CONSPECIFIC POLLEN ON INSECTS VISITING FEMALE FLOWERS ON THE OAK PARASITE *PHORADENDRON CORYAE* (VISCACEAE)

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ABSTRACT.—*Phoradendron coryae* (Viscaceae) is a dioecious, parasitic plant on oak trees and shrubs in *Quercus* (Fagaceae), and it occurs from Arizona to Texas and into northern Mexico. The species produces minute spherical flowers during summer. Dioecious flowering requires pollinating insects to carry pollen from male to female plants. I investigated the pollination of *P. coryae* parasitizing *Quercus turbinella* shrubs at 3 sites at different elevations in the Cerbat Mountains of northwestern Arizona during August–September 2015. I examined pollen from male flowers, aspirated insects landing on female flowers, and counted conspecific pollen grains carried by insects. The tricolpate pollen of *P. coryae* was semiangular to subangular in polar view and circular to depressed oval in equatorial view. Female flowers were visited by 2 species of Coleoptera in 2 families, 6 species of Diptera in 6 genera and 3 families, and 1 species of Hymenoptera. Insects on flowers were extremely small (most <3 mm in length), and nearly all (99%) of the pollen carried by insects was from *P. coryae*. Conspecific pollen was found on 67% of the insects identified. Pollen loads were low, with only 25% of the insects carrying ≥ 5 grains. The beetle *Attalus futilis* (Melyridae) was the most frequently aspirated species, comprising 71% of the insects collected and occurring at all 3 sites. Most *A. futilis* (64%) carried *P. coryae* pollen. The second most frequently collected insects were 2 species of *Hippelates* and *Lihippelates* flies (Chloropidae). The *Lihippelates* carried the most *P. coryae* pollen. Other insects with pollen included 2 additional species of Chloropidae, 2 species of flies in Tachinidae and Tephritidae, a species of beetle in Chrysomelidae, and a species of parasitic wasp in Figitidae. *Phoradendron coryae* appeared to be pollinated mostly by *A. futilis* beetles due to their apparent abundance and by *Lihippelates* flies due to their relatively high pollen loads.

RESUMEN.—*Phoradendron coryae* (Viscaceae) es una planta dioica y parásita de robles y arbustos de *Quercus* (Fagaceae), que se distribuye desde Arizona a Texas y en el norte de México. La especie produce flores diminutas esféricas durante el verano. La floración dioica requiere la polinización de los insectos para llevar el polen desde las plantas macho hasta las plantas hembra. Investigué la polinización de *P. coryae* que parasita arbustos *Quercus turbinella* en 3 áreas a distintas alturas en las montañas Cerbat, en el noroeste de Arizona, durante agosto y septiembre del 2015. Examiné el polen de las flores macho, insectos aspirados que se posaron en flores hembra y contabilicé los granos de polen conspecifico transportados por los insectos. El polen tricollado de *P. coryae* era de semi-angular a sub-angular, desde el punto de vista polar, y de circular a ligeramente ovalado, bajo vista ecuatorial. Las flores hembra fueron visitadas por 2 especies de coleópteros de 2 familias, 6 especies de dípteros de 6 géneros y 3 familias, y 1 especie de himenópteros. Los insectos en las flores fueron extremadamente pequeños (la mayoría <3 mm de longitud), y casi todo el polen transportado (99%) por insectos fueron *P. coryae*. El polen conespecifico se encontró en el 67% de los insectos identificados. Las cargas de polen fueron bajas, con tan sólo el 25% de los insectos transportando ≥ 5 granos. Los escarabajos *Attalus futilis* (Melyridae) fue la especie más frecuentemente succionada, comprendiendo el 71% de los insectos colectados y presentes en los tres sitios. La mayoría de *A. futilis* (64%) transportaron polen de *P. coryae*. Los segundos insectos colectados con mayor frecuencia fueron 2 especies de moscas *Hippelates* y *Lihippelates* (Chloropidae). La mayor parte del polen transportado por la *Lihippelates* fue de *P. coryae*. Otros insectos con polen incluyeron 2 especies adicionales de Chloropidae, 2 especies de moscas Tachinidae y Tephritidae, una especie de escarabajo Chrysomelidae, y una especie de avispa parásita Figitidae. *Phoradendron coryae* pareció ser polinizado principalmente por escarabajos *A. futilis* debido a su aparente abundancia, y por moscas *Lihippelates* debido a sus cargas relativamente altas de polen.

Phoradendron (Viscaceae), or mistletoe, is a genus of perennial plants that parasitize a wide variety of woody plants (Trelease 1916, Wiens 1964, Kuijt 2003). The genus includes 234 species distributed from the northern United States to northern Argentina and from eastern Pacific Islands to the eastern Caribbean (Kuijt 2003). *Phoradendron* plants

obtain water and other inorganic nutrients from their host plants by tapping into xylem with their haustoria, and they produce organic nutrients from photosynthesis in leaves and stems (Kuijt 1969, 2003).

Flowers on *Phoradendron* (Kuijt 2003) are unisexual and typically around 1 mm in diameter. Male flowers are spherical, with a

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cavity enclosed by 3 or 4 petals that each supports a minute sessile anther. Female flowers are similar but contain a short style with an indistinct rounded or faintly bilobed stigma atop an inferior ovary. Both sexes of *Phoradendron* flowers contain a small vestigial nectar gland, described by Trelease (1916) as “apparently adapted to pollination by such short-tongued insects as flies and small bees.” *Phoradendron* fruits are eaten by birds that disperse plants by defecating seeds (Kuijt 2003).

Dioecious flowering in many *Phoradendron* species makes it possible to study pollination by examining conspecific pollen loads on insects visiting flowers on female plants. This approach was used to examine pollination of *Phoradendron californicum* Nuttall (Wiesenborn 2016), a species found on trees and shrubs of Fabaceae in southwestern deserts. I found 13 species of flies in Diptera and 3 species of bees and wasps in Hymenoptera carrying *P. californicum* pollen to female flowers. Fruit flies in Tephritidae and blow flies in Calliphoridae appeared most likely to pollinate the species due to their high abundances on flowers or large loads of conspecific pollen.

Phoradendron coryae Trelease is a dioecious species of mistletoe found mostly on oaks, or *Quercus* (Fagaceae). It is the only mistletoe on *Quercus* in Arizona (Kearney and Peebles 1951). The systematics of the species is unsettled. Trelease (1916) first described *P. coryae* in his monograph of *Phoradendron* from plants examined on *Quercus* in Arizona, New Mexico, and northern Mexico. Kearney and Peebles (1951) also recognized the species in their flora and described it as nearly exclusive to various oak species and very common from Arizona to western Texas. Wiens (1964) reduced *P. coryae* to the rank of subspecies within *Phoradendron villosum* (Nuttall) Nuttall, also reflected in the flora by Munz (1974) and flora section by Hawksworth and Wiens (2002). In Kuijt's (2003) monograph of the genus, the subspecies was considered a synonym of *Phoradendron serotinum* ssp. *tomentosum* (Candolle) Kuijt. Despite these revisions, *P. coryae* retains acceptance (Allred and Ivey 2012) and is therefore used in the present study.

Phoradendron coryae is morphologically distinct from *P. californicum* in that it produces leaves, instead of scales, that are round

to elliptic and up to 3 cm wide and 3.5 cm long (Trelease 1916). The species also differs from *P. californicum* in its near restriction to a single host genus within a different family, occurrence at higher elevations (1100–2600 m compared with <1200 m in Arizona; Kearney and Peebles 1951), and more easterly distribution. Flowering seasons also differ between the 2 species, with *P. coryae* producing flowers during July–September (*P. villosum* in Munz 1974) instead of winter. Both species produce similar spherical flowers on spike-like inflorescences. Seeds of *P. coryae* and *P. californicum* may also be similarly dispersed by birds. Seeds of *P. villosum* are dispersed by a variety of fruit-eating birds in coastal California (Wilson et al. 2014).

I investigated pollination of *P. coryae* parasitizing *Quercus turbinella* E. Greene growing in different plant communities in northwest Arizona by examining pollen loads on insects visiting female flowers. I considered (1) what insect species carry *P. coryae* pollen to female flowers, (2) how specific these insects are to *P. coryae* flowers based on pollen loads, (3) whether there was any variation in amounts of *P. coryae* pollen carried by the individuals of these species, (4) which taxa of insects are more likely to pollinate *P. coryae*, and (5) whether the taxa of insects carrying pollen to female flowers are different between *P. coryae* and *P. californicum*.

METHODS

The study was conducted in the Cerbat Mountains, 33 km northwest of Kingman, Mohave County, Arizona. I collected insects from *P. coryae* plants parasitizing *Q. turbinella* shrubs at 3 sites at different elevations along Big Wash Road, an unpaved road that ascends eastward from U.S. Highway 93. The only oaks growing at the sites were *Q. turbinella*, keyed to species with Kearney and Peebles (1951). The lowest site (35.464° N, 114.202° W) was at an elevation of 1380 m within interior chaparral (Pase and Brown 1982) and supported mostly *Q. turbinella*, with scattered *Pinus monophylla* Torrey & Frémont (Pinaceae), *Juniperus osteosperma* (Torrey) Little (Cupressaceae), *Acacia greggii* A. Gray (Fabaceae), *Cercocarpus* sp. (Rosaceae), and *Gutierrezia* sp. (Asteraceae). Cattle were present at the site in low density. The middle site (35.465° N,

114.179°W) was 2.1 km east at an elevation of 1620 m, also within interior chaparral and predominated by *Q. turbinella*, with scattered *P. monophylla*, *Cercocarpus* sp., *Gutierrezia* sp., *Nolina microcarpa* S. Watson (Agavaceae), *Arctostaphylos pringlei* Parry (Ericaceae), and *Garrya flavescens* S. Watson (Garryaceae). The highest site (35.452°N, 114.170°W) was 1.6 km southeast of the middle site at an elevation of 1864 m within Great Basin conifer woodland (Brown 1982). This site supported mostly *P. monophylla* followed by *Q. turbinella*, with scattered *Cercocarpus* sp., *A. pringlei*, and *G. flavescens*. *Quercus turbinella* flowers during spring (Nixon 1997), and the only plants seen in flower at the sites were herbaceous. The distribution of *P. coryae* and *Q. turbinella* extended 2.3 km west of the lowest site, down to an elevation of 1280 m, along Big Wash Road. *Phoradendron californicum* occurred in the area but appeared to be parapatric with *P. coryae*. The closest *P. californicum* plant along Big Wash Road grew on an *A. greggii* shrub 0.6 km west of the furthest west *P. coryae* plant and at a lower elevation of 1248 m. Maximum air temperatures averaged 13 °C in January and 37 °C in July, and yearly precipitation (occurring mostly during December to March and July to September) averaged 262 mm during 1901–1967 at Kingman (DRI 2015). Rainfall (12 mm) occurred at the beginning of the study near the upper site at Packsaddle Mountain during 13–15 August 2015 (MCFCD 2015).

I collected insects from 2 female *P. coryae* plants (or clumps of plants) 0.5–1.0 m in diameter on different *Q. turbinella* host shrubs (1.5–3.0 m tall) at each site. I recognized female plants by the presence of fruit (Fig. 1a). Proximities of male *P. coryae* plants differed among the 6 female plants sampled: 3 female plants were next to a male plant on the same host, and 3 female plants were 1–2 m away from a male plant on the same host or on a different host. I collected insects at the lower site on 8 dates during 14 August–1 September 2015, at the middle site on 8 dates during 16 August–1 September 2015, and at the upper site on 6 dates during 22–31 August 2015. Flowers on female and male plants (Fig. 1b, 1c) viewed with a hand lens were open during collections. Insects on female flowers were individually aspirated into a 125-mL plastic screw-capped flask containing a 4-dram

glass vial with 4 mL of 70% EtOH. Each insect was aspirated through a 13-cm-long tube with a 3-mm-diameter opening to the top of the flask where it dropped into the alcohol. Insects were aspirated from each plant for 15–100 min on each date, for a total 25.2 h, during 06:10–10:50 Mountain Standard Time. Air temperature during collections was 25–36 °C, relative humidity 21%–26%, cloud cover 0%–95%, and wind speed <10 km · h⁻¹. I deposited a pressing (UNLV 64429) of a host *Q. turbinella* shrub, a sampled *P. coryae* female plant, and a nearby male plant at the Wesley E. Niles Herbarium, University of Nevada, Las Vegas.

I examined pollen from *P. coryae* after mounting each sample in polyvinyl alcohol (Dafni 1992). I collected male inflorescences at the upper site into 70% EtOH on 26 August 2015 and vortexed pollen from flowers. Alcohol containing pollen was centrifuged at 3400 revolutions · min⁻¹ for 5 min, and the alcohol was drawn off and replaced with 3.5 mL of water. The water and suspended pollen was then poured into a 100-mL teflon evaporating dish, and 1 mL of a 12% solution of hydrolyzed polyvinyl alcohol was added. The mixture was vortexed and dried 2 h at 55 °C. I viewed pollen grains embedded in the resulting clear-plastic film in brightfield microscopy, measured them with an eyepiece reticle at 40×, photographed them through a 100× oil-immersion objective lowered onto the film, and described them following figure 11.3 in Faegri et al. (1989).

I also extracted, mounted, and examined pollen on insects aspirated from female flowers. Each collection vial was vortexed for 30 s, and the alcohol and suspended pollen was centrifuged as described above. I drew off the alcohol, replaced it with 4 mL of water, centrifuged the pollen suspension a second time, drew off the water, and added 0.8 mL of water. I mixed the water and pollen, then transferred it with a pipette into a 35-mL porcelain evaporating dish. I added 0.3 mL of the polyvinyl alcohol solution to the dish and vortexed and dried the mixture 1.5 h at 40 °C. This process produced a circular film 25 mm in diameter containing pollen from each insect. Insects were mounted on points after drying in hexamethyldisilazane (HMDS) to prevent shrinkage (Brown 1993).

I examined the entire area of each circular film for pollen. I pressed the film between 2

Fig. 1. *Phoradendron coryae* parasitizing *Quercus turbinella* in the Cerbat Mountains near Kingman, Arizona, during August 2015: a, stem with fruit and female flowers; b, female flowers; c, male flowers; d, pollen from male flowers in equatorial view (upper grains) and polar view (lower grains); e, face of *Attalus futilis* melyrid beetle aspirated from a female flower showing white clypeus between upper frons and lower labrum and white paired maxillae with haired tips extended below labrum. Scale bars in panels a, b, and c are 1 mm; scale bar in panel d is 10 μ m; scale bar in panel e is 0.1 mm.

microscope slides and scanned it at 100 $\times$ with a compound microscope by moving the stacked slides with a mechanical stage. I recognized pollen grains by their yellow color and symmetrical shape, categorized grains as *P. coryae* or as differing from *P. coryae*, and counted grains in each category. I counted pollen as *P. coryae* unless it differed in size, shape, color, or exine sculpture. If I could

not distinguish pollen as *P. coryae* at 100 $\times$, I viewed it at 200 $\times$.

I identified insects collected on *P. coryae* to the lowest taxonomic rank possible. I only identified insects with >1 specimen in a species. Coleoptera were keyed to family with Triplehorn and Johnson (2005). Melyridae were keyed to Malachiinae with Mayor (2002) and identified to species by matching specimens

against those in the subfamily at the Entomology Research Museum, University of California, Riverside (UCRC). One specimen was photographed at different focal planes that were overlaid with CombineZP (Hadley 2013). Chrysomelidae were identified to genus by keying specimens with Riley et al. (2002) and comparing them with specimens at UCRC. Diptera were keyed to family with McAlpine (1981). Chloropidae were identified to genus by keying specimens with Sabrosky (1987) and comparing them with specimens at UCRC and at the Los Angeles County Museum of Natural History (LACM). Tachinidae were keyed to genus with Wood (1987) and to species with Reinhard (1942) and matched against specimens at UCRC and LACM. Tephritidae were keyed to species with Foote et al. (1993) and compared with specimens at UCRC. Hymenoptera were keyed to family and identified to subfamily with Triplehorn and Johnson (2005). An eyepiece reticle was used to measure lengths of insects, and vouchers were deposited at UCRC (ENT 460754–460767).

Amounts of *P. coryae* pollen carried by insects were compared among the predominant taxa collected. I used SYSTAT (version 10.2, Chicago, IL) to rank numbers of pollen grains on specimens and calculate the first quartile (containing the lower 25% of observations), median, and third quartile (containing the lower 75% of observations). Ranked pollen counts were compared among insect species with a one-way analysis of variance using GLM in SYSTAT. I decomposed the variation among species into independent contrasts (Neter et al. 1996) in GLM that compared pollen counts between Coleoptera and Diptera, between Chloropidae and other Diptera, and between the 2 most collected species in Chloropidae.

RESULTS

Pollen grains from *P. coryae* were tricolpate but variable in shape. Grains in polar view varied from semiangular (rounded) in shape with intruding furrows (Fig. 1d, lower left) to subangular (flattened) with open furrows (Fig. 1d, lower right). Grains in equatorial view were spherical but varied in shape from circular (Fig. 1d, upper right) to depressed oval with round sides and flat ends (Fig. 1d, upper left). Widths of furrows appeared to differ

between the 2 shapes in equatorial view. Dimensions of pollen grains in equatorial view were also variable. Grains ($n = 12$) averaged $19\ \mu\text{m}$ (range $18\text{--}20\ \mu\text{m}$) from corner to opposite side in polar view and $20\ (17\text{--}24)\ \mu\text{m}$ long $\times$ $18\ (15\text{--}21)\ \mu\text{m}$ wide in equatorial view. Pollen grains had smooth exines with 2 distinct layers apparent in polar view (Fig. 1d, lower right).

I aspirated and identified 146 insects from *P. coryae* female flowers: 2 species of Coleoptera in 2 families, 6 species of Diptera in 6 genera and 3 families, and 1 species of Hymenoptera (Fig. 2). The most abundant insect on female flowers was the flower beetle *Attalus futilis* Fall (Melyridae) (Fall 1917). This small beetle, around $2.4\ \text{mm}$ in length, comprised 71% of the insects identified and was found at all 3 sites. *Attalus* females ($n = 72$) were more frequently aspirated than males ($n = 31$). A distinctive feature found on both sexes of *A. futilis* was the white clypeus that appeared as a band between the black frons and dark-brown labrum (Fig. 1e). The character needed to key *A. futilis* to genus in Mayor (2002), a distinct dorsal lobe on the second tarsal segment of the front legs of males (absent at UCRC), was variable and indistinct in this species. The lobe, weak but bearing 2 teeth, was visible on a leg that I removed (from a specimen kept in EtOH), treated with NaOH, mounted on a slide, and examined with the compound microscope.

Flies in Chloropidae ($n = 33$), all in the subfamily Oscinellinae, were the second most abundant insects collected and included 4 species in different genera. Most (85%) of the chloropids were keyed to *Hippelates* or to neotropical *Lioscinella*, now considered *Liohippelates* (Wheeler 2010). Specimens keyed to *Lioscinella* resembled *Liohippelates* at UCRC and LACM but possessed a short hind tibial spur instead of a long spur as seen on *Hippelates*. *Liohippelates* flies were distinctive by their shining black bodies and white eyes. All but one of the chloropids in *Hippelates* and *Liohippelates* were collected at the lower site, and except for 2 *Liohippelates*, the 2 genera occurred at the site on different plants. Other less common Chloropidae on flowers were keyed to *Conioscinella* and *Olcella*.

Other insects found on female flowers in low numbers included the flies *Microchaetina valida* Townsend (Tachinidae) and *Neaspilota*

Fig. 2. Insects aspirated from female flowers on *Phoradendron coryae* parasitizing *Quercus turbinella* in the Cerbat Mountains near Kingman, Arizona, during 14 August–1 September 2015. Insect taxa are listed along the x-axis, with families in bold: a, numbers of aspirated insects with (closed bars) and without (open bars) *P. coryae* pollen in pollen load; b, numbers of *P. coryae* pollen grains in pollen load on each insect. Horizontal bars are medians. Vertical bars connect the first and third quartiles (= pollen counts if $n = 2$).

viridescens Quisenberry (Tephritidae), the flea beetle *Glyptina* sp. (Chrysomelidae: Galerucinae: Alticini), and a parasitic wasp in Figitidae: Eucoilinae. Except for the tachinid fly, which was 5.0 mm in length, the insects identified on flowers were extremely small: *A. futilis* was the largest and the figitid wasp was the smallest at 1.4 mm in length.

Nearly all (99.2%) of the pollen on insects aspirated from female flowers was identified as *P. coryae*. Only 9 pollen grains differing from the plant species were found on 5

insects, and most of these grains were distinguished by their darker brownish color or spiny sculpture. *Phoradendron coryae* pollen was found on 98 (67%) of the insects collected and on all of the specimens in only 3 species (all chloropids) of the 9 species identified (Fig. 2). Only 37 insects (25%) carried ≥ 5 pollen grains, and 18 insects (12%) carried ≥ 10 grains. A *Liohippelates* fly in Chloropidae carried the most *P. coryae* pollen (265 grains).

Insects aspirated from *P. coryae* female flowers carried different amounts of conspecific

pollen (Fig. 2). Amounts of *P. coryae* pollen on insects (n ; median, 1st–3rd quartiles) did not differ ($F_{1,137} = 0.88$, $P = 0.35$) between Coleoptera (105; 1.0, 3.0–3.3 grains) and Diptera (39; 2.0, 1.0–8.8 grains). Both beetles, the melyrid *A. futilis* and the chrysomelid *Glyptina* sp., carried low amounts of conspecific pollen. The total amount of pollen carried by the more abundant *A. futilis* was 422 grains. Ranked amounts of *P. coryae* pollen on *A. futilis* did not differ ($t = 1.1$, $df = 101$, $P = 0.27$) between males (31; 1.0, 0.0–2.0 grains) and females (72; 1.0, 0.0–4.0 grains). Amounts of *P. coryae* pollen also did not differ ($F_{1,137} = 2.46$, $P = 0.12$) between flies in Chloropidae (33; 3.0, 1.0–11 grains) and those in Tachinidae and Tephritidae (6; 0.5, 0.0–2.0 grains). The 2 species of chloropids that were more frequently aspirated carried different amounts of pollen ($F_{1,137} = 10.1$, $P = 0.002$), with the *Liohippелates* (14; 8.5, 3.0–25 grains) carrying more pollen than the *Hippelates* (14; 1.0, 0.0–3.0 grains). The species of *Liohippелates* carried a total of 452 grains. On the other less frequently collected chloropids, *P. coryae* pollen loads were high on the *Conioscinella* species and low on the *Olcella* species. Both species of Tachinidae and Tephritidae carried low amounts of pollen, with pollen loads being more variable in the tachinid. Only a few pollen grains were found on the species of parasitic wasps in Figitidae: Eucolilinae.

DISCUSSION

Co-occurrence of the collected insect species and *P. coryae* flowers is dependent on the food and habitat requirements of larvae and adults. Although flower beetles in Melyridae do not have a well-known biology, those in Malachiinae are believed to be scavengers or predators as larvae, with adults also consuming pollen and nectar (Mayor 2002). Larvae of *Collops georgianus* Fall and *Malachius ulkei* Horn, which are also in Malachiini with *Attalus*, have been found in rocky soil beneath plants (King 1985) or underneath tree bark feeding on insect eggs (Dix 1990). Larvae of *Collops* have developed in the lab on honey and yeast (King 1985) and on mite and insect eggs, immature mites, insect pupae, and dead insect adults (Walker 1957). *Attalus futilis* is a widespread species that has been collected

from California eastward to Colorado and Texas (Fall 1917, Marshall 1953, Tanner and Tanner 1974; UCRC specimens). The apparent abundance of *A. futilis* on *P. coryae* suggests its larvae may have developed on or near the plant or its host *Q. turbinella*. Beetles in Curculionidae and Bostrichidae, but not Melyridae, have been collected on *Phoradendron tomentosum* Engelmann in Texas (Whittaker 1984). In contrast, oak trees and shrubs can support a diverse coleopteran fauna: 150 species of beetles including a melyrid were collected from *Quercus robur* L. trees in Britain (Stork and Hammond 2013). Larvae of *A. futilis* may develop beneath oak bark similar to *M. ulkei* (Dix 1990) or in soil beneath oak trees or shrubs, similar to *C. georgianus* (King 1985).

Flies in Chloropidae also have varied larval diets. Larvae of most chloropids in Oscinellinae eat living or decomposing herbaceous plants, although they also consume immature insects, decomposing wood, and fungi (Nartshuk 2014). Adult chloropids in *Hippelates* and *Liohippелates* are commonly called eye gnats because of the propensity of many species to feed on secretions, especially at the eyes of humans and domestic animals. Flies at the lower site were landing in my eyes at the plant where *Hippelates* were aspirated but not at the plant where most *Liohippелates* were aspirated. Larvae of both genera develop in soil containing organic matter such as dung (Nartshuk 2014). The presence of cattle at the lower site, where most *Hippelates* and *Liohippелates* were collected, corresponds to a larval habitat of dung-enriched soil. Tachinidae larvae are primarily parasites of insects (Wood 1987). Larvae of the widely distributed tephritid *N. viridescens* develop in flower heads of various Asteraceae (Goeden and Headrick 1992, Foote et al. 1993). Larvae of chrysomelid beetles including *Glyptina* are phytophagous, and larvae of wasps in Figitidae: Eucolilinae are parasites of fly pupae (Triplehorn and Johnson 2005).

All insects identified were specific to *P. coryae* flowers based on the very high proportion of conspecific pollen carried. Flower constancy was most likely due to the small size of the insects collected and their weak flight capabilities. Beetles and flies also do not transport pollen from flowers to nests, as do bees, and are unlikely to move between flowers

on distantly separated plants. Weak flight by pollinating insects requires male and female *P. coryae* plants to be near each other. This closeness in proximity was observed at the female plants I sampled, as the furthest male plant was 2 m away. Proximity of male and female *P. coryae* plants may result from the behavior of seed-dispersing birds. Male and female *P. californicum* plants likely become clumped from *Phainopepla*, *Phainopepla nitens* (Passeriformes: Ptilonotidae), eating fruits and defecating seeds on the same host plants (Larson 1996).

Beetles and flies likely transport pollen from male to female *P. coryae* plants on different mouthpart structures. *Attalus futilis* may have carried pollen on the hairs at the ends of their maxillae (Fig. 1e). Maxillae with dense hairs for pollen collection have been found on other beetles including the European *Malachius bipustulatus* L. (Barth 1991). Flies likely carried pollen attached to hairs on the labella at the tip of the proboscis, as observed in *P. californicum* (Fig. 1d, 1e in Wiesenborn 2016). Relatively high conspecific pollen loads on the *Liohippелates* may have been due to the structure of their labellae, which were large and supported much longer hairs than the labellae of the other chloropids collected.

Phoradendron coryae was most likely pollinated by the melyrid *A. futilis* and chloropid flies, especially the *Liohippелates*. *Attalus futilis* was the most frequently aspirated insect on female flowers, and individual *Liohippелates* carried the most conspecific pollen. Total numbers of *P. coryae* pollen were similar on both species. The potential pollination of *P. coryae* by a beetle is unexpected and contradicts Trelease's (1916) hypothesis that *Phoradendron* is pollinated by flies and small bees. Despite their occurrence in flowers, melyrids are not generally known as effective pollinators (Bernhardt 2000). Musty-smelling *Ferraria* (Iridaceae) flowers in South Africa are visited by melyrid beetles that carry pollen on their dorsum (Goldblatt et al. 2009). Chloropidae are known pollinators of a few plant species (Larson et al. 2001). The orchid *Genoplesium littorale* D.L. Jones (Orchidaceae), an Australian species with small flowers, is pollinated exclusively by chloropid flies, primarily females (Bower et al. 2015). Chloropid flies in *Liohippелates* and *Hippelates* may not

be widespread pollinators of *P. coryae*. The localized abundances of the 2 species at the lower site may have resulted from cattle providing dung-enriched soil for larvae and eye secretions for adults. Cattle grazing may increase populations of some insects (while decreasing populations of others) that potentially pollinate the plant.

Phoradendron californicum and *P. coryae* appear to be pollinated very differently. One obvious difference is the size of insect visitors. Insects collected from female flowers on *P. californicum* (Wiesenborn 2016) and measured with the reticle varied in length from 2.2 mm in a parasitic wasp (Pteromalidae: *Heteroschema* sp.) to 22 mm in honey bees (Apidae: *Apis mellifera*). Nearly all (98%) of the insects identified on *P. coryae* were <3 mm in length. Flower size is unlikely to account for this difference, because female flowers on both species are around 1 mm in diameter. One possible difference between plants is the extent that flowers were open. Female flowers appeared to be open further on *P. californicum* (Fig. 1c in Wiesenborn 2016) than on *P. coryae* (Fig. 1b). This was apparent in the field, as a hand lens was required to determine if flowers were open on *P. coryae* but not on *P. californicum*. Flower opening in both species may be influenced by rainfall, which affects plant water content. A second difference in pollination between the 2 plants was the diversity of insects visiting flowers. Female flowers on *P. californicum* were visited by 16 species of insects in 13 genera, 9 families, and 2 orders compared with 9 species and genera, 6 families, and 3 orders in *P. coryae*. A third difference between plants was the taxa of insects aspirated. Most insects on *P. californicum* were flies in Tephritidae followed by Calliphoridae and Syrphidae (Wiesenborn 2016). Calliphorids and syrphids were not found on *P. coryae*, and only 3 tephritids (in a genus not found on *P. californicum*) were identified. Conversely, flowers on *P. californicum* were not visited by Coleoptera or Chloropidae.

Insect visitors to flowers were unique between the 2 *Phoradendron* species. Insect size, diversity, and taxa are not independent of each other because a size limitation would affect diversity and taxa. Compositions of insects visiting flowers on both species may have been influenced by relative amounts of nectar, plant water content, and pollen. The

different plant communities and flowering seasons of *P. californicum* and *P. coryae* would also influence the diversity and taxa of available insects. Although *Phoradendron* flowers are simple and similar, pollination may differ among species more than expected.

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