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Pollinator trapping in selfing carnivorous plants, *Drosera makinoi* and *D. toyoakensis* (Droseraceae)

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Abstract Carnivorous plants use insects not only as prey, but also as pollinators. Whereas outcrossing carnivorous plants are known to avoid trapping pollinators, selfing carnivorous plants may capture the pollinators as prey. Here, we provide evidence that two selfing carnivorous plant species with short flower-trap separation, *Drosera makinoi* (white-colored flowers) and *D. toyoakensis* (pink-colored flowers), caught some major pollinator species belonging to Diptera and Hymenoptera: four out of five species in *D. makinoi* and one out of six species in *D. toyoakensis*. We also tested the function of flowers to attract pollinator or prey insects by experimentally removing *Drosera* flowers. Flower removal did not significantly affect the number of trapped insects. On the other hand, the removal of flowers of co-flowering neighbor plants, *Eriocaulon decemflorum* for *D. makinoi* and *Lysimachia fortunei* for *D. toyoakensis*, significantly decreased the number of trapped insects. This finding suggests an exploitative relationship between *Drosera* spp. and co-flowering species.

Keywords Carnivorous plants · Droseraceae · Pollinator · Self-pollination · Sundew

Introduction

Carnivorous plants use specialized traps to catch insects and absorb nutrients from their bodies. This unique feeding habit has been considered as an adaptation to nutrient-poor habitats because carnivorous plants can fill deficiency of nutrients in soil by digesting trapped insects (Thum 1988; Zamora et al. 1997; Thoren and Karlsson 1998). Probably due to this advantage, carnivory evolved at least six times independently in the angiosperms (Ellison and Gotelli 2001). Catching insects is, however, not always advantageous for carnivorous plants because insects may serve as both prey and pollinators (Ellison and Gotelli 2001). If the same insect species serves as both, catching pollinators may decrease pollination success. Most carnivorous plant species may avoid this Pollinator-Prey Overlap (PPO) by making traps functional only after a flowering season (temporal separation) or placing traps apart from flowers (spatial separation) (Jürgens et al. 2012). The degree of PPO has been studied in some sundew species (*Drosera* spp.) in which traps are arranged in a rosette close to the ground, whereas their flowers are located high at the top of erect stems. For *D. pauciflora*, Anderson (2010) demonstrated that no pollinators were caught in traps. Murza et al. (2006) showed that basal traps of another sundew *D. anglica* caught a minor pollinator species *Thrips* sp. (Murza et al. 2006). However, it comprised only 3% of all flower visitors and major pollinators (Diptera, 95% of the total) were not caught by the traps of *D. anglica*.

On the other hand, high PPO may be observed in highly selfing carnivorous species in which trapping pollinators may not reduce fitness under negligible inbreeding depression (Sciligo 2009; Jürgens et al. 2012). Sciligo (2009) tested this idea using autonomously selfing *D. arcturi* that showed no inbreeding depression, and showed that 96% of pollinator fly families were trapped. To test the expectation of high PPO in highly selfing species, further studies on other *Drosera* species are needed (Jürgens et al. 2012). Here, we examine this

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expectation in two selfing annuals *Drosera makinoi* Masamune and *D. toyoakensis* M. Watanabe in which the inbreeding coefficient is 0.497 and 0.260, respectively (Watanabe, unpublished), indicating that selfing rate is higher in *D. makinoi*. In *D. makinoi* and *D. toyoakensis*, flowers are close to trap leaves arising from flowering stems and pollinators may approach trap leaves more frequently.

We also examine whether the flowers of two *Drosera* species attract pollinator and prey insects. Because two species are moderately inbreeding, it may be unnecessary to attract many pollinators required for high outcrossing. On the other hand, it may be advantageous to attract more insects by flowers as prey (Zamora 1999; Salces-Castellano et al. 2016). To test how the flowers are attractive to pollinators and prey insects, we experimentally removed flowers of *Drosera* spp. In addition, we also experimentally removed flowers of co-flowering neighbor species because those could also increase the number of insects trapped by the two *Drosera* species.

Specific questions addressed in this paper are as follows. (1) How large is the degree of PPO in two selfing carnivorous species, *D. makinoi* and *D. toyoakensis*? (2) Does the experimental removal of the flowers of *Drosera* spp. decrease the numbers of insects trapped by *Drosera* spp.? (3) Does the experimental removal of the flowers of co-flowering neighbor plants decrease the number of insects trapped by *Drosera* spp.?

Materials and methods

Study species and sites

Drosera makinoi Masamune and *D. toyoakensis* M. Watanabe, previously included in *D. indica* (Watanabe et al. 2013; Kagawa 2015), are both annual plants with a single stem growing up to 10–20 cm. Linear and alternate trap leaves 5–7 cm long are scattered along the stem and trap leaves at the upper position are close to flowers (Fig. 1a). Traps have glandular hairs called tentacles and glands secrete sticky liquid and digestive enzyme (Sun et al. 2014). The two species are different in flower color: white in *D. makinoi* and pink in *D. toyoakensis*. Both *Drosera* species grow in open bogs of a few restricted localities and have been listed as threatened plants (Japan Wildlife 2015). *Drosera makinoi* has a scattered distribution in Japan and the distribution of *D. toyoakensis* is now restricted to Aichi Prefecture, Japan. *Drosera toyoakensis* germinates early in May and has three to four flowers at the top of the stem from July to September. Flowers open around 8 am and close by 1 pm. A flower blooms only once, and it does not open again after closing even if closing is due to strong rain or wind. About 500 seeds per flower mature in the middle of September, and the plants begin to wither in the middle of October. *Drosera makinoi* has similar phenology but a longer flowering period from July to

October. We made observations and field experiments of *D. makinoi* in a *Sphagnum* bog at Watarase (Tochigi City, Tochigi Pref., Japan). The bog is about 200 m² and neighboring to a population of common reed *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae). Studies of *D. toyoakensis* were carried out in a *Sphagnum* bog at Toyoake (N 35°4'26" E 137°1'7", Toyoake City, Aichi Pref., Japan). The bog of about 200 m² is surrounded by a protection fence and is neighboring to paddy fields.

Flower visitor observations

To determine whether pollinator species were trapped by *D. makinoi* and *D. toyoakensis*, we observed flower visitors from August to September for three years (2012–2014). For *D. makinoi*, we observed pollinators from 8 am to 2 pm, and for *D. toyoakensis*, from 7 am to 2 pm while careful not to damage the bog. We observed each flower visitor until it visited five flowers of *Drosera* or it flew away before visiting five flowers, and recorded the taxonomic identity of insect species and whether it touched stamens and/or pistils. Some flower visitors of *D. makinoi* and *D. toyoakensis* visited *Eriocaulon decemflorum* Maxim. (Eriocaulaceae) and *Lysimachia fortunei* Maxim. (Primulaceae), respectively (Fig. 1b, c). The plant species was recorded if the flower visitor moved from *Drosera* species to another species (co-flowering neighbor species) and vice versa. A pollinator was defined as an individual that (1) touched a stamen and/or a pistil and (2) carried pollen grains. Flower visitors were caught with a butterfly net and fixed with 95% ethanol. Later in the laboratory, the entire body of each insect visitor was stained with 45% aceto-carmine solution and observed under a stereomicroscope to check whether it carried pollen grains. Based on results from the flower-visitor survey and the following prey survey, we calculated an index of pollinator-prey species overlap J as the number of trapped pollinator species divided by the total number of pollinator species; $J = 0$ when no pollinator species was trapped, while $J = 1$ when all pollinator species were trapped.

We computed all statistical analyses using R 3.1 (R Core Team 2010). To examine whether there is a difference in the number of flower visits between *Drosera* and co-flowering neighbor plant species, we used a generalized linear mixed model (GLMM) with the plant species, pollinator species, and the interaction term as explanatory variables, and survey date as a random factor. At first, we verified the significance of the interaction term by comparing the model with and without the interaction term. In Watarase, we adopted the model without the interaction term because the effect of the interaction was not significant. In Toyoake, the interaction term was significant because some pollinators visited *Drosera* flowers more frequently than flowers of neighbor plant species, and others visited flowers of neighbor plant species more frequently than *Drosera* flowers. Thus, we only used the data of pollinator species

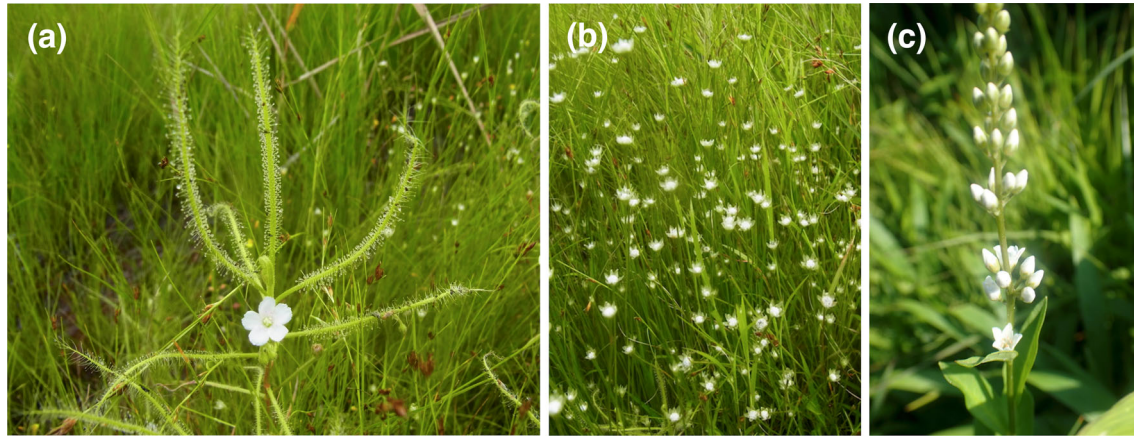


Fig. 1 *Drosera makinoi* and two co-flowering neighbors at the study sites of *Drosera* spp. **a** *Drosera mainoi*. **b** *Eriocaulon decemflorum*, a co-flowering species growing with *D. makinoi* at

Watarase site. **c** *Lysimachia fortunei*, a co-flowering species growing with *D. toyoakensis* at Toyoake site. Color figure online

that visited flowers of both *Drosera* and neighbor plant species at least once in our survey. We used a likelihood-ratio test (type II) to determine any significant effect of explanatory variables. These GLMM analyses were performed with a log link and a Poisson distribution (Crawley 2005) using the R package “lme4” (Douglas et al. 2015). To describe the degree of pollinator sharing between *Drosera* and co-flowering neighbor plant species, we calculated the niche overlap index (NOI) (Pianka 1973); the index ranges from 0 (no overlap) to 1 (complete overlap) using the R package “EcoSimR” (Gotelli et al. 2015).

Flower removal experiments

To determine the effect of flowers of *Drosera* and neighbor plants (*E. decemflorum* for *D. makinoi* and *L. fortunei* for *D. toyoakensis*) on the number of insects trapped by *D. makinoi* or *D. toyoakensis*, we removed flowers of *D. makinoi*, *D. toyoakensis* and neighbor plants during the flowering periods at study sites of *D. makinoi* and *D. toyoakensis*: September 5 and 6, 2014 for *D. makinoi* and September 2 and 3, 2014 for *D. toyoakensis*. For each species, we set the following four classes of 40 cm × 40 cm quadrats at an interval of 40 cm or longer: (1) a treatment where flowers of both *Drosera* species and neighbor species were left, (2) a treatment where flowers of *Drosera* species were left but flowers of neighbor plants were removed, (3) a treatment where flowers of neighbor plants were left but flowers of *Drosera* species were removed, and (4) a treatment where flowers of both *Drosera* species and neighbor plants were removed. For each treatment, we set one quadrat containing 20 individuals of each *Drosera* species and co-flowering neighbor species. When the quadrat had more than 20 individuals, we cut flowers of excessive individuals to equalize the sample size; here, we regarded the sample size as 20 by considering a plant as a unit of

replication. On each observation day (from 6 am to 7 am), we removed all flower buds of *Drosera* and/or neighbor plants that were just before flowering and we removed all dead insects on the surface of traps. For both *Drosera* species, we collected prey insects on traps from noon to 1 pm to identify species and recorded the number of prey individuals per day per plant in each quadrat. We then measured the body length of a prey insect, distance between each prey insect and the nearest flower, the presence/absence of flowers, and the height (from the ground) of traps where the prey was trapped.

To determine whether the flowers of *Drosera* species and neighbor species affected the number of prey individuals trapped, we used a generalized linear model (GLM) with the number of insects trapped per day per plant, the number of pollinators trapped per day per plant or the number of non-pollinators trapped per day per plant as the response variable. At first, the presence/absence of flowers of *Drosera*, the presence/absence of flowers of neighbor species and the interaction of these two variables were considered as the explanatory variables. Because the interaction effect on the response variable was not significant, we used a model without the interaction term to test effects of the two variables. Because the observed number of prey insects showed over-dispersion, we used a negative-binomial error distribution and a log link (Zuur et al. 2009) with a function “glm.nb” in the R package “MASS” (Venables and Ripley 2002).

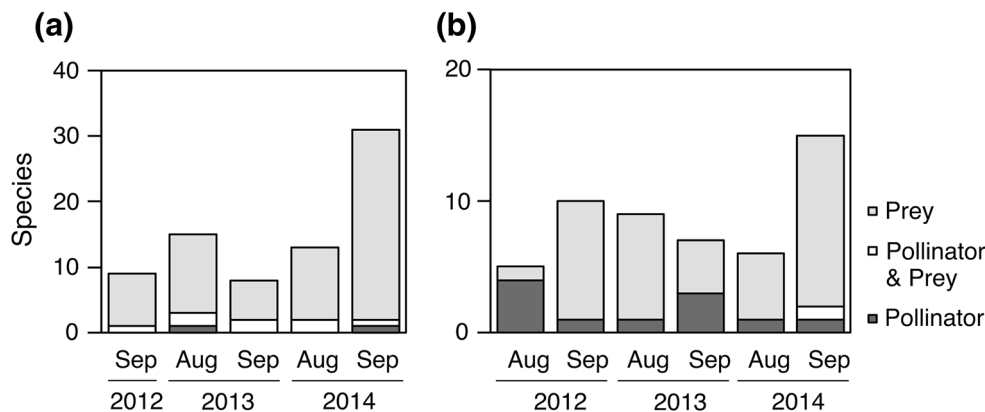
Results

Pollinator-prey species overlap

In *D. makinoi*, five pollinator species of Diptera, Hymenoptera and Lepidoptera were recorded (Table 1a, Fig. 2a) and all five pollinator species except *Mathias oberthueri* (Lepidoptera) were trapped as prey (Table 1

Table 1 Pollinator and prey species of *Drosera* and co-flowering neighbor species

Pollinator species	<i>D. makinoi</i> flower visits (mean ± SD)	<i>E. decemflorum</i> flower visit (mean ± SD)	Trapped (mean)
(a) <i>Drosera makinoi</i> and <i>Eriocaulon decemflorum</i>			
<i>Mesembrius flaviceps</i>	5.0 ± 4.0	4.5 ± 4.5	1.2
<i>Sphaerophoria menthastri</i>	3.3 ± 1.7	6.7 ± 4.8	1.4
<i>Andrena</i> sp.	0.50 ± 0.50	0.50 ± 0.50	0.2
<i>Apis mellifera</i>	3	–	0.13
<i>Mathias oberthueri</i>	1	1	0
Pollinator species	<i>D. toyoakensis</i> flower visits (mean ± SD)	<i>L. fortunei</i> flower visits (mean ± SD)	Trapped (mean)
(b) <i>D. toyoakensis</i> and <i>Lysimachia fortunei</i>			
<i>Eupeodes corollae</i>	0.25 ± 0.43	4.5 ± 4.0	0
<i>Lucilia</i> sp.	0	5	0
<i>Paragus haemorrhous</i>	0	3.0 ± 2.0	0
<i>Sphaerophoria menthastri</i>	4.5 ± 7.6	9.7 ± 8.5	2.5
<i>Eurema hecabe</i>	5.5 ± 5.5	2.5 ± 0.50	0
<i>Lycaena phlaeas</i>	0	10	0
<i>Zizeeria mahargia</i>	0.33 ± 0.47	5.3 ± 3.7	0

**Fig. 2** Monthly variations of pollinator and prey species composition. Green, blue and red bars respectively indicate the number of prey species that were not regarded as pollinators, the numbers of species regarded as both prey and pollinators, and the number of pollinator species not regarded as prey. **a** *Drosera makinoi*, **b** *D. toyoakensis*

a). In *D. toyoakensis*, six pollinator species of Diptera and Lepidoptera were recorded (Table 1b, Fig. 2b) among which only a syrphid fly *Sphaerophoria menthastri* (Diptera) was trapped as prey (Table 1b). The index of pollinator-prey species overlap J was 0.83 ± 0.21 (mean ± SD, $n = 5$) in *D. makinoi* and 0.071 ± 0.18 (mean ± SD, $n = 6$) in *D. toyoakensis*; it was positive in every month in *D. makinoi*, but positive only in September 2014 in *D. toyoakensis*.

A syrphid fly (*S. menthastri*, Fig. 3) was the most frequent visitor to flowers of *D. makinoi* (22.6% of all flower visits; mean ± SD = 1.3 ± 1.8) and *D. toyoakensis* (67.3% of all flower visits; mean ± SD = 3.3 ± 7.3). *Sphaerophoria menthastri* carried 4.6 ± 3.2 (mean ± SD, $n = 5$) pollen grains of *D. makinoi* and 14 ± 8.2 (mean ± SD, $n = 5$) pollen grains of *D. toyoakensis*.

Four pollinator species visited *E. decemflorum*, a co-flowering neighbor species of *D. makinoi*. All four species were overlapped with pollinator species of *D. makinoi* and three of four species were overlapped with prey species of *D. makinoi* (Table 1a). *Drosera makinoi*

and *E. decemflorum* showed a large overlap of their pollinator species (NOI = 0.761). There was no significant difference between the number of flower visits in *D. makinoi* and *E. decemflorum* (Fig. 4a GLMM $P = 0.730$). Seven pollinator species visited *L. fortunei*, a co-flowering neighbor species of *D. toyoakensis*. Four out of seven species were overlapped with pollinator species of *D. toyoakensis* and one of seven species was overlapped with prey species of *D. toyoakensis* (Table 1b). *Drosera toyoakensis* and *L. fortunei* showed a large overlap of their pollinators (NOI = 0.834). The effect of the interaction of plant species and pollinator species on the number of flower visits was significant (GLMM $P < 0.001$), and some pollinator species visited *D. toyoakensis* more frequently (e.g. *Eurema hecabe*, 5.5 ± 5.5 times on *D. toyoakensis*, 2.5 ± 0.50 times on *L. fortunei*) while *S. menthastri* visited *L. fortunei* more frequently (4.5 ± 7.6 times on *D. toyoakensis*, 9.7 ± 8.5 times on *L. fortunei*). The number of flower visits by pollinators was significantly higher in *L. fortunei* than in *D. toyoakensis* when we used the data of pollinator



Fig. 3 The most frequent pollinator species: *Sphaerophoria menthastris*. The hoverfly *S. menthastris* was a pollinator species common to *Drosera makinoi* and *D. toyoakensis*. **a** *S. menthastris* landing on a *D. toyoakensis* flower. **b** *S. menthastris* landing on a *D. makinoi* flower. **c** *S. menthastris* trapped by *D. makinoi* (also trapped in *D. toyoakensis*, not shown). Color figure online

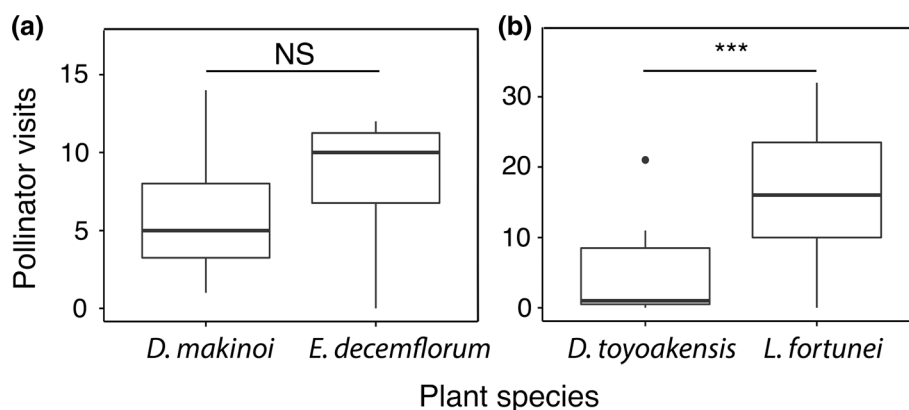


Fig. 4 Number of pollinator visits for *Drosera* and co-flowering neighbor species. **a** There was no significant difference in pollinator visits between *D. makinoi* and a co-flowering neighbor species *Eriocaulon decemflorum* at the Watarase site (GLMM $P = 0.73$). **b** Pollinators visited a co-flowering neighbor species *Lysimachia fortunei* more frequently than *D. toyoakensis* at the Toyoake site (GLMM $P < 0.001$)

species that visited *D. toyoakensis* and *L. fortunei* at least once in our survey (Fig. 4b, GLMM Estimate \pm SE = 1.8 ± 0.82 , $P < 0.001$).

Flower removal experiments

Flowers of *D. makinoi* had no significant effect on the number of insects trapped, whereas flowers of a co-flowering neighbor species *E. decemflorum* had a significant positive effect on the number of both pollinator and non-pollinator species trapped (Table 2a, Fig. 5a–c). Flowers of *D. toyoakensis* had no significant effect on the number of insects trapped, whereas flowers of a co-flowering neighbor species *L. fortunei* had a significant positive effect on the number of pollinator species trapped (Table 2b, Fig. 5d–e). Flowers of co-flowering neighbor species *L. fortunei* had no significant effect on the number of non-pollinator species trapped (Table 2b, Fig. 5f).

Discussion

The two *Drosera* species trapped their pollinators, four of five pollinator species in *D. makinoi* and one of six species in *D. toyoakensis*, including syrphids that are known as effective pollinators of many flowering plants (Willmer 2011; Woodcock et al. 2014). This finding supported our prediction that selfing species may show large PPO. Because both *D. makinoi* and *D. toyoakensis* do not have mechanisms such as temporal, spatial, and chemical separation of traps from flowers (Jürgens et al. 2012; El-Sayed et al. 2016), flying pollinators are likely to be trapped by accident. A similar case is reported in a selfing species *D. arcturi*, which has flowers close to traps and catches major pollinator species (Sciligo 2009).

Whereas the two *Drosera* species trapped their pollinators, the experimental removal of flowers of neither *D. makinoi* nor *D. toyoakensis* significantly changed the number of insects trapped. This may be because autonomous selfing species like *D. makinoi* and *D.*

Table 2 Results of generalized linear model analyses on the effect of flowers of *Drosera* and co-flowering neighbor plants on (a) Watarase site (*Drosera makinoi* and *Eriocaulon decemflorum*) and (b) Toyoake site (*D. toyoakensis* and *Lysimachia fortunei*)

Explanatory variable	Estimate ± SE	Z	P
(a) Watarase site			
Response variable: all prey individuals			
(Intercept)	- 1.2 ± 0.27	- 4.6	4.9 × 10⁻⁶***
<i>Drosera makinoi</i>	0.089 ± 0.26	0.35	0.73
<i>Eriocaulon decemflorum</i>	0.90 ± 0.28	3.2	0.0015**
Response variable: prey overlapped with pollinator species			
(Intercept)	- 2.5 ± 0.52	- 4.8	3.7 × 10⁻⁶***
<i>Drosera makinoi</i>	- 0.097 ± 0.43	- 0.23	0.82
<i>Eriocaulon decemflorum</i>	1.1 ± 0.54	2.1	0.038*
Response variable: prey not overlapped with pollinator species			
(Intercept)	- 1.6 ± 0.30	- 5.3	1.1 × 10⁻⁷***
<i>Drosera makinoi</i>	0.15 ± 0.27	0.53	0.60
<i>Eriocaulon decemflorum</i>	0.81 ± 0.31	2.6	0.0084**
(b) Toyoake site			
Response variable: all prey individuals			
(Intercept)	- 1.4 ± 0.38	- 3.6	2.7 × 10⁻⁴***
<i>Drosera toyoakensis</i>	0.22 ± 0.37	0.61	0.54
<i>Lysimachia fortunei</i>	0.87 ± 0.37	2.3	0.019*
Response variable: prey overlapped with pollinator species			
(Intercept)	- 2.3 ± 0.60	- 3.9	1.0 × 10⁻⁴***
<i>Drosera toyoakensis</i>	0.020 ± 0.57	0.036	0.97
<i>Lysimachia fortunei</i>	1.2 ± 0.60	1.9	0.050*
Response variable: prey not overlapped with pollinator species			
(Intercept)	- 1.8 ± 0.44	- 4.2	2.7 × 10⁻⁷***
<i>Drosera toyoakensis</i>	0.32 ± 0.43	0.75	0.45
<i>Lysimachia fortunei</i>	0.66 ± 0.42	1.6	0.12

Bold *P* values indicate the significant effects

P* < 0.05; *P* < 0.01; ****P* < 0.001

toyoakensis allocate small amounts of resources to pollinator attraction (Barrett 2002). On the other hand, the experimental removal of flowers of co-flowering neighbor plants significantly reduced the number of pollinator insects trapped. This finding shows that the number of flowers of not *Drosera* but neighbor plants maintains the density of pollinator species, although the sample size is small and further tests using more quadrats are desirable. This positive relationship is similar to the relationship called pollination facilitation in pollination biology: the presentation of flowers by one species attracts pollinators to the other neighboring plant species (Feldman et al. 2004; Ghazoul 2006). Pollination facilitation can occur when two or more co-flowering plants form large and collective floral displays (Morales and Traveset 2009; Ye et al. 2014) that increase pollinator density in a patch. Facilitative pollination especially benefits species occurring at low densities (Schemske 1981; Morales and Traveset 2009) and rewardless species growing near rewarding species (Johnson et al. 2003). In our study, the existence of flowers of co-flowering plants benefits *Drosera* plants by increasing the density of prey insects in a patch. Therefore, *Drosera* plants may experience pollination facilitation in the presence of co-flowering neighbors. On the other hand, *Drosera* plants may impose a cost on co-flowering neighbors by decreasing the density of pollinators and pollination efficiency. Therefore, co-flowering neighbors may experience exploitation rather than facilitation.

Drosera makinoi trapped more pollinator species than *D. toyoakensis*. This difference may be explained by the difference of flower color: *D. makinoi* has white flowers, which are similar to neighboring *E. decemflorum*, whereas *D. toyoakensis* has pink flowers, which are not similar to neighboring *L. fortunei*. Corresponding to this difference, the frequency of flower visits was not significantly different between *D. makinoi* and *E. decemflorum* in all pollinator species, but was significantly different between *D. toyoakensis* and *L. fortunei* for some pollinator species. Under these circumstances, pollinator species visiting neighboring plant flowers are expected to be trapped more frequently in *D. makinoi*, because pollinators of *D. makinoi* probably share a similar search image to white flowers of *Drosera* and *L. fortunei*. Alternatively, it may be explained by the difference of selfing level between the two species: the inbreeding coefficient was higher in *D. makinoi* ($F = 0.497$) than in *D. toyoakensis* ($F = 0.260$) (Watanabe, unpublished). Pollinator dependence is expected to be lower in the more highly selfing species *D. makinoi* in which trapping pollinator species is considered to be more advantageous. This result may support the prediction that species with a higher selfing rate are likely to trap pollinators more frequently. For a more rigorous test of this prediction, however, further studies on the degree of PPO in plants with a wide range of selfing rates are needed.

In conclusion, by studying selfing species of *Drosera*, we showed evidence of trapping major pollinator species

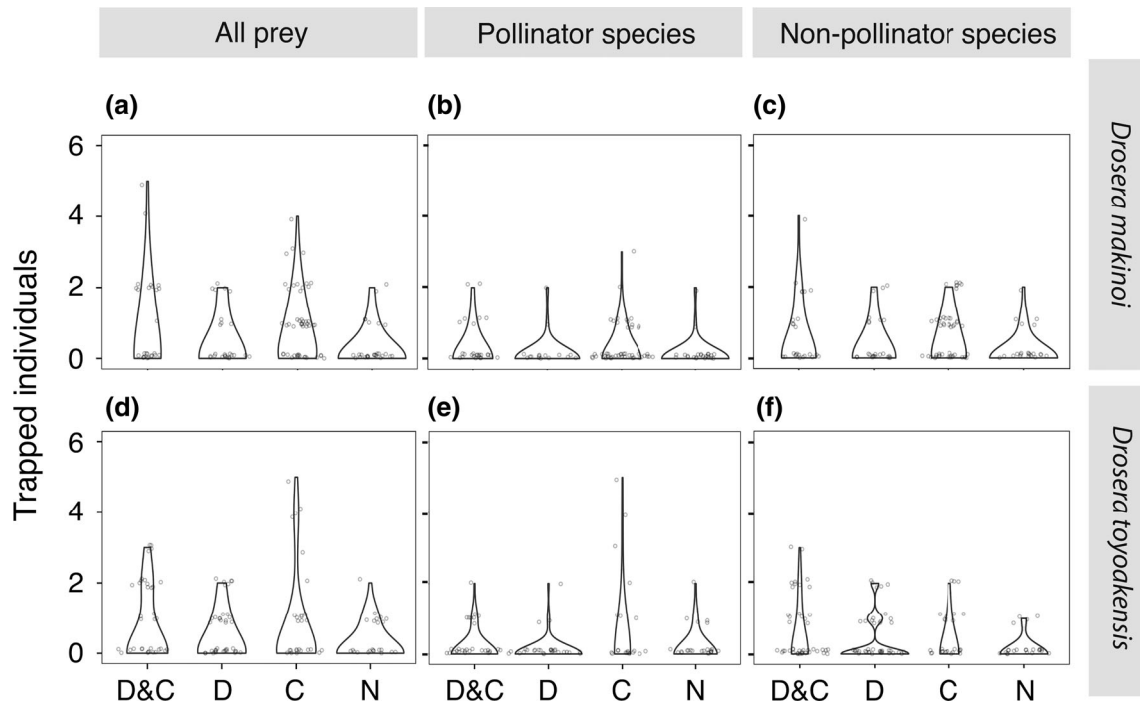


Fig. 5 Kernel density (black line) and observed value (gray circles) of trapped prey individuals on four treatments with the combination of presence/absence of *Drosera* and presence/absence of co-flowering neighbor plants flowers. *D&C* both *Drosera* and co-flowering neighbor plants, *D* only *Drosera*, *C* only co-flowering neighbor plants, *N* neither *Drosera* nor co-flowering plants existed. Flowers of

neighbor plants positively affected the number of **a** all prey species and **b** pollinator species trapped by *Drosera makinoi* and **d** all prey species and **e** pollinator species trapped by *D. toyokensis*. Flowers of neighbor plants positively affected the number of **c** non-pollinator species trapped by *D. makinoi*, while did not affect significantly the number of **f** non-pollinator species trapped by *D. toyokensis*

in carnivorous plants that were attracted by flowers of neighbor plants. This finding suggests that *Drosera* plants are exploiting pollinator resources of co-flowering neighbor species. We suggest that selfing carnivorous species provide a unique opportunity to test various ideas on pollinator-prey relationships in carnivorous plants. More species of selfing carnivorous plants are known in *Drosera* and other carnivorous plants and further studies on those species would deepen our understanding on PPO as well as possible exploitative relationship between carnivorous species and co-flowering neighbor species.

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