Importance of non-native honeybees (*Apis mellifera*) as flower visitors to the Hawaiian tree ‘Ōhi‘a lehua (*Metrosideros polymorpha*) across an elevation gradient

By Camila Cortina*, Clare E. Aslan and Stacey J. Litson

Abstract

Pollinator populations are in decline worldwide. These declines are likely to impact native Hawaiian species and their interactions. To explore spatial heterogeneity in interactions between a foundational native Hawaiian tree and flower visitors, we examined how flower visitation varied for *Metrosideros polymorpha* over an elevational gradient, on the Island of Hawai‘i. We conducted a short-term, observational study at sites of high human activity, spanning a 1500-m elevational gradient. We predicted that native flower visitors would be most important, where importance is defined as the product of the number of flower visitors observed and the number of flowers visited per visitor, at the highest elevations where human impacts have historically been less consistent and human populations are lower. We predicted that non-native bee visitation would be most important at the lowest elevations where human impact is highest. Contrary to our expectations, we found that the non-native honeybee, *Apis mellifera*, was the most important visitor at both the lowest and highest-elevation sites and second only to native species of *Hylaeus* bees in visitor importance at mid-elevation sites. We recorded *A. mellifera* interacting with flowers during 16.3% of all observation blocks and *Hylaeus* spp. during 9.4% of observation blocks, with all other visitors appearing more rarely. Although this study was short in duration and occurred at only six study sites in disturbed areas, our results suggest that the high importance of *A. mellifera* as a flower visitor of *M. polymorpha* is consistent across a range of environmental conditions. Hawaii’s shifting suite of pollinators may impact gene flow and reproduction for *M. polymorpha*, a species with immense ecological and cultural importance.

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Introduction

Along with the multitude of other organisms that are at risk of anthropogenic extinction, pollinators are exhibiting major population declines (Abrol 2012, Tylianakis 2013, but see Martin 2015). Bees in particular are undergoing major population losses due to anthropogenic stressors such as changing land use patterns, herbicides, and the use of neonicotinoid pesticides on crops (Smart et al. 2016, Tison et al. 2016, Jumarie et al. 2017). These anthropogenic threats, along with invasion of hives by Varroa destructor mites and virus outbreaks, have led to population declines among managed European honey bees (Apis mellifera) (Evans et al. 2009, Potts et al. 2010). Losses in managed and wild pollinators alike have led to widespread alarm (Allsopp et al. 2008, Goulson et al. 2015).

Global conservation issues are particularly pronounced in Hawaii, which has been termed the “extinction capital of the United States” (Ragone 2002). In 2016, seven endemic Hawaiian bee species in the genus Hylaeus were listed under the U.S. Endangered Species Act (US Fish and Wildlife Service Rule 81 FR 67786). Plants have experienced declines (Wagner et al. 1999) driven by a combination of biological invasions and habitat transformation. In addition to habitat loss through conversion of native forest to agriculture and development, widespread introductions of mosquitoes, avian diseases, and disease-transmitting birds have resulted in the extinction of 71% of Hawaiʻi’s native non-migratory land bird species (Boyer 2008) and major population declines for those that were not extirpated. These environmental changes impact species and also interspecific interactions. Endemic Hawaiian species now interact with novel competitors (Aslan et al. 2016), predators (Shiels and Drake 2011), seed dispersers (Foster and Robinson 2007), and pollinators (Aslan et al. 2013; Hanna et al. 2013; Shay et al. 2016). Such transformed interactions could have implications for the reproductive success and population sizes of native species.
Among pollinators, remnant populations of native birds are predominantly relegated to higher-elevation remnant habitats (Hart et al. 2011) outside the range of introduced mosquitoes (although the endemic honeycreepers ‘amakihi (*Hemignathus virens*) and ‘apapane (*Himatione sanguinea*) retain small low-elevation populations and demonstrate some disease resistance (Atkinson and LaPointe 2009)). Among introduced insects, the non-native and cosmopolitan *A. mellifera* is particularly adapted to human-modified landscapes and may be expected to be more abundant than other pollinator species at lower elevations where humans dominate ecosystems, although recent arrival in Hawaii of the parasitic *Varroa* mite threatens *A. mellifera* colonies (Martin et al. 2012). Native bees, including diverse members of the genus *Hylaeus*, a quintessential example of Hawaiian adaptive radiation (Magnacca and Danforth 2006), persist across elevational gradients, but are likely impacted by habitat modifications common at lower and more disturbed elevations and have been shown to experience predation and competition from non-native *Vespula pensylvanica* in woodlands (Magnacca 2007, Wilson and Holway 2010, Hanna et al. 2014, US Fish and Wildlife Service Rule 81 FR 67786).

To further our understanding of these populations, we examined the question: How do flower visitors interacting with the dominant tree on the island of Hawai‘i differ over an elevational gradient spanning a range of environmental contexts and human impacts? We performed a short-term observational study across a 1500-m elevational gradient to assess the relative importance of birds, native bees, and non-native bees as flower visitors for the Hawaiian tree *Metrosideros polymorpha* Gaudich. (‘ōhi‘a). The most abundant native tree in the Hawaiian Islands, *M. polymorpha* is both a forest dominant and a lava pioneer, growing on new lava flows; it exhibits a wide range of growth forms and can be found from sea level to the high-elevation tree line on the island of Hawai‘i. The flowers of *M. polymorpha* are bottlebrush-shaped and range in color from dark red to yellow. Known pollinators include birds as well as both native
and non-native insects, particularly bees (Hanna et al. 2013). Because flowers are bright in color and possess long stamens and stigmas, it is likely that nectarivorous bird pollinators are particularly effective visitors of *M. polymorpha*, since their feathers necessarily contact reproductive structures when the bird forages for nectar (Carpenter 1976), whereas insects may be small enough to crawl inside flowers for nectar without contacting reproductive structures (Junker et al. 2010, Hanna et al. 2013). Both *A. mellifera* and *Hylaeus* bees are known to be effective pollinators of *M. polymorpha*, with *A. mellifera* depositing more pollen per visit (Junker et al. 2010).

In this study, climate, habitat type and duration and intensity of human impact vary with elevation, allowing us to examine how flower visitation for a single tree species varies over a range of environmental conditions. Previous research has detected elevational trends in *M. polymorpha* flower visitation, finding that flower visitation rates overall were higher at middle elevations and dominated by native *Hylaeus* spp. bees (Koch and Sahli 2013). That work provided an important snapshot of the current pollinator community interacting with *M. polymorpha* in various portions of its range. We aimed to complement this previous research by extending observations of flower visitation to lower elevations and targeting study sites with high human activity and high occurrence of non-native species, to broaden our understanding of the role of non-native flower visitors across different conditions. Lower elevations in this study are warmer, have full-time human residence, and contain a diversity of non-native plant and animal species. Middle elevations in this study are easily accessible by humans for recreation and hunting and visited by humans on a daily basis, but contain no permanent human residents. Higher elevations in this study are cooler and drier and experience limited human visitation on a daily basis.

We predicted that, out of the full flower visitor community at each study site, non-native
A. mellifera would be the most important component of the flower visitor community in the most human-modified systems, at lower elevations. This prediction emerged from both the known close association between humans and A. mellifera and our prediction that a long history of human impact and thus high habitat modification at low elevations would result in decreased native flower visitor presence at these sites. This pattern has previously been found in other systems where native flower visitors have been reduced in occurrence and diversity relative to A. mellifera in sites of high habitat modification (e.g., Aizen and Feinsinger 1994, Smith and Mayfield 2018). We also predicted that the relative importance of native visitors (bees and birds) as flower visitors would increase as elevation increased, since the intensity of human activity and habitat modification is greatest at lowest elevations. Note that our purely observational approach compares frequency of visitation and flower interactions among visitors but does not attempt to measure effectiveness of visitors as pollinators.

Materials and Methods

Study Sites

Flower visitation observations took place in June and July of 2017 at six woodland study sites, at each of which M. polymorpha was the dominant tree and human activity was frequent, spanning an elevational gradient on windward Hawai‘i Island (Fig. 1). Sites included a residential area at 180 m elevation (Site A), a county park at 280 m elevation (Site B), a national park at 1150 m elevation (Site C), a young forest area at 1126 m with high hunter and recreational use (Site D), a military training area at 1407 m (Site E), and a popular birdwatching and hunting trail at 1760 m (Site F). Approximately a tenth of trees across all sites were in flower during this study, and flowering trees occurring in clusters.

<Figure 1>

<Table 1>
**Flower Visitation Observations**

We used systematic flower visitation observations to estimate number of visitors per open flower by each visitor taxon, adjusted by the total amount of observation time at each study site. We multiplied these estimates by the average number of flowers visited by observed visitor individuals (rate of flower probing) to estimate flower visitation importance.

Each site was observed in non-rainy weather on at least four randomly-selected dates. Each site was observed at least once in early morning (three-hour observation start time 0630 h), midday (start time 0930 h), early afternoon (start time 1230 h), and late afternoon (start time 1530 h). Each observation period lasted three hours, divided into 10-minute blocks. Observers used high-powered binoculars (16x50) to observe flower visitation. To begin each block, observers performed a scan of visible open flowers, recording any flower visitors to functional group (e.g., native bird, non-native bird, native bee, non-native bee, non-native wasp, etc.) and, when possible, to taxon (e.g., *Hylaeus* sp., *A. mellifera*, *Hemignathus virens*, *Himatione sanguinea*, *Zosterops japonicus*). Following each such scan, observers conducted focal individual observations (after Uetz et al. 1994) for the remainder of the time block, observing individual flower visitors and recording the number of flowers and plants they visited as well as the total amount of time they were visible. Because these flowers can be visited by both insects and birds, we alternated conducting these 10-minute observation blocks from a distance of 3 m from flowering trees and a distance of 10 m, in order to observe both small and large visitors. Observed flowers ranged from approximately 1.5-8.5 m above the ground; in most sites, we were able to use the rugged lava terrain to stand slightly higher than the base of the tree, in order to observe even small insect interactions with flowers. Nevertheless, the distance from some flowers prevented us from verifying the presence of the smallest interactors, such as ants, which are known to deter bee visitation (Lach 2008a, Sidhu and Wilson Rankin 2016) and may have
influenced visitors across all elevations.

In total, 94 hours of *M. polymorpha* flower visitation observations were conducted in this study. Total observation time per site varied from 12 hours at Site F to 19 hours at Site A; this variation was the result of heavy rain events preventing observations at some sites on some days. Because this was observational research and some visitor taxa are rare or threatened, we made no attempt to capture flower visitors for species-level identification: for insects, this often relegated observation data to genus or lower resolution. For this reason, we analyzed much of our data by visitor functional groups (see Data Analysis). Also, we discuss “flower visitors” rather than “pollinators” because no visitors were captured to verify pollen transport and we did not attempt to examine deposition of pollen on stigmas following visitation.

**Transect Surveys of Potential Pollinators across Study Sites**

In addition to systematic observations of visitation to *M. polymorpha* flowers, we performed three rapid censuses of potential pollinators at all sites to evaluate the relative densities of potential pollinators across each site. We established a 2-km transect cutting across the center of each site along a north-south orientation. We surveyed each transect for potential pollinators by walking the transect slowly (1 km/hour) on three separate occasions (morning, midday, afternoon) and three separate dates per site. On each occasion, the transect was surveyed twice, first for birds and then for insects. We treated the transect as a belt transect 6m in width (3m on either side of the center line) for insect detections and 30m in width for bird detections; any potential pollinator individual detected within the transect was recorded, along with its location along the transect. The difference in transect width was due to detectability constraints: we could not be certain that insects further than 3m were being detected, but recognized that birds were likely to avoid the transect center line due to observer presence so extended bird observations to a greater distance. We chose this method of rapid comparison of potential
pollinator occurrence across sites rather than more robust and established methods such as bird
distance sampling (Buckland et al. 2001) because of the need to consider insect and bird
pollinators simultaneously.

Data Analysis

We pooled flower visitation observation data across observation periods for each study
site. We used those pooled data to calculate flower visitor importance (FVI) as the product of the
average number of individuals of each visitor taxon or functional group visiting focal flowers per
open flower per minute and the average number of flowers visited per minute per individual
(after Renne et al. 2000, Aslan et al. 2013). A higher importance value can result from a higher
frequency of visitation by a visiting taxon, a higher number of flowers visited by each individual,
or both. FVI is a useful metric for a baseline assessment of visitor frequency in observational
pollination ecology because it standardizes visitation rate by the number of open flowers and by
the amount of time spent observing, enabling sites varying in flower availability and observer
effort to be compared. However, it does not compare the effectiveness of each visit by different
visitors. Data used in this study are archived at the Dryad Digital Repository
(https://datadryad.org/).

Results

A total of 19 taxa were observed visiting *M. polymorpha* flowers. The most frequent
visitors were non-native *A. mellifera* (observed on 92 of 564 (or 16.3%) of scans), followed by
native *Hylaeus* spp. bees (not identified to species level) (on 9.4% of scans), non-native *Z.
japonicus* (6.6% of scans), and native *Hemignathus virens* (2.0% of scans). Remaining visitors
appeared during fewer than one percent of scans and included native and non-native insects
(unspecified Lepidoptera, non-native *V. pensylvanica*, unspecified non-native Formicidae (as
stated above, there may have been ant visitations that were not observed due to the distance from
which viewing occurred), and unspecified Diptera), native (*Himatione sanguinea* and *Drepanis coccinea*) and non-native birds (see list in Figure 2 below), and unspecified Gekkonidae. Most of these less common visitors (all non-native birds, ants, and geckos) failed during focal individual observations to contact the reproductive parts of flowers (i.e., they interacted with flower bases or pedicels but did not display probing behavior with the potential to transfer pollen).

*Apis mellifera* was the most important flower visitor (by FVI) in the lowest (sites A and B) and highest (sites E and F) elevation sites in this study. Native *Hylaeus* spp. bees were most important at mid-elevation sites C and D (Fig. 2), followed by *A. mellifera*.

<Figure 2>

Transect surveys of potential pollinators at each site detected *Z. japonicus* most commonly and *Hylaeus* spp. least commonly at Sites A and B (Fig. 3). *Apis mellifera* was the most commonly detected potential pollinator along transects at sites C, D, and F (Fig. 3). *Hemignathus virens* was the most commonly detected potential pollinator at Site E, followed by *A. mellifera* (Fig. 3).

<Figure 3>

Discussion

We found that non-native honey bees dominated visitation at all elevations, with *A. mellifera* as the most important visitors in the highest- and lowest-elevation sites in this study (although there are no known managed hives in the vicinity of any of the study sites) and native *Hylaeus* spp. bees as most important at mid-elevation sites. The non-native *Z. japonicus*, which is resistant to mosquito-borne diseases, was also a major flower visitor at the lowest elevations. Insects as frequent pollinators of *M. polymorpha* have been observed elsewhere (Hanna *et al.* 2013; Junker *et al.* 2010, Lach 2008b), but the consistency of *A. mellifera* as one of the most important visitors across all elevations is notable, indicating that this native tree may now be
consistently interacting with a non-native pollinator across sites spanning a range of habitat types and human activity types.

As a super-generalist (Aizen et al. 2008), *A. mellifera* generally visits upwards of one hundred different plant species in any particular region (Goulson 2003). As was observed in this study, *A. mellifera* has been observed to be the most frequent flower visitor in many natural areas and the only visitor to some native plant species, although its per-visit effectiveness (and thus efficiency) as a pollinator is lower than that of many other pollinators (Rader et al. 2009, Hung et al. 2018). In Hawaii, *A. mellifera* individuals have been shown to carry more pollen than *Hylaeus* spp. individuals but also to carry mixed pollen loads, likely diminishing their effectiveness at conspecific pollen transfer (Miller et al. 2015). Additionally, *A. mellifera* has also been observed to displace and outcompete native bees in some cases (e.g., Roubik 1978; Kato et al. 1999; Shavit et al. 2009). For *M. polymorpha*, however, *A. mellifera* demonstrates more frequent stigmatic contact and deposits more pollen compared to *Hylaeus* spp. (Junker et al. 2010). Furthermore, Kuppler et al. (2017) demonstrated that exotic flower visitors at Hawaii Volcanoes National Park were more generalized than native species, could forage in more diverse weather conditions, and were more abundant, indicating that they may alter pollination dynamics in a variety of ways.

Pollinator communities in Hawaii are shifting as a result of environmental change (e.g., see listings of endemic *Hylaeus* bees and *D. coccinea* under the Endangered Species Act; US Fish and Wildlife Service Rule 81 FR 67786; US Fish and Wildlife Service Rule 82 FR 43873). Hawaiian native birds have declined precipitously over the past few centuries (Boyer 2008); non-native birds now dominate most ecosystems in the Hawaiian Islands. Birds generally transport more pollen per interaction than insects, and bird-mediated pollen transfer has been deemed more efficient per-visit in other systems (e.g., Ramsey 1988; Hingston et al. 2004; Aslan 2015),
including for *M. polymorpha* and relatives (Carpenter 1976; Schmidt-Adam et al. 2009). Birds may also fly longer distances, move pollen at different times of day, and seek foraging sites with more cover relative to insect pollinators, all behaviors that could influence pollen transfer patterns for native plants. We have little knowledge regarding historical pollination of *M. polymorpha*; we cannot know what the relative densities of insect vs bird pollinators may have been in the past, nor how much each contributed to historical gene flow of *M. polymorpha*. However, the current rarity of bird visitation found in our study and previous research (e.g., Hanna et al. 2013) implies that bird contributions to *M. polymorpha* gene flow are limited today. Meanwhile, the introduction of the *Varroa* mite to Hawaii may impact *A. mellifera* populations on the islands (Martin et al. 2012). This is a recent phenomenon, however; a survey in 2003 documented no mites in managed or feral hives on four Hawaiian Islands (Culliney 2003). Decline of *A. mellifera* populations in Hawaii could impact *M. polymorpha* reproduction across habitat types, particularly since they are known effective pollinators and *M. polymorpha* has been shown to be pollen limited in previous studies (Junker et al. 2010, Hanna et al. 2013).

Species assemblages and interaction networks are changing rapidly as climate change, biological invasions, and habitat fragmentation drive species to decline or shift their ranges. The role of *A. mellifera* in pollination networks worldwide remains nebulous, given its context-dependent effectiveness coupled with its consistently high abundance across varying environmental conditions and varying degrees of anthropogenic disturbance. This was a short-term, observational study, intended to explore how flower visitation varies in human-disturbed sites across a 1500-m elevational gradient. Extending observations over time and space will be necessary in order to understand whether the importance of *A. mellifera* in flower visitation persists across a broader spatial scale and broader range of contexts.
Acknowledgments

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Shavit, O., A. Dafni, and G. Ne’eman. 2009. Competition between honeybees (Apis mellifera)


Table 1. Study sites, spanning a 1500-m elevational gradient, at which flower visitation to *M. polymorpha* was observed in this study. Selected sites contained high levels of human activity and mixed native and non-native insect and bird communities.

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Elevation</th>
<th>Approx. ave. annual precip.</th>
<th>Approx. age of lava flow</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>19.705502, -155.115164</td>
<td>180 m</td>
<td>355 cm</td>
<td>3500 yrs</td>
</tr>
<tr>
<td>B</td>
<td>19.686672, -155.131042</td>
<td>280 m</td>
<td>430 cm</td>
<td>150 yrs</td>
</tr>
<tr>
<td>C</td>
<td>19.417322, -155.252891</td>
<td>1150 m</td>
<td>203 cm</td>
<td>300 yrs</td>
</tr>
<tr>
<td>D</td>
<td>19.689906, -155.270927</td>
<td>1126 m</td>
<td>270 cm</td>
<td>150 yrs</td>
</tr>
<tr>
<td>E</td>
<td>19.740579, -155.693188</td>
<td>1407 m</td>
<td>203 cm</td>
<td>2500 yrs</td>
</tr>
<tr>
<td>F</td>
<td>19.671541, -155.387507</td>
<td>1760 m</td>
<td>203 cm</td>
<td>1000 yrs</td>
</tr>
</tbody>
</table>
Figure 1. Map showing study sites on the island of Hawai‘i, ranging in elevation from 180 to 1750 m.
**Figure 2.** Quantitative matrix displaying flower visitor importance (FVI) values for all recorded *M. polymorpha* flower visitors at each site. Darker shading denotes more important visitors. FVI is calculated as the number of visitor individuals per open flower per minute multiplied by the total number of flowers visited by each individual. Values are then scaled such that the most important visitor at each site is set equal to 1.00, with other visitor importance values proportional to that most important visitor. *Other non-native birds included: red-billed leiothrix (*Leiothrix lutea*), yellow-billed cardinal (*Paroaria capitata*), northern cardinal (*Cardinalis cardinalis*), common waxbill (*Estrilda astrild*), nutmeg mannikin (*Lonchura punctulata*).
Figure 3. Detections of potential pollinators via surveys of 2-km transects at each site. Transects were surveyed three times during the course of the study, and the average number of detections over the three surveys is displayed here.