

Venus Flytrap Rarely Traps Its Pollinators

Elsa Youngsteadt,^{1,*} Rebecca E. Irwin,² Alison Fowler,² Matthew A. Bertone,¹
Sara June Giacomini,² Michael Kunz,³ Dale Suiter,⁴ and Clyde E. Sorenson¹

1. Department of Entomology and Plant Pathology, North Carolina State University, Raleigh, North Carolina 27695; 2. Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695; 3. North Carolina Botanical Garden, University of North Carolina, Chapel Hill, North Carolina 27599; 4. US Fish and Wildlife Service, Raleigh, North Carolina 27606

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ABSTRACT: Because carnivorous plants rely on arthropods as pollinators and prey, they risk consuming would-be mutualists. We examined this potential conflict in the Venus flytrap (*Dionaea muscipula*), whose pollinators were previously unknown. Diverse arthropods from two classes and nine orders visited flowers; 56% of visitors carried *D. muscipula* pollen, often mixed with pollen of coflowering species. Within this diverse, generalized community, certain bee and beetle species appear to be the most important pollinators, on the basis of their abundance, pollen load size, and pollen fidelity. *Dionaea muscipula* prey spanned four invertebrate classes and 11 orders; spiders, beetles, and ants were most common. At the family and species levels, few taxa were shared between traps and flowers, yielding a near-zero value of niche overlap for these potentially competing structures. Spatial separation of traps and flowers may contribute to partitioning the invertebrate community between nutritional and reproductive functions in *D. muscipula*.

Keywords: Venus flytrap, *Dionaea muscipula*, pollination ecology, pollinator-prey conflict, niche overlap.

Introduction

Plants typically interact with multiple species of animals and exhibit ecological and evolutionary responses to the conflicting pressures imposed by mutualists (such as pollinators) and antagonists (such as herbivores; e.g., Strauss and Irwin 2004; Sun et al. 2016). Carnivorous plants present a special case of potentially conflicting pressures. Because many carnivorous plants rely on arthropods as pollinators and prey, they risk consuming their would-be mutualists (Givnish 1989; Ellison and Gotelli 2001). They may therefore face trade-offs between pollination services and nutrient intake, known as

pollinator-prey conflict (Juniper et al. 1989; Zamora 1999; Jürgens et al. 2012). For example, recent experiments suggest that the red color of sundew (*Drosera*) traps reduces pollinator bycatch but at the expense of total prey capture (Jürgens et al. 2015). With few exceptions, however, the extent and strength of pollinator-prey conflict is poorly quantified (but see Zamora 1999; Murza et al. 2006; El-Sayed et al. 2016). The pollination systems of most carnivorous species are poorly documented, while the composition of their prey is often reported at coarse taxonomic resolution (Jürgens et al. 2012).

Remarkably, Venus flytrap, *Dionaea muscipula* J. Ellis (Droseraceae), is among the species whose pollinators have never been reported. Of more than 600 species of carnivorous plants in the world, *D. muscipula* is the only terrestrial species with an active snap trap (Ellison and Gotelli 2009). Since *D. muscipula* came to the attention of Victorian naturalists in the 1800s, the rapid movement of its traps has prompted cultural fascination and extensive physiological study (e.g., Darwin 1875; Forterre et al. 2005; Chase et al. 2009). The species is now cultivated in many countries for research, education, and horticultural trade, but its native range is restricted to a small area of North Carolina and South Carolina, where it is threatened by habitat loss, fire suppression, and poaching. The International Union for Conservation of Nature and the North Carolina Plant Conservation Program list the species as vulnerable, and it has been petitioned for listing under the US Endangered Species Act (Schnell et al. 2000; Robinson and Finnegan 2016; Waller et al. 2016).

Despite the conservation status and unique trap biology of *D. muscipula*, its pollination ecology is relatively unknown. From mid-May to early July, it produces white, saucer-shaped flowers, approximately 2 cm in diameter, in a cymous raceme atop a scape 15–35 cm long (Smith 1929; Roberts and Oosting 1958). Roberts and Oosting (1958, p. 202) reported that it is self-infertile and that pollination is “presumably . . . entomophilous, apparently by various

* Corresponding author; e-mail: ekyoung@ncsu.edu.

ORCIDiDs: Youngsteadt, <http://orcid.org/0000-0003-2032-9674>; Fowler, <http://orcid.org/0000-0002-9263-2253>; Suiter, <http://orcid.org/0000-0002-7494-7227>; Sorenson, <http://orcid.org/0000-0002-7127-7272>.

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beetles, small flies, and possibly spiders,” although they did not present data or more specific taxonomic determinations. Prey have been better quantified; spiders, ants, and beetles compose the largest share (Ellison and Gotelli 2009; Hutchens and Luken 2015).

The goal of this study was to document the potentially conflicting insect interactions of *D. muscipula* flowers and traps to inform further study of its evolutionary ecology and conservation management. Specifically, we asked the following: (1) Which invertebrate species visit *D. muscipula* flowers? (2) Which of these are the most important potential pollinators? (3) To what extent do flowers and traps interact with the same suite of invertebrates?

Methods

Study System

Dionaea muscipula is native only to southeastern North Carolina and northeastern South Carolina, where it grows in wet longleaf (*Pinus palustris*) and pond pine (*Pinus serotina*) savannas and the ecotone between evergreen shrub bogs and dry pine stands (Luken 2005; Schafale 2012). These habitats have frequent fire return intervals and waterlogged, low-nutrient soils. Because of these conditions, *D. muscipula* captures prey to satisfy nutrient requirements and co-occurs with a diverse community of other carnivorous plants (Ellison and Gotelli 2001). This habitat is well represented in Pender County, North Carolina, where our study took place.

Sampling

We sampled *D. muscipula* flower visitors and prey from three sites, separated by 2.5–3.7 km. Each site comprised hundreds to thousands of flowering stems. We sampled on four dates in 2016 during peak *D. muscipula* bloom (May 17, May 24, June 2, and June 10). We collected flower visitors between 1000 and 1820 hours during fair weather for a total of 29.5 person-hours of collecting (68–670 person-minutes per site each time a site was visited). During sampling, we searched the site and collected all arthropods observed on anthers, stigmas, and flower petals. Arthropods were collected directly into individual vials or netted and transferred into vials, and then they were sacrificed and transported on dry ice. We regularly washed nets with 70% ethanol to avoid pollen contamination. To develop a local pollen library, we removed a sample of anthers (or pollinia) from *D. muscipula* and all nearby flowering species and transported them in vials on dry ice.

We sampled prey from traps during the same flower-collecting periods. We used fine forceps to remove prey from a maximum of one closed trap per plant. Prey removal

did not damage plants. We transferred prey into individual vials of 70% ethanol.

We identified arthropods from flowers and traps to the lowest taxonomic level possible; target resolution was family for spiders and Orthoptera (most of which were immature or poorly preserved in traps) and species/morphospecies for other insects. We used standard references (e.g., Stehr 1987; Arnett et al. 2002 and references therein; Gibbs 2011) and comparison to reference material in the North Carolina State University Insect Museum, where voucher specimens will be deposited.

Pollen Analysis

To identify potential pollinators of *D. muscipula*—defined here as taxa that carry *D. muscipula* pollen on their bodies—we sampled and stained pollen from each flower visitor by swabbing all surfaces of its body with a small piece of fuchsin gel (Kearns and Inouye 1993). Hereafter, we refer to the pollen swabbed off the insects as the pollen load, and we assumed that pollen on the insect’s body was available for transfer to another plant. We mounted the pollen by melting the jelly on a microscope slide and sealing it with a coverslip. Similarly, we prepared slides of reference pollen from anthers and pollinia. We assessed all flower visitor slides under a compound microscope for the presence or absence of *D. muscipula* pollen and heterospecific pollen by comparison to the reference pollen. *Dionaea muscipula* pollen is large (~100 μm diameter) and easily distinguished from that of coflowering species.

For the subset of flower visitors that carried *D. muscipula* pollen, we subjected pollen slides from the 10 most abundant taxa to more detailed analysis. We counted a sample of pollen grains from up to 10 randomly selected slides per taxon (or all available slides if fewer than 10 individuals carried pollen). At $\times 200$ magnification, we counted the number of grains of *D. muscipula* pollen and heterospecific pollen in five fields of view per slide (one in the center of the stained sample and four peripheral fields of view from the center sampling point). The final sample count was the sum of the number of pollen grains in all five fields of view.

Data Analysis

All analyses were conducted using R v.3.3.1 within R studio v.1.0.136 (R Development Core Team 2013; RStudio Team 2015). To estimate the number of taxa that might be detected at flowers and traps with further sampling, we computed the Chao1 asymptotic richness estimator in the iNEXT package, using the subset of specimens identified to our target taxonomic resolution (Chao 1984; Hsieh et al. 2016). To determine whether the likelihood of carrying *D. muscipula* pollen varied across flower visitor taxa at the order level,

we used Fisher's exact test (implemented in the stats package). From this analysis, we excluded the orders Odonata and Neuroptera because of low sample sizes (two specimens and one specimen, respectively). To quantify differences among species/morphospecies in the amount of pollen carried, we constructed a generalized linear model in which pollen sample count was the response and species was the predictor. Because pollen counts were overdispersed, we used a binomial error distribution and log link function, implemented in the MASS package. One sample count of 343 pollen grains from one *Trichiotinus piger* beetle was a statistical outlier and was excluded from the analysis.

The relative importance of a flower-visiting animal species depends on the animal's abundance, pollen carrying capacity, pollen transfer efficiency, and floral fidelity (Primack and Silander 1975; Schemske and Horvitz 1984). To represent the likely relative importance of the 10 most abundant pollen-carrying taxa in this study, we modified methods of Lindsey (1984) and Gibson et al. (2006) to summarize aspects of pollinator quantity and quality into a single pollinator importance (PI) index. Because of the diversity of flower visitors considered, we followed Gibson et al. (2006) by summarizing quality in terms of fidelity, not pollen deposition. We calculated PI for taxon X as follows:

$$PI_X = (\text{relative abundance of } X) \times (\text{pollen carrying capacity of } X) \times (\text{fidelity of } X),$$

where relative abundance is the proportion of all insects carrying *D. muscipula* pollen that are of taxon X, pollen carrying capacity is the mean number of *D. muscipula* pollen grains sampled from individuals of taxon X (given pollen presence), and fidelity is the mean proportion of *D. muscipula* pollen within individual pollen loads of taxon X. The index cannot be compared across studies but indicates relative importance within a study.

To visualize overlap between prey and potential pollinators, we used the package bipartite (Dormann et al. 2008) to construct a quantitative interaction network in which *D. muscipula* traps and flowers were treated as species that interact with multiple invertebrates. We included only taxa that were identified to our target taxonomic resolution; among flower visitors, we included only individuals that carried *D. muscipula* pollen on their bodies (since consumption of nonpollinating flower visitors presents no conflict of interest for the plant). The analyzed data included 183 prey and 233 potential pollinators representing 107 taxa (including 55 singletons). To further assess niche overlap between flowers and traps, we used the package EcoSimR (Gotelli et al. 2015) to compute *O* (Pianka's index of niche overlap; Pianka 1973) and to assess its significance through a null model analysis. We used algorithm ra3 to reshuffle invertebrates between flowers and traps 1,000 times while retaining the original

niche breadth of each and then compared the observed value of *O* to the distribution generated by the null model.

Results

Flower Visitors

From *Dionaea muscipula* flowers, we collected a total of 426 arthropods representing two classes (Arachnida and Insecta) and eight insect orders. Of these, 409 specimens (96%) were identified to target taxonomic resolution (family for spiders and Orthoptera, species/morphospecies for all other groups), representing 98 taxa, of which 56 were singletons (table A1 is available online). The value of the Chao1 richness estimator was 218 (95% confidence interval [CI], 155–352), suggesting that continued sampling would detect more flower visitor taxa.

Overall, 69% of individual flower visitors carried pollen (*D. muscipula* and/or heterospecific pollen), but only 56% carried *D. muscipula* pollen; of these, 25% bore pure *D. muscipula* loads while 75% bore a mixture of *D. muscipula* and other pollen. Arthropods that carried *D. muscipula* pollen included 64 taxa (61 of which were identified to our target taxonomic resolution). Hymenoptera (principally bees) and Coleoptera were the most abundant orders on flowers and were the most likely to carry *D. muscipula* pollen (fig. 1A).

At finer taxonomic resolution, the quantity and quality of pollen loads on insect bodies varied across the 10 most common flower visitor taxa (table 1). Within the pollen-carrying community, the sweat bee *Augochlorella gratioiosa* (Halictidae) and the longhorned beetle *Typocerus sinuatus* (Cerambycidae) had the highest relative abundance, while *A. gratioiosa* and the checkered beetle *Trichodes apivorus* (Cleridae) carried the largest pollen loads (figs. 1B, 2; table 1). Across the 10 common taxa, the mean percentage of *D. muscipula* pollen within pollen loads ranged from 50% to 94% (table 1). Summarizing relative abundance, load size, and load composition into a single index suggested that *A. gratioiosa* was the most important pollinator of *D. muscipula* during the study (PI = 3.68), with the beetles *T. apivorus* (PI = 0.82) and *T. sinuatus* (PI = 0.72) in distant second and third places because of their lower abundance, more heavily mixed loads, and smaller mean load size.

Prey

From *D. muscipula* traps, we collected a total of 212 individual invertebrates representing four classes: Gastropoda, Arachnida (two orders), Crustacea (one order), and Insecta (seven orders). Of these, 40% were spiders (principally Salticidae and Lycosidae) and 58% were insects. Among the insects, the most abundant were Hymenoptera (26% of prey, principally ants) and Coleoptera (11%; fig. 2). Of the specimens

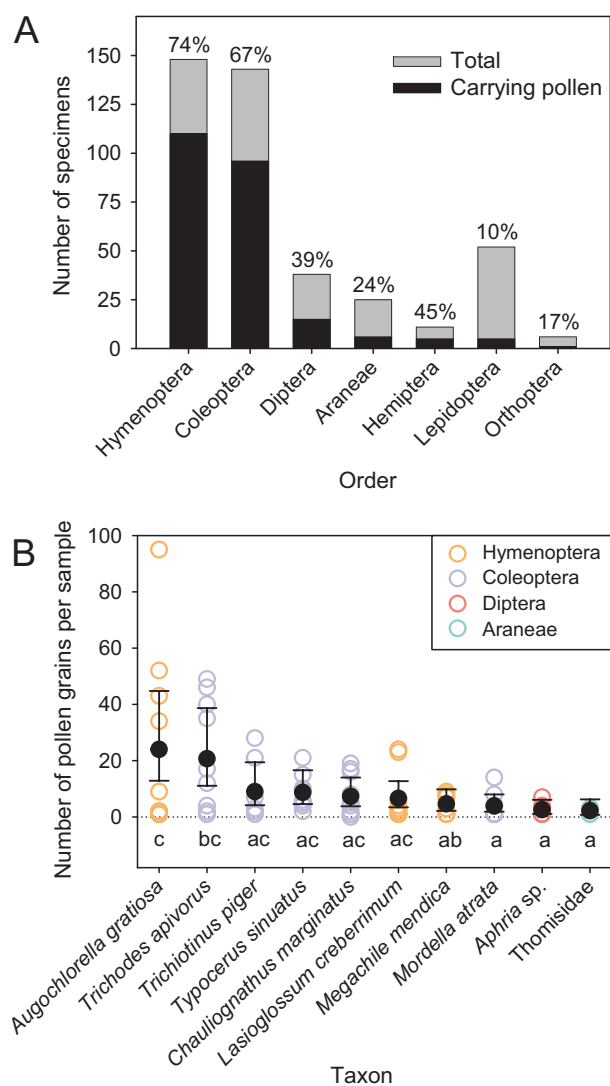


Figure 1: Components of *Dionaea muscipula* pollinator importance at the level of arthropod order (A) and species (B). Arthropod orders (A) differed in the likelihood of carrying *D. muscipula* pollen on their bodies (Fisher's exact test, $P < .0001$); values above bars are percentages of specimens bearing *D. muscipula* pollen. The 10 most abundant pollen-carrying taxa (B) differed in the number of *D. muscipula* pollen grains they carried. Colored circles are sample counts; black symbols show means and asymmetrical 95% confidence intervals from a negative binomial model. Taxa with the same letter are not significantly different. Data underlying the figure are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p8s64> (Youngsteadt et al. 2017).

collected, 182 individuals (86%) were identified to our target taxonomic resolution, representing 54 taxa, of which 32 were singletons (table A1). The Chao1 richness estimate was 224 (95% CI, 105–623), suggesting that continued sampling would detect more prey taxa.

Pollinator-Prey Overlap

Prey and flower visitor communities overlapped very little (fig. 2). Among taxa identified to our target resolution, 13 occurred in both traps and flowers. Nine of these 13 taxa included specimens that were potential pollinators but in low numbers. The overlapping taxa totaled 68 prey specimens (32% of individual prey) and 61 flower visitor specimens (14% of individual flower visitors). Among these 61 flower visitor specimens, only 17 carried *D. muscipula* pollen on their bodies (accounting for 7% of potential pollinators). The shared taxa that did not carry pollen (not shown in fig. 2) were grasshoppers (Acrididae), jumping spiders (Salticidae), the chrysomelid beetle *Paria aterrima*, and the ant *Crematogaster pilosa/atkinsoni*. The most extensive overlap between prey and potential pollinators occurred in the ant *Solenopsis invicta*, with 12 individuals in traps and three individuals at flowers, and the butterfly *Junonia coenia*, with five larvae in traps and 15 adults at flowers (of which two carried pollen). Except for one crab spider, the 10 most abundant flower-visiting taxa never occurred in traps. Pianka's index of niche overlap was 0.019 (on a scale from 0 to 1, where 0 represents no overlap). The null model analysis indicated that flower visitors and prey overlapped significantly less than expected compared with a random distribution of taxa between traps and flowers ($P < .001$). The value and significance of O were unchanged when we repeated the analysis excluding the 58 singleton taxa.

Discussion

We provide the first report of the flower-visiting community of the Venus flytrap. The species relies on a suite of generalist pollinators, primarily from the orders Hymenoptera and Coleoptera, embedded in a diverse flower visitor community. The most important vector of flytrap pollen in this study was the sweat bee *Augochlorella gratiosa*, but other bees (e.g., *Lasioglossum creberrimum*) and beetles (*Typocerus sinuatus* and *Trichodes apivorus*) also contributed to pollen movement. The per-visit efficiency with which any of the potential pollinators remove pollen from anthers and deposit pollen on stigmas remains to be determined. *Dionaea muscipula* attracted more diverse flower visitors than its closest terrestrial relatives (members of the genus *Drosera*). Studies of *Drosera* report flower visitors from three to seven insect families, while we documented 48 arthropod families at *D. muscipula* flowers (Murza et al. 2006; Anderson 2010; El-Sayed et al. 2016; table A1). Although some of these visitors, such as the scarabaeid and cerambycid beetles, are floral herbivores, their hirsute bodies and potentially long-distance movements also make them important pollen vectors in generalist pollination systems, assuming they do contact stigmas and are

Table 1: Characteristics of the 10 most abundant pollen-carrying taxa collected at *Dionaea muscipula* flowers

Taxon	Order	Family	No. caught	Proportion carrying <i>D. muscipula</i> pollen				No. pollen loads sampled	Mean proportion of <i>D. muscipula</i> pollen in load \pm SE	Mean no. <i>D. muscipula</i> grains in sample ^a	PI index
				Relative abundance	<i>D. muscipula</i> pollen	Relative abundance	No. pollen loads sampled				
<i>Augochlorella gratiosa</i>	Hymenoptera	Halictidae	49	.82	.17	.91 \pm .05	10	24.0	3.68		
<i>Trichodes apivorus</i>	Coleoptera	Cleridae	19	1.00	.08	.50 \pm .12	10	9.00	.82		
<i>Typocerus sinuatus</i>	Coleoptera	Cerambycidae	32	.94	.13	.66 \pm .11	10	8.70	.72		
<i>Lasioglossum creberrimum</i>	Hymenoptera	Halictidae	25	.68	.07	.87 \pm .10	10	7.30	.41		
<i>Chaulioognathus marginatus</i>	Coleoptera	Cantharidae	11	1.00	.05	.85 \pm .11	10	6.60	.29		
<i>Trichiotinus piger</i>	Coleoptera	Scarabaeidae	8	1.00	.03	.68 \pm .12	8	20.7	.21		
<i>Mordella atrata</i>	Coleoptera	Mordellidae	43	.28	.05	.94 \pm .06	9	4.63	.18		
<i>Megachile mendica</i>	Hymenoptera	Megachilidae	8	1.00	.03	.55 \pm .06	8	3.89	.07		
<i>Aphria</i> sp.	Diptera	Tachinidae	10	.60	.03	.88 \pm .09	7	2.57	.06		
Thomisidae	Araneae	Thomisidae	14	.36	.02	.90 \pm .10	5	2.20	.04		

Note: Pollinator importance (PI) index summarizes a taxon's relative abundance, pollen fidelity, and load size such that larger values are assumed to indicate greater pollination service to *D. muscipula*.

^a Pollen load samples represent a subsample of total pollen load for each individual. Values exclude one influential sample of 343 *D. muscipula* grains from *Trichiotinus piger*. See figure 1B for asymmetrical 95% confidence interval around these means, derived from negative binomial model of pollen counts.

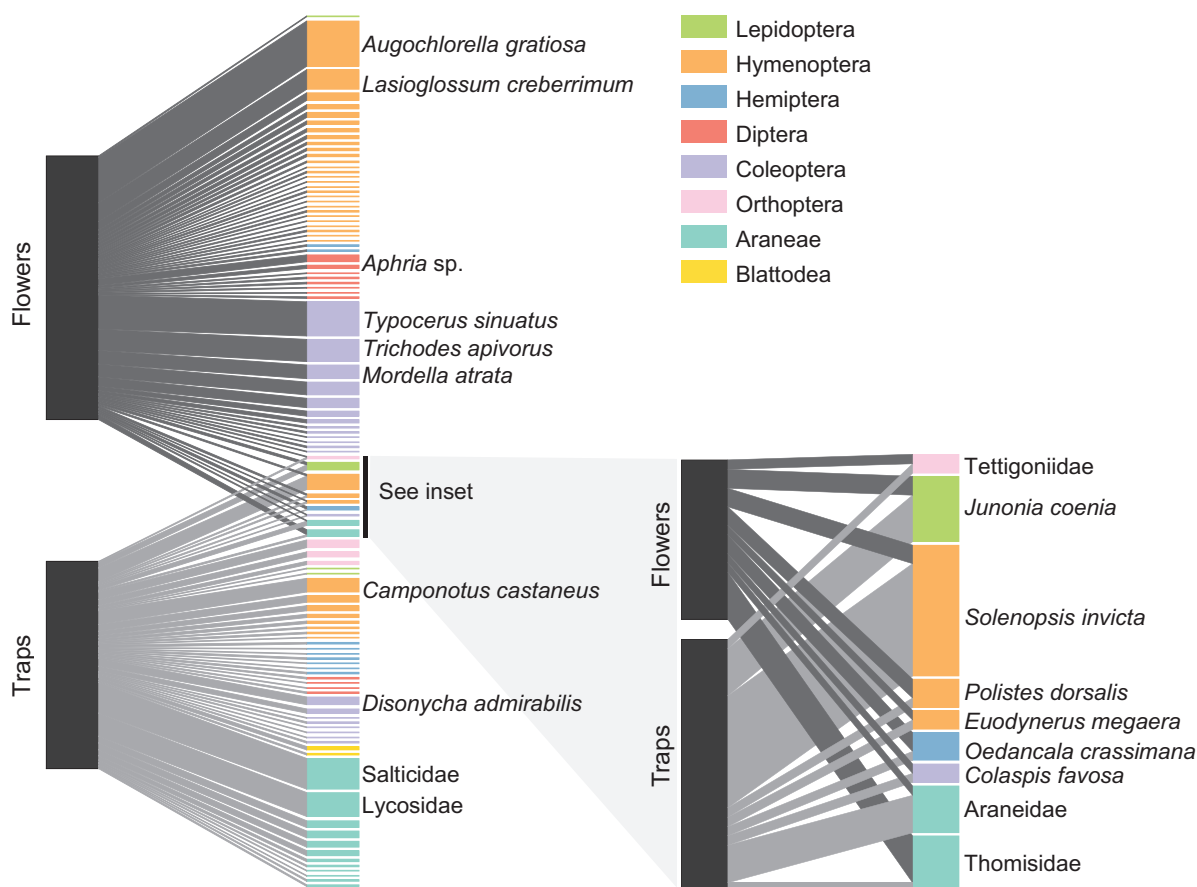


Figure 2: Quantitative network illustrating the extent of overlap between *Dionaea muscipula* prey and flower visitors. Only flower visitors that carried pollen are shown. In each network, block heights in the left bar represent the relative sample sizes of arthropods from flowers and traps; block heights in the right bar represent relative abundance of each taxon in the combined sample from traps and flowers. Taxa shared between traps and flowers are connected both to traps (light gray connections) and to flowers (dark gray connections); shared taxa are expanded in the inset. Data underlying the figure are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.p8s64> (Youngsteadt et al. 2017).

not strictly pollen thieves (Bernhardt 2000; Matsuki et al. 2008; Hargreaves et al. 2009).

We detected little overlap between pollen-carrying and prey communities, suggesting that *D. muscipula* traps and flowers partition the invertebrate community and largely avoid the pollinator-prey conflict. Studies in several *Drosera* species and *Sarracenia purpurea* also report zero to minor overlap (Murza et al. 2006; Ne'eman et al. 2006; Anderson 2010; El-Sayed et al. 2016), while in *Pinguicula vallisnerii-fofolia*, the capture of thrips and small beetles depleted a limited pollinator community in shaded habitats (Zamora 1999). Direct comparison across pollinator-prey overlap studies is not straightforward because of differing levels of taxonomic resolution and inconsistent reporting of arthropod sample sizes. Addressing pollinator-prey overlap as a quantitative question of niche overlap between flowers and traps may add clarity to comparative studies across carnivorous species.

Three mechanisms have been proposed for minimizing pollinator-prey overlap (Juniper et al. 1989; Jürgens et al. 2012): flowers and traps may (1) be separated in time, (2) be separated in space, or (3) deploy different attractants (such as different colors or scents). *Dionaea muscipula* does not employ temporal separation. Although it does not produce new traps during flowering (Roberts and Oosting 1958), pre-existing traps remain active; 73% of our prey specimens, including live and freshly caught individuals, were retrieved from plants with flowering stems. We speculate that spatial separation has some role in partitioning flower visitors and prey: flowers are elevated 15–35 cm above traps, and most flower visitors arrived through flight, while most prey walked into traps from the ground. In our sample, 87% of individual flower visitors (but only 20% of prey) were capable of flight. Finally, we cannot exclude the possibility of differential attraction. Although traps produce fluorescent and ultraviolet

reflectance patterns, carbohydrates, and volatile organic compounds (Joel et al. 1985; Givnish 1989; Jürgens et al. 2009; Kurup et al. 2013; Kreuzwieser et al. 2014), comparative data for flowers are lacking.

For any mechanism that partitions the pollinator and prey communities of a carnivorous plant, a key question is what selective pressures shaped that mechanism. In other words, is the lack of overlap between prey and pollinators a “ghost of competition past” (Connell 1980), reflecting selection for divergence in the niches occupied by flowers and traps? Or is it the product of independent selection pressures that separately shaped flowers and traps? In *Drosera* species, some of which also bear flowers on tall scapes, absolute height aboveground (and thus visibility to pollinators)—rather than flower-trap separation—appears to be the trait under selection, even though separation may sometimes reduce pollinator bycatch (Anderson and Midgley 2001; Anderson 2010; El-Sayed et al. 2016). Red *Drosera* trap color, on the other hand, deters pollinators but does not attract prey; Jürgens et al. (2015) suggest that selection against pollinator-prey overlap may favor this trait. The results we present for *D. muscipula* build a foundation for its inclusion in evolutionary ecological studies of the carnivore’s dilemma.

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Left, *Dionaea muscipula* in bloom, illustrating the spatial separation between traps and flowers. Photo credit: Clyde E. Sorenson. Right, two of the most important potential pollinators of *D. muscipula*: *Augochlorella gratiosa* (top) and *Typocerus sinuatus* (bottom). Photo credits: Elsa Youngsteadt (top), Clyde E. Sorenson (bottom).