Minute pollinators: The role of thrips (Thysanoptera) as pollinators of pointleaf manzanita, *Arctostaphylos pungens* (Ericaceae)

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Abstract—The feeding habits of thrips on plant tissue, and their ability to transmit viral diseases to their host plants, have usually placed these insects in the general category of pests. However, the characteristics that make them economically important, their high abundance and short- and long-distance movement capability, may also make them effective pollinators. We investigated this lesser-known role of thrips in pointleaf manzanita (*Arctostaphylos pungens*), a Southwestern US shrub. We measured the abundance of three species of thrips (*Orothrips kelloggii*, *Oligothrips oreios*, and *Frankliniella occidentalis*), examined their pollen-carrying capability, and conducted an exclusion experiment in order to determine whether thrips are able to pollinate this species, and if they do, whether they actually contribute to the reproductive success of the plant. Our data suggest that indeed thrips pollinate and do contribute significantly to reproductive success. Flowers exposed to thrips only produced significantly more fruit than did flowers from which all visitors were excluded. The roles of thrips as antagonists/mutualists are examined in the context of the numerous other floral visitors to the plant.

Keywords: Frankliniella occidentalis, Orothrips kelloggii, Oligothrips oreios, pollination mutualism, fruiting success, self-incompatibility, pollen-carrying

Introduction

In his studies of cross- and self-fertilization in plants, Darwin (1876) noticed small pollen-carrying insects, specifically thrips, that could not be excluded by any net, and that might have cross-pollinated those plants he had intended for self-fertilization. Nevertheless, he assumed that these visits did not contribute to plant reproduction. Being small and seemingly less mobile than other floral visitors, thrips do not match the profile of effective pollinators, and Darwin's view has persisted throughout the years. Furthermore, the extensive damage caused by a few species of thrips on certain crop plants, either directly or through vectoring plant pathogens, has led to a focus on their economic impact rather than on their potential roles as ecological players in natural environments (Lewis 1973; Lewis 1997b). However, in recent years researchers have found that thrips can act as pollinators. Fossil thrips in Cretaceous amber have been found to hold many grains of pollen in specialized structures, indicating intentional pollen collection (presumably for larval feeding) and suggesting a role in pollination (Peñalver et al. 2012). Similarly, extant species of thrips specialize in feeding on the pollen of cycads; *Cycadothrips* spp., for example, can collectively transfer more than 5,000 grains of pollen of *Macrozamia* sp. plants in a single afternoon (Terry 2001). Unlike many flowering plants, cycads are specifically adapted to small pollinators, attracting thrips and weevils to narrow spaces not accessible to larger insects (Terry 2001). Some species of plants, such as *Xylopia aromatica* (Annonaceae), produce floral scents that attract thrips, their main pollinators (Jürgens et al. 2000; Gottsberger 1999). Evidence for thrips as major pollinators has also been found in *Castilla elastica* (Moraceae; Sakai 2001), *Macaranga hullettii* (Euphorbiaceae; Moog et al. 2002), and *Popowia pisocarpa* (Annonaceae; Momose et al. 1998).

A notable exception to the rule of dismissing thrips as pollinators in earlier parts of the 20th century is an observation made by Hagerup & Hagerup (1953) of an abundance of thrips on a member of the plant family Ericaceae. The structure of *Erica tetralix* flowers suggested to the authors that, unlike many Ericads, they are not pollinated by bees, as their corollas are longer than the proboscis of the most common visiting bee, the honey bee. Instead, the authors determined that the main form of fertilization is autogamy, augmented with transfer of pollen between plants by thrips (Hagerup & Hagerup 1953).

Another member of the Ericaceae, *Arctostaphylos pungens* (pointleaf manzanita), is similarly visited by multitudes of thrips (Richardson 1999). However, unlike *E. tetralix*, *A. pungens* flowers are visited by many conventional

pollinators, such as bees, wasps, flies, and butterflies (Richardson & Bronstein 2012). The question then arises whether thrips have any role in pollinating *A. pungens*, and if so, to what extent they contribute to reproduction. Thrips, mostly of the species *Ceratothrips ericae* and *Haplothrips setiger*, were found to contribute approximately 20% of the fruiting success of kinnikinnick manzanita, *Arctostaphylos uva-ursi* (García-Fayos & Goldarazena 2008), in Spain. Like its congener, *A. uva-ursi* is visited by many insects, but unlike *A. pungens*, it is self-compatible. Hence, even assuming that thrips mobility is limited, the contribution of thrips to reproductive success is not surprising in this case.

A. pungens is a perennial shrub that is native to the Southwestern US and Northern Mexico. Flowering occurs in late January-early March, making *A. pungens* the first plant in these habitats to flower each year (N. Rafferty, unpublished data). Unlike other Ericaceae in which thrips pollination has been observed, *A. pungens* is mostly self-incompatible: self-fertilized flowers do on rare occasions produce fruit, but their seeds are much smaller and apparently inviable (Richardson & Bronstein 2012). For thrips to effectively pollinate *A. pungens*, movement between plants is essential. The delicately-fringed wings of many thrips species are well adapted for flight, which is the most common form of dispersal (though aided by wind and results in widespread scattering), as well as short-distance movement between plants (Lewis 1973). Thus, if thrips are abundant and have the capacity to carry pollen while moving between plants, we hypothesize they could be effective pollinators of pointleaf manzanita.

To test our hypothesis, we conducted observational and manipulative experiments in the Santa Catalina Mountains in southern Arizona. We surveyed thrips populations throughout the season to determine their abundance. While doing so, we also collected data on plant size, number of open flowers, and the presence or absence of petal damage, as it related to the presence of thrips. We wanted to see if thrips are more associated with open flowers and their abundance. In addition, although preliminary studies (D. Eliyahu, unpublished data) provided no evidence that thrips perforate the corolla, we wondered whether thrips might use perforations to access the interior of buds. We also used electron microscopy to establish thrips' capacity for carrying manzanita pollen. Lastly, we manipulated inflorescences to exclude large and/or small pollinators in order to determine whether thrips contribute to fruiting success of *A. pungens*.

MATERIALS AND METHODS

Study species

Pointleaf manzanita (*Arctostaphylos pungens*) grows at elevations of about 1,200-2,500 m in chaparral and woodland habitats, including in the sky island mountain ranges of Arizona (Whittaker & Niering 1975; Richardson & Bronstein 2012). Plants can reach a height of 3 m and produce hundreds to thousands of small pink urceolate (pitcher-shaped) flowers in racemes. The plant blooms roughly from mid-January to mid-March, with peak season usually around mid-February. As one of the only flowering species at the beginning of its season, it attracts abundant and diverse floral visitors, primarily Hymenoptera and Diptera; some of these visitors perforate the flowers to rob nectar, and many of them feed through perforations made by others (Richardson & Bronstein 2012).

Flowers contain 10 stamens with pollen dehisced via pores in the anthers, and possess 5-10 ovules. Pollen of this species adheres in tetrads (Richardson 1999). Pointleaf manzanita is largely self-incompatible, as flowers fertilized with pollen from other plants produced heavier seeds that were more viable than flowers that were fertilized by pollen from the same plant (Richardson & Bronstein 2012). The fruits are berries that produce an average of 6.38 seeds and a maximum of 15 seeds per fruit. They remain and dry on the plant and are likely dispersed by a wide array of vertebrates (Richardson 1999).

Thrips (Thysanoptera) is a diverse order of small insects whose members primarily feed on plant tissue. Thrips range in size from 0.5 to 14 mm in length, but most temperate species do not exceed 2 mm. The order is divided into two suborders, Terebrantia and Tubulifera. These are distinguished by the shape and function of the ovipositor, with the former capable of piercing plant tissue for oviposition (Lewis 1973). All the species found on pointleaf manzanita (Richardson 1999; and see results below) belong to the Terebrantia, and therefore lay their eggs inside plant tissue. Thrips have a unique incomplete metamorphosis life cycle in that they have two feeding life stages (larva) followed by 1-3 non-feeding immature stages ("pre-pupa" and "pupa"). Species belonging to the Terebrantia most commonly spend their resting stage in the soil or litter and move there once their feeding during the second larval stage is complete (Lewis 1973). Other life stages spend their time in and around the tissue they consume, such as inside flowers, as in the case of pointleaf manzanita (Richardson 1999; and see results below).

Study site

The study was conducted in the Santa Catalina Mountains, Arizona, USA (32.20°N, 110.33°W), at the Gordon Hirabayashi Recreation Site (1,500 m elevation). At this site, *A. pungens* is a dominant shrub species. The study plants are situated on the northern and western aspects of a hill, as well as at its apex.

Thrips survey

At the peak of the 2012 flowering season (22 Feb), fifteen haphazardly-chosen racemes with at least one open flower were collected from each of 17 haphazardly-chosen *A. pungens* plants. The chosen plants were measured for maximum height and width. The racemes were placed into small plastic cups that were immediately capped and kept in a -20°C freezer until further analysis. In 2014, three similar collections were made, one at the beginning of the flowering season (20 Jan), one at the peak of the season (5 Feb), and another at the end of the season (19 Feb). These collections allowed us to look for patterns in thrips abundance and species composition over time. At each collection in 2014, five racemes from the same 20-22 plants were chosen

haphazardly. The flowers from all racemes were later dissected, and the thrips were removed, counted, and identified to species under a dissecting microscope using the *Thrips of California 2012* keys (Hoddle et al. 2012). Larvae were counted, but it was not possible to identify them to species. The individual flowers collected in 2012 were also measured for height and width, and the number of open flowers per raceme was recorded, as well as the number of floral perforations.

Visitor exclusion experiment

In the flowering season of 2012 we conducted an exclusion experiment to determine the relative contribution of thrips to reproductive success of pointleaf manzanita. Ten plants with at least 15 racemes with intact flower buds (no possible opening for thrips) were haphazardly chosen. On each plant, 5 racemes were tagged and left uncovered; 5 racemes were tagged and covered with a 1.0 mm mesh bag tightened around the peduncle with a twist-tie; and 5 racemes were tagged and covered with a drawstring 0.125 mm mesh bags tightened around the peduncle. The 1.0 mm (hereafter referred to as coarse) mesh bags allowed access of thrips to the flowers, but excluded all other floral visitors, while the 0.125 mm (hereafter referred to as fine) mesh bags inhibited access of nearly all insects, including thrips. Although small insects other than thrips (such as aphids, wasps, and staphylinid beetles) are found in pointleaf manzanita flowers, they are vastly outnumbered by thrips, as observed in racemes collected for the thrips survey (see above). Once all flowers on the tagged racemes had senesced, racemes were covered with fine mesh bags to protect developing fruit. Once fruits were ripe, they were harvested for quantitative and qualitative comparisons between the three treatments. Fruits were counted and dried in an oven at 40°C for 5 days. In addition to counting the fruit, it was necessary to determine if the seeds in the fruit contain an embryo, as an estimate of their viability. This is because self-fertilized flowers sometimes produce fruit, and when they do, these fruits lack embryos and are therefore lighter in weight than fruit that result from cross-fertilization (Richardson & Bronstein 2012). Seeds were soaked in water to soften the outer shell, and dissected to reveal the embryo. Seeds that did not appear to have an embryo (revealing empty space where the embryo should have been), were considered inviable. The number of total fruit, and the subset with apparently viable seeds, per raceme were compared among treatments.

Electron microscopy

A few thrips among those collected in the survey were chosen for electron microscopy analysis to assess their ability to carry pollen grains. Thrips were mounted on double-sided conductive carbon tape on metal stubs, sputter-coated with gold–palladium and viewed in a scanning electron microscope (SEM Hitachi S-3400N; Hitachi, Tokyo, Japan) at an accelerating voltage of 1-3 kV. The presence of pollen grains on the body of the thrips, as well as their location on the body, were observed.

Statistical analysis

Correlations between the number of thrips per raceme and plant maximum diameter were analyzed by calculating Pearson's product-moment correlation coefficients. Pearson's product-moment coefficients were also used to analyze correlations between the number of thrips and the number of open flowers per raceme, as well as the number of floral perforations. These perforations were divided into two types: one corresponding with nectar robbing, and the other with florivory. Florivory perforations are complete openings that can be found anywhere on the corolla, and are often associated with damage to reproductive parts of the flower. Nectar-robbing perforations, on the other hand, often include flaps, and can be found within a distinct range from the base of the flower, a position that corresponds with the location of nectaries. For correlations involving florivory perforations, nectar-robbing perforations, and open flowers per raceme, we first ran a regression of the number of thrips per raceme on florivory perforations, robbing perforations, and the number of open flowers with plant identity as a random independent variable. This was done because we wished to remove the effects of individual plants in the analysis. The residuals from these regressions were then used in the correlation analyses. For each correlation set, we used a sequential Bonferroni correction to account for the multiple correlations computed. There were three measurement periods (beginning, peak, and end) within the 2014 flowering season, so we used a sequential Bonferroni correction within each period. Correlations were performed in JMP 10 (SAS Institute, Cary, NC).

We analyzed the data from the visitor exclusion experiment in the same way for the two dependent variables, total fruit number per raceme and viable fruit number per raceme. We first constructed a linear mixed model using the lme function in the package lme4 (v. 1.1-6) in the R statistical environment (v. 3.03; R Core Team 2014), with treatment as the independent fixed effect and plant identity as the independent random effect. Both dependent variables were log-transformed to improve homogeneity of variances. We then tested the significance of the treatment effect using a Wald Chi-square test with the Anova function in the R package car (v. 2.0-19). If the treatment effect was significant, we tested the differences among treatment levels (control, coarse mesh, fine mesh) with the glht function in the multcomp package (v. 1.3-2). This function tests each pair of comparisons using Tukey's contrast method.

RESULTS

Thrips species and abundance

Four species of thrips were present on pointleaf manzanita inflorescences in both 2012 and 2014: *Frankliniella occidentalis*, *Oligothrips oreios*, *Orothrips kellogii*, and *Erythrothrips arizonae*, with the latter represented by a single specimen. The number of thrips per raceme, as measured in 2014, was much higher at the beginning of the flowering period, averaging 22.3 ± 1.9 (mean ± SEM) thrips per raceme, compared with 2.1 ± 0.2 thrips per raceme at the peak of the flowering period, and

TABLE 1. The abundance of thrips in different parts of the season, by species and lifestage. *Including a single *Erythrothrips arizonae* specimen. Larvae were not identified to species.

Season	Date of collection	No. of racemes	Number of thrips:				
			Total	*Frankliniella occidentalis*	*Oligothrips oreios*	*Orothrips kellogii*	Larvae
Beginning	1/20/14	110	2367	52	259	2056	0
Peak	2/20/12	255	307	107	76	40	86
	2/5/14	110	230*	49	27	111	42
End	2/19/14	97	716	88	12	26	590

7.4 ± 0.7 thrips per raceme at the end of the flowering period. Considering the high numbers of racemes per plant, thrips abundance is far from being negligible, even at its lowest. Thrips community composition also varied across the season, with *Orothrips kelloggii* dominating the beginning and *F. occidentalis* and *Oligothrips oreios* more dominant by the end of the flowering period. The number of larvae also increased as the season progressed. The results are summarized in Tab. 1.

Thrips abundance by plant

Thrips were found on all plants sampled, and in 54 - 98% of sampled racemes, with the highest abundance at the beginning of the season. Thrips were found in the plastic container in which the racemes were collected, as well as inside flowers. Since field observations showed that thrips are mostly visible when the inflorescence is shaken lightly, it is reasonable to assume that most of the thrips we found in the container were initially inside the flowers. Plants varied in thrips abundance, ranging from an average of 0.133 per raceme on the plant with the lowest number of thrips to 6 per raceme on the plant with the highest number of thrips in 2012 (mean number of thrips collected per plant 1.8, SD 1.9; median 1.6). Much higher numbers were found in the beginning of the flowering period of 2014 ranging from 6.1 to 21.9 per raceme (mean number of thrips collected per plant 112, SD 49; median 92).

The number of thrips per raceme was positively correlated with estimated plant size in both 2012 (Fig. 1A; $r = 0.56$, $N = 18$, $P = 0.015$) and 2014 (Fig. 1B; $r = 0.71$, $N = 17$, $P = 0.015$). In 2012, there were no significant correlations between the number of thrips per raceme and the number of open flowers per raceme (data not shown; $r = 0.11$, $N = 252$, $P = 0.09$). However, at the beginning of the flowering period of 2014, there was a significant correlation between the number of thrips per raceme and the number of open flowers per raceme (Fig. 2A; $r = 0.38$, $N = 106$, $P < 0.0001$). In neither 2012 nor the beginning of the flowering season in 2014, were there significant correlations between the number of thrips and the number of nectar-robbing perforations per raceme (data not shown; $r = 0.04$, $N = 252$, $P = 0.51$ for 2012; $r = 0.04$, $N = 106$, $P = 0.07$ for Beginning 2014), or the number of florivory perforations per raceme (data not shown; $r = 0.02$, $N = 252$, $P = 0.81$ for

2012; $r = -0.16$, $N = 106$ $P = 0.11$ for Beginning 2014). At the peak of the 2014 flowering period, there were no significant correlations between the number of thrips per raceme and open flowers per raceme (Fig. 2B; $r = 0.08$, $N = 110$, $P = 0.39$), nectar-robbing perforations per raceme,
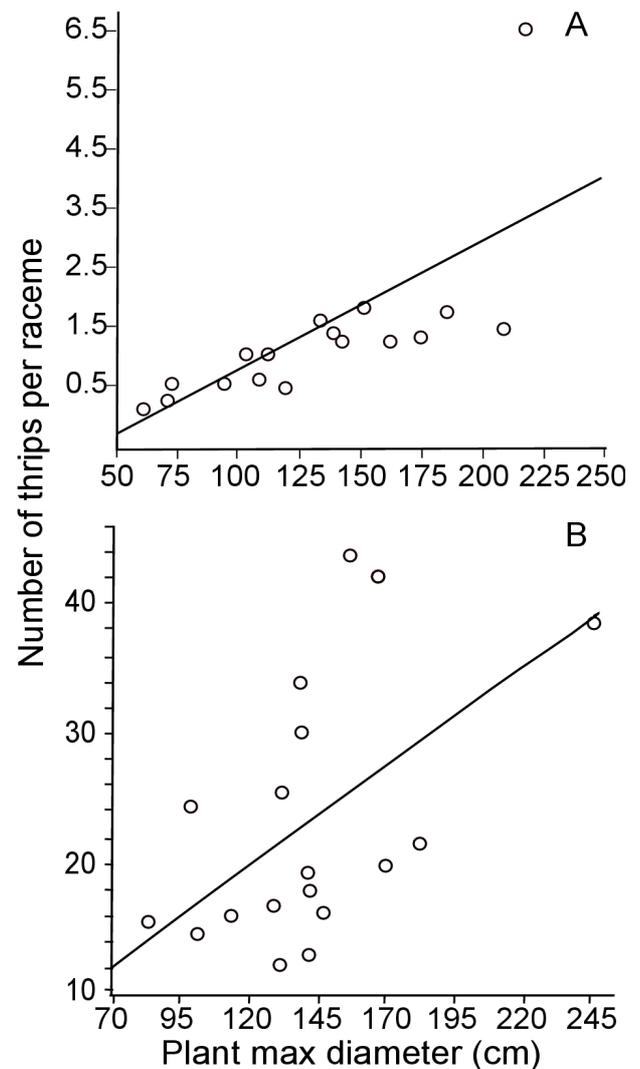

FIGURE 1. Number of thrips and estimated plant size in (A) 2012 and in (B) 2014.
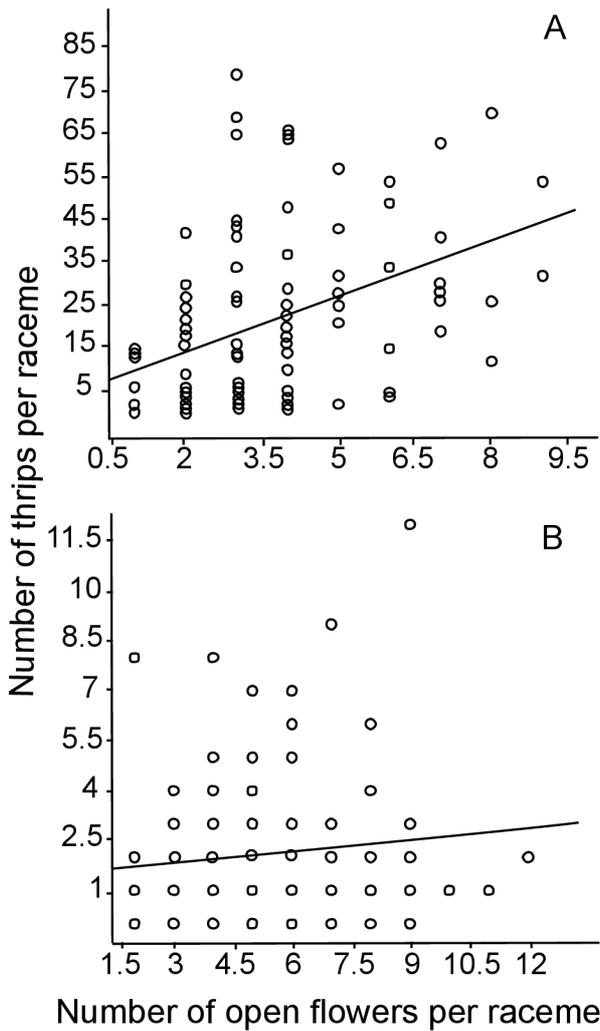
FIGURE 2. Number of thrips and number of open flowers (A) at the beginning of the flowering period and (B) the peak of the flowering period.

(Fig. 3A; $r = 0.18$, $N = 110$, $P = 0.054$) or florivory perforations per raceme (Fig. 3B; $r = -0.20$, $N = 110$, $P = 0.041$, not significant after Bonferroni correction), although there were trends in the relationships with nectar-robbing and florivory perforations. At the end of the flowering period, there was again a significant correlation between the number of thrips per raceme and the number of open flowers per raceme (data not shown; $r = 0.41$, $N = 97$, $P < 0.0001$). There was again a nonsignificant trend in the correlation between the number of thrips per raceme and the number of nectar-robbing perforations per raceme (data not shown; $r = 0.19$, $N = 97$, $P = 0.06$), but no significant correlation between the number of thrips and the number of florivory perforations ($r = 0.04$, $N = 97$, $P = 0.72$).

Pollen-carrying capacity of thrips

Scanning electron microscope images suggest that the adults and larvae of the two thrips species examined, *Orothrips kelloggii* and *Oligothrips oreios*, carry *A. pungens* pollen grains on the surface of their body (Fig. 4). Pollen tetrads were found in crevices between segments, attached to flat surfaces, in clumps and individually. On average, each

thrips observed had 4.6 ± 1.2 (mean $\pm$ SEM) pollen tetrads attached to their bodies, ranging from 1 to 13 ($N = 13$; median = 3).

Effect of thrips presence on fruiting success

The results of the exclusion experiment are summarized in Tab. 2. *Post hoc* analysis revealed that the number of fruit with apparently viable seeds (i.e., those seeds that contained an embryo) per raceme in the fine mesh treatment (which excluded thrips and all larger insects) was significantly smaller than the numbers in either the coarse mesh (which excluded only larger visitors) and control (open access) treatments (Tukey contrasts; fine mesh - coarse mesh, $z = -6.96$, $P < 0.0001$; fine mesh - control, $z = -6.50$, $P < 0.0001$; control - coarse mesh, $z = 0.55$, $P = 0.85$).

DISCUSSION

Our results suggest that thrips potentially play an important role in pollinating pointleaf manzanita. Thrips are able to carry pollen, are very abundant, and produce a high
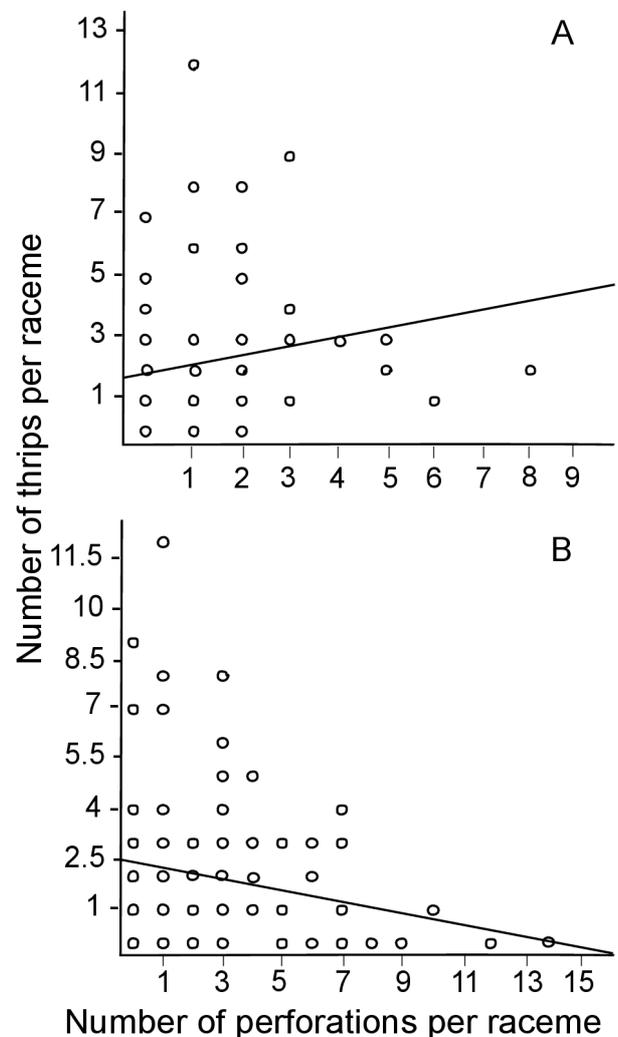

FIGURE 3. Number of thrips and number of floral perforations at the peak of the 2014 flowering period. (A) Number of thrips and number of nectar-robbing perforations per raceme.
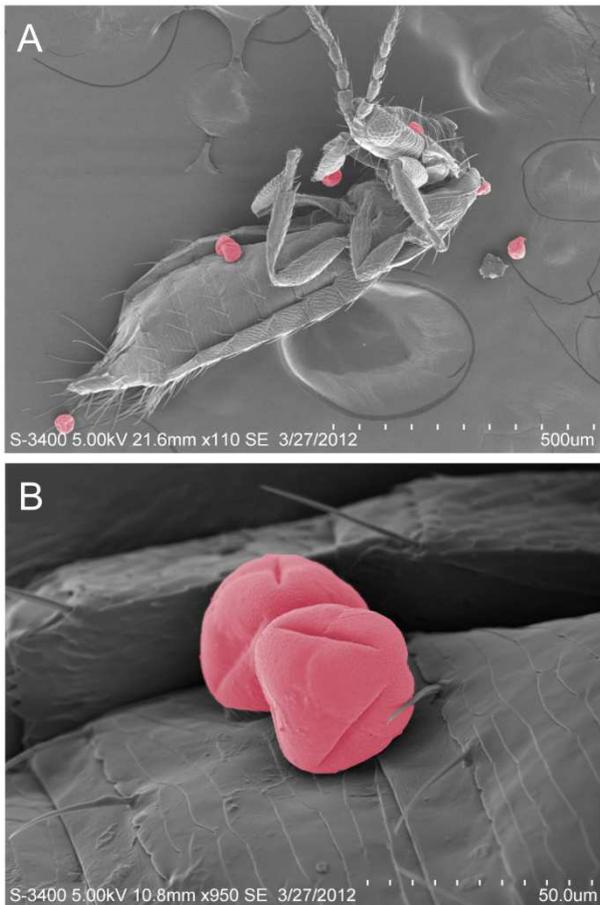
FIGURE 4.   Scanning electron micrograph of *O. kelloggii* with *A. pungens* pollen grains (A) with a closer view of the pollen tetrads attached to the abdomen of the thrips (B).

number of viable fruit. Since thrips number per raceme is highest early in the season, when fewer of the larger visitors frequent the flowers (Rafferty et al., unpublished data), it might be that thrips' contribution to reproductive success would be most significant then. However, their actual significance is dependent on the effectiveness of other visitors, which is yet unknown. Our exclusion experiment was conducted during the peak of the flowering season, when floral visitation by larger potential pollinators peaks as well, and thrips number per raceme plummets. Despite the thrips' relatively low numbers per raceme, flowers that could have been pollinated solely by thrips had a significantly higher fruiting success than those that received no floral visitors.

Although we did not collect direct evidence for movement of thrips between plants, evidence suggests that they may have regularly done so, given that pointleaf manzanita is largely self-incompatible (Richardson & Bronstein 2012). A few sticky traps that were placed between plants at our field site indeed trapped thrips (data not shown), further supporting the existence of such behaviors. Moreover, the ability of thrips to move short and long distances is well established, especially for those species that are fully winged, such as all four species we found in flowers of pointleaf manzanita (Lewis 1973; Lewis 1997a; Richardson 1999).

Thrips are capable of carrying pollen, and the scanning electron micrographs probably provide an underestimate of this ability. It is very probable that most of the pollen that was originally on the thrips was dislodged between the time of thrips collection and micrograph production.

The results of our exclusion experiment are similar to those found in the study of thrips pollinating another manzanita species, *A. uva-ursi,* in Spain. García-Fayos and Goldarazena (2008) found evidence that thrips were responsible for about 20% of its fruiting success. Unlike *A. pungens*, however, *A. uva-ursi* is self-compatible. For *A. uva-ursi*, fruiting success was measured by the number of fruits per raceme. Since *A. pungens* produces fruits (although effectively seedless ones) even when it is not cross-pollinated, we could not use this measure to estimate fruiting success. Indeed, we did not find significant difference in the number of fruits per raceme between the three visitor exclusion treatments. A preferred measure for fruiting success in this species is the number of fruits with viable seeds per raceme, since the few fruit produced by self-fertilized flowers are greatly reduced in size and weight compared to cross-fertilized flowers (Richardson & Bronstein 2012) and are often inviable. Our thrips-pollinated flowers produced a number of viable fruit indistinguishable from the number of viable fruit produced by flowers that were accessible to all floral visitors. Those flowers from which all visitors were excluded produced significantly fewer viable fruit. This suggests that thrips are quite effective in pollinating pointleaf manzanita. Interestingly, some thrips did manage to get into the fine mesh bags, which possibly accounts for the few viable fruit found in the fine mesh treatment.

The effect of thrips on reproductive success of pointleaf manzanita seems larger than that found in the *A. uva-ursi* study. This could be the result of the lower abundance of thrips found on *A. uva ursi* – only about 40% of plants and 5% of racemes. This is much lower than in *A. pungens*, in which thrips were present on 100% of the plants and 54% of the racemes sampled at the time the experiment was conducted (peak of the flowering period, 2012). An additional factor could be differences in mobility or pollen-carrying capacity of the thrips species in the two studies. However, the capacity to carry pollen is largely determined by the number of setae on the body, while the mobility of the thrips is largely dependent on the presence or absence of wings (Lewis 1973). All of the thrips species found in *A. uva ursi* are fully winged and are equipped with a similar number of setae as found on the thrips in the present study (Hoddle et al. 2012).

Thrips abundance and changes in population age structure over the season, with only adults at the beginning of the season, and many larvae at the end of the season, suggest that thrips' eclosion to adults (from the resting stages found in the soil; see Study Species in Materials and Methods) corresponds with the beginning of manzanita flowering. This agrees with the fact that the most abundant thrips at the beginning of the season, *O. kelloggii,* is univoltine (Bailey 1949). It lays its eggs in the pedicels of the flowers it feeds on, and provisions pollen grains to the emerging larvae (Richardson 1999). The larvae feed on the

TABLE 2.   Results of exclusion experiment. Control = racemes remained uncovered, allowing access to all visitors, coarse mesh allowed access to only small insects, mostly thrips, and fine mesh did not allow access to any visitors.

	Control	Coarse mesh	Fine mesh	Wald χ^2 statistics
Number of fruit per raceme	4.9 ± 0.52	4.3 ± 0.25	3.85 ± 0.34	$\chi^2 = 5.08$, 2 df, $P = 0.08$
Number of fruit with apparently viable seeds per raceme	4.33 ± 0.47	4.04 ± 0.25	1.83 ± 0.26	$\chi^2 = 61.91$, 2 df, $P < 0.0001$

flowers during their larval stages, and then drop to the ground to pupate inside a cocoon before they eclose as adults in the next year (Bailey 1949).

It is interesting to note the abundance of thrips on a related species of manzanita, *Arctostaphylos pringlei*, which is common at higher elevations (~2,000 m) at our study site, and whose flowering period begins roughly when the flowers of *A. pungens* have all senesced (Richardson 1999). On this higher elevation species, we did not find the univoltine thrips *Orothrips kellogii*, but we did find the two other species, *Oligothrips oreios* and *F. occidentalis* (Eliyahu, unpublished data). The thrips species most abundant at the end on the flowering season on *A. pungens* is *F. occidentalis*. This species is multivoltine, has a very short life cycle, with only a few days from egg to adult, and can therefore reproduce multiple times during a flowering period. Moreover, it does not have an obligatory developmental or reproductive diapause (Reitz 2009). Since this species can travel long distances assisted by wind currents (Reitz 2009), it might take up residence in the flowers of *A. pringlei*. Indeed *F. occidentalis* was found in *A. pringlei* at an average of 2.57 ± 0.5 (mean ± SEM) adults per raceme (Eliyahu, unpublished data). Data on the third thrips species we found in pointleaf manzanita, *Oligothrips oreios*, is lacking, so we cannot speculate about its life history and migratory abilities, aside from pointing out the fact that it was the most dominant species on *A. pringlei*, with 5.75 ± 0.74 (mean ± SEM) adults per raceme (Eliyahu, unpublished data).

Variation in thrips abundance among shrubs reflected plant size and number of open flowers per raceme, though the latter only holds true at the beginning and at the end of the flowering period. At those times, the number of open flowers is not as great as during the peak of the period, and therefore the collected racemes may have had less competition from other racemes in attracting visitors. This same rationale can explain the reduced number of thrips per raceme we observed during the peak of the season.

The presence of floral perforations was not significantly correlated with the number of thrips. Corolla perforations could be caused by nectar robbers and/or by florivores, and further experiments (Eliyahu, in prep.) show that they are unlikely to be caused by thrips. The two types of perforations can be distinguished based on their morphological characteristics, as described in the methods. However, there was a trend, at times, for a positive correlation between the number of thrips and the number of

nectar-robbing perforations, as well as a tendency for a negative correlation between the number of thrips and the number of florivory perforations. Nectar-robbing perforations may provide necessary entrance to flowers that have not yet opened, as we only found thrips inside buds when those buds had been perforated by a nectar robber or a florivore (data not shown). However, florivory perforations showed a tendency for a negative correlation to the number of thrips, possibly because flowers with such perforations were either hollowed out (caterpillars, the makers of these holes, feed on all the reproductive parts inside the flowers), or still in the process of being hollowed out, and therefore occupied by one or more caterpillars (D. Eliyahu, pers. obs.).

At least two of the species we found, *Orothrips kelloggii* and *F. occidentalis*, feed on flower parts, including pollen (Bailey 1949; Richardson, 1999; Reitz 2009). It is assumed that *Oligothrips oreios* also feeds on flower parts (Bailey 1960). Richardson (1999) observed *Orothrips kelloggii* oviposit in the pedicels of flowers they were feeding on, forming necrotic lesions that were topped with *A. pungens* pollen. This suggests a form of specialized pollen collection, for purposes other than immediate feeding. Moreover, this suggests that thrips, in addition to shelter and warmth in the flowers (thrips show thermotaxis and thigmotaxis; Gilbert 2014), use manzanita as a brooding site, which is an important step in the early evolution of certain obligate pollination mutualisms (Sakai 2002).

Thrips were among the first groups of insects, along with some beetles and flies, to pollinate plants, even prior to the appearance of angiosperms (Willmer 2011). Pollination in thrips is thought to have evolved through pollen parasitism, attraction to heat or to nutritious secretions (Willmer 2011; Peñalver et al. 2012). Our data suggest that thrips may be effective pollinators of an angiosperm that is commonly visited by numerous potential pollinators, and that thrips numbers per raceme are the greatest at times when other visitors are less frequent, though the effect of other floral visitors, in general and compared to that of thrips, is yet to be measured. Although thrips' contribution to the reproductive success of pointleaf manzanita was not conclusively shown here, this study cautions against regarding thrips as mere annoyance, or pests, even when found on generalist plants that attract numerous visitor species.

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