Pollination biology of the Hawaiian coastal vine *Jacquemontia sandwicensis* (Convolvulaceae)

By Kimberly R. Shay* and Donald R. Drake

Abstract

As human impacts on island ecosystems increase, so does the importance of understanding the life histories of island plants for conservation. Yet, surprisingly little is known about the reproductive ecology of many common island plant species. We experimentally investigated the breeding system and observed pollinators of the endemic Hawaiian vine *Jacquemontia sandwicensis* (Convolvulaceae), a common species in the coastal strand habitat. To evaluate the breeding system, experiments involving natural and hand pollination treatments were performed in the field and with cultivated plants. To identify natural pollinators, flower-visiting insects were observed in three sites on the southeast coast of Oʻahu. *Jacquemontia sandwicensis* is a self-compatible, hermaphroditic species with a flexible, mixed mating system. High levels of fruit set, seed set, and germinating seeds seem to depend on pollen being deposited on the stigma by an active pollinator rather than a passive vector (wind or autogamy). However, this species still produced some fruit and seeds even in the absence of manipulation, suggesting a limited degree of reproductive assurance when pollinators are absent or in low abundances. At the observed sites, this species was visited by a variety of mostly non-native Hymenoptera (especially *Apis mellifera* and *Lasioglossum* spp.). The endangered native bee *Hylaeus anthracinus* also visited flowers, but at a much lower rate than the non-native insects. Non-native insects appear to be effective pollinators for *J. sandwicensis*, and now play an important role as native pollinators decline.

*Corresponding Author E-mail: kimlesnock@gmail.com

Introduction

Island plants are threatened by multiple phenomena: the fragmentation and loss of habitat, the decline and extinction of mutualists, and the invasion of non-native species (Whittaker and Fernández-Palacios 2007, Kaiser-Bunbury et al. 2010, Traveset et al. 2013). As these impacts on island systems intensify, so does the importance of understanding life histories of native species for conservation (Anderson et al. 2001, Caujapé-Castells et al. 2010). For example, Weller et al. (2017) recently demonstrated the importance of a newly-described endemic moth for pollination of the endangered plant *Schiedea kaalae* (Caryophyllaceae) in Hawai'i. Unfortunately, such basic ecological information exists for very few island species, either common or rare (Anderson et al. 2001, Caujapé-Castells et al. 2010, Kueffer et al. 2014).

The reproductive features of island plants, including breeding systems and pollinator interactions, are the result of two processes: filters that affect the likelihood of island colonization, and subsequent evolution in disharmonic and depauperate island communities (Carlquist 1974, Whittaker and Fernández-Palacios 2007, Kaiser-Bunbury et al. 2010, Watanabe and Sugawara 2015). As a result, the flower biology of island floras often differs from that of continental floras. For example, many island floras have relatively high proportions of plants that are dioecious or self-compatible (Carlquist 1974, Sakai et al. 1995, Anderson et al. 2001, Schlessman et al., 2014), and have relatively generalized pollinator interactions (Sakai et al. 1995, Abe 2006, Kaiser-Bunbury et al. 2010, Traveset et al. 2016). Some island plants are even considered supergeneralists, having wide pollination niches and interacting with a disproportionately large fraction of the pollinator community, such as *Azorina vidalii* (Campanulaceae) in a pollination network from Ile aux Aigrettes, Mauritius (Olesen et al. 2002).

Little is known about the breeding systems of the great majority of native Hawaiian plants, beyond what can be inferred from floral morphology (Sakai et al. 1995, Price and Wagner

2004). As with certain other isolated island systems, such as New Zealand and New Caledonia (Schlessman et al. 2014), Hawaiʻi has a higher proportion of dioecious species (ca. 15%; Sakai et al. 1995) than is found on continents (typically 4–6%; Renner and Ricklefs 1995). Some Hawaiian species have shifted their breeding system and pollination biology during the process of colonizing and adapting to new habitats (Sakai et al. 2006). Many Hawaiian species are adapted for pollination by birds, whereas much of the remaining flora has small, white or green flowers, which are associated with unspecialized pollinators or wind (Sakai et al. 1995, Price and Wagner 2004). The few coastal species that have been examined are hermaphroditic (Wagner et al. 1999, Yorkston and Daehler 2006), self-compatible (Hopper 2002, Pleasants and Wendel 2010), and appear to interact with a wide range of flower-visiting insects (Hopper 2002, Elmore 2008, Shay et al. 2016).

Pollinator communities on islands are naturally depauperate and disharmonic compared to those of continental ecosystems (Carlquist 1974, Abe 2006, Traveset et al. 2016, Hiraiwa and Ushimaru 2017). The Hawaiian Islands are renowned for their endemic, nectar-feeding birds (Carlquist 1974), but the role of native insects as pollinators is less well known. In Hawaiʻi, native insect pollinators may include roughly 1,000 moth species (Ziegler 2002), nearly 100 *Nesodynerus* potter wasps (Carpenter 2008), 63 species of *Hylaeus* yellow-faced bees (Magnacca 2007), yet only two species of butterflies (Zimmerman 1958), among others. *Hylaeus* spp., Hawaiʻi's only native bees, have radiated from one colonizing species (Magnacca 2007). They have been observed visiting flowers of many native plant species in habitats across the islands (Wilson et al. 2010, Koch and Sahli 2013, Krushelnycky 2014). *Hylaeus* spp. are sometimes among the most frequent flower visitors for native coastal plants, including *Jacquemontia sandwicensis* (Hopper 2002, Shay et al. 2016). *Hylaeus* and other lowland insects have been impacted by negative interactions with non-native insects (Howarth 1985, Cole et al. 1992),

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novel predators (e.g., Kraus et al. 2012), and habitat destruction (Asquith and Messing 1993). Consequently, insects such as *Hylaeus* are declining in abundance and becoming rare and endangered (Magnacca and King 2013). In 2016, the coastal species *H. anthracinus* was classified as federally endangered. Its decline may have consequences for native plants, because the loss of just one species in a plant-pollinator relationship may reduce the fitness of its partner (Kiers et al. 2010).

Invasive, non-native insects are increasingly ubiquitous and ecologically significant in ecosystems around the world (Cameron et al. 2016). Over 2,500 species of non-native insects have established in Hawai'i (Pimental et al. 2005), and non-native flower visitors range from likely pollinators to nectar thieves (Hopper 2002, Elmore 2008, Pleasants and Wendel 2010, Junker et al. 2011, Shay et al. 2016). Non-native insects may increase or decrease the pollination activities of other insects in a community (Ings et al. 2005, Bartomeus et al. 2008), and in Hawai'i, non-native flower visitors visit many native plant species and may compete with native flower visitors for native plant floral resources (Kuppler et al. 2017).

Jacquemontia sandwicensis (pā'ū'ohi'iaka, Convolvulaceae), is an endemic, creeping, perennial vine found on all Hawaiian Islands (Robertson 1974, Namoff et al. 2010). It was formerly classified as *J. ovalifolia* subsp. *sandwicensis*, but molecular and morphological data supported the Hawaiian plants as being a distinct species (Namoff et al 2010). It is a consistent and sometimes dominant component that defines the coastal vegetation, where it is often mixed with other low-growing species, especially *Sida fallax* (Richmond and Mueller-Dombois 1972, Gagné and Cuddihy 1990). Despite its ecological importance, little is known about its ecology or reproductive biology. *Jacquemontia sandwicensis* produces hermaphroditic flowers (Carlquist 1966, Wagner et al. 1999, Sakai et al. 1995), but no one has tested its breeding system experimentally and its pollinators have not been thoroughly documented (but see Shay et al.

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2016). In the pollination network at Kaʻena Point, a site with the most intact, native-dominated, coastal strand vegetation on Oʻahu, *J. sandwicensis* was an important generalist species in terms of plant-pollinator interactions, interacting with native *Hylaeus* spp. and 10 non-native taxa (Shay et al. 2016). In one of two years, it was visited by more insect species than any other plant species in the network; it received 4.6% of the community's pollinator visits, and 8.3% of its visits involved *Hylaeus* (Shay et al. 2016).

The objectives of this study were to: 1) investigate the breeding system of *J. sandwicensis* to determine its reliance on pollinators for reproduction, and 2) investigate variation in the floral visitors and their effects on reproduction of *J. sandwicensis* in several communities of mixed native and alien species on Oʻahu. We predicted that *J. sandwicensis* would have a mixed mating system, reproducing by both selfing and outcrossing (Goodwillie et al. 2005), similar to *J. reclinata*, a related coastal species in Florida (Pinto-Torres and Koptur 2009). We expected that Hymenoptera (bee and wasp) species, including native *Hylaeus*, if present, would be common floral visitors to *J. sandwicensis* (Shay et al. 2016), and would be effective pollinators.

MATERIALS AND METHODS

Study Sites

This study involved plants from four field sites along 3.5 km of coastline on southeast Oʻahu: near Halona Blowhole (21°16'50" N, 157°40'44" W; 23.8 m elevation), Ka Iwi Scenic Shoreline (21°17'50" N, 157°39'20" W; 3 m elevation), a cliff near the Makapuʻu Lighthouse Trail (21°17'59" N, 157°39'06" W, 66 m elevation) and Wawamalu Beach Park (21°17'13.98"N, 157°40'08.23"W; 2 m elevation). These low elevation, low rainfall (670 mm/yr; Giambelluca et al. 2013) sites experience harsh environmental conditions such as intense solar radiation, high temperature and salt spray, and support dry, coastal plant communities with a mix of native and

non-native species (Richmond and Mueller-Dombois 1972, Gagné and Cuddihy 1990, Alpha et al. 1996).

Floral Description

The inflorescence of *J. sandwicensis* has from one to a few flowers in an axillary cyme (Wagner et al. 1999). The corolla is sympetalous and broadly campanulate, ca. 13.8 mm wide x 13.1 mm deep (Shay 2014), and flowers typically have two long stamens and three short stamens (Figure 1). The long stamens are of similar length to the style. The flowers range in color from white to pale blue. The fruit is a capsule (Wagner et al. 1999).

Pollen-ovule Ratio

Pollen-ovule ratio is often suggestive of a plant's breeding system: the greater the number of pollen grains/ovule, the more likely it is that the species depends on outcrossing for seed set (Cruden 2000). Pollen counts were done by using a gridded hemocytometer and dissecting microscope to count pollen grains from single, randomly-selected anthers, from one random flower, from each of seven individuals (Kearns and Inouye 1993). We did not distinguish between short and long stamens because anther size did not differ between them, and pollen size was not measured. The number of ovules per flower is consistently four in this genus (Wagner et al. 1999).

Breeding Experiments

Cuttings of *Jacquemontia sandwicensis* were collected at the four study sites in southeast Oʻahu (20 to 25 individuals per site) in May 2013 for a lab breeding experiment. The cuttings were trimmed to between 10 cm and 15 cm with 3 to 5 nodes, and leaves below the 3rd or 4th node from the apex were removed to reduce water loss from transpiration. The cuttings were planted in 15.2 cm diameter x 12.7 cm height pots with a mix of 3 parts perlite to 1 part vermiculite, and kept well-watered. After 16 weeks, when the surviving plants had reached approximately 1 to 1.5

m in length, they began branching and regularly flowering. They were then transplanted into 25.4 cm diameter x 25.4 cm height pots with a mix of 4 parts commercial potting soil to 3 parts perlite to 1 part vermiculite and a slow-release fertilizer. The plants were grown outdoors in full sunlight, on the roof of a six-story building, where they were allowed to mature and flower. Plants were grown in a common setting to facilitate daily cross-pollination experiments among plants from four separate populations, and to minimize between-site environmental effects on fruit and seed set. The pollination treatments for the breeding experiments were conducted from 1 January to 11 February, 2014.

A total of 51 plants received each of the following treatments in the lab breeding experiment: control (C), autogamy (A), selfing (S), within-population cross (W), and between-population cross (B) (Dafni et al. 2005, Pinto-Torres and Koptur 2009). The order of application of treatments was randomized for each plant. The C flowers were not bagged and sexual structures received no manipulation; this tested for reproduction in flowers that were exposed to insect flower visitors (in practice, insects were unexpectedly not observed on this rooftop site). The A flowers were bagged and the sexual structures received no manipulation. This tested for within-flower, self-pollination in the absence of pollinators (autonomous autogamy). In the S treatment, the flower was bagged and received pollen from another flower on the same plant, testing for self-compatibility in the absence of pollen limitation (facilitated autogamy). In the W and B treatments the flower was pollinated with pollen either from a different, haphazardly-chosen individual from within the same site (W) or from another site (B); this assessed effects of possible inbreeding (within a population) vs. outcrossing (between populations), and maximum potential seed set among populations (Dafni et al. 2005, Schoen and Lloyd 1992, Pinto-Torres and Koptur 2009).

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All treatments except C used a bag made of organza fabric to isolate the bud and flower from pollinators and pollen sources (Dafni et al. 2005). We used twist ties to ensure bags were tightly closed and inaccessible to ants. Because it is difficult to isolate individual flowers in a bag, other flowers and buds in the same inflorescence as the treated flower were removed. Pollination was effected by using forceps to apply an open anther to a stigma (Dafni et al. 2005). After treatment, flowers were bagged again, to exclude other possible pollen donors. Because flowers of *J. sandwicensis* last only one day, bags were removed the day following the treatment to avoid any effects of the bag on fruit development. Treated flowers were checked every other day. The developing fruits were collected when ripe and easily detached. All fruits were collected by 14 March, 2014.

The breeding experiment was also performed in the field on 31 haphazardly-chosen plants at Makapuʻu in May 2013; they received four treatments: C, A, S (like S in the lab experiment, except the flower was hand pollinated with its own anthers, rather than anthers from another flower on the same plant), and W. The W treatment involved crosses with haphazardly-chosen pollen donors that were approximately 5 m from the recipient, to reduce the likelihood of selfing between different ramets of a clone. Cross-pollination between populations was not logistically practical. The order of application of treatments was randomized for each plant. Fruits were collected by 2 June, 2013.

The C treatment was also performed in the field at three sites (Ka Iwi, Makapuʻu, and Halona) on June 14, 2013, testing for natural rates of fruit and seed set. At each site, individuals and flowers were selected at random points. One flower on each of 40 plants from every site was tagged and left open to pollinators. Fruits were checked every other day for 25 days. They were collected when they were ripe and about to detach from the individual, and all remaining fruits were collected on the 25th day.

For all studies, collected fruits were stored at 20º C in wax paper envelopes in a dry environment (Pinto-Torres and Koptur 2009). Fruit and seed set were recorded for each treatment in all experiments. There was no evidence of fruit removal by animals. Fruit from the field breeding experiment at Makapuʻu was collected too early to test for seed germination, but developing seeds were counted. For germination tests, seeds were carefully removed from the fruit capsule and scarified by nicking the seed coat with a razor blade (Baskin and Baskin 1998). Seeds were placed on a wet paper towel in a petri dish and placed under continuous fluorescent light (irradiance = 85-120 μmol m^{-2} sec^{-1}) at 20º C. Every other day seeds were moistened and dishes rearranged to avoid positional effects. After 2 weeks, seeds with an emerged radicle or cotyledon(s) were counted as germinated (Pinto-Torres and Koptur 2009).

Pollinator Observations

We observed flower visitors to *Jacquemontia sandwicensis* in May and June of 2013 at three of the four study sites (Halona, Ka Iwi, and Makapuʻu) for a total of 30 hours of observations. Ten individuals were observed per day of observations. The individuals were chosen haphazardly and observed for 15 minutes each during non-rainy weather. All sites and time of day (8 a.m. – 5 p.m.) were sampled equally.

When a flower visitor made contact with a flower, we recorded the species of flower visitor, the number of flowers visited by the flower visitor, the duration of the visit per flower, if the reproductive structures (stigma and/or anthers) of the flower were touched by the visitor, and if the visitor foraged for nectar, pollen, or both. We also recorded the total number of flowers under observation. Flower visitors were not examined for pollen quantity or identity. When field identification of flower visitors was not possible, specimens were collected. These were later identified by Paul Krushelnycky (University of Hawaiʻi), Sheldon Plentovich (US Fish & Wildlife Service), and Karl Magnacca (University of Hawaiʻi) (pers comm). Each visitor

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approaching the observed flowers on an individual was considered a new individual and a separate visit. The frequency of visits (FV) were calculated as:

$$FV = \sum (V / O) / T$$

The number of flowers visited by an insect (V) is divided by the number of flowers observed during an observation period (O), which is divided by the total number of hours of observations (T). T was 10 hours for each site (30 hr total). The FV rate is a sum by flower visitor: the proportion of flowers visited by flower visitors per hour (Castro-Urgal et al. 2012).

Flower abundance counts were performed at Ka Iwi and Makapuʻu on 24 May, 2013 and Halona on 27 May, 2013 to help interpret floral community resource abundance for flower visitors. Thirty plots (2 m x 2 m) were placed every 2 m on alternating sides of a transect through *Jacquemontia* habitat, each plot a random distance of 0 to 5 m off of the transect, and the numbers of open flowers of all species were counted and recorded in each plot.

Statistics

In our study, fruits per flower (0 or 1), seeds per flower, and germinated seeds per flower were measures of reproductive success. Seeds germinated per flower were not tested for the field breeding experiment because fruits were collected before seeds were fully mature. Because data from the breeding system experiment in the lab were not normally distributed, treatments were compared using Friedman's test, controlling for plant individual, followed by Tukey's test for pairwise comparisons among treatments. Data from the breeding system experiment in the field were normally distributed, so treatments were compared using a one way repeated measures ANOVA. Data for fruits/flower and seeds/flower for C flowers at three field sites were not normally distributed, so sites were compared using a Kruskal-Wallis test, followed by Dunn's test for pairwise comparisons among sites. All tests were significant if $p < 0.05$. Standard error of the means are reported.

RESULTS

Pollen-ovule Ratio

Mean pollen grains per anther was 489.6±38.2 (n = 7). The pollen-ovule ratio was 612 : 1.

Lab Breeding Experiments

In the lab, hand pollinated flowers (S, W, and B) had two to three times the reproductive output of flowers that were not hand pollinated (C and A) regardless of pollen source (Figure 2). There appeared to be no flower visitors in the lab setting, as indicated by the low reproductive output of the C treatment. Controlling for the plant individual, significant differences were found for fruits/flower ($\chi^2_{4, N=255} = 50.2$, $p < 0.001$), seeds/flower ($\chi^2_{4, N=255} = 57.5$, $p < 0.001$), and germinated seeds/flower ($\chi^2_{4, N=255} = 46.4$, $p < 0.001$). Tukey tests revealed that reproductive output in C and A treatments was always significantly lower than in S, W, and B treatments ($p < 0.01$ in all tests).

Field Breeding Experiments

For treatments in the field, fruits/flower and seeds/flower in all treatments were only slightly lower than for hand-pollinated treatments in the lab experiment (Figure 3). However, unlike in the lab, there was no significant difference among pollination treatments for fruits/flower ($F = 2.08$, $p = 0.11$) or seeds/flower ($F = 1.12$, $p = 0.33$) in the field.

The range of fruit set and seed set for unmanipulated flowers (C treatment) at three field sites (Figure 4) overlapped with the C treatment in the field breeding experiment but not the C treatment in the lab experiment. There were slight differences in fruits/flower among sites ($H = 11.2$, $p < 0.005$), but no significant difference in seeds/flower among sites ($H = 3.81$, $p = 0.15$).

Pollinator Observations

Jacquemontia sandwicensis flowers started to open around 7 a.m. and began to close in early-to-late afternoon, with most closed by 5 p.m. (pers obs). Open flowers of *Jacquemontia*

sandwicensis were present at densities of 2.3/m^2 at Makapu'u, 2.1/m^2 at Ka Iwi, and 0.5/ m^2 and

Halona. Overall visitation rates from insects that touched reproductive structures (and were

considered potential pollinators) were 0.6 visits/flwr/hr at Makapu'u, 1.0 visits/flwr/hr at Ka Iwi,

and 0.9 visits/flwr/hr at Halona (Table 1). Across the three sites, we observed five insect genera

(four bee and one wasp) visiting flowers throughout the day (approximately 8 a.m. through 4

p.m.) and frequently contacting reproductive structures (Table 2). Non-native bees, *Apis*

mellifera and *Lasioglossum* spp., provided most of the visits (37.8% and 45.6% respectively).

Three species of *Lasioglossum* were present in and near the sites: *L. imbrex, L. microlepoides,*

and *L. impavidum* (Magnacca, pers comm). *Lasioglossum* species could not be distinguished in

the field, and are here referred to as *Lasioglossum* spp. Other non-native visitors included

Tachysphex sp., which is the only wasp observed, and *Ceratina smaragdula.* The native bee

Hylaeus anthracinus, was present at Ka Iwi and Makapu'u, and provided 4.2% of the total visits.

Males of *Hylaeus* species can be identified by their distinctive facial markings, but females are

indistinguishable in the field, and were assumed to be *H. anthracinus*. Unidentified ants also

visited *J. sandwicensis* 28 times, but were removed from further analysis. While some studies

indicate that they have a complex role in plant-pollinator interactions by impacting plant floral

resources (Bleil et al. 2011, Junker et al. 2011) and flower visitors behavior and habitat (Lach

2008, Krushelnycky and Gillepsie 2008), their behavior on *J. sandwicensis* indicated they were

unlikely pollinators, mostly collecting nectar and rarely contacting the reproductive structures.

Sites varied in pollinator assemblages and in flower visitation rates (Table 1). The least

diverse pollinator community was at Halona, where only two taxa, *Lasioglossum* spp. and

Ceratina smaragdula, visited flowers, and *Lasioglossum* spp. provided 81.1% of the visits. At

Makapu'u, four species were present, but *A. mellifera* provided 72.2% of the visits. Ka Iwi had

the most diverse assemblage of pollinators with five species present and *A. mellifera* providing

the most visits, 51.3%. The only native pollinator observed, *Hylaeus,* provided 11.5% of visits at Makapu'u and 3.9% of the visits at Ka Iwi.

All bee and wasp flower visitors observed were considered potential pollinators because they consistently contacted reproductive structures during our observations (67% of visits; Table 2). *Lasioglossum* spp., *H. anthracinus,* and *C. smaragdula* collected pollen and nectar, whereas *A. mellifera* and *Tachysphex* sp. collected only nectar. *Lasioglossum* spp. often crawled over anthers and contacted the stigma, and were covered with pollen in the process. They searched the base of the flower, presumably for nectar, and groomed in *J. sandwicensis* flowers. *Apis mellifera* foraged at the base of the flower (for nectar presumably) and accidentally contacted anthers and/or the stigma. *Ceratina smaragdula* spent more time on a flower (mean 39.2 s / 15 minute observation period ± 12.9) than did *A. mellifera* (mean 3.2 s / 15 minute observation period ± 0.7).

DISCUSSION

Breeding System

Reproductive output of hand-pollinated *Jacquemontia sandwicensis* flowers, as measured by fruit set, seed set, and seed germination, was similar regardless of pollen source: self, within population, or between populations. This suggests that *J. sandwicensis* has a mixed mating system, is self-compatible, and is unlikely to suffer severely from inbreeding, at least up through the seed germination stage (Dafni et al. 2005, Lloyd and Schoen 1992). Cruden (2000) found an average pollen-ovule ratio of 796.6 +/- 87.7 (SEM) for facultatively xenogamous plants and 168.5 +/- 22.1 facultatively autogamous plants. *Jacquemontia sandwicensis* had a ratio of 612:1, which is consistent with a mixed mating system (facultative xenogamy). Mixed mating systems are prevalent in animal-pollinated plants, and are considered the "best of both worlds"

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because they allow reproduction through both selfing and outcrossing (Lloyd 1992, Goodwillie et al. 2005).

The lab experiment and the field experiment had contrasting results for the C and A treatments. We believe the C treatment differed because pollinators were common in the field and rare or absent in the rooftop lab setting. The A treatment in the lab suggests that although autonomous autogamy (self-pollination in the absence of flower visitors) is possible in *J. sandwicensis*, it is not as effective as having pollen deposited on the stigma by a pollinator (Figure 2). However, tests for autogamy in the field did not show significantly reduced fruit and seed set in the absence of pollinators; this reason for this difference is unclear, but may be a result of the strong winds on the coastal cliffs shaking the bagged flowers without allowing pollen to blow away, thus resulting in within-flower pollination. Rooftop plants were in the lee of a wall and experienced less wind. It is also possible some pollen is moved by wind under natural conditions.

The breeding system of *J. sandwicensis* contrasts with that of at least some congeners. In pollination experiments with *J. reclinata*, an endangered species of coastal dunes in Florida, reproductive success, defined as fruit set per flower, seed set per flower, and seed set per fruit, was greater for outcrossed flowers than for selfed flowers, and generally increased as the degree of outcrossing (distance from pollen donor) increased (Pinto-Torres and Koptur 2009, Maschinski et al. 2013). Nevertheless, *J. reclinata* did produce a few seeds via autogamy. The Brazilian caatinga species *J. bracteosa* likewise produced more seeds from outcrossing than from selfing, and very few seeds from facultative autogamy (Santos and Gimenes 2016). However, another species from Brazilian xeric shrubland, *J. nodiflora,* interestingly had higher rates of fruit set from self-pollination than outcrossing (Kiill and Simao-Bianchini 2011).

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Jacquemontia sandwicensis did not seem to experience pollen limitation at Makapuʻu because there was no difference in fruit set or seed set between unmanipulated control flowers and hand-pollinated flowers. In addition, fruit set and seed set of unmanipulated flowers at the other two field sites were at least as high as at Makapuʻu. This suggests that plants are being adequately pollinated despite the pollinators having changed to a non-native community. Therefore, the reduction in overall reproductive output of field plants relative to lab plants was possibly a result of an environmental factor or resource (e.g., water) limiting production of viable seeds in the field relative to the well-watered and fertilized lab plants.

Flower Visitors

Although the three field sites in southeastern Oʻahu were separated by < 3.5 km, they differed somewhat in pollinator abundance and activity. The most frequent visitors to *J. sandwicensis* were the non-native bees *Lasioglossum* spp., *Apis mellifera*, *Ceratina smaragdula*, the native bee *Hylaeus anthracinus*, and the non-native wasp *Tachysphex* sp. *Jacquemontia sandwicensis* received zero to 11.5% of its visits from *Hylaeus* spp. across the 3 sites. These results are similar to visitation rates from diverse, native, coastal vegetation at the far northwestern tip of Oʻahu, where *Lasioglossum imbrex*, *C. smaragdula*, and *H. anthracinus* were common visitors to *J. sandwicensis* in 2008 and 2009, along with a number of other insect species, and 8.3% of visits to *J. sandwicensis* were from *Hylaeus* spp.(Shay et al. 2016). The honey bee *Apis mellifera* was not recorded at Kaʻena Point in 2009, but has been observed there since (Shay et al. 2016).

Many *Hylaeus* species across Hawaiʻi are declining in abundance (Magnacca and King 2013), and *H. anthracinus* was one of seven species in the genus that were listed as federally endangered in 2016. This species was an uncommon visitor to *J. sandwicensis* at two sites. However, it was a frequent visitor to flowers of another native coastal plant, *Sida fallax,* at the same two sites during the same time period (Shay and Togikawa unpub.). Overall, *Hylaeus* was

the dominant flower visitor to *Sida*, providing 43.4% of visits. Out of 59 *Hylaeus* spp. visits to *Sida*, 94.9 % contacted reproductive structures, 64.4% collected pollen, and 33.9% collected nectar. At Ka Iwi, the dominant flower visitor for *Sida* was *Hylaeus*, providing 79.8% of visits, and at Makapuʻu, they provided 38.8% of visits to *Sida* (Shay and Togikawa unpub.).

Populations of Hawaiian *J. sandwicensis* may be sustained by both its ability to form interactions with diverse pollinators and through autogamy, which should allow some reproduction even when mates or pollinators are scarce (Lloyd and Schoen 1992, Kalisz and Vogler 2003, Goodwillie et al. 2005). The ancestor of *J. sandwicensis* is thought to have colonized Hawaiʻi by seeds drifting in the ocean through the Central American Seaway, before the Isthmus of Panama fully closed around 3 to 4 million years ago (Namoff et al 2010). The known native pollinators, *Hylaeus* spp., are estimated to have colonized Hawaiʻi 500,000–700,000 years ago (Magnacca and Danforth 2006). Prior to the arrival of *Hylaeus, J. sandwicensis* would have required other pollinators or had to rely on autogamy for reproduction by seed. The same conditions exist for the coastal *Gossypium tomentosum* (Pleasants and Wendel 2010), suggesting that at least these two coastal plant species are able to adjust to the changing pollinator assemblage or can rely on their mixed mating systems to survive.

Other species of *Jacquemontia* elsewhere are visited mostly by small to medium sized bees. In Florida, *J. reclinata* was visited by 18 taxa of Hymenoptera (15 taxa of bees) (Pinto-Torres and Koptur 2009). In Brazil, *J. montana, J. nodiflora, J. multiflora,* and *J. bracteosa* are visited by predominantly small to medium sized bees (Silva et al. 2010, Kiill and Simao-Bianchini 2011, Kiill and Ranga 2000, Santos and Gimenes 2016).

Body size in bees correlates with foraging range (Greenleaf et al. 2007), which could affect pollen-mediated gene flow between individuals and populations of *J. sandwicensis*. The observed bees in this study included both small (*Lasioglossum* spp., *Hylaeus* females) and

medium-sized bees (*A. mellifera*). The small bees are predicted to move pollen within a population due to their smaller foraging range of 150–600 m, whereas *A. mellifera* can move 1-10 km, depending on resources in the landscape (Greenleaf et al. 2007). The sites we observed are approximately 3.5 km (Halona to Makapuʻu), 2.9 km (Halona to Ka Iwi), or 586 m (Ka Iwi to Makapuʻu) apart, but the vegetation is semi-continuous through these sites and could allow for bee foraging throughout the region.

Hawaiian *Jacquemontia* and *Sida* are both potentially important resources for *Hylaeus anthracinus*. *Hylaeus* visit and collect nectar and pollen from both of these plants, which are common along the southeast coastline of Oʻahu. *Jacquemontia* occurs consistently through this region, dependably providing resources for *Hylaeus*.

CONCLUSION

Jacquemontia sandwicensis, a common Hawaiian plant in the coastal strand habitat, has a mixed mating system. Maximum fruit set, seed set, and germinating seeds seem to depend on abundant pollen being deposited on the stigma by an insect pollinator, rather than autogamy. However, this species still produces some fruit and viable seeds, even in the absence of flower visitation, suggesting it can reproduce when pollinators are absent or in low abundances. In the field sites observed, this plant was visited by a variety of mostly non-native Hymenoptera (*Apis mellifera* and *Lasioglossum* spp.) and occasionally by one endangered native bee flower visitor, *Hylaeus anthracinus*. Non-native insects appear to be effective pollinators for *J. sandwicensis* and could provide pollination services in the face of absent or declining native pollinators.

ACKNOWLEDGMENTS

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Table 1. Flower visitation rates to *Jacquemontia sandwicensis* for three sites, Halona, Ka Iwi, Makapuʻu, and all 3 sites combined. Rate refers to the flower visitation rate as described in Methods. Percent indicates the percent of visits at a site that were attributed to a given visitor taxon.

Sites	Halona		Ka Iwi		Makapuʻu		All 3 Sites	
Species	Flower visit rate	%	Flower visit rate	%	Flower visit rate	%	Flower visit rate	%
Apis mellifera	0	0	0.53	51.3	0.41	72.2	0.31	37.8
Ceratina smaragdula	0.17	18.9	0.04	3.9	0	0	0.07	8.3
Hylaeus anthracinus	0	0	0.04	3.9	0.07	11.5	0.04	4.2
Lasioglossum spp.	0.72	81.1	0.37	36.1	0.04	7.5	0.38	45.6
Tachysphex sp.	0	0	0.05	4.9	0.05	8.8	0.03	4.0
Sum	0.88	100	1.03	100	0.57	100	0.83	100

Table 2. Flower visitor behavior on *Jacquemontia sandwicensis*. Behaviors recorded included contacting the reproductive structures (stigma and/or anthers), collecting nectar, and collecting pollen.

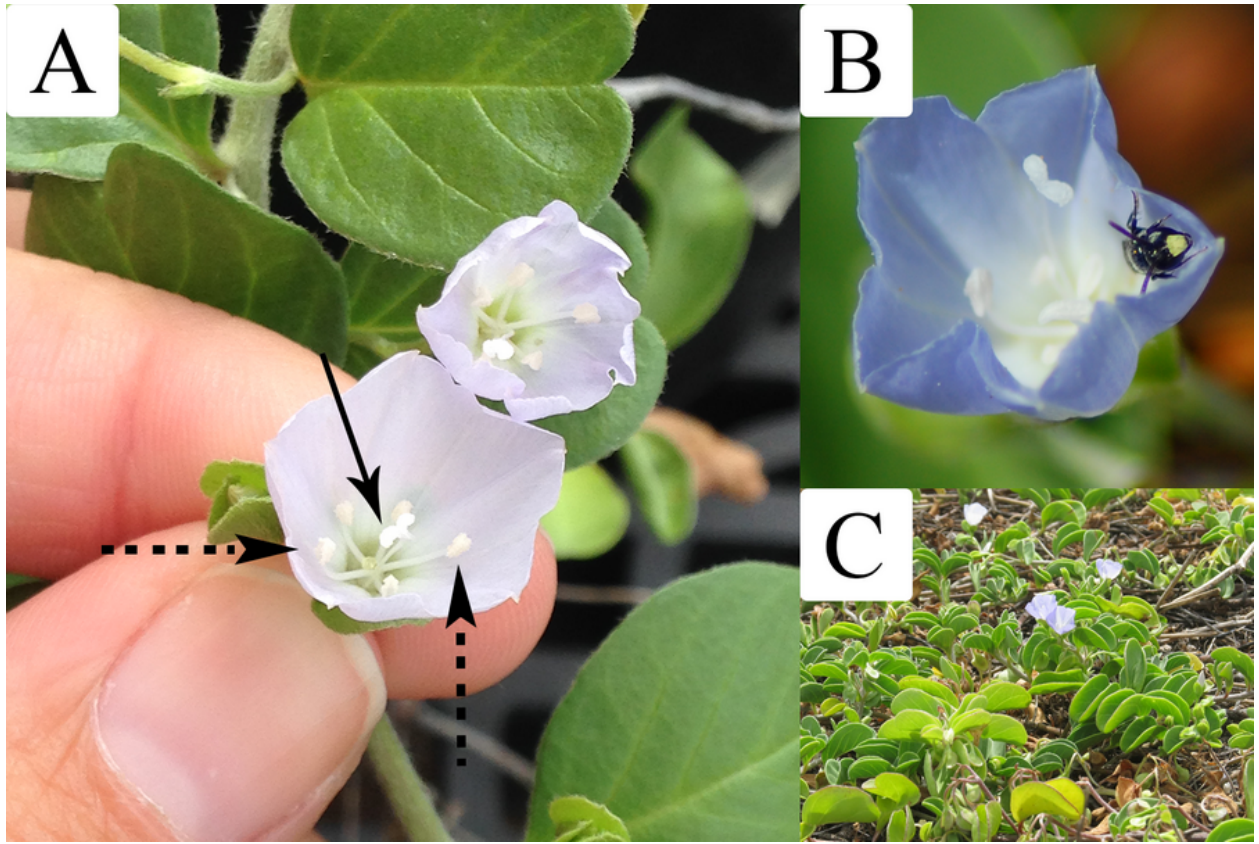| Species	No. Visitors Observed	Mean visit duration (s)	Reproductive Structures		Nectar		Pollen	
			No. Contacting	% Contacting	No. Collecting	% Collecting	No. Collecting	% Collecting
Apis mellifera	15	3.2	13	87	14	93	0	0
Ceratina smaragdula	3	39.2	2	67	1	33	2	67
Hylaeus anthracinus	4	32.9	3	75	1	25	2	50
Lasioglossum spp.	27	36.7	21	78	19	70	15	56
Tachysphex sp.	3	19.5	2	67	3	100	0	0

Figure 1. Flowers and habit of *Jacquemontia sandwicensis*. (A) The solid black arrow points to the bilobed stigma and the dashed black arrows point to the two longer stamens. (B) A male *Hylaeus anthracinus* visiting *J. sandwicensis* (Photo: Kobey Togikawa). (C) *J. sandwicensis* in coastal habitat at Ka Iwi Shore, Oʻahu.
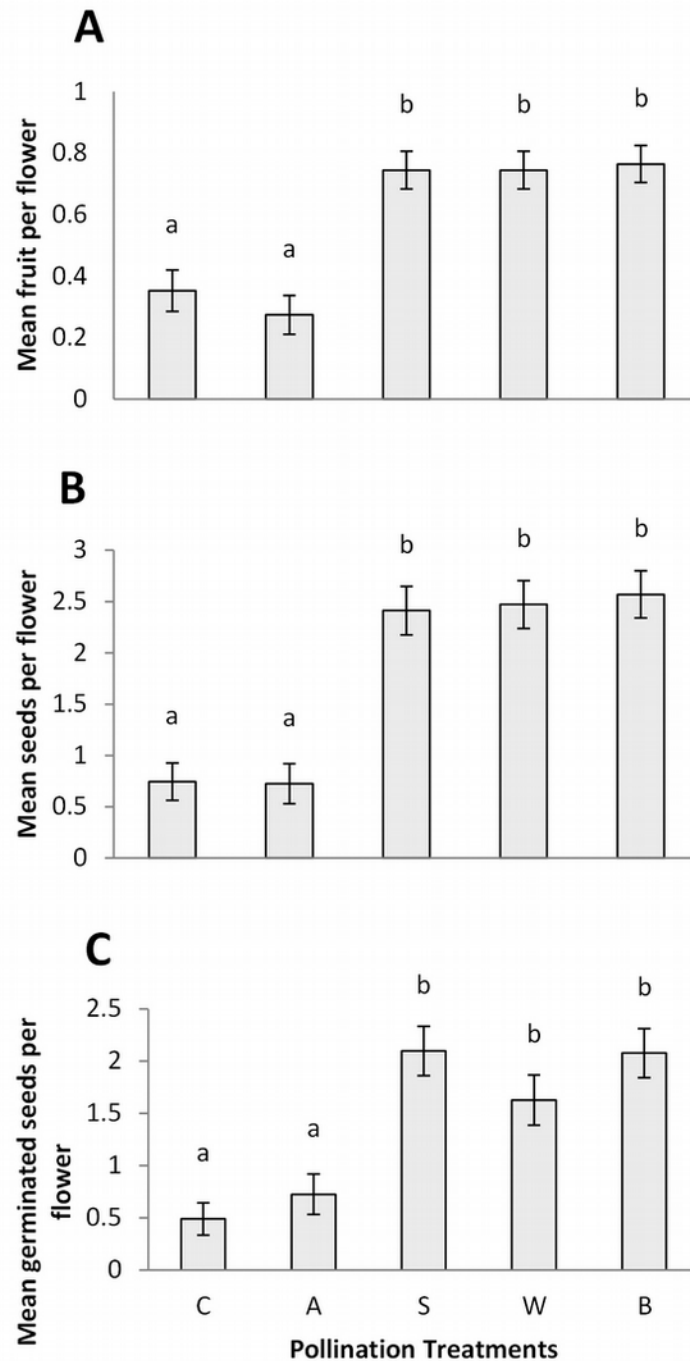
Figure 2. Reproductive output of *Jacquemontia sandwicensis* from lab pollination experiment (N = 51 plants). Treatments are: C=Control, no pollen applied, open to pollinators; A=Autogamy, no pollen applied, pollinators excluded; S=Self, pollen applied from a different flower of the same individual, pollinators excluded; W=Within population, pollen applied from a different individual from the same site, pollinators excluded; B=Between populations, pollen applied from a different site, pollinators excluded. Treatments with the same letter do not differ significantly from each other ($P < 0.05$). From top to bottom, (A) mean fruit set per flower ± 1 SEM, (B) mean seed set per fruit ± 1 SEM, and (C) mean germinated seeds per flower ± 1 SEM.
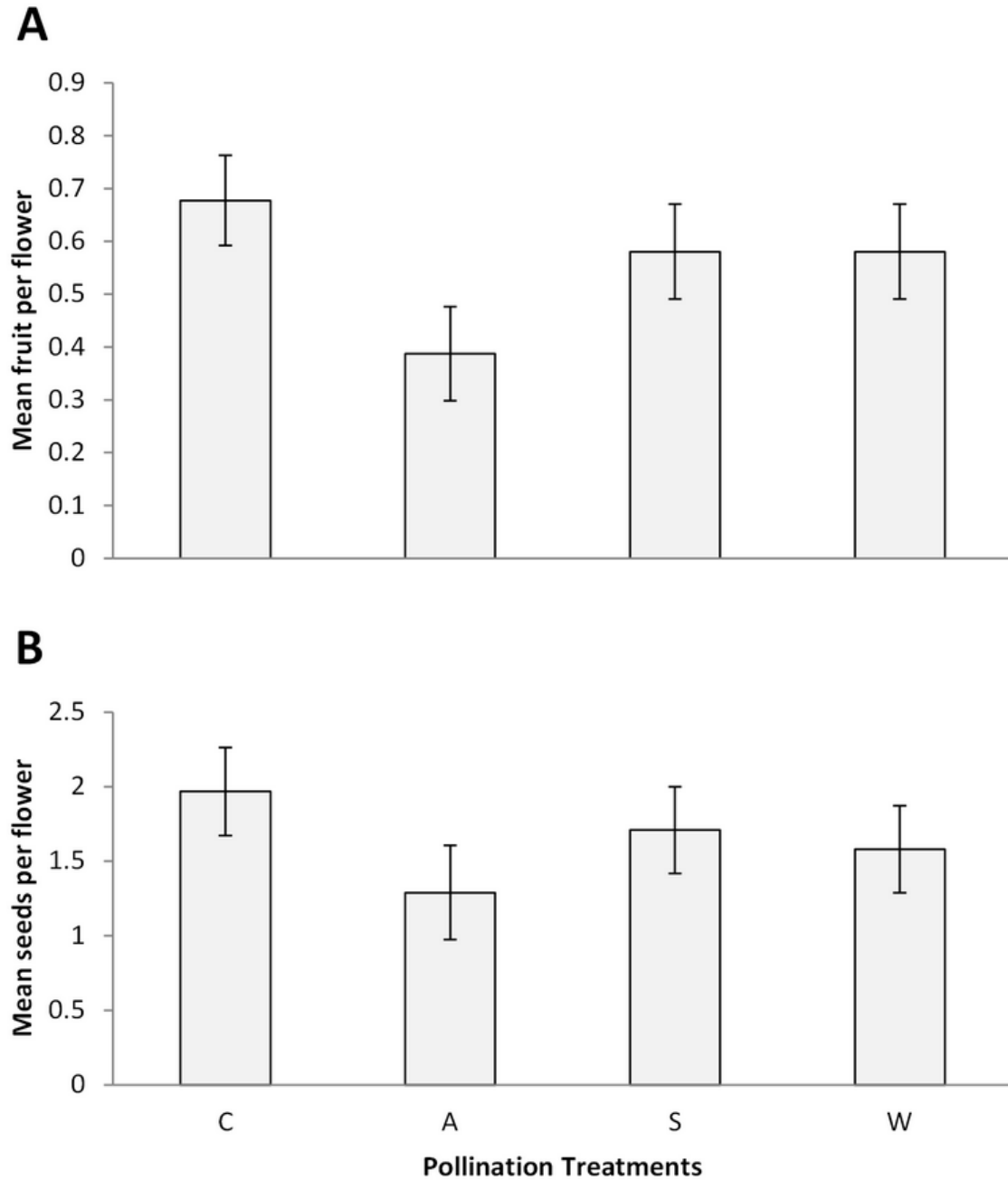
Figure 3. Reproductive output of *Jacquemontia sandwicensis* from field pollination experiment (N = 31 plants). Treatments are: C=Control, no pollen applied, open to pollinators; A=Autogamy, no pollen applied, pollinators excluded; S=Selfing, pollen applied from anther to stigma within the same flower, pollinators excluded; W=Within population, pollen applied from a different individual from the same site, pollinators excluded. From top to bottom, (A) fruit set per flower ± 1 SEM, and (B) mean seeds per flower ± 1 SEM. No significant differences detected between treatments ($P > 0.05$).
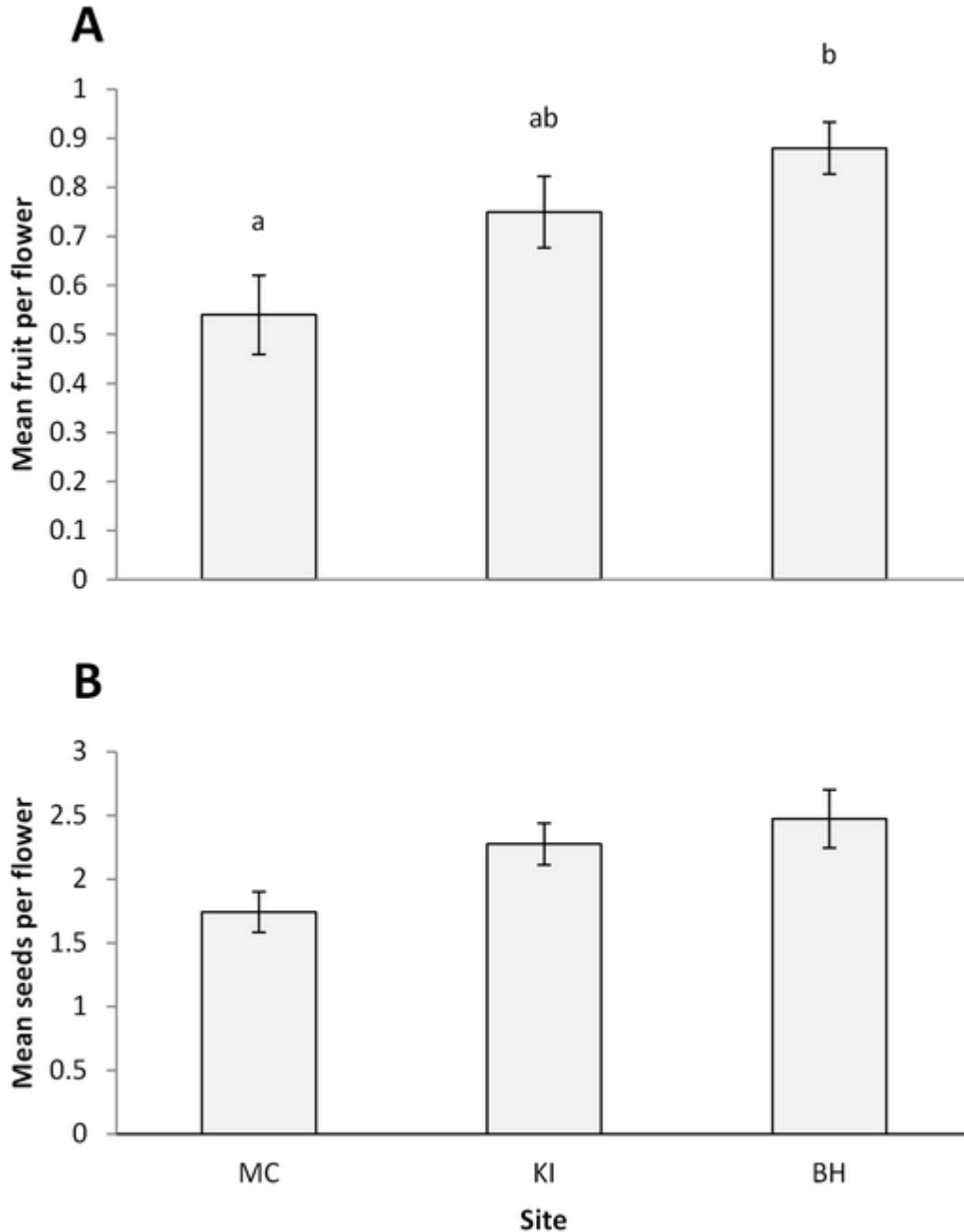
Figure 4. Reproductive output of *Jacquemontia sandwicensis* from 3 field sites. After tagging 40 flowers as at each site, we followed through fruit development and retrieved 39 fruits at Makapuʻu Cliff (MC), 36 at Ka Iwi Shore (KI), and 40 at Halona Blowhole (BH). All flowers tagged were treated as the control treatment: no pollen applied, open to pollinators. Sites with the same letter do not differ significantly from each other ($P > 0.05$). From top to bottom, (A) fruit set per flower $\pm$ 1 SEM, and (B) mean seed set per fruit $\pm$ 1 SEM.