly understood to be products of millennia of coevolution, by which stationary plants have developed strategies to increase outcrossing sexual reproduction through attraction and sometimes exploitation of mobile floral visitors, and animals such as birds, bats, small mammals, or especially insects have in turn taken advantage of floral provisions including foodstuffs and sheltering architecture. Direct selection pressures exerted by these symbiotes on one another has contributed to expansive taxonomic radiations over time; angiosperms serviced by biotic pollen vectors, versus wind, are estimated to account for ~87.5 percent of assumed species-level diversity in the flowering plant clade (Ollerton et al. 2011).

Evolution is not a directed process, however, and neither are all plant-pollinator relationships as simple or entirely mutualistic as popular audiences may frequently imagine them to be. For instance, a plethora of descriptions of mimicry or other bargain-breaking acts on the part of one participant or another exist throughout the literature—from rewardless orchids producing attractive olfactory signals (Schiestl 2005), to nectar-robbing bumblebees (floral larcenists) that feed on floral resources without significantly contributing to pollination (Irwin et al. 2010). Plants and their pollinators do not set out to somehow assist one another intentionally, yet pollination is closely intertwined with angiosperm reproduction. Thus, a multitude of selection factors acting on these organisms both individually and in combination can lead to complex and sometimes contradictory trait evolution.

Branching out: spider-plant interactions

Although it is not entirely clear how and why spiders choose their respective host plants and develop fidelity behaviors to them, there are a number of current hypotheses. First, as reviewed by Gavini et al. (2019a), spider presence is commonly associated with plant traits including flower color, rosette leaf arrangement, overall size, inflorescence height, and the presence and length of glandular trichomes. These mainly morphological characteristics can be evaluated by a discerning arachnid seeking a specific microhabitat; exact trends or values for relevant traits vary between study systems (Gavini et al. 2019a), as well as across life stages within some spider species (Su et al. 2020). In addition to aspects of plant architecture, more transient, often induced signals in the form of volatile chemicals have also been shown to attract spiders to certain plants. A 2018 study by Knauer et al., for example, described local adaptation of *Biscutella laevigata* (Brassicaceae) to the presence of the crab spider *Thomisus onustus* via emission of the attractive floral monoterpene β-ocimene as a consequence of florivore infestation. The authors additionally noted that β-ocimene is found across a multitude of other plant species, as an herbivory-induced compound in leaves as well as flowers, and so may influence plant-spider interactions in other systems besides that covered by their paper.

In studies on mechanisms of specifically spider-plant relationships (less directly focused on pollinator elements), symbioses are often classified in relation to the consequences of spiders' predation on herbivores. Such consumption can function as an indirect defense for an associated host plant, as seen in the above example of florivory-induced olfactory signals attracting *T. onustus* to threatened plant individuals. At the same time, however, spiders' generalist predation habits do not only cover herbivores, but also extend to potentially beneficial floral visitors, including pollinators. Depending on the study system, and its own abundances and traits of predator and prey species, researchers have drawn variable conclusions about the ecological partnerships between spiders and plants.

For instance, Kersch-Becker et al. (2018) explored the independent and interactive effects of different spider foraging habits on floral herbivory and fitness of a glandular trichome-bearing plant, *Trichogoniopsis adenatha* (Asteraceae), by contrasting the sit-and-wait crab spider *Misumenops argenteus* (Thomisidae) with active-hunting lynx spiders of the genus *Peucetia* (Oxyopidae).

Host-plant fitness was positively impacted by the presence of each spider type, as measured in herbivore suppression and increased ovary fertilization compared to spiderless controls, but the combined presence of the two taxa had an additive beneficial effect weaker than that of either spider taxon's presence alone. In this case, spiders and plants were generally considered to be engaged in a mutualistic relationship.

On the other hand, the work of Gavini et al. (2019a) on the ecological role of *Misumenops pallidus* (Thomisidae) relative to its host *Anemone multifida* (Ranunculaceae) found more of a commensal spider-plant association. Specifically, the presence of spiders did not appear to affect pollinator visitation rate, florivory, or overall plant fitness. According to the authors, the asymmetrical benefit (favoring spiders) may result from a combination of factors weakening top-down effects on plant fitness, including the low-to-medium abundance of spiders observed, the generalist diet of *M. pallidus*, and the presence of ecologically redundant pollinators in the region. They also noted that upward variation in spider population density could further increase asymmetrical benefits attained from inhabiting *A. multifida* plants, likely causing a shift from commensalism to antagonism.

Overall, several authors have commented on how variation in abundance—of spiders and/or prey species—is known or hypothesized to affect fitness for plant individuals as well as populations. With respect to floral-dwelling spiders generally, Silva et al.'s (2020) study of *Peucetia flava* (Oxyopidae) and *Chamaecrista neesiana* (Leguminosae Caesalpinioideae) in the tropical savanna found that plant benefits from indirect herbivory defense were conditional on predator abundance over time, and highest during the rainy season (the period of peak abundance for *P. flava*). The aforementioned Kersch-Becker et al. (2018) work also indicated that suppression of herbivory may be more effective with higher abundance, rather than diversity, of predators. Regarding prey species, modeling by Higginson et al. (2010) suggests that plants' net fitness effects are strongly influenced by the relative density and effectiveness of pollinators, as well as strength of florivory, in a system. Moreover, Telles et al. (2018) found that when flower-dwelling predators have access to, and experience with, abundant non-pollinator prey, they may attack other species less frequently—and even indirectly benefit their host plants.

Bringing it together: pollinator-spider interactions

By consuming pollinators, as well as altering their behavior through a so-called "landscape of fear" (Cuny et al. 2020), flower-dwelling predators can disrupt plant-pollinator mutualisms to varying degrees, with a multitude of potential consequences for plant fitness. Focusing on interactions between spiders and floral visitors—specifically insect pollinators—there exists a complex interplay between the morphological, physiological, and behavioral traits of predators and prey. As described by Rodríguez-Morales et al. (2020), sit-and-wait predators such as crab spiders typically must use patient stillness (avoiding motion-detection cues in prey) and attain some form of crypsis or signal exploitation relative to the sensory system(s) of their targets, while prey use a blend of visual and olfactory information to identify ambush predators, and then potentially engage in behavioral strategies to avoid a novel or repeated attack.

Crypsis, Signaling, and Sensory Perception

Under selective pressure to avoid detection by potential prey, ambush-hunting thomisids have evolved a complex blend of camouflage strategies. For example, depending on the exact species—and sometimes instar—individuals may exhibit different degrees of preference for certain host-plant flower-colourations (Gavini et al. 2019a, Su et al. 2020), or even specific positions (such as on flower heads versus receptacles) on individual plants' inflorescences (Rodríguez-Morales et al. 2018). Body colouration is also a variably employed strategy for evading notice; some species are known for their plasticity—altering their appearance over several days to mimic the colouration of particular flowers—while others exhibit more permanent color-polymorphisms that may help them blend in with certain plant species or features of floral architecture (Ajuria Ibarra et al. 2018, Rodríguez-Morales et al. 2018).

Rather than attempting to escape detection by potential prey items, some thomisids have alternatively evolved to exploit plants' visual and olfactory signals that are attractive to pollinators and other floral visitors. Manipulation or exploitation of a signal its prey is sensorily biased towards can increase a spider's chances of foraging success (Heiling et al. 2004). The previously discussed floral volatile β-ocimene, for instance, serves as an attractive signal for not just crab spiders but also some pollinator species (Knauer et al. 2018). Further overlap in host-plant choice factors can also be found for *Thomisus spectabilis* and honeybees (*Apis mellifera*) in relation to *Chrysanthemum frutescens* (Asteraceae), in the contexts of olfactory cues and flower symmetry (Heiling et al. 2004, Wignall et al. 2006). Another way in which crab spiders take advantage of insect pollinators' perception biases is through mimicry of visual cues; visual luring is a common strategy among sit-and-wait predators (White and Kemp 2020). For example, UV+-white colouration, functioning as a conspicuous and attractive visual lure, has recurrently evolved across several species of flower-dwelling thomisids in Australia (Gawryszewski et al. 2017), and UV-induced fluorescence has been proposed as an additional possible signal to draw in prey (Brandt and Masta 2017, Suetsugu and Morihisa 2020). A leaf-dwelling crab spider, *Epicadus heterogaster* has even been observed successfully attracting pollinators, via its own mimicry of flower shape and UV reflectance, in the absence of a nearby floral model (Vieira et al. 2017). Exploitation of existing signals can contribute to conflicting selection pressures on the plants exhibiting those traits, because they may suffer a decline in reproductive success if a greater proportion of would-be pollinators are consumed or otherwise deterred by predators-in-residence. Knauer et al. (2018) specifically call out floral-dwelling predators' influences on floral trait evolution as a currently enigmatic and underexplored area of research.

Importantly, the relative effectiveness of a camouflage or attraction strategy is highly dependent on the sensory system(s) of whatever animals are potentially attempting to identify and interact (or not) with the organism engaged in passive deception. Factors such as visual acuity and color sensitivity are particularly crucial to consider, as are decision-trees and sense-prioritization, when attempting to evaluate the perception and responsiveness of an individual confronted with abiotic and biotic stimuli. Bees' ability to see into the UV portion of the electromagnetic spectrum is one reason researchers have been exploring spider signaling through signals in that light range, and models of honeybee vision specifically have been used to check hypothetical conspicuousness of variously pigmented, distanced, and positioned, flower-dwelling spiders (Rodríguez-Morales 2018). With respect to decision-making and interpretation of sensory input, insect prey species have been shown to exhibit differential responses to color, morphology, and/or presence of ambush predators (Morse 2007, Gavini et al. 2018, Rodríguez-Morales et al. 2020). By keeping in mind the biases of human sensory perception (e.g., emphasis on color cues) relative to research on non-human organisms, researchers can hopefully construct more objective experimental conditions, and so also draw more useful conclusions.

Behavior and Learning by Prey

In a similar vein to predators' exploitation of floral traits influencing foraging success and pollinator attraction, prey behavioral responses can observably affect ongoing selection on predators' morphological traits. Ajuria Ibarra et al. (2018) explored a notable example of this phenomenon, examining how honeybees' (*Apis mellifera*) learned experiences contribute to subsequent predator avoidance and so also selection on the colouration of *Synema globosum* (Thomisidae). Results indicated that based on a prior, simulated attack, honeybees learn to avoid spider color morphs associated with that experience. This gives less-common morphs a fitness advantage (more opportunities to catch prey), and contributes to cyclical modulation of each discrete, heritable color-pattern's frequency in the population over time. Thus, in contrast to the perhaps traditional model of predator-on-prey selection mechanisms, this study offers empirical evidence for negative frequency-dependent selection on predators' conspicuous polymorphisms as a consequence of prey behavior—a concept which could have potentially significant implications for ecological and evolutionary study even beyond spider-pollinator systems.

Pollinators' behavioral responses to predation risk, mediated by sensory perception and sometimes also learned experience, also more generally provide a link between direct dynamics of spider-pollinator interactions and cascading, indirect impacts of spiders on host-plant fitness. Not all species are equally capable of discerning the presence of a floral-dwelling predator while foraging, and not all species react the same way to such a potential threat even after it has been successfully identified (Brechbühl et al., 2009; Rodríguez-Gironés and Jiménez 2019). A significant portion of extant research on spider-pollinator interactions in this context has primarily focused on hymenopterans—and among those, mostly social bees (Howard 2021)—but some generally proposed influences affecting pollinator responses to perceived predation risk include ecological factors (bee size and sociality, abundance of available resources), as well as organisms' previous experience with predators (Rodríguez-Gironés and Jiménez 2019). At least at the species level, bees that are larger and/or habituated to less frequent occurrences of spider attack are more likely to respond to perceived predator presence with indifference, while those that are smaller and/or have experienced a prior predation attempt (real or simulated) typically exhibit more avoidance behaviors (Gavini et al. 2018, Telles et al. 2018, Gavini et al. 2019b). In systems with generalist pollinators, especially in abundance, such a mix of behaviors combined with opportunities for ecological redundancy could impact the magnitude of negative plant-fitness cascades resulting from arachnid-on-pollinator predation (Higginson et al. 2004). Moreover, considering these behavioral variations in complement to abundance effects on spider foraging patterns (Telles et al. 2018), it seems that the fitness effects of these tritrophic interactions are in yet another way highly context dependent.

Conclusion

This review summarized and synthesized major themes of current literature regarding tritrophic interactions of spiders, plants, and pollinators—primarily focusing on how angiosperm fitness is impacted by thomisid predation, and additionally discussing contextual topics including florivory, sensory signals, and foraging behaviors. While some authors emphasize core subsets of the triad (e.g., spider-pollinator interactions) and argue a paradigm of majority-positive or negative fitness cascades, others offer a more nuanced, often system-specific analysis of net effects. In short, consideration of context dependency and spatiotemporal variation is critically important for exploration of multitrophic interactions' inputs and outcomes. Developing research in this area has already provided, and will likely continue to contribute, significant insight about broader themes of biological communities' structures, functions, and dynamism.

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