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Breeding system and pollination of *Dubautia menziesii* (Asteraceae), a self-incompatible Hawaiian alpine shrubJuan Francisco Guisado Chavez^{a,*}, Paul Krushelnycky^b, Kasey E. Barton^a, Donald R. Drake^{a,c}^a School of Life Sciences, University of Hawai'i at Mānoa, 3190 Maile Way, Honolulu, HI 96822, USA^b Department of Plant and Environmental Protection Sciences, University of Hawai'i at Mānoa, 3050 Maile Way, Honolulu, HI 96822, USA^c Harold L. Lyon Arboretum, University of Hawai'i at Mānoa, 3860 Mānoa Rd., Honolulu, HI 96822, USA

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ABSTRACT

Islands host unique biodiversity that faces threats from global change. Understanding plant reproduction is vital to conserve and restore island ecosystems, in turn ensuring stable population dynamics and preserving biodiversity. *Dubautia menziesii* (Asteraceae) is a common shrub endemic to the alpine and subalpine ecosystem of Haleakalā volcano on Maui. The purpose of this study is to: (i) characterize the breeding system of *D. menziesii*, (ii) identify its main pollinators, (iii) determine how plant isolation affects seed set and seed parasitism, and (iv) estimate the abundance of *D. menziesii* and its flower resources in the habitat. Hand pollination treatments were conducted to assess seed set and determine the breeding system. Flower-visiting insects were observed, to identify pollinators. The impact of isolation was assessed by analyzing seed set and seed predation at varying distances from the nearest flowering neighbor. Species abundance was estimated using belt transects and plotless sampling. *Dubautia menziesii* is self-incompatible and requires outcrossing to set seeds (66 % seed set for outcrossed flowers vs. 3 % for manually self-pollinated and bagged unmanipulated flowers). The most frequent flower visitors were endemic *Hylaeus* bees (44 %), and non-native honeybees (34 %), followed by *Nysius* spp. seed bugs (15.9 %). Isolation had no significant effect on either seed set or seed predation at 2 sites. The relative dominance of *D. menziesii* at high elevations on Haleakalā suggests it plays an important role in maintaining insect populations and may benefit other plants with which it shares floral visitors, such as the Haleakalā silversword.

1. Introduction

Although islands represent only 6.7 % of the Earth's total land surface (Sayre et al., 2019), their high level of species endemism, taxonomic diversity, and unique ecological scenarios (Carlquist, 1974; Kier et al., 2009; Caujapé-Castells et al., 2010) have made them invaluable sources of biodiversity (Caujapé-Castells et al., 2010; Schrader et al., 2024). Islands harbor one-quarter of all plant species on Earth (Kreft et al., 2008), and are therefore particularly important for conserving global plant diversity (Caujapé-Castells et al., 2010; Fernández-Palacios et al., 2021; Schrader et al., 2024). Despite this, island plant species present important knowledge gaps, including their interactions with animals or breeding systems (Anderson et al., 2001; Kaiser-Bunbury et al., 2010; Crawford et al., 2011; Chamorro et al., 2012). Given that 87.5 % of the world's flowering plants are pollinated by animals (Ollerton et al., 2011), understanding plant-pollinator interactions is crucial for

advancing the biology and conservation of these species (Kevan and Viana, 2003; Sánchez-Bayo and Wyckhuys, 2019). Plants produce multiple resources (pollen and nectar) for the flower-visiting animal species that may promote pollination and subsequent seed set and plant population regeneration (Kearns et al., 1998; Willmer, 2011).

In the Hawaiian archipelago, the role of endemic nectar-feeding honeycreeper and honeyeater birds as pollinators has been the focus of much attention (Carlquist, 1974); however, the role of insects as pollinators is less well studied (Medeiros et al., 2013). Yet, it is estimated that 67 % of the endemic flora is insect pollinated (Medeiros et al., 2013). Among flower-visiting insects, bees are considered one of the most important pollinator groups globally (Tepedino, 1979; Ballantyne et al., 2017). The only native bees in Hawai'i are in the genus *Hylaeus* (Colletidae, yellow-faced bees), with more than 60 endemic species (Daly and Magnacca, 2003). These bees occur across a wide range of habitats and elevations (Daly and Magnacca, 2003; Koch and Sahli,

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2013; Shay et al., 2016), where they visit and pollinate many native plants (Daly and Magnacca, 2003), including threatened and endangered species (Krushelnicky, 2014; Shay et al., 2016). However, little is known about the potential pollinators for most of the common Hawaiian plant species, and the role of *Hylaeus* as pollinators needs further study (Koch and Sahli, 2013).

As with pollination, there is a general lack of knowledge of the breeding systems of island plant species (Anderson et al., 2001; Crawford et al., 2011), which is particularly useful to understand the life history, evolution, and speciation of island taxa (Sun and Ganders, 1988; Sakai et al., 2006). Additionally, in the Hawaiian archipelago, this is one of the urgent needs for the conservation of native biodiversity (Caujapé-Castells et al., 2010).

Establishment of a new population following long-distance dispersal is one the major filters that limits the ability of species to colonize islands, and the breeding system plays an important role in the likelihood of success (Whittaker and Fernández-Palacios, 2007). Self-compatibility provides an advantage for establishment in a new land after long-distance dispersal (Baker, 1955) because a single propagule could potentially generate a sexually reproducing population without the need to cross pollinate with a conspecific. This principle, known as Baker's rule (Baker, 1955, 1967), has been the focus of attention of ecologists, and has been discussed and tested in multiple scenarios (Carlquist, 1966; Cheptou, 2012; Patiño et al., 2013; Pannell et al., 2015). A potentially contradictory pattern occurs in the Hawaiian archipelago (Carlquist, 1966), which contains the highest percent of dioecy of any flora worldwide (14.7 %; Sakai et al., 1995), and some species belonging to the endemic silversword alliance (Asteraceae) show strong self-incompatibility (Carr et al., 1986).

The family Asteraceae is one of the most successful and diverse colonizers of oceanic islands (Lenzner et al., 2017; Roebler et al., 2024); however, surprisingly little is known about its reproductive biology on islands (Crawford et al., 2023; Roebler et al., 2024). This family is well represented in Hawai'i (Wagner et al., 1990), including the Hawaiian silversword alliance, a monophyletic group of 35 species in endemic genera *Argyroxiphium*, *Dubautia*, and *Wilkesia* (Baldwin, 1997; Wagner et al., 1990, 2012), and considered as one of the most remarkable and well-described plant adaptive radiations (Robichaux et al., 1990; Baldwin and Sanderson, 1998; Carlquist et al., 2003; Raven et al., 2005; Crawford et al., 2023; Roebler et al., 2024). Colonization of the Hawaiian archipelago has been traced to a self-incompatible ancestral tarweed reaching the island of Kaua'i 4–6 Mya (Baldwin and Sanderson, 1998; Barrier et al., 1999; Landis et al., 2018). The breeding systems for one species of *Argyroxiphium* and one species of *Wilkesia* have been identified as self-incompatible (Carr et al., 1986; Baldwin, 1997; Forsyth, 2003), but the presumed sporophytic self-incompatibility mechanism for other taxa in the alliance (Carr et al., 1986) remains unproven, and little quantitative research has been published with the most diverse genus in the alliance, *Dubautia* (but see Aslan et al., 2019). *Dubautia* is represented by 28 species and is present across all major Hawaiian Islands, in diverse habitats, across a wide elevational range, and exhibits diverse growth forms such as shrubs, trees, and lianas (Carr, 1985; Robichaux et al., 1990; Blonder et al., 2016; Wagner et al., 1990, 2012).

The species *Dubautia menziesii* (A. Gray) D.D. Keck is a perennial shrub adapted to high elevations of Haleakalā volcano (1800–3075 m.a.s.l.) on the island of Maui (Carlquist, 1959; MacLachlan et al., 1992). The flower visitors of this species include endemic *Hylaeus* bees, such as *H. difficilis* and *H. volcanicus* (Daly and Magnacca, 2003; Wilson et al., 2010), upon which other plants, such as the threatened Haleakalā silversword or 'āhinahina (*Argyroxiphium sandwicense* subsp. *macrocephalum*) depend for pollination (Krushelnicky, 2014). In addition, seed predation has been documented for the Haleakalā silversword, in particular by the native arthropod species *Rhynchephestia rhabdotis* (Lepidoptera: Pyralidae) and *Trupanea cratericola* (Diptera: Tephritidae) (Krushelnicky, 2014), but there is no information on seed predation for *D. menziesii*. Spatial isolation among conspecifics is a factor that can

influence seed production through pollination and seed parasitism and predation (Kunin, 1992; Elzinga et al., 2005), as in the Haleakalā silversword (Krushelnicky, 2014), but it is unclear how *D. menziesii* is affected by spatial isolation from conspecifics. This factor can influence seed production through both pollination and seed predation (Kunin, 1992; Elzinga et al., 2005), and may have a significant impact on plants, such as in the Haleakalā silversword (Krushelnicky, 2014).

Despite being among the most widespread plant species in the high elevation ecosystem of Haleakalā (Wagner et al., 1990; Friar et al., 2006; Ainsworth and Drake, 2020), the ecological role of *D. menziesii* remains obscure. Endangered species are often the focus of conservation, but common species, such as *D. menziesii*, are crucial for supporting ecosystems and maintaining their structure and function (Gaston, 2010; Jansen et al., 2020). Common species should be a major target for conserving habitats, especially those vulnerable to climate change (Ainsworth and Drake, 2020, 2023a; Gaston and Fuller, 2008; Gaston, 2010; Fortini and Dye, 2017; Cubas et al., 2022). Biodiversity in alpine ecosystems is highly vulnerable to climate change owing to the progressive reduction in alpine area with elevation, resulting in reduced distribution ranges and smaller populations, together with the limited capacity of alpine plants to respond to rapid environmental shifts (Buytaert et al., 2011; Krushelnicky et al., 2020; Fortini et al., 2022). Upper Haleakalā includes 11 % of the total alpine land in the Hawaiian archipelago, and is considered one of the most intact remaining environments in the state (Frazier and Brewington, 2020). With climate change, ecosystem boundaries are expected to change (Buytaert et al., 2011; Ainsworth and Drake 2023a, 2023b), and the risk of extinction or extirpation for some plants in the lower region of the alpine ecosystem of Maui may be expected to increase over the next century, as is already the case for silverswords (Krushelnicky et al., 2013, 2016; Fortini et al., 2022).

The objectives for this study were to: (1) Investigate the reproductive system of *D. menziesii* by determining both its ability to reproduce through self-pollination (self-compatibility) and its reliance on pollination vectors to transfer pollen between individuals, (2) document the flower visitors (presumed pollinators) and compare overlap with the related Haleakalā silversword, (3) understand plant isolation as a factor in seed production and seed predation, and (4) estimate the abundance of *D. menziesii* in the habitat, relative to other flowering species, to understand floral resource availability for pollinators and seed predators. We predicted that *D. menziesii* is self-incompatible, similar to most other tested species of the silversword alliance (Carr et al., 1986; Forsyth, 2003). We expected that native *Hylaeus* bees and introduced honey bees (*Apis mellifera*) would be common floral visitors, and that plant isolation would reduce seed set and seed predation as in the Haleakalā silversword (Krushelnicky, 2014). Finally, we expected that *D. menziesii* is one of the most abundant plants in the ecosystem (Wagner et al., 1990; Kitayama and Mueller-Dombois, 1992) and may have an important role in sustaining pollinator communities through provision of floral resources.

2. Materials and methods

2.1. Study species

Dubautia menziesii (Asteraceae) or Kūpaoa is a perennial shrub that can reach up to 2.5 m in height (Pérez, 2019). This single-island endemic species, derived less than 1 million years ago (Friar et al., 2006), is one of the most widespread species in the subalpine and alpine ecosystems of Haleakalā, with many thousands of individuals (Wagner et al., 1990; Friar et al., 2006) between 1800 m above sea level and the summit (3055 m.a.s.l.), where it forms the *D. menziesii* vegetation unit above 1950 m.a.s.l. (Gagne and Cuddihy, 1990; Kitayama and Mueller-Dombois, 1992; Friar et al., 2006; Pérez, 2019). Flowering occurs annually, over multiple years, from July to December (Friar et al., 2006). Inflorescences (capitula) consist of 12–25 yellow-orange flowers (florets; Carr, 1985,

1995; Friar et al., 2006), each having a single ovule (Wagner et al., 1990; Crawford et al., 2023). Flowers of *D. menziesii* are bisexual and protandrous. Pollen is released on the first day of anthesis, and stigma lobes open and become receptive to pollen on the second day. By the third day, the stigmas senesce and are no longer receptive (Fig. 1). Flowers mature sequentially, in a spiral pattern, beginning at the outer edge of the inflorescence, over a period of 5–7 days.

2.2. Study sites

The study site is located on the island of Maui, the second largest island of the Hawaiian archipelago (1883 km²). Fieldwork was carried out in Haleakalā National Park. Haleakalā—House of the Sun—is a shield volcano of the Pleistocene, originating around 0.8 million years ago, with an elevation of 3055 m.a.s.l. The upper elevation region consists of an arid zone with dry and cold air, strong seasonal drought, and intense radiation (Blumenstock and Price, 1967; Gagne and Cud-dihy, 1990). Vegetation at the highest elevations of Haleakalā is sparse, represented by the alpine *D. menziesii* vegetation unit (Gagne and Cud-dihy, 1990; Kitayama and Mueller-Dombois, 1992; Friar et al., 2006; Pérez, 2019), together with several herbs, tufted grasses, nano shrubs and silversword rosettes (Pérez, 2017; Ainsworth and Drake, 2023a) (Fig. 2).

The study was carried out from August to November of 2023 in a roughly 4 hectare plot (site A) on the western slope of the crater (20°43'14"N 156°14'52"W; 2930 m.a.s.l.; Fig. 3). This site was selected for the abundance of *D. menziesii* (and *Argyroxiphium sandwicense*), and it overlaps with the area uninvaded by non-native ants in Krushelnycky's (2014) study of the reproduction of the Haleakalā silversword.

This plot was used for breeding system studies and observation of pollinators (see below), and another (site B) was added to increase sample size for investigating how isolation affects seed set. Site B covered roughly 11.4 ha (20°42'50"N 156°15'14"W; 2945 m.a.s.l.), 885 m southwest of site A (Fig. 3).

2.3. Pollen-ovule ratio

The ratio between pollen and ovules produced by a plant can be a rough indicator of its breeding system (Cruden, 1977). It is expected that self-compatible plants will have a lower pollen: ovule ratio than those that require outcrossing (Cruden, 1977; Mione and Anderson, 1992). We estimated the pollen: ovule ratio for *D. menziesii*. Flowers in the Asteraceae have only one functional ovule per floret. To count pollen, ten random mature florets were collected from 4 different capitula belonging to 4 different individuals. One stamen from each floret was selected and mounted in a 3 × 3 mm cube of glycerin jelly stained with basic fuchsin and mounted on a microscope slide. Pollen grains were detached from the stamen using fine forceps and counted under a compound microscope at 100x magnification. The number of pollen grains per stamen was averaged and multiplied by 5 (total stamens per floret) to estimate pollen production per floret (Kearns and Inouye, 1993; Krushelnycky, 2014).

2.4. Breeding system

Pollination treatments were performed from 1 to 6 August 2023, early in the flowering season. A total of 40 flowering individuals were unsystematically selected in Site A. On each plant, at least four branches containing only capitula with unopened flowers were bagged (organza fabric mesh with pore size 0.2 × 0.2 mm). Because of the difficulty of bagging one isolated capitulum, the entire flowering branch tip was bagged, and the target capitulum was marked with a waterproof pen on the peduncular bracts. On each of four branches on the plant, one haphazardly-selected capitulum received one of the following four treatments: self-treatment (S), autonomous autogamy (A), outcrossing (O), or control (C) (Gross, 2001). The S inflorescence was examined daily to monitor number of flowers and floral development, and each day the number of female receptive florets was noted and hand-pollinated with pollen from male-phase flowers from a bagged donor inflorescence elsewhere on the same plant. This was done on two consecutive days; in some cases, a third day was added so that at least five female-phase florets were pollinated. This tests for capacity to set



Fig. 1. *Dubautia menziesii* inflorescence and flowers. A: flowers of a single inflorescence (capitulum). B: flower breaking bud. C: one-day-old flower in male phase, releasing pollen. D: two-day-old flower in female phase, stigmatic areas of style branches unpollinated. E: two-day-old flower in female phase, stigmatic areas of style branches pollinated. F: three-day-old flower in female phase, style branches senescent.



Fig. 2. Vegetation at high elevation, the alpine ecosystem, in Haleakalā. Vegetation is sparse and the landscape is well-represented by bare soil and rocks. The species *Dubautia menziesii*, *Deschampsia nubigena* and *Argyroxiphium sandwicense* are visible.

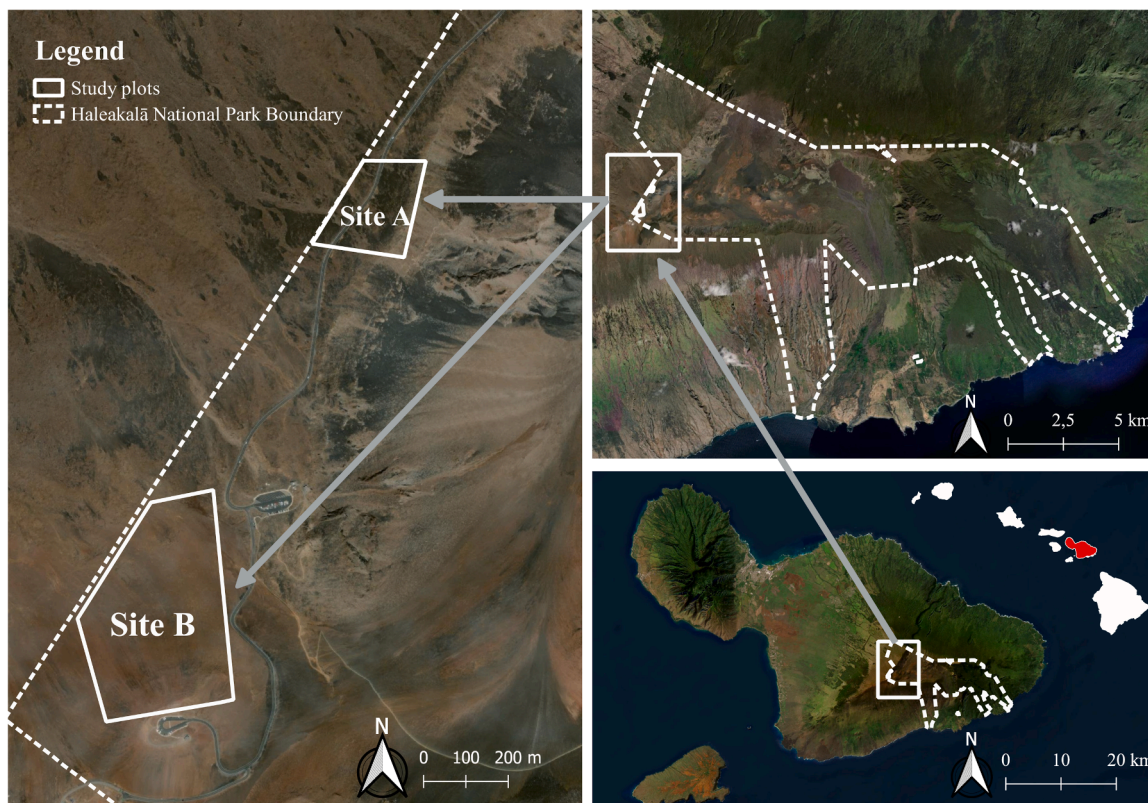


Fig. 3. Geographic location of the study site (sites A and B) across Haleakalā National Park. Map produced with QGIS 3.18.2 Zurich. Geographic limits of the National Park and coastlines were obtained from NPS - Land Resources Division Boundary and Tract Data Service and the Hawaii Statewide GIS Program. Base map: ESRI Satellite.

seed via self-pollination when pollination is not limited. The **A** inflorescences remained bagged and unmanipulated throughout the experiment, which tests the capacity to set seed via self-pollination in the absence of an animal pollination vector. The **O** inflorescence was

treated the same way as the **S** inflorescence, but female-phase florets were pollinated with pollen from male-phase florets from inflorescences from two other plants (therefore four donors over two days) located at least 5 m away. This tests for capacity to set seed with non-self pollen

when pollination is not limited. The C inflorescences were unbagged, tagged with a plastic twist tie below the marked capitulum and left unmanipulated. This tests for maximum reproductive output when pollination (quantity and source) is done by natural pollination vectors.

Pollination was performed by selecting male phase florets with open anthers showing pollen. Flowers begin opening around 09.00. Florets were picked with forceps and rubbed against the stigma of the female-phase treatment floret after opening the mesh bag. Forceps were sterilized with 70 % ethanol after each pollination treatment. Bags were tied again to exclude other pollen donors once pollination was performed, and the branches were left bagged until maturing capitula were collected on August 26 (Kearns and Inouye, 1993). The total number of florets in each marked capitulum and the total number of florets subjected to the hand pollination treatments were noted. Proportions and other calculations for the S and O treatments were done considering the number of florets subjected to the treatments. By contrast, calculations for C and A treatments were done by considering the total number of florets in the capitulum because each had an equal chance to receive the “treatment.”

Collected capitula were stored individually in plastic bags and left open for at least two days at room temperature to facilitate air-drying and avoid fungal growth. Subsequently, bags were closed and stored in a refrigerator (4 °C) until examination. For each capitulum, phyllaries were removed and achenes were observed under a dissecting microscope (10x magnification). The achenes were opened by making an incision on the seed coat and the number of filled, empty and/or depredated achenes were counted and recorded. Depredated achenes were observed as a group of compacted achenes with a black pupa inside covering the inner part of the achenes, with the achenes lacking an embryo and part of the epicarp. Any insect found was stored in a vial with 70 % ethanol for identification.

2.5. Insect observations

We performed observations of flower visitors on unsystematically selected *D. menziesii* in site A on September 9, 10, 30, and October 1, coinciding with the peak flowering season of the species, to determine flower visitor identities, abundance, and rate of flower visits. Observations consisted of 10-minutes intervals during sunny and non-windy days from 09.30 to 16.00, which were the times of highest insect activity. If a plant was so large that not all flowering branches could be observed, the side that was facing the sun was selected. The observer was at least one meter away from the plant and started observing the flower visitors with binoculars after a one-minute period in order to minimize disturbance to flower visitors (Padrón et al., 2009). For each observation, we identified each flower visitor to the lowest taxonomic group possible, and the number of individuals per taxon that contacted the reproductive structures of the plant during the interval. Flower visitors were not collected. To assess the abundance of total visitors throughout the day, the observations were divided into hourly counts throughout the period (except for 14.30 to 16.00, which were combined owing to the reduced number of observations conducted from 15.30 to 16.00), and visits were averaged per unit time. Finally, floral display for each plant observed was estimated by counting the number of flowering branches on the plant ($n = 244$ plants) and number of capitula per flowering branch ($n = 50$ branches).

2.6. Isolation effect

In order to assess whether isolation is a factor related to seed set and seed predation, as demonstrated for *Argyroxiphium sandwicense* in the Haleakalā alpine ecosystem (Powell, 1992; Krushelnicky, 2014), the distance to the nearest flowering neighbor was measured, and seed set and predation rate were analyzed. Three mature capitula were randomly chosen and collected from each of 49 plants at site A on August 26 and from 38 plants at site B on September 30, with plants located at varying

distances (measured with a meter tape) from their nearest flowering neighbor. Data sets from the two locations were treated independently due to the possibility that different pollinator communities could generate different pollination rates, and therefore seed set rates, from one site or time to the other. Capitula were processed, and achenes were counted similarly to those in the breeding system experiment (see Materials and methods – Breeding system). The proportions of filled, empty, and depredated achenes were calculated among all florets in the capitulum and averaged per plant.

2.7. Vegetation survey

We surveyed vegetation in the subalpine ecosystem of Haleakalā at sites A and B to characterize the vascular plant community and understand the overall abundance of *D. menziesii* and its relative abundance in the vascular plant community. This information may suggest floral resource availability during the survey period for the pollinator community. Vegetation cover was examined by using the line-intercept method (Canfield, 1941). A transect was established in both site A (400 m) and B (240 m). For each, the species, phenology (flowering or vegetative), and linear distance overlapping the transect were recorded for each plant intersecting the transect. For species identification, we followed Wagner et al. (1990, 2012) and Palmer (2003). Percent cover was then calculated based on the percent of total transect distance covered by each species. Plant abundance (density) was estimated using plots. Two rows of 20 consecutive 20 m x 5 m plots were distributed along a transect covering the area in site A (40 plots covering a total of 4000 m²) and 12 plots of the same size in site B (24 plots covering a total of 2400 m²). The following information was recorded: i) number of species inside the plot, ii) number of individuals per species, iii) and the phenology of each individual.

2.8. Statistical analysis

Differences in seed set and seed predation rates were compared among the four treatments (Outcrossing $n = 39$; Control = 40; Autogamy = 39; Self-treatment = 40) using generalized linear models (GLMs). Each model included treatment as the explanatory variable and either proportion of filled achenes or proportion of depredated achenes per capitulum as the response, using the binomial distribution and logit link function. Likelihood ratio contrasts were used to evaluate significant differences among treatment levels.

Numbers of flower visitors were summed over all observations to estimate the abundance of each taxon and total visitation. Total visitor abundances, and abundances of the three most common visitor groups, were compared over the one-hour periods using GLMs fit with the negative binomial distribution and log link function. For each model, visitor number was the response variable and time period was the explanatory variable. Similarly, GLMs fit with the negative binomial distribution and log link function were used to assess the relationships between floral display size of *D. menziesii* and total numbers of floral visitors as well as numbers of the three most common visitor groups. For each model, visitor number was the response variable and number of floral heads (log-transformed) was the explanatory variable.

To assess the relationship between seed set rate and isolation distance, a GLM with binomial distribution and logit link function was used, grouping data from sites A and B. The proportion of filled achenes was the response variable, and distance (log-transformed), site, and the distance*site interaction were included as explanatory variables. A similar model was used to assess the relationship between seed predation rate and isolation distance, in which proportion of depredated seeds was the response variable.

All data were analyzed using SAS JMP v. 17.0 and the “MASS” (Venables and Ripley, 2002), “dplyr” (Wickham et al., 2023) and “dev. tools” (Wickham et al., 2022) packages in the statistical platform R (R version 4.1.2; R Core Team, 2021).

3. Results

3.1. Pollen-ovule ratio

A single floret was estimated to produce a total of 6040 ± 660.9 SE pollen grains (mean number of pollen grain per anther = 1209.16 ± 132.1 SE, $n = 10$). Therefore, pollen-ovule ratio is 6040: 1. This ratio falls within the range of xenogamous (outcrossing) breeding systems according to Cruden's (1977) classification in which a mean ratio of 5859 ± 937 was determined for this type of breeding system.

3.2. Breeding system

We collected 2720 florets, belonging to 158 different capitula of 40 *D. menziesii* individuals that were exposed to treatments. Two capitula, one from the outcrossing and other from the autogamy treatment, were not collected due to floral branch breakage. Seed set was highly significantly different among the four-pollination treatments ($\chi^2 = 68.07$, $df = 3$, $P < 0.001$; Fig. 4). The outcrossing and control treatments (65.7 ± 4.6 % SE and 49.7 ± 3.9 % filled achenes, respectively) did not significantly differ from each other ($\chi^2 = 2.106$, $df = 1$, $P = 0.15$), but produced nearly twenty times as many filled fruits as the selfing and autogamy treatments (2.5 ± 1.1 %; 2.7 ± 1.0 %, respectively) and significantly differed from these treatments ($P < 0.001$ for all contrasts). The majority of achenes for the self-fertilization and autogamy treatments were empty (92.5 ± 2.1 %; 93 ± 2.3 %, respectively) and these treatments did not differ from each other ($\chi^2 = 0.002$, $df = 1$, $P = 1.00$).

We found no significant differences in the frequency of depredated achenes among the four treatments ($\chi^2 = 1.83$; $df = 3$; $P = 0.61$). Predation rates were very low, with less than 5 % of achenes affected in any treatment. Surprisingly, no depredated achenes were found for the capitula collected from the control treatment, which was the only one unbagged throughout the study. The percentage of damaged achenes within an affected capitulum ranged from 15 % to 63 %, with an average of 28.19 ± 2.8 %. This usually involved from 3 to 10 achenes destroyed by larvae of endemic *Trupanea* fruit flies (Diptera: Tephritidae). Three

adult specimens of *Trupanea cratericola* and two parasitic wasps that emerged from *Trupanea* pupae (*Spalangia* sp. and an unidentified species in the family Pteromalidae) emerged from the achenes collected.

3.3. Insect observations

A total of 246 insect censuses were performed, totaling over 41 h. The mean visitation rate for insects that were in contact with the reproductive structures of *D. menziesii* was 7.33 ± 0.4 SE visits per 10 min. Of 1810 visits that were recorded during the observations, at least sixteen taxa were identified. Native *Hylaeus* bees were the most common visitors, accounting for 44 ± 0.27 % of all visits, and averaging 4.2 visits (± 0.27 SE) per 10-min observation period per plant. Most *Hylaeus* visitors were females, which cannot be identified to species in the field. Only two males were observed during the census, and could be recognized as either *H. volcanicus* or *H. difficilis* (Fig. 5a). The next most common visitors were introduced honeybees, *Apis mellifera* (34 ± 0.18 %), with 3.22 visits (± 0.18 SE) per 10 min and seed bugs *Nysius* spp. (Hemiptera: Lygaeidae; 16 ± 0.44 %) with 3.5 visits (± 0.44 SE) per 10 min. This latter taxonomic group consisted of mostly sedentary insects occurring in high abundance on the plants, and only those in the flowers were counted at the end of each observation; this average better represents the mean number of *Nysius* individuals present on flowers per plant, rather than the number of individuals moving between plants. The rest of the groups accounted for less than 6 % of the total visits and were taxonomically diverse: hoverflies (Diptera: Syrphidae; *Allograpta* spp., *Eristalis* sp.), fruit flies (Diptera: Tephritidae; *Trupanea* spp.), unidentified flies (Diptera: Tachinidae and Calliphoridae), wasps and solitary bees (Hymenoptera: Megachile sp; *Vespa pensylvanica*; *Pristomerus* spp.; *Nesodynerus* spp. and Pteromalidae), ladybugs (Coleoptera: Coccinellidae), and an unidentified moth (Lepidoptera) (Fig. 5).

Flower visitor abundance was similar throughout the day, and no significant differences were found among the hourly time periods ($\chi^2 = 5.28$; $df = 5$; $P = 0.382$). The time with the greatest rate of visitation was between 14.30 and 16.00, with an average of 8.66 ± 0.89 SE per ten-minute observation. Similarly, there was no significant difference in

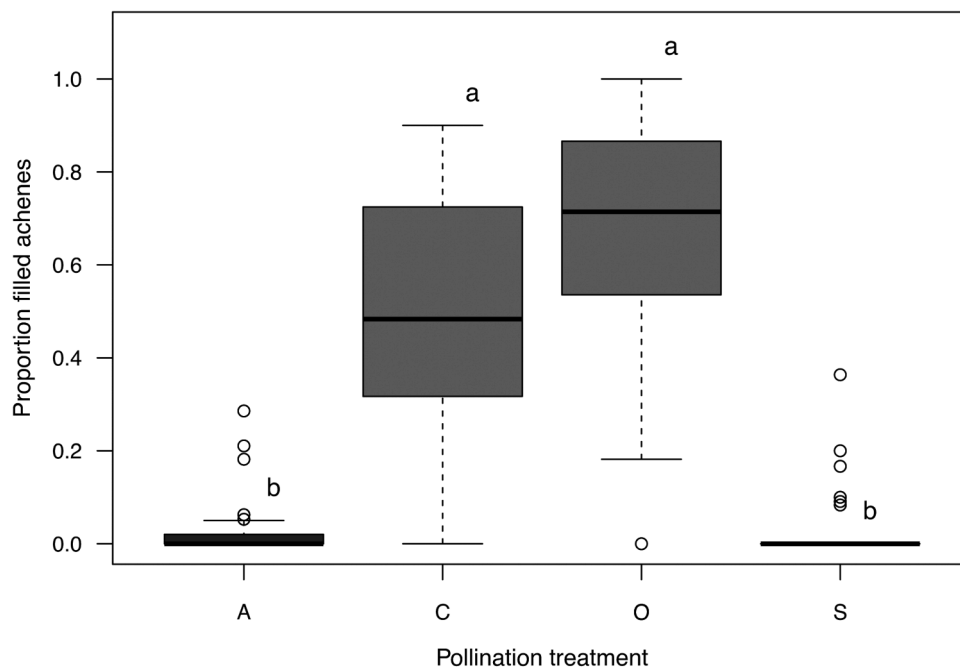


Fig. 4. Proportion of filled achenes of *D. menziesii* after florets were exposed to the pollination experiments. Treatments are as follows: A (Autonomous Autogamy; $N = 39$); C (Control; $N = 40$); O (Outcrossing; $N = 39$) and S (Selfing; $N = 40$). Grey boxes represent the quartiles 25–75 %; the horizontal line in the boxes is the median value; whiskers represent variability outside the lower and upper quartiles; and empty circles outliers. Treatments sharing the same letter are not significantly different.

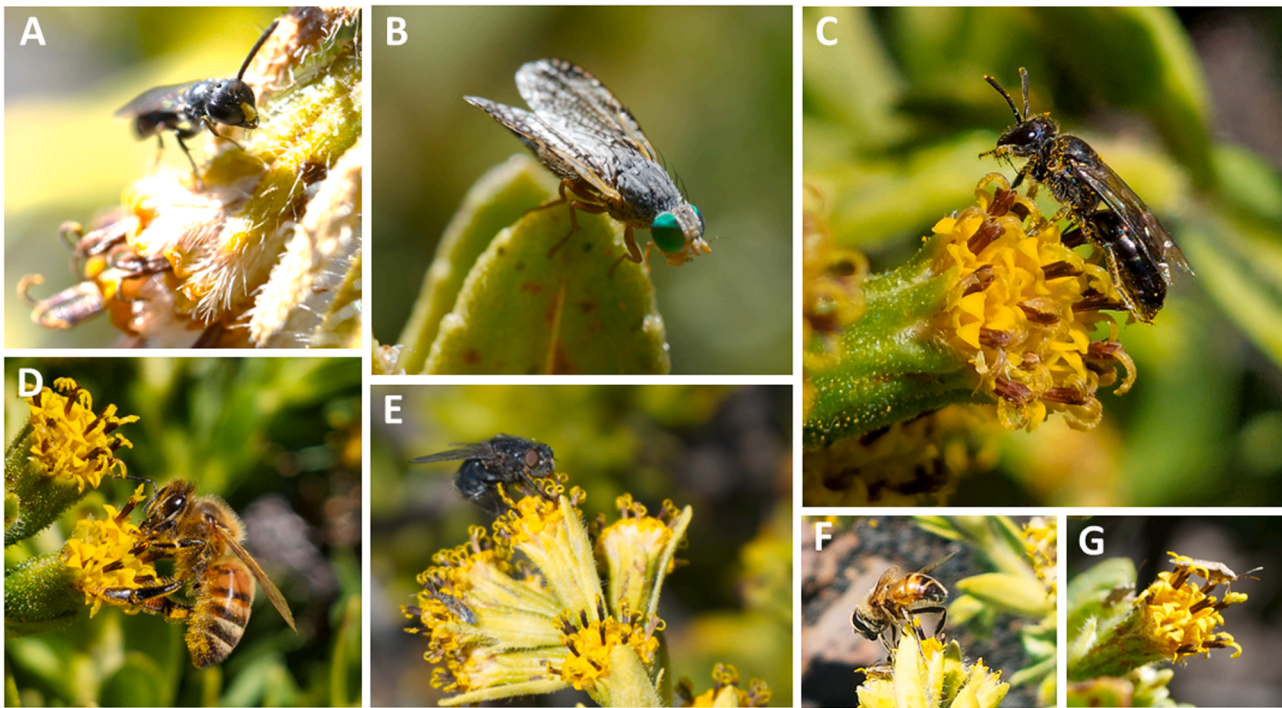


Fig. 5. Most common floral visitors observed during the 10-min observations. A: *Hylaeus* sp. male. B: *Trupanea* sp. C: *Hylaeus* sp. female. D: *Apis mellifera*. E: Diptera. F: *Eristalis tenax*. G: *Nysius* sp. All these visitors contacted the reproductive parts of *D. menziesii*. Pollen grains are visible on *Hylaeus* sp. female and *Apis mellifera* (C, D).

abundance of the three major visitors (*Hylaeus*, *Apis*, and *Nysius*) across time of day ($\chi^2 = 4.67$; $df = 5$; $P = 0.457$; $\chi^2 = 5.66$; $df = 5$; $P = 0.34$; $\chi^2 = 4.72$; $df = 5$; $P = 0.45$; respectively). The greatest numbers of native bees, *Hylaeus* spp., were observed during 14.30 to 16.00, accounting for a total of 22 % of total visits, and a similar pattern was seen for the introduced honeybees, with 22.9 % of visitation. The two main visitors for *D. menziesii* share a similar visitation pattern (Fig. 6).

Finally, we found a significantly positive relationship between the

size of the floral display (log number of floral branches) and the number of visitors per observation period for *D. menziesii* ($\chi^2 = 51.11$; $df = 1$; $P < 0.001$) (Fig. 7). Similarly, there was a significantly positive but diffuse relationship between floral display size and the most abundant visiting insect groups: *Hylaeus* ($\chi^2 = 25.32$; $df = 1$; $P < 0.001$), *A. mellifera* ($\chi^2 = 29.56$; $df = 1$; $P < 0.001$) and *Nysius* ($\chi^2 = 14.76$; $df = 1$; $P < 0.001$).

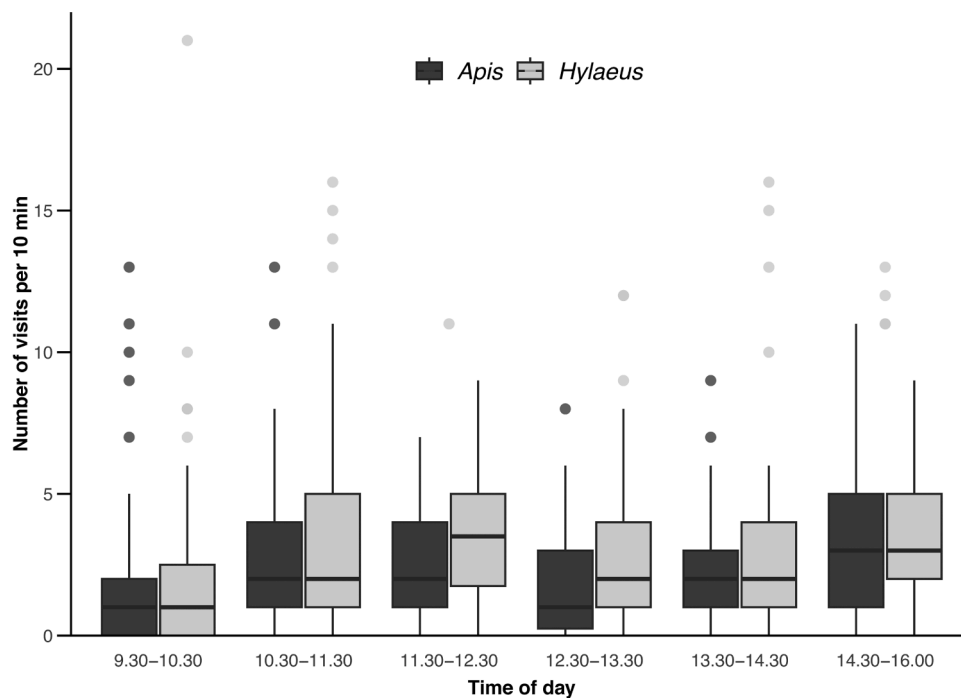


Fig. 6. Flower visitation rate (visits/10 min) throughout the day for the two most common visitors of *D. menziesii*: *Hylaeus* and *Apis*. Observations were grouped into hourly intervals across the diurnal observation period (09.30 to 16.00). Both bee taxa had similar diurnal visitation patterns and abundances.

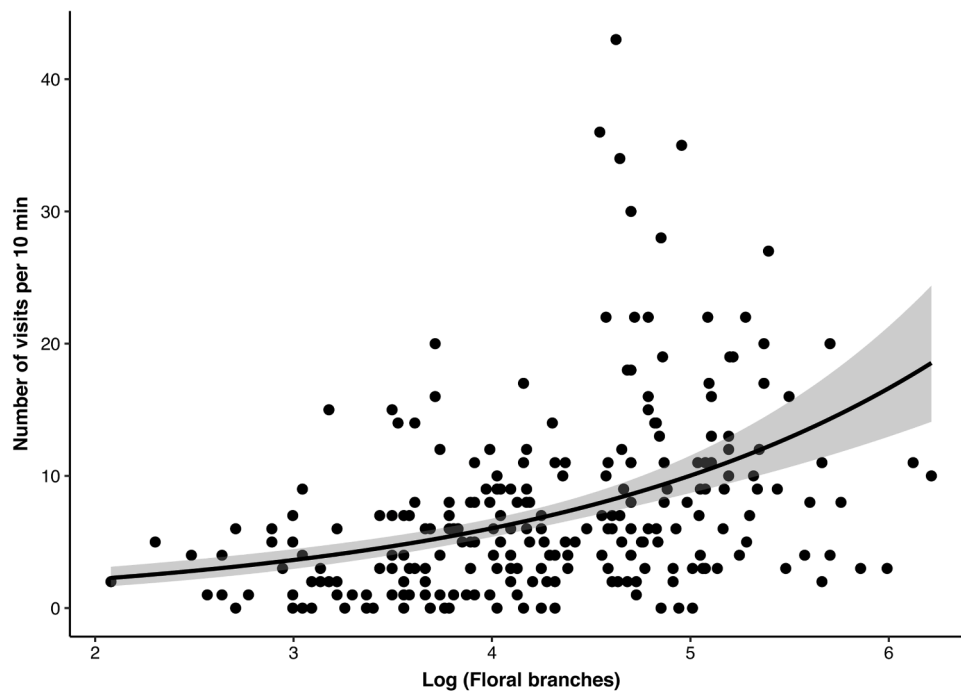


Fig. 7. Relationship between the floral display size (log number of floral branches) of *D. menziesii* and the total number of floral visitors observed per 10 min observation period ($\chi^2 = 51.11$; $df = 1$; $P < 0.001$).

3.4. Isolation effect

We collected 2393 florets belonging to 147 different capitula of 49 *D. menziesii* individuals at site A, where distance to the nearest flowering neighbor ranged from less than 1 to 15 m. At site B, we collected 1699 florets belonging to 114 different capitula of 38 *D. menziesii* individuals. Individuals were sparser than at site A, with distance to the nearest flowering neighbor ranging from 1 to 86.7 m.

We found no significant relationship between seed set and the isolation of *D. menziesii* individuals ($\chi^2 = 1.18$, $df = 1$, $P = 0.28$), and there was no significant influence of site on this relationship ($\chi^2 = 0.52$, $df = 1$, $P = 0.47$ for site; $\chi^2 = 0.02$, $df = 1$, $P = 0.86$ for site*isolation distance). The individual with the most distant flowering neighbor in this study (86.7 m) had 74 % filled achenes.

Less than 1 % of the capitula collected showed any sign of seed predation at either site. Four capitula were depredated at site A, with an average of 39 ± 8.9 % of the achenes affected in the four capitula. Nine capitula were depredated at site B, with 25.4 ± 2.7 % of the achenes in those capitula being destroyed. All damage was caused by the native *Trupanea* flies. Isolation was not significantly associated with predation rate ($\chi^2 = 0.08$, $df = 1$, $P = 0.78$), and there was no significant influence of site on this relationship ($\chi^2 = 0.12$, $df = 1$, $P = 0.73$ for site; $\chi^2 = 0.11$, $df = 1$, $P = 0.73$ for site*isolation distance).

3.5. Vegetation cover

Vegetation cover in the Haleakalā alpine ecosystem is sparse: more than 96 % of the area surveyed is bare soil and rocks (96.52 % for site A and 99 % for site B). The most common plant species is *D. menziesii*, with 1.42 % cover for site A and 0.8 % for site B, followed by *Deschampsia nubigena* (Poaceae) with 0.82 % in site A, and *Argyroxiphium sandwicense* subsp. *macrocephalum* with 0.2 % in site B. Other plant species with minor cover in site A included *A. sandwicense*, *Trisetum glomeratum* (Poaceae), *Vaccinium reticulatum* (Ericaceae), *Leptocophylla tameiameia* (Ericaceae) and the fern species *Pellaea ternifolia* and *Asplenium adiantum-nigrum*. For site B, *Hypochaeris radicata* (Asteraceae, non-native) was also found.

For the plot vegetation survey, 14 different plant species were recorded, with 14 species found at site A and 9 species at site B. Similar to the cover data, the most common plants in site A are *D. nubigena*, with 9.63 individuals per 100 m², *D. menziesii* with 3.95 individuals/100 m² (of which 2.63 were flowering), and *T. glomeratum* with 2.03 individuals/100 m². For site B, *D. menziesii* was the most abundant plant with 2.5 individuals/100 m² of which 1.29 were flowering, followed by *A. sandwicense* with 1.75 individuals/100 m².

3.6. Floral display and seed production for *D. menziesii*

The average *D. menziesii* shrub in the study area produces 94.0 ± 5.0 SE floral branches ($n = 246$ plants), each of which contains 11.0 ± 0.4 SE capitula ($n = 50$ branches). As a result, each plant produces 1030.6 ± 65.4 SE capitula. Considering that each capitulum produces 16.2 ± 0.3 SE florets ($n = 299$ capitula), an individual produces $16,714.8 \pm 767.8$ SE total florets. If 49.7 % of the achenes are filled (based on the control experiment under natural conditions - see Section 3.2), a single individual would produce 8307.35 filled achenes. There is an average of 1.31 *D. menziesii* flowering individuals per 100 m² (average from site A and B). As a result, the density of filled achenes produced in 100 m² is 10,882.5.

4. Discussion

Two species from the Hawaiian silversword alliance were experimentally demonstrated to be self-incompatible, *Argyroxiphium sandwicense* subsp. *macrocephalum* and *Wilkesia gymnoxiphium* A. Gray (Carr et al., 1986; Forsyth, 2003). In addition, self-incompatibility was inferred for several species of the largest genus, *Dubautia*, based on lack of non-hybrids resulting from interspecific hand-crosses in the presence of self-pollen (Carr et al., 1986). However, Carr et al. (1986) noted evidence of variation in breeding system within *Dubautia*, though few previous studies have focused on it (Carr et al., 1986; Aslan et al., 2019). The reproductive output of hand pollinated *Dubautia menziesii*, measured by seed set in this study, confirms that the species is self-incompatible. The deposition of non-self-pollen on the stigma of the

flowers shows a twenty-four fold increase in seed set relative to when self-pollen is applied ($65.7 \pm 4.6\%$ versus $2.7 \pm 1\%$). These results are consistent with the high pollen: ovule ratio, which suggests that *D. menziesii* is a self-incompatible species producing an abundant amount of pollen that increases the probability of cross pollination (Cruden, 1977). Pollination under natural conditions (control treatment), produced slightly fewer filled seeds (49.7 %) than the outcrossing treatment. A possible explanation for this is the prevalence of extreme winds caused by a pressure gradient created by a nearby hurricane which occurred for several consecutive days immediately after the pollination treatment (i.e., during the time when florets on the marked “control” capitula were continuing to open). This extreme weather could have limited pollinator activity when some of the later female florets were receptive.

The breeding system of *D. menziesii* supports the idea of the Hawaiian Madiinae as an exception to Baker’s rule (Baker, 1955; Carr et al., 1986). The family Asteraceae is known for characteristics favoring long-distance dispersal (Nielsen et al., 2003; Roebler et al., 2024), which could facilitate the arrival on a remote island, but establishment could pose a major challenge (Carlquist, 1966; König et al., 2021). In fact, it is expected that self-incompatible species have less than half of the probability to occur on islands compared to self-compatible species, including within the Asteraceae (Grossenbacher et al., 2017). Still, the presence of self-incompatible species on oceanic islands is an exception to this expectation, and makes further studies necessary to understand the establishment of these species and their reproductive systems (Carr et al., 1986; Nielsen et al., 2003; Crawford et al., 2008, 2023; Grossenbacher et al., 2017). The colonization and establishment of the ancestor that originated the Hawaiian silversword alliance 5.1 million years ago remains obscure, and multiple scenarios have been proposed (Carr et al., 1986; Landis et al., 2018). The ancestral continental group in this clade is primarily self-incompatible (Baldwin et al., 1991; Barrier et al., 1999), making the establishment after long-distance dispersal a challenge. One hypothesis proposed to explain colonization of the Hawaiian Islands was the presence of pseudo-self-compatibility, in which a self-incompatible species is capable of producing at least some seeds by self-fertilization (Carr et al., 1986; Levin, 1996). In this study, the self-pollination treatment produced a small number of seeds (2.7 %), similar to other species from the alliance under field conditions (Carr et al., 1986), including *Dubautia linearis* (Aslan et al., 2019). This could support the idea of pseudo-self-compatibility facilitating the establishment in the Hawaiian Islands (Baker, 1955, 1967). The family Asteraceae on other oceanic islands includes similar cases of pseudo-self-compatibility, such as the genus *Tolpis* in the Canary Islands (Crawford et al., 2008) or the genus *Scalesia* in the Galápagos Islands (Nielsen et al., 2003). However, the possibility of contamination during hand pollination or the possible presence of small insects carrying external pollen and entering into the bags should be considered. Other hypotheses, such as the arrival of multiple self-incompatible propagules during island colonization should not be ruled out (Baldwin and Wagner, 2010).

Flowers of *D. menziesii* were visited by 16 insect taxa from multiple orders, suggesting a generalized pollination system, as commonly found in the Asteraceae (Crawford et al., 2008; Philipp et al., 2004). Given the structure of the florets - in which pollen and the stigmatic surface are exposed at the tips of the small flowers, we predict that all observed visitors are capable of transporting and transferring pollen grains, and thus were treated as potential pollinators, regardless of efficiency (but see King et al., 2013). The most frequent visitors for *D. menziesii* were the native yellow-faced *Hylaeus* bees (44 % of the visits), several species of which occur on Haleakalā (Daly and Magnacca, 2003; Krushelnicky et al., 2007; Wilson et al., 2010). Some of these, such as *H. volcanicus* and *H. nivicola*, have previously been recorded as flower visitors for *D. menziesii* (Daly and Magnacca, 2003). In addition, the foraging of these native bees on *D. menziesii* has been confirmed by DNA identification of pollen grains recovered from *H. difficilis* (Wilson et al., 2010).

The *Hylaeus* bees also visit many other plants at Haleakalā, including the threatened species *Argyroxiphium sandwicense* (Daly and Magnacca, 2003). In fact, a study conducted by Krushelnicky (2014) found that more than 80 % of the total visits to *A. sandwicense* were from *Hylaeus* bees, and therefore it is likely that the silversword depends on these bees for its reproduction. Since *D. menziesii* and *A. sandwicense* share *Hylaeus* bees as flower visitors, the abundance of *D. menziesii*, with an average of 1.98 flowering individuals per 100 m² (compared to 0.02 flowering individuals of silversword), together with its consistent annual flowering, may provide resources to sustain *Hylaeus* populations and indirectly benefit *A. sandwicense* (a monocarpic species in which flowering frequency varies strongly from year to year) and other species at Haleakalā. This highlights the importance of common plant species in sustaining ecosystems (Gaston, 2010; Jansen et al., 2020). A similar example includes the common plants *Jacquemontia sandwicense* and *Sida fallax*, which provide resources to the endangered bee *H. anthracinus* in Hawaiian coastal habitat (Shay and Drake, 2018). The present study supports *Hylaeus* bees as an important pollinator for native plants, in this case at high-elevations, similar to findings of other studies in other Hawaiian ecosystems (Koch and Sahli, 2013; Sahli et al., 2016; Shay and Drake, 2018; Aslan et al., 2019). On Haleakalā, one of the major threats to *Hylaeus* bees is the presence of invasive species such as Argentine ants (*Linepithema humile*; Cole et al., 1992; Krushelnicky et al., 2011; Krushelnicky, 2014; Sahli et al., 2016). These ants have been established in some parts of the high elevation shrubland of Haleakalā for more than 25 years, resulting in the sometimes dramatic reduction of *Hylaeus* bee abundances and likely decreasing their pollination activity where their distributions overlap (Cole et al., 1992; Krushelnicky, 2014; Sahli et al., 2016). Given the important role of *Hylaeus* bees as pollinators, their conservation is urgently needed (Magnacca, 2007).

The second dominant flower visitor for *D. menziesii* was the non-native honeybee (*A. mellifera*), which accounted for 34 % of the visits. The impact of honeybees on native insect populations and the reproduction of native plants has been the focus of attention for many years. In some cases, their presence can lead to the decrease of native pollinator populations and reduction in fitness for native plants (Roubik, 1978; Sugden and Pyke, 1991; Gross and MacKay, 1998; Gross, 2001; Dupont et al., 2004; Schaffer et al., 2016; Valido et al., 2019). On the other hand, introduced species also have the potential to form mutualistic interactions with native species and can contribute to key functions, such as pollination (Rodríguez, 2006; Hanna et al., 2013; Miller et al., 2015; Shay et al., 2016; Aslan et al., 2019). In Hawai’i, Miller et al. (2015) found that *Hylaeus* bees have higher pollination fidelity than honeybees, despite carrying much less pollen. In our observations, we found a similar pattern of visitation rates to *D. menziesii* for both species, with both species being attracted to flowering plants showing larger displays. This indicates that native and exotic bees are sharing some of the same resources in the ecosystem. Pollination efficiency and ability to transfer pollen depend on several factors such as pollinator morphological features (i.e., bee size, hairiness) and foraging behavior (Daly and Magnacca, 2003; Greenleaf et al., 2007; Miller et al., 2015; Aslan et al., 2019), and the effectiveness of honeybees and native bees as pollinators was not assessed in this study. Further research is therefore needed to understand how the impact of honeybees affects *D. menziesii* reproductive success and native bee populations.

Nysius spp. seedbugs were the third most common insect group found on flowers during the surveys. *Nysius* seedbugs are mostly sedentary insects that remained in the same position on the reproductive parts of *D. menziesii* during the 10-min observations. Insect behavior can be an important factor in pollination efficiency and the reproductive output of a plant (Rossi et al., 2014). Sedentary insects spend much time at a single plant individual, touching the reproductive parts and walking among neighboring flowers in the same capitulum or flowering branch, and therefore increase the chances of carrying self-pollen and transferring it to the stigma of a flower on the same individual. This behavior promotes self-fertilization, which leads to a reduction in seed set (Rossi et al.,

2014), and suggests that these insects are likely poor pollinators for *D. menziesii*. Although the rest of the flower visitors account for a small percent of the visits, these additional 13 taxa included native and endemic insects, such as the *Trupanea* flies, of which *D. menziesii*, apart from providing floral resources, can represent a host plant for larval stages. This study shows how *D. menziesii* represents an important resource for arthropod diversity at Haleakalā and highlights the importance of the plant to the ecosystem.

Isolation, at the scale of tens of meters, does not significantly affect seed production for *D. menziesii*. There was a weak negative trend between seed production and distance to the nearest neighbor, although the most isolated individual (almost 90 m from the nearest flowering individual) produced 74 % filled achenes. These results differ greatly from those of the silversword, in which isolation had a strong significant impact on the proportion of filled achenes, and explained 73 % of the variation in seed set (Krushelnicky, 2014). These differences could be related to the foraging behavior of the flower visitors for each plant. Some studies suggest that body size in bees is correlated with their foraging range (Greenleaf et al., 2007). Honeybees have longer flight distances, of up to 10 km, and are larger than *Hylaeus*, the latter are known for their small to medium size, with forewing length ranging from 3 to 8 mm (Daly and Magnacca, 2003; Greenleaf et al., 2007). This could explain the impact of isolation on seed set for *A. sandwicense*, which was visited mainly by *Hylaeus* bees, in which seed set was severely reduced when plants were more than 15 m apart (Krushelnicky, 2014). Isolation in *A. sandwicense* also had an effect on predation rate by *Trupanea* flies, increasing when plants were aggregated, although other factors, such as the presence of another species of predator, influenced the degree of depredation by *Trupanea* (Krushelnicky, 2014). In contrast, there was no correlation between isolation and predation rate for *D. menziesii* in the present study.

The average *D. menziesii* shrub in our study area produced 8307.3 filled achenes in 2023. This falls within the range of the related Haleakalā silversword, which produces from 3000 to 45,000 achenes, of which an average of 42 % suffers seed predation (Forsyth, 2002; Krushelnicky, 2014). Predation does not have an important impact on seed set in *D. menziesii*, as indicated by the low percentage of achenes damaged per plant (less than 5 %), assuming 2023 was a typical year. The bagging treatment could have had some impact on predation rates, though it is unclear why no damaged seeds were found in the unbagged control treatment. However, studies in previous years have shown an impact of seed predators on *D. menziesii* seeds of up to 20 % (D. Drake, unpublished data). These differences could be caused by insect populations varying yearly depending on environmental factors. The rate of depredation for *D. menziesii* differs greatly from that of *A. sandwicense*, which can have up to 60 % of its achenes parasitized (Krushelnicky, 2014). However, most of this damage was due to caterpillars from the genus *Rhynchephestia*, which were not found on *D. menziesii*. *Trupanea* flies, the other predator for *A. sandwicense*, accounted for a smaller portion of silversword achene damage, with 5.8 % of achenes depredated per individual. Only the endemic species of *Trupanea* flies were found to depredate the seeds of *D. menziesii*.

Although *D. menziesii* is not listed as an endangered species, threats such as climate change may pose a risk to its populations, as it already does for the silversword (Krushelnicky et al., 2013, 2016, 2020), and even common species in high elevation ecosystems on oceanic islands (Ainsworth and Drake, 2020, 2023a, 2023b; Cubas et al., 2022). High mountain climates are expected to change (Buytaert et al., 2011; Krushelnicky et al., 2020; Fortini et al., 2022), and understanding the biology of species that comprise these ecosystems, especially common species, is fundamental for their conservation and restoration (Gaston and Fuller, 2008; Gaston, 2010; Fortini and Dye, 2017; Ainsworth and Drake, 2020, 2023a, 2023b; Cubas et al., 2022). *Dubautia menziesii* is one of the most abundant plants at high elevations on Haleakalā. It provides a considerable amount of flower resources, and thus may be important for sustaining arthropod populations, especially keystone species such as

Hylaeus bees. A decline of *D. menziesii* might have serious negative impacts for the alpine and subalpine ecosystems of Haleakalā, by reducing arthropod density and diversity and possibly initiating cascading effects, for example, for the threatened *A. sandwicense*. Insufficient knowledge of plant breeding systems, pollination interactions, and ecology limit our ability to protect the future of island plants (Fernández-Palacios et al., 2021; Crawford et al., 2023), and the integration of ecological and evolutionary research is needed for the conservation and restoration of Hawaiian plant communities (Barton et al., 2021). By understanding the reproduction and ecology of *D. menziesii*, the protection, restoration and conservation of the Haleakalā ecosystem can be enhanced.

5. Conclusions

Dubautia menziesii, an endemic shrub from Haleakalā (Maui), is self-incompatible and therefore requires pollen from a different individual to set seed. This is consistent with the self-incompatibility demonstrated for other species from the Hawaiian silversword alliance and poses an exception to Baker's rule. Flowers from *D. menziesii* attracted a wide variety of insects in the alpine ecosystem. The most common flower visitors were the native *Hylaeus* bees, followed by the introduced *Apis mellifera*. Seed bugs (*Nysius* spp.) were also common on flowers but were mainly sedentary and were not likely to be moving pollen between plants frequently. The impact of the honeybee on the Hawaiian ecosystem is still unclear, as it may compete with native species. However, for *D. menziesii*, it could promote outcrossing and replace lost ecological function if native insects decline or disappear. Spatial isolation within the population does not have a significant effect on seed set and seed predation, in contrast to *Argyroxiphium sandwicense*. The high abundance of *D. menziesii* in the barren alpine ecosystem of Haleakalā and its interactions suggest that its presence is critical for the continued functioning of the ecosystem. *Dubautia menziesii* provides floral resources supporting the pollinator community on which other plants depend, including the threatened *A. sandwicense*.

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CRediT authorship contribution statement

Juan Francisco Guisado Chavez: Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Paul Krushelnicky:** Writing – review & editing, Formal analysis, Conceptualization. **Kasey E. Barton:** Writing – review & editing, Conceptualization. **Donald R. Drake:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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