

Ant-Plant Mutualism in Hawai'i? Invasive Ants Reduce Flower Parasitism but Also Exploit Floral Nectar of the Endemic Shrub *Vaccinium reticulatum* (Ericaceae)¹

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Abstract: Ants had been absent from the Hawaiian Islands before their human introduction. Today they cause severe alterations of ecosystems and displace native biota. Due to their strong demand on carbohydrate-rich resources, they often exploit floral nectar of native Hawaiian plant species with largely unknown consequences for the plants' reproduction. We examined effects of flower-visiting invasive ants on reproduction of the endemic shrub *Vaccinium reticulatum* (Ericaceae) in Hawai'i Volcanoes National Park. Ant densities in flowers were high and floral nectar was excessively exploited, which may lead to a reduced visitation rate of pollinators. However, the ants' presence on flowers strongly reduced flower parasitism by caterpillars of the introduced plume moth *Stenoptilodes littoralis* and thus decreased the loss of flowers and buds. This is, to our knowledge, the first documented mutualism between invasive ants and an endemic plant species in Hawai'i. Developed fruits of this partly self-incompatible plant, however, bore relatively low proportions of viable seeds, irrespective of the experimentally controlled visitor spectrum of the flowers. This may indicate that ants do not function as pollinators and that effective pollinators (probably *Hylaeus* bees) are scant or absent.

INVASIVE ANTS ARE generally characterized as widespread, abundant, aggressive, and omnivorous (Holway et al. 2002, Lach et al. 2010). They often cause severe alterations of ecosystems by displacing native species and thereby breaking up mutualistic interactions and key ecological functions such as nutrient

cycling, seed dispersal, or pollination (Christian 2001, Holway et al. 2002). Island ecosystems are particularly vulnerable to invasions due to disharmonic floras and faunas and their isolation from other terrestrial habitats (Loope and Mueller-Dombois 1989). With a distance of 3,600 km to the closest continent, the Hawaiian Islands are among the most isolated archipelagos of the world. They bear a high percentage (90%) of endemic species (Adersen 1995), more than any region of similar size on earth (Kaneshiro 1995). Ant invasions are particularly severe on these Islands, where plants and animals have evolved in the absence of any social hymenopterans (but see Medeiros et al. 1986), and their spreading has had devastating consequences for native ecosystems (Zimmerman 1970, Beardsley 1980, Howarth 1985, Reimer 1994, Krushelnicky and Gillespie 2008).

Ants require carbohydrate-rich resources to fuel their colony's nutrition. Sources of carbohydrates may be honeydew (sugary exudates of insects), as well as extrafloral and floral nectar (Blüthgen and Fiedler 2004, Blüthgen et al. 2004). However, few Hawaiian

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endemic plants possess extrafloral nectaries (Keeler 1985). Floral nectar may be an important sugar supply for ants in Hawai'i and can be heavily exploited (Lach 2005, 2008*b*). Flower-visiting ants are detrimental to the reproduction of many plant species because they usually are poor pollinators (Armstrong 1979, Hölldobler and Wilson 1990) due to their relatively low mobility, central-place foraging, often hairless cuticles, and glandular secretions that can reduce pollen viability (Beattie et al. 1984, Galen and Butchart 2003). Thus, ants are generally referred to as nectar thieves (Inouye 1980) that often drive off pollinators (Tsuiji et al. 2004, Ness 2006, Junker et al. 2007). As a response to detrimental flower-visits by ants, many plant species defend their flowers via mechanical barriers (Harley 1991, Willmer et al. 2009), unpalatable nectar (Feinsinger and Swarm 1978, Guerrant and Fiedler 1981, Kessler and Baldwin 2007, Junker and Blüthgen 2008), and by repellent floral scents (Junker and Blüthgen 2008, Willmer et al. 2009). Endemic Hawaiian plants often lack such defense mechanisms, likely due to the absence of ants during their evolution (Junker et al. 2011).

Flower visitation by ants can also positively affect the plant's reproduction by means of ant pollination (Hickman 1974, Wyatt 1981, Gomez and Zamora 1992, Beattie 2006) or an increase in cross-pollination through disturbance of pollinators (e.g., Altshuler 1999, Maloof and Inouye 2000, Lach 2003). Furthermore, several studies have shown that ants effectively protect flowers from damage by herbivores (e.g., Bentley 1977, Rico-Gray and Thien 1989, Oliveira 1997, Oliveira et al. 1999). In those studies, ants were attracted to extrafloral nectaries on pedicels, bracts, or flower buds and increased fruit set by reducing herbivore damage to flowers and buds. Flower protection by ants that consume floral nectar has also been documented (Lach 2008*a*) but seems to be less common.

In this study, we quantified the consumption of nectar by invasive ants on flowers of the endemic shrub *Vaccinium reticulatum* Sm. (Ericaceae) and investigated its associated effects on the plants' reproduction and on flower parasitism by caterpillars of the introduced plume moth *Stenoptilodes littoralis*

Butler, which occurred in high abundances and parasitized flower buds and flowers of this plant species, leading to their abortion.

MATERIALS AND METHODS

Study Sites and Organisms

The study was conducted at two woodland sites dominated by *Metrosideros polymorpha* Gaudich, (Myrtaceae) within Hawai'i Volcanoes National Park (HAVO) between March and May 2009. One site, Kīpuka Kahali'i (897 m above sea level [a.s.l.]; 19° 20.70' N, 155° 12.65' W), had a cinder substrate, very sparse ground vegetation, and was inhabited by the ant species *Pheidole megacephala*, *Paratrechina bourbonica*, and *Plagiolepis alluaudi*, all of which were observed visiting flowers of *Vaccinium reticulatum*. The other site, Broomsedge Burn Area (1,230 m a.s.l.; 19° 26.23' N, 155° 17.97' W), had a weathered *pāboeoe* lava substrate. The dense ground vegetation consisted mainly of invasive grasses such as *Andropogon virginicus* and *Schizachyrium condensatum* (both Poaceae) and was inhabited by a single ant species, *Linepithema humile*, which also visited flowers of *V. reticulatum*.

V. reticulatum (Hawaiian: 'ōbelo) is a small shrub (10–130 cm in height) usually occurring as a member of the pioneer flora on lava flows, ash dunes, and cinder beds or as a member of communities at exposed sites such as alpine and subalpine shrubland. It is common on the islands of Maui and Hawai'i (Wagner et al. 1990). *V. reticulatum* is an important plant in Hawaiian tradition, being the inherbation of goddess Pele's sister Ka'ōhelo. Branches of the plant are traditionally used as offerings to the goddess, and berries are eaten raw or in jams, jellies, or pies. The berries are also an important food source for native animals like the endangered Hawaiian Goose, Nēnē (*Branta sandvicensis*) (Black et al. 1994), which in turn is an important disperser of *V. reticulatum* seeds (Wagner et al. 1990). Yellow-faced bees (*Hylaeus* spp.) have been recorded to be by far the most abundant flower visitors (Heather Sahli, pers. comm.) and probably pollinate the flowers. Adults of the caterpillars that parasitized in flower buds and flowers were identified as *Stenoptilodes*

littoralis (Pterophoridae) by Bernard Landry (Muséum d' Histoire Naturelle, Geneva). The species has been reported to occur on *Vaccinium* spp. and is considered to be introduced (Zimmerman 1958, Henneman and Memmott 2001).

Treatment of Plants

Four haphazardly selected branches of 10 *V. reticulatum* plants at Kīpuka Kahali'i and Broomsedge Burn Area, respectively, were treated in one of the following categories: (1) ants excluded: the basal section of the branch was covered with a sticky barrier (Raupenleim, Schacht, Germany) to prevent ants from accessing inflorescences; (2) all visitors allowed: no modifications were done; (3) flying visitors excluded: a plastic cup was put over the branch's inflorescence with the bottom facing the basis of the branch. The bottom had a small opening for the stem and a crescent-shaped one of about one-third of the bottom's diameter through which ants were able to access the flowers. The top of the cup reaching beyond the tip of the inflorescence was covered with pollen mesh (Pollen Protection Sheet, GCM, Germany) to keep out flying visitors and pollen; (4) all visitors excluded: instead of using a plastic cup, the inflorescence of each branch was covered entirely with pollen mesh to keep out all visitors and pollen. This treatment was not included in the statistical analysis, because most of the flowers were eaten by caterpillars that were trapped inside the pollen meshes.

In addition, 16 plants at Broomsedge Burn Area were treated in categories 1 and 2 only, 11 of which were used only for nectar measurements and five were included in the fruit- and seed-set analysis. We checked all flowers and flower buds for evidence of presence of caterpillars. One plant at Broomsedge Burn Area was lost because the ants circumvented the barrier. One plant at Kīpuka Kahali'i could not be considered for ant density counting because it had too few flowers.

Availability of Nectar

On 2 days from 0745 to 0900 hours four flowers from ant-free and four flowers from

ant-visited branches of a total of 11 plants at Broomsedge Burn Area were chosen haphazardly, and nectar volume (μl) was measured using microcapillary tubes ($5 \mu\text{l}$). Means of the four measurements per plant were compared in a paired design with a Wilcoxon signed-rank test ($n = 11$ pairs). We used non-parametric tests whenever log-transformed data did not meet assumptions of parametric tests.

Flower Parasitism

V. reticulatum readily self-pollinates (Wagner et al. 1990), and self-pollination in this species leads to 100% fruit set (Vander Kloet 1993). Thus, we considered fruit set (developed fruits per initial number of flower buds) to be independent from pollination but dependent on the rate of flower abortion through parasitism. Therefore, fruit set was used as a measure for flower parasitism. Self-pollination in *V. reticulatum* leads to very low proportions of viable seeds (Vander Kloet 1993). Thus, we considered seed set (proportion of viable seeds per fruit) to be dependent on pollination but independent from flower parasitism and used it as a measure for pollination. Ant density on flowers of each plant was estimated by haphazardly selecting up to 30 flowers of control and other untreated branches and counting ants inside the corolla once a week. For analysis of fruit set we counted flower buds and, if present, open flowers on the four treated branches before the preparation of the branches. Then, on a weekly basis, all branches were checked for newly developed buds. Finally, when the last flower of each branch had senesced, we counted the developing fruits. Groups were compared with a Friedman test for both sites combined. The ants' density effect on fruit set was investigated with a Spearman rank correlation.

Seed Set

After all flowers had senesced, the cups and mesh of treatments in categories 3 and 4 were removed to provide equal microclimatic conditions to all branches in terms of fruit development. The berries were collected about 2 months after bloom. We washed out the seeds

from the flesh and counted viable seeds containing an embryo and unviable seeds without an embryo. Both were easily distinguishable under a dissecting microscope (Vander Kloet 1993). For each experimental plant, the proportions of viable seeds in the berries of each treatment were averaged. Seed set was compared with a Kruskal-Wallis test. No paired test was performed because many plants did not set fruit in all of the treatments. A potential relation between berry diameter and proportion of viable seeds was tested with a Pearson's product-moment correlation.

RESULTS

We observed numerous pierced flower buds that were prone to die-off. Some pierced flower buds, however, still developed into flowers that lacked reproductive structures. We observed a caterpillar of the plume moth *S. littoralis*, apparently coming from a consumed bud, moving to a new bud and entering it through a hole pierced into the petals. During those interchanges of host buds, caterpillars are particularly exposed to predation by ants. In addition, we observed an Argentine

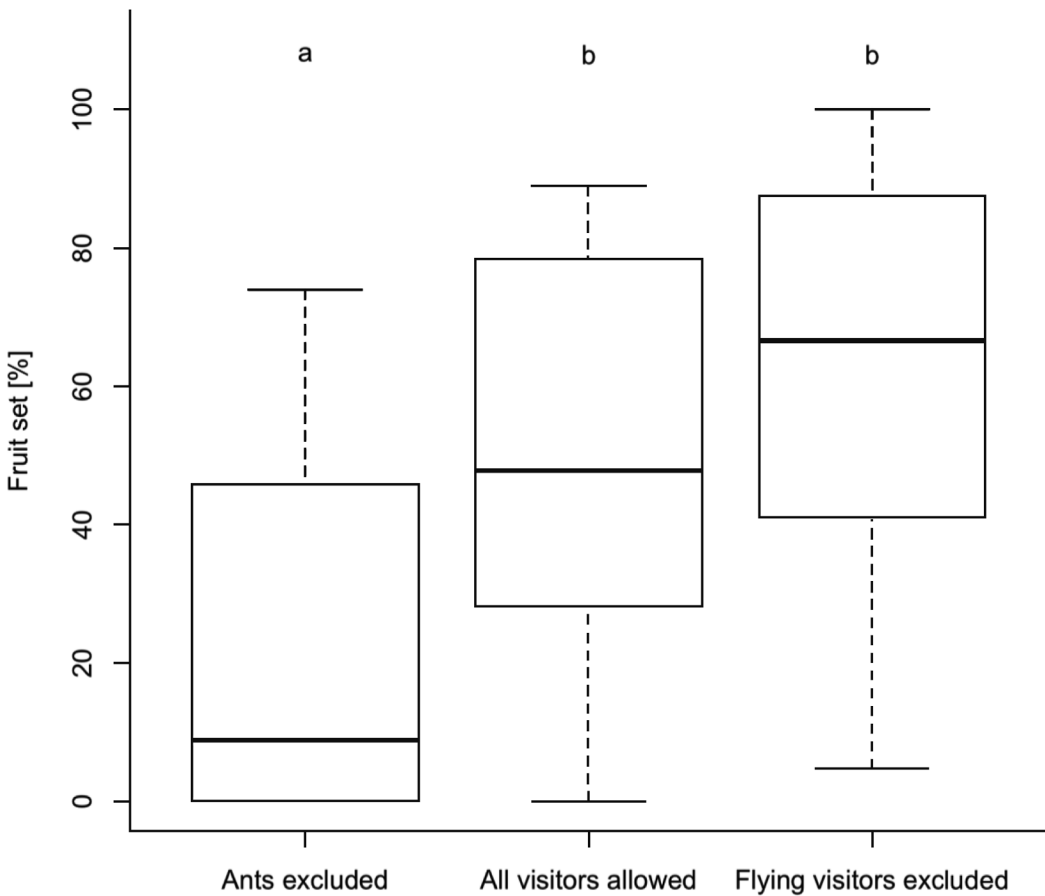


FIGURE 1. Fruit set of inflorescences with experimentally altered visitor spectrums averaged across both field sites. Box plots show medians (heavy lines), quartiles (boxes), and range (whiskers). Treatments with different letters indicate significant differences ($P < .05$) among treatments according to Wilcoxon signed-rank tests, performed after a Friedman test.

ant (*L. bumile*) entering a flower bud through a caterpillar hole and reappearing with the head of a caterpillar. We offered caterpillars of *S. littoralis* to both *P. megacephala* and *P. bourbonica* ants outside flowers. They were readily taken and transported to the nest.

On flowering branches of *V. reticulatum* new buds appear regularly, so nectar-producing flowers and buds are most often in direct proximity to each other (R.B., pers. obs.). This ensures contact of flower-visiting ants with bud-feeding caterpillars. Furthermore, the ants may drive off adult female plume moths and thus prevent them from ovipositing.

Availability of Nectar

Ants excessively exploited the floral nectar of *V. reticulatum*. No nectar could be extracted from flowers on ant-accessible branches in any of the samples. Consequently, the volume of available nectar in ant-excluded flowers (median, quartiles: 0.13, 0.00–0.56 $\mu\text{l flower}^{-1}$) was significantly higher than in flowers that were accessible by ants (Wilcoxon signed-rank test, $z = -2.13$, $P = .022$, $n = 11$).

Flower Parasitism

At both sites, ant-free branches produced fewer fruits (percentage of initial flower bud set) than ant-visited branches (i.e., more flowers and flower buds were lost to parasitism on branches without ants). On average, the presence of ants increased fruit set more than fivefold compared with the fruit set on ant-excluded branches irrespective of other allowed visitors (Friedman test, $\chi^2 = 17.69$, $P < .01$, $n = 19$) (Figure 1).

Fruit set was generally higher at Broomsedge Burn area, where ant density was higher (median, quartiles: 0.72, 0.45–0.93 ants flower^{-1}) than at Kīpuka Kahali'i (0.06, 0.03–0.35 ants flower^{-1}). Fruit set was significantly correlated with ant density in flowers of individual plants. Plants with high ant densities in their flowers set more fruit than individuals with lower ant densities (Spearman

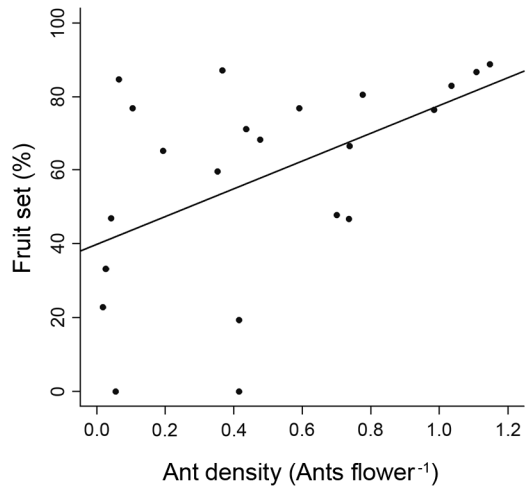


FIGURE 2. Relationship between ant density in flowers (ants flower^{-1}) and fruit set (%) of the control (all visitors allowed) branches.

rank correlation, $r = 0.56$, $P < .01$, $n = 23$) (Figure 2).

Seed Set

No flower visitors other than ants and caterpillars of *S. littoralis* were observed during the whole study period. *Hylaeus* spp. bees, the most common visitors of *V. reticulatum* elsewhere (Heather Sahli, pers. comm.) and probably the main pollinator of *V. reticulatum*, were rare (Broomsedge Burn Area) or absent (Kīpuka Kahali'i) from the study sites (personal observations by the authors on other flowers in the same habitat).

The proportion of viable seeds was low (median: <10%) for all treatments (Figure 3). Consequently, the different treatments showed no effects on seed set of *V. reticulatum* (Kruskal-Wallis test, $\chi^2 = 0.52$, $P = .77$, $n = 14$ plants [ants excluded], 23 [all visitors allowed], 14 [ants only]). The proportion of viable seeds was weakly positively correlated with berry diameter (Spearman rank correlation, $r = 0.27$, $P < .01$, $n = 100$ berries). However, treatments and ant density had no effect on berry diameter (Kruskal-Wallis test, $\chi^2 = 0.91$, $P = .63$, $n = 52$ berries [all visitors allowed], 30 [ants excluded], 18 [ants only]), (Pearson's product-

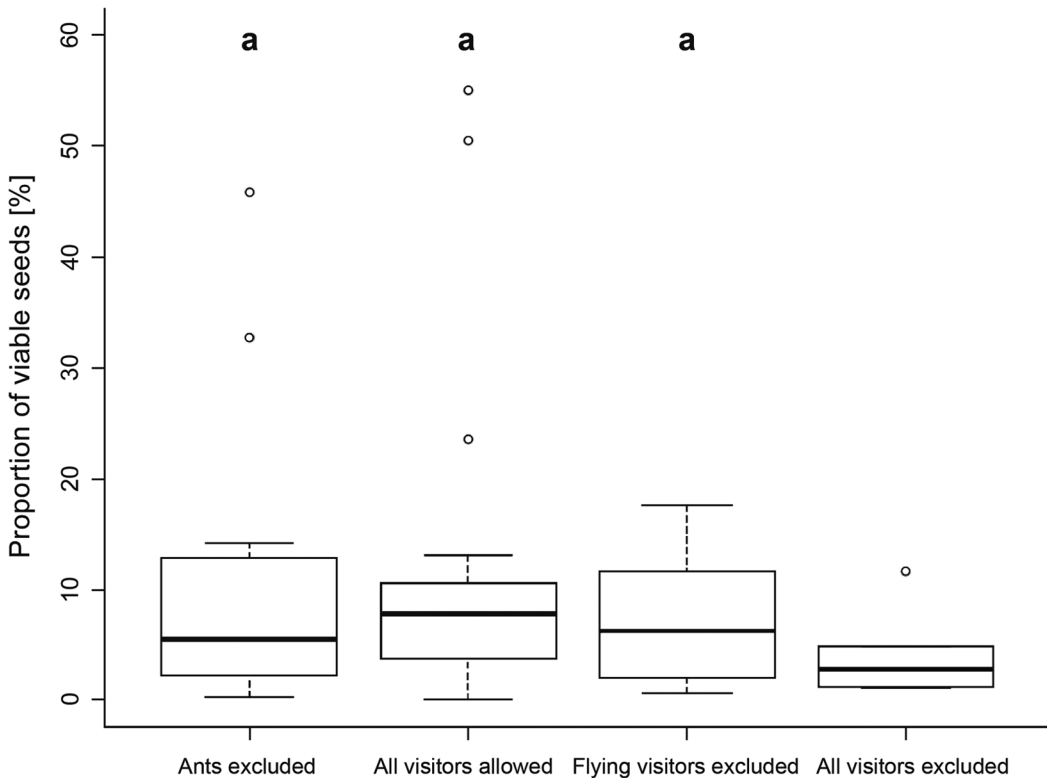


FIGURE 3. Proportions of viable seeds in berries from inflorescences with experimentally altered visitor spectrums averaged across both field sites. Box plots show medians (lines), quartiles (boxes), range (whiskers), and outliers (circles). Treatments with different letters indicate significant differences ($P < .05$) among treatments according to pairwise Wilcoxon signed-rank tests. Treatment “All visitors excluded” was not included in statistical analysis.

moment correlation, $r^2 = 0.03$, $P = .57$, $n = 13$ plants).

DISCUSSION

Ants were frequent flower visitors and depleted floral nectar of *Vaccinium reticulatum*. The presence of ants in flowers did not affect the proportion of viable seeds per fruit but had a positive effect on the plant's reproduction by decreasing flower parasitism, leading to increased fruit set. Thus, invasive ants efficiently protected flower buds and flowers of an endemic Hawaiian plant species that is neither adapted to the introduced moth nor to ants. These results constitute a contrasting example to other studies, which demonstrated devastating effects of invasive ants on native

organisms in Hawai'i (e.g., Zimmerman 1970, Howarth 1985, Cole et al. 1992, Reimer 1994, Krushelnycky and Gillespie 2008). The magnitude of floral ant protection for *V. reticulatum* (fruit set increased more than fivefold) is even greater than shown in studies of co-evolved ant-plant mutualisms, where ants increased fruit set usually less than fourfold (Rico-Gray and Thien 1989, Oliveira 1997, Oliveira et al. 1999). However, co-evolved systems of ant flower protection fundamentally differ from the system studied here. In co-evolved systems, ants are often attracted to extrafloral nectaries on pedicels, bracts, or flower buds (see Bentley 1977, Rico-Gray and Thien 1989, Oliveira 1997, Oliveira et al. 1999) but are mostly repelled from flowers of the same plant during anthesis (Willmer and

Stone 1997, Agarwal and Rastogi 2008). Thus, protection of the reproductive structures is enhanced while an interference of ants with pollination is avoided. *V. reticulatum*, which did not coevolve with ants, apparently lacks floral defense mechanisms. The plant profits from ant protection of its reproductive structures but cannot avoid interference with pollination. It is well known that both *P. megacephala* (Lach 2008b) and *L. humile* (Blancafort and Gomez 2005, Lach 2007, 2008a, Junker et al. 2010) negatively interfere with other flower visitors. However, we were not able to observe this proposed interference with pollinators because we never observed any potential pollinators visiting the flowers. This apparent lack of pollinators suggests that there was virtually no cross-pollination in any treatment. Our finding that the treatments that allowed visitation of flying insects did not produce more viable seeds than the treatments with all visitors excluded supports this assumption. Pollination by ants is unlikely because ant-visited treatments did not produce more viable seeds than the ant exclusion treatment.

We propose three potential reasons for the apparent lack of flower visitors: (1) reduced activity of pollinators caused by uncommonly cold temperatures from March to May 2009 (mean monthly maximum temperature March–May was 17.3°C instead of 19.8°C, which is usual during that time of the year [Karin Schlappa, pers. comm.]); (2) decline of populations of potential pollinators caused by competition with ants and honeybees for floral resources; (3) decline of populations of potential pollinators caused by ant predation. Numerous authors have demonstrated that ants are responsible for an intense decline of native arthropods in Hawai'i (e.g., Zimmerman 1970, Beardsley 1980, Howarth 1985, Reimer 1994, Krushelnycky and Gillespie 2008) and particularly of *Hylaeus* spp. bees (Cole et al. 1992, Daly and Magnacca 2003). In a study on the seed set of *V. reticulatum* in HAVO and Haleakalā National Park, Maui, Vander Kloet (1993) found 32.6% of the seeds from field collections to be viable—four times more than what we found. Studies by Gagné (1979) and Medeiros et al.

(1986) indicate that *L. humile* ants were generally present at Vander Kloet's collection sites, but one-third of those sites (those above 1,650 m a.s.l.) hosted only two locally restricted populations of *L. humile* and were mostly uninvaded at that time (Krushelnycky et al. 2005). Lower predatory pressure by ants in that area may have supported a denser population of *Hylaeus* spp. bees. This may be one explanation for the higher ratio of viable seeds. *Hylaeus* spp. bees were rare (Broomsedge Burn Area) or absent (Kīpuka Kahali'i) from our study sites. However, it remains unclear whether ants influenced their populations in our case.

Despite the fact that ants effectively protected the flowers of *V. reticulatum* in our study, their strong resource exploitation and their negative effect on native pollinator populations (Cole et al. 1992, Daly and Magnacca 2003) may outweigh this positive effect. Therefore, potential positive effects (e.g., reduction of flower parasitism) by ants and potential negative effects on pollination need to be considered in concert to assess net effects of ants on the reproduction of endemic Hawaiian plants.

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