The Role of Honey Bees as Pollinators in Natural Areas

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ABSTRACT: The western or European honey bee (*Apis mellifera*) is the primary managed pollinator in US agricultural systems, and its importance for food production is widely recognized. However, the role of *A. mellifera* as an introduced species in natural areas is potentially more complicated. The impact of *A. mellifera* on native insect pollinators can depend on broad community context, as can the relative effectiveness of *A. mellifera* in pollination of both native and nonnative plant species outside of agricultural systems. *Apis mellifera* is highly generalist and able to interact with hundreds of native plant species following its naturalization. It is unlikely to wholly replace native pollinators as visitors of specialized plant species, and its behavioral characteristics tend to reduce *A. mellifera's* per-visit efficiency, even when its overall effectiveness is high. Preliminary results of our case study exploring the importance of *A. mellifera* vs. native bees as pollinators of native plants in Hawai'i indicate that *A. mellifera* is less important than native *Hylaeus* bees as a flower visitor of focal native plant species. In light of current global declines in *A. mellifera* populations, maintenance of a diversity of pollinators and pollinator habitat are critical conservation needs in natural areas.

Index terms: Apis mellifera, competition, mutualistic networks, native bees, pollination

INTRODUCTION

Pollination serves as the backbone of complex ecological systems (Heithaus 1974) and is essential to agricultural production (Bommarco et al. 2013). To boost pollination and fruit production, European honey bees (*Apis mellifera* Linnaeus) have been introduced to agricultural systems worldwide (Moritz et al. 2005). Following these introductions, *A. mellifera* has repeatedly naturalized and spread, now occurring in natural areas in most parts of the globe (Moritz et al. 2005).

The establishment of the nonnative *A. mellifera* as a pollinator and forager carries the potential to alter mutualistic and competitive interaction networks worldwide (Traveset and Richardson 2006). *Apis mellifera* may directly boost native plant fitness through pollination, or indirectly reduce native plant fitness by pollinating nonnative invasive plant species (Kato et al. 1999). By competing with native pollinators for resources, *A. mellifera* may reduce native pollinator fitness (Paini 2004). More subtle impacts are possible as well; *A. mellifera* may differ from native bees in spatial and/or temporal pattern of pollen transport, in nectar foraging, or the quantity of pollen dispersed vs. consumed (Freitas 1997; Freitas and Paxton 1998). Here, we review these factors to evaluate the role of *A. mellifera* in native communities and the importance of the species as a pollinator in natural areas. Additionally, to illustrate the conservation implications of this topic, we present a brief case study and early results of ongoing research exploring the importance of *A. mellifera* as a pollinator of native Hawaiian plants. Finally, we discuss the global implications of *A. mellifera* naturalization on native species. Widespread population declines among both native and nonnative pollinators could impact both food security and native ecological community dynamics (Meffe 1998; Steffan-Dewenter et al. 2005; Biesmeijer et al. 2006; Potts et al. 2010). The relative influence of *A. mellifera* on pollination in natural areas will be an important determinant of how current pollinator declines impact native biodiversity and could guide land managers in determining how to manage *A. mellifera* colonies in natural areas.

REVIEW: Honey Bees in Natural Systems

Upon naturalization and spread into natural systems, *A. mellifera* becomes a member of complex ecological communities structured by mutualism, competition, and resource flows. This integration of *A. mellifera* has occurred worldwide, following introductions from its native Europe, Asia, and Africa. In North America, *A. mellifera* was introduced as early as 1622, with subsequent introductions beginning in 1859 (Whitfield et al. 2006). The unique ecology of *A. mellifera* contributes to the success of the species. *Apis mellifera* exhibits a complex society characterized by the simultaneous presence of several generations within a colony, cooperation in offspring care, and division of labor into queens, drones, and workers. Older workers forage for pollen and nectar, and the dance communication between *A.*

mellifera individuals boosts foraging effectiveness (Okada et al. 2012). Individual workers forage across varied locations and seasons, exhibit great flexibility in flight performance, and can carry substantial loads during flight (Harrison and Fewell 2002). Mature *A. mellifera* colonies can range from 20,000 to 70,000 worker bees (Lee and Winston 1987). By contrast, the vast majority of native bees in systems where *A. mellifera* has naturalized are solitary. As a result of its sociality and behavior, *A. mellifera* makes up a very high proportion of pollinator individuals in any natural area where it is found. The presence of *A. mellifera* therefore exerts a strong influence on pollination patterns (stemming from foraging distance and foraging preferences) in inhabited sites (e.g., Steffan-Dewenter and Tscharntke 2000; Jha and Vandermeer 2009), even though *A. mellifera* is a single species and native bees may comprise dozens or hundreds of species in a particular locale. The introduction of *A. mellifera* has altered the behavioral and ecological characteristics of pollinators within both the agricultural and natural landscape.

Apis mellifera is able to partner with a large number of plant species because of its morphology and behavior, making it a supergeneralist interactor (Giannini et al. 2015). Direct competition for resources between *A. mellifera* and native bees may also indirectly impact the fitness of native plants through declines in native bees (Abrol 2012). An early review identified unrelated correlates of *A. mellifera* introduction impacting both native plants and native bees, and claimed a lack of evidence of direct negative effects on native biota from introductions of *A. mellifera* (Huryn 1997). Since then, a large number of studies have explored the various roles of *A. mellifera* in natural areas, finding that effects vary widely by context, and we review these studies here.

Effectiveness and Efficiency of Honey Bees as Interactors with Individual Native Plant Species

The effectiveness of *A. mellifera* as a pollinator of native plants varies enormously among plant species and systems. The quantitative effectiveness of a pollinator depends on visitation frequency as well as the abundance of pollen transferred. Effectiveness relates the overall visits of a pollinator to seed set (Motten et al. 1981). Furthermore, effectiveness must be evaluated in comparison to pollination received by native pollinators; in theory this is the pollination context within which a given focal plant species evolved. Hypothetically it is an indicator of the quantity of pollen transfer required to maintain population growth rate. Although *A. mellifera* is a single introduced species, the sheer abundance of *A. mellifera* in most systems can transform patterns of pollination in a region, giving *A. mellifera* a disproportionate effect on community dynamics. This abundance results in a high number of visits and, probabilistically, a high occurrence of seeds attributable to *A. mellifera* visits (Rader et al. 2009). Efficiency, on the other hand, is generally assessed as the amount of seed set resulting from each visit: a high-efficiency pollinator can generate high seed set with fewer individual visits (Rader et al. 2009). Some studies have demonstrated low efficiency of *A. mellifera* as a pollinator of native plants. This is because each individual visit results in lower seed set than a visit by native bees, although effectiveness may be high (Westerkamp 1991; Osorio-Beristain et al. 1997; Spira 2001). Very different patterns have been observed elsewhere; the efficiency of *A. mellifera* visits to two native species of *Jatropha* in Brazil, for example, was extremely high (100% and 85%, respectively) (Neves and Viana 2011). This result was attributable to the generalist floral characteristics of *Jatropha*: the flowers are easily accessible to *A. mellifera* due to their size and shape. Such generalist characteristics are likely to sustain pollination for many plants in transformed ecosystems by enabling them to interact with nonnative visitors such as *A. mellifera* (Schweiger et al. 2010). Similarly, *A. mellifera* was the most frequent visitor to the California native *Triteleia laxa* Benth. and appeared to be responsible for most seed set (Chamberlain and Schlising 2008).

In Brazil, *A. mellifera* is the principle pollinator of the native plant *Melochia tomentosa* L. (Machado and Sazima 2008). One study in Hawaiian forests where avian pollinators have declined in abundance found that the primary pollinator of the native *Metrosideros polymorpha* Gaudich. was now *A. mellifera*, although native bees are present and interacting with the tree as well (Hanna et al. 2013). Native bees are the primary visitors to the declining *Acacia carneorum* Maiden in Australia, but *A. mellifera* is the primary visitor to its abundant congener *A. ligulata A. Cunn. ex Benth.*, which displays high fecundity (Gilpin et al. 2014). In China native bumble bees deposited more pollen during their first floral visit to the endemic plant *Pedicularis densispica* Franchet ex Maximowicz, but *A. mellifera* significantly elevated overall seed set for the species by increasing out-crossing (transfer of pollen between plants) (Sun et al. 2013). In Spain, native *Crataegus monogyna* L. and *Vaccinium myrtillus* L. displayed higher fruit set when an *A. mellifera* apiary was located closer to the plants, although this effect was not observed for *Prunus avium* L. (Cayuela et al. 2011). Native bees and *A. mellifera* were equally effective pollinators when fruit set was examined following single visits from each potential pollinator for *Psychotria carthagenensis* (Faria and Araujo 2015), and also for *Dillwynia juniperina* Lodd. in Australia (Gross 2001). The endemic herb *P. densispica* exhibited enhanced reproduction and constant outcrossing rates following introduction of *A. mellifera*, suggesting that *A. mellifera* was as effective a pollinator as the native bumblebee (Xia et al. 2007). Both *A. mellifera* and native bees adjust their foraging in response to seasonal floral changes that occur in the native tree *Magnolia grandiflora* L. (Allain et al. 1999). The native shrub *Dillwynia sieberi* Steud. was visited primarily by *A. mellifera* in revegetated pastures, whereas native pollinators dominated in remnant native woodland patches; total seed set was similar between the two site types (Lomov et al. 2010). As these examples illustrate, *A. mellifera* has been shown to be an effective pollinator of some native plants.

In other cases, *A. mellifera* appears to be an ineffective pollinator of native plant species. Compared to visitation by *A. mellifera*, more seed set was produced by native pollinator visitation to the native plant *Phacelia parryi* Torrey in California

(Bruckman and Campbell 2014), native bird visitation to the native *Kniphofia linearifolia* Baker in South Africa (Duffy et al. 2013), native hummingbird visitation to the native cactus *Melocactus intortus* Link and Otto in Puerto Rico (Fagua and Ackerman 2011), and native parrot visitation to the native *Eucalyptus globulus* Labill. in Tasmania (Hingston et al. 2004). Exclusion of birds reduced seed set of the native Australian shrub *Brachyloma ericoides* (Schltdl.) Sond., but exclusion of *A. mellifera* did not (Celebrezze and Paton 2004). *Apis mellifera* appeared relatively ineffective at promoting outcrossing of rare plant individuals of *Persoonia* spp. (Rymer et al. 2005). *Apis mellifera* was found to steal 99% of the pollen grains of the native *Clusia arrudae* Planchon & Triana, and there was a negative correlation between frequency of *A. mellifera* visits and seed set (Carmo et al. 2004). For the native plant *Melastoma affine* L. in Australia, *A. mellifera* deposited less pollen and removed more pollen than native bees and also disturbed the foraging of native pollinators (Gross and Mackay 1998).

Effectiveness of *A. mellifera* compared to native pollinators is often unknown (e.g., Kaiser-Bunbury and Müller 2009). For a suite of endemic Cunoniaceae plants in New Caledonia, *A. mellifera* is a common flower visitor along with native insects, birds, bats, and geckos (Hopkins et al. 2015), but the effectiveness of *A. mellifera* compared to that of native visitors has not been explored. In Australia, *A. mellifera* began foraging on *Eucalyptus costata* Behr & F. Muell. flowers earlier in the day than native pollinators, but collected pollen rather than nectar. The overall impact on *E. costata* reproduction of a switch to pollination by *A. mellifera* rather than native pollinators is unclear (Horskins and Turner 1999). On Tenerife, an island with a restricted number of individual plants due to small land area, plants at a site with high occurrence of *A. mellifera* demonstrated rapid nectar depletion and higher frequency of visits to multiple flowers on the same plant; seed set and viability, however, appeared unaffected (Dupont et al. 2004). Although the importance of *A. mellifera* in natural areas can only be satisfactorily evaluated with reference to native community pollination, knowledge for many systems is too limited to draw confident comparisons.

Honey Bees as Pollinators of Nonnative Plant Species in Natural Areas

Because of its highly generalist behavior and morphology, *A. mellifera* often pollinates nonnative plant species, with the potential to facilitate spread rates (Stokes et al. 2006). Such dynamics could affect natural areas by increasing invasiveness of nonnative plants requiring management. These effects have been documented in highly disturbed locations such as in Australia and New Zealand (Goulson 2003). Pollination by *A. mellifera* is responsible for the spread of the invasive *Lantana camara* L. in Australia (Goulson and Derwent 2004). In Tasmania, the invasive ecosystem engineer *Lupinus arboreus* Sims is pollinated by *A. mellifera* (Stout et al. 2002). When the nonnative *Acacia saligna* (Labill.) H.L.Wendl. was present in South African study sites, visitation to the native *Roepera fulva* L. was reduced; *A. mellifera* is largely responsible for the high floral visitor overlap, and thus pollination competition, between the two species (Gibson et al. 2013). In Kansas, the invasive *Lespedeza cuneata* (Dum.Cours.) G.Don, but not its native congeners, was visited frequently by *A. mellifera* (Woods et al. 2012). In California and Oregon, *A. mellifera* is the principal pollinator of the nonnative *Centaurea solstitialis* L. (Barthell et al. 2001; Mciver et al. 2009; Swope and Parker 2010), a major rangeland invader. In South Africa, *A. mellifera* is the primary pollinator of nonnative *Araujia sericifera* Brot. (Coombs and Peter 2010). Examining a broad community of interacting native and nonnative species, nonnative pollinators including *A. mellifera* were significantly more likely to visit nonnative than native plants (Morales and Aizen 2006). Similar effects have been observed in many systems; pollination by *A. mellifera* and other exotic pollinators likely exacerbates plant invasions in many natural areas (Hanley and Goulson 2003). Therefore, the interaction between *A. mellifera* and nonnative plants is a necessary consideration for natural area managers faced with the need to balance pollination management (perhaps by management of *A. mellifera* colonies) and nonnative plant species control.

The Position of Honey Bees in Pollination Networks and Communities

Apis mellifera can interact with large numbers of species and potentially alter the composition of ecological communities, but its role varies widely across time and space. For *Eucryphia cordifolia* Behr & F. Muell., a native tree in Chile, only three out of 137 pollinators were observed in every year of a ten-year study; *A. mellifera* dominated at times, but not always (Smith-Ramírez et al. 2014). Spatial variation may be important, as well. In native and introduced ranges of *Hedysarum coronarium* D., a perennial native to Spain, seed set and pollinator richness were greater in the native than the introduced range, but pollen loads on *A. mellifera* were equivalent in the two locations (Montero-Castaño et al. 2014).

Some studies of communities have shown that *A. mellifera* was the most frequent flower visitor, such as in a Garry oak ecosystem in Canada and an endemic New Caledonian ecosystem (Kato and Kawakita 2004; Parachnowitsch and Elle 2005). However, *A. mellifera* visited only a small proportion of all local floral species in a regrowth forest patch in Brazil (Pedro and De Camargo 1991), in forested systems in the Philippines (Fajardo and Cervancia 2003), in wildflower gardens in Montana (Pearce et al. 2012), and in New Zealand honey production (Huryn 1997). By contrast, 23 out of 43 native plants were visited by *A. mellifera* in managed field margins in Michigan (Tuell et al. 2008). Fragmented systems in the Argentinian chaco serrano were dominated by *A. mellifera*, with smaller fragments exhibiting increasing occurrence of *A. mellifera* relative to native insect species (Aizen and Feinsinger 1994). Similar context dependence was observed for pollination of *Schinus terebinthifolius* (Cham. and Schlecht.) F. Muell., which was visited predominantly by *A. mellifera* in beach grass shrubland but by native halictid bees in restinga forest (Cesario

and Gaglianone 2013).

The generality of *A. mellifera* is pervasive in networks. In mutualisms such as pollination, a specialist interactor is one that interacts with one, or perhaps a restricted guild of partner species. Generalist interactors (whether plants or pollinators) will interact with many and diverse species, with supergeneralist interactors interacting with a very high diversity of partners. Generalization is more common than specialization in pollination (Johnson and Steiner 2000; Waser 2006). In shrubland ecosystems in Mexico, *A. mellifera* dominated the pollinator community in both a conservation area and a disturbed area (Campos-Navarrete et al. 2013). *Apis mellifera* performed the majority of flower visits in a frequently disturbed cerrado-atlantico forest site, perhaps demonstrating the capacity of the species to quickly recolonize after disturbance (Polatto and Chaud-Netto 2013). In a Pantanal, Brazil, network, the most generalist bee species was *A. mellifera*, visiting 27 out of 63 plant species (Boff et al. 2013).

In network calculations, *A. mellifera* exhibits high centrality, uniting multiple modules with its generalist interaction behavior (Santos et al. 2012). In the Brazilian caatinga, *A. mellifera* strongly affected network structure by reducing modularity and increasing nestedness (Santos et al. 2012). Modularity measures the amount to which a network of interactors is divided into a number of natural subsets wherein species interact much more with each other than with species outside the subset (Olesen et al. 2007). Nestedness refers to the tendency of specialist species to interact with generalists (James et al. 2012). *A. mellifera* impacts these metrics by partnering with a high proportion of the species in the system, changing the linkages of native species with one another. In study systems in Brazil and South Africa, *A. mellifera* was the most abundant species, again generating high nestedness via its generalist behavior (Dubet da Silva Mouga et al. 2012; Gibson et al. 2012). In a common garden in the eastern US, pollination of native plants was heavily dominated by native *Bombus impatiens* Cresson and nonnative *A. mellifera* (Tuell et al. 2008).

Broad community context affects the role of *A. mellifera*. In the Seychelles, *A. mellifera* altered plant linkage and interaction evenness in networks including large numbers of nonnative plants (Kaiser-Bunbury et al. 2011). For coflowering *Asclepias* species, visitation frequency and, by extension, pollinator importance of *A. mellifera* vs. native insect species varied by plant species even among such similar plants (Theiss et al. 2007). In burned and unburned sites, nonnative *A. mellifera* and *B. terrestris* as well as native bees were primary visitors to *Satureja thymbra* L., and seed set was high in both habitats (Potts et al. 2001). In disturbed islands within the Bonin Islands, *A. mellifera* dominated visitation to both native and nonnative flowers and were seasonally dependent on nonnative flowers; this contrasted with intact native communities on less disturbed islands, which were dominated by native bees (Kato et al. 1999). Depending on its abundance, the role of *A. mellifera* varies across communities, but its generality gives it the potential to heavily influence the structure of any given network.

Impact of Honey Bees on Native Pollinators

When competing for limiting resources, *A. mellifera* may be expected to impact native pollinators (Thomson 2004; Traveset and Richardson 2006; Shavit et al. 2009). Tests of such effects, once again, indicate that context matters. Habitat fragmentation was associated with declines in native insects and increases in *A. mellifera* abundance in Argentina, but there was not strong evidence in that system that *A. mellifera* itself contributed to the native bee decline (Aizen and Feinsinger 1994). In Brazil, however, studies have indicated that declines in native bees may be due at least in part to competition with *A. mellifera* (Martins et al. 2013) and that depletion of *Spondias mombin* L. pollen by *A. mellifera* reduced native bee foraging benefit (Carneiro and Martins 2012). Niche overlap between *A. mellifera* and native bumble bees depended on total floral resource availability (Franco 2009). A lengthy study of native bee populations on Barro Colorado Island following colonization of the island by *A. mellifera* found no measurable competitive effect of the nonnative (Roubik and Wolda 2001).

Competition between *A. mellifera* and native pollinators is likely to be highest when the ecological requirements of the two groups are similar (Dohzono and Yokoyama 2010). In New Caledonia, *A. mellifera* is "ubiquitous," and competes with native bees for nectar and pollen (Donovan et al. 2013). In protected areas in Israel, *A. mellifera* introduction resulted in decreased frequency of floral visitation by native bees (Shavit et al. 2009). Proximity to *A. mellifera* hives reduced reproductive success and altered the foraging strategy of native *Bombus occidentalis* Greene individuals (Thomson 2004). Niche overlap between *A. mellifera* and native *Melipona* bees in Brazil indicated competition for nectar (Wilms and Wiechers 1997). For two *Sideroxylon* tree species in Mauritius, *A. mellifera* was a low-efficiency pollinator but depleted nectar each day, likely interfering with the native mutualism (Hansen et al. 2002). *Apis mellifera* could also impact native bees through pathogen transmission and reproductive interference, but these have been less studied than competition (Stout and Morales 2009). When natural area managers are concerned about native pollinators, it may be important to consider broad availability of flowering plants and densities of *A. mellifera* to determine how much the non-native bee may compete with natives.

As our review demonstrates, the role of *A. mellifera* in natural ecosystems and communities is context-dependent. When evaluating the impact of *A. mellifera* in a particular system, natural area managers must consider effects on native plants, nonnative plants, and native pollinators. Those impacts will vary according to the abundance of *A. mellifera*, the level of ecological similarity between *A. mellifera* and native pollinators, and the relative effectiveness of *A. mellifera* vs. native pollinators for particular plant species of concern. *Apis mellifera* pollinates some native plants successfully, even replacing extinct pollinators in certain cases, but

it interferes with effective pollination of other native plants. The pollination needs of a given natural system, the conservation status of native pollinators, and the relative occurrence of specialist vs. generalist pollinators may all be important determinants of the relative costs vs. benefits of *A. mellifera* introductions and may influence *A. mellifera* management decisions.

CASE STUDY: Honey Bees vs. Native Bees as Pollinators of Native Hawaiian Plants

The Hawaiian Islands have been heavily impacted by humans and exhibit very high extinction rates (e.g., Hadfield et al. 1993; Boyer 2008). Hawai'i is the most isolated archipelago on the planet (Price 2004); only a restricted suite of species have been able to colonize Hawai'i on their own, resulting in a limited diversity of native species within any given functional group (Eldredge and Evenhuis 2003). This low diversity leaves a high number of vacant niches, allowing rapid diversification and adaptive radiation and the evolution of unique forms and specialized interactions (Price and Clague 2002). Hawaiian pollination was historically dominated by a restricted number of native bees, butterflies, and moths, and a remarkably high proportion of native plants are bird-pollinated (Wagner et al. 1999). Due to habitat loss, invasion of exotic predators, and rampant introduced disease, native pollinators in Hawai'i have experienced high extinction rates (Cox and Elmqvist 2000). Given such widespread extinction among native pollinators, *A. mellifera* may be critical to reproduction of a diversity of endemic and native plants. However, because *A. mellifera* is highly generalist and differs behaviorally from native pollinators, it is unlikely that *A. mellifera* wholly replaces endemic pollinators as a partner of all plant species. Furthermore, current declines in *A. mellifera* populations in Hawai'i could indicate that *A. mellifera*'s relative abundance in pollinator communities may decline in the future. We set out to understand the relative importance of *A. mellifera* vs. native species as pollinators of a diversity of native plant species in Hawai'i, and we present here preliminary data relevant to three cooccurring native plant species in early successional mesic forest on the Island of Hawai'i.

METHODS

To quantify the relative importance of *A. mellifera* vs. native species as pollinators of native plant species in Hawai'i, we performed flower visitation observations for three common Hawaiian plant species: endemic *Metrosideros polymorpha* Gaudich. ('ōhi'a, Myrtaceae), endemic *Styphelia tameiameiae* (Cham. and Schltdl.) F. Muell. (pūkiawe; Ericaceae), and native *Vaccinium reticulatum* Sm. ('ōhelo 'ai; Ericaceae). For all of these species, we had casually observed visitation of both *A. mellifera* and native bee species (especially *Hylaeus* spp.) before conducting the present study. We quantified flower visitation by *A. mellifera* and other pollinators using systematic visitation observations. All observations were performed over six weeks in the summer of 2015 at a montane mesic forest site on Mauna Loa Volcano, Hawai'i Island, at approximately 1200 m elevation. Because these data were collected in one flowering season and one study site, we consider them to be preliminary; our next step is to expand these data collection methods to a wider diversity of endemic plants, additional field sites, and multiple years of data collection. Additionally, we report here solely observational flower visitation data, determined to be effective in some systems (Vázquez et al. 2005) and ineffective in others (King et al. 2013) at identifying pollinators; to supplement these observations and further explore the role of particular visitor groups, we are currently performing controlled pollination treatments on flowers of these species to evaluate fruit and seed set in the absence and presence of *A. mellifera* visitation.

Flower Visitation Observations

Observations took place in July and August 2015. Plants were observed in 10-minute blocks by four observers. *Metrosideros polymorpha* Gaudich. was observed for a total of 1610 minutes, *S. tameiameiae* (Cham. and Schlecht.) F. Muell. for a total of 1510 minutes, and *V. reticulatum* Sm. for a total of 1530 minutes. Plants flowered on a rolling basis, therefore observations moved among flowering plants on each succeeding observation day. In all, 32 *M. polymorpha* individuals and 231 flowers were observed, 45 *S. tameiameiae* individuals and 663 flowers were observed, and 41 *V. reticulatum* individuals and 1224 flowers were observed. Each 10-minute observation period was divided into a 1-minute scan sample and a 9-minute focal individual observation period (Aslan 2011; Aslan et al. 2014). During the scan sample, focal plants were observed from a fixed point to determine the total number of individuals of each species of flower visitor interacting with the focal flowers. During the focal individual observation period, individual visitors were observed, and the observer recorded the number of flowers visited as well as visitor behavior (pollen or nectar foraging, nectar robbing, etc.) during those visits. New focal individuals were selected and observed in sequence as long as they were present until the 9-minute period had ended, at which point the observation block ended and a new block began with a new scan sampling period.

Analysis

Flower visitation observation data were used to calculate Pollinator Importance (adapted from Renne et al. 2000; Aslan et al. 2014; Aslan 2015), a systematic method of comparing visitor *importance* (sensu Renne et al. 2000) and identifying important visitors as those that visited large numbers of flowers or were present in high abundance. Pollinator Importance (FPI) is calculated as the average number of visiting individuals of each flower visitor group per minute from scan samples, multiplied by the total number of flowers visited by each individual per minute, for each plant/flower visitor combination. This total flower visitation is then divided by the total average number of open flowers observed. We examined resulting FPI values to determine which visitors emerged as most important, and compared those values using a simple one-way analysis of variance for each focal plant species.

RESULTS

The visitor taxon with highest FPI across all three focal plant species was native *Hylaeus* spp. bees (Figure 1). This result was largely driven by the tendency of *Hylaeus* bees to visit multiple flowers within a single observation (Table 1). FPI values for *A. mellifera* and *Hylaeus* as visitors of *M. polymorpha* were quite similar and considerably greater than values for the other flower visitors (Lepidopteran moths, Hymenopteran wasps, and nonnative Syrphidae flies; and the native birds *Vestiaria coccinea* Forster and *Himatione sanguinea* Gmelin and nonnative *Zosterops japonicas* Temminck and Schlegel). For the Ericaceae species *S. tameiameiae* and *V. reticulatum*, *Hylaeus* again exhibited the highest FPI, with *A. mellifera* visiting flowers much more rarely than *Hylaeus*. One-way analysis of variance results revealed significant differences among FPI only for *S. tameiameiae* ($F = 22.63$; $P < 0.0001$; df = 2). Due to large variances, there were no significant differences in FPI for visitors of *M. polymorpha* ($F = 0.104$; $P = 0.996$; df = 6) or *V. reticulatum* ($F = 1.43$; $P = 0.262$; df = 2).

Implications

Because observations took place within a single season and because visitation data alone can vary in significance based on system, we consider these results preliminary and will expand this study to encompass flower treatments as well as additional plant species in future seasons. Nevertheless, these initial results imply that the effectiveness of *A. mellifera* in this system is once again context-dependent. For *M. polymorpha*, *A. mellifera* exhibited the second greatest FPI, but its importance did not differ significantly from that of the native *Hylaeus* bees (Figure 1). This result contrasted somewhat with results exploring pollination of *M. polymorpha* in a lower-elevation system further south on Hawai‘i Island, wherein *A. mellifera* was found to be the most important pollinator (Hanna et al. 2013); the relative importance of *A. mellifera* in pollinator networks may vary even over relatively short spatial distances and within ecosystem types and between years.

Apis mellifera as a pollinator appeared even less important for *S. tameiameiae* and *V. reticulatum*. Visitation observations suggested that native *Hylaeus* bees were by far the most important visitors for both species, followed by nonnative Syrphidae spp., with *A. mellifera* as significantly less important (Figure 1).

CONCLUSIONS

The impact of *A. mellifera* on pollination in natural areas is context-dependent, varying by focal plant species and by ecological community. *Apis mellifera* acts as an effective pollinator of generalist plants, in particular, and occupies a highly influential role in interaction networks but is likely to serve in many cases as an imperfect replacement for native pollinators. In some circumstances, such as for plants with specialist floral characteristics requiring specialized morphology or behavior on the part of pollinators, *A. mellifera* may be ineffective compared with native pollinators; in other cases, the high abundance typical of *A. mellifera* populations may generate high pollination rates for certain native species. In some systems, *A. mellifera* appears to compete with native pollinators for resources. This is most likely when niche overlap is great and floral resources limited and is a phe-

Table 1. Components of flower visitation importance (FPI) for each visitor taxon to each focal native plant species. Overall FPI for each visitor taxon is calculated from presence (i.e., the average number of visitors of each taxon per unit time) and activity (i.e., the average number of flowers visited by each visitor). The native *Hylaeus* spp. bees exhibited the highest FPI for all three plant species.

	Visitor taxon	Importance ± SE	Presence ± SE	Activity ± SE
Plant species				
Metrosideros polymorpha	*Apis mellifera*	0.13 ± 0.02	0.069 ± 0.0054	1.88 ± 0.14
	Hylaeus spp.	0.14 ± 0.19	0.031 ± 0.006	4.49 ± 0.36
	Vestiaria coccinea	0.0050 ± 0.05	0.00049 ± 3.94E-05	10.09 ± 1.82
	Zosterops japonicus	0.013 ± 0.21	0.00093 ± 0	13.44 ± 4.22
	Lepidopteran	± 0	0.00018 ± 0	0.34 ± 0
	Himatione sanguinea	0.011 ± 0.17	0.0021 ± 0	5.50 ± 0.5
	Hymenopteran wasps	0.0025 ± 0.038	0.00048 ± 0	5.22 ± 0
Styphelia tameiameiae	*Apis mellifera*	0.017 ± 0.0024	0.0036 ± 0.00023	4.62 ± 0.57
	Hylaeus spp.	0.25 ± 0.026	0.044 ± 0.0042	5.60 ± 0.23
	Syrphidae	0.067 ± 0.013	0.015 ± 0.0016	4.45 ± 0.75
Vaccinium reticulatum	*Apis mellifera*	0.0024 ± 0.00072	3.2 ± 0.8	0.00076 ± 0.00012
	Hylaeus spp.	0.030 ± 0.0096	3.51 ± 0.6	0.0085 ± 0.0023
	Syrphidae	0.0072 ± 0.0019	2.86 ± 0.6	0.0025 ± 0.00039

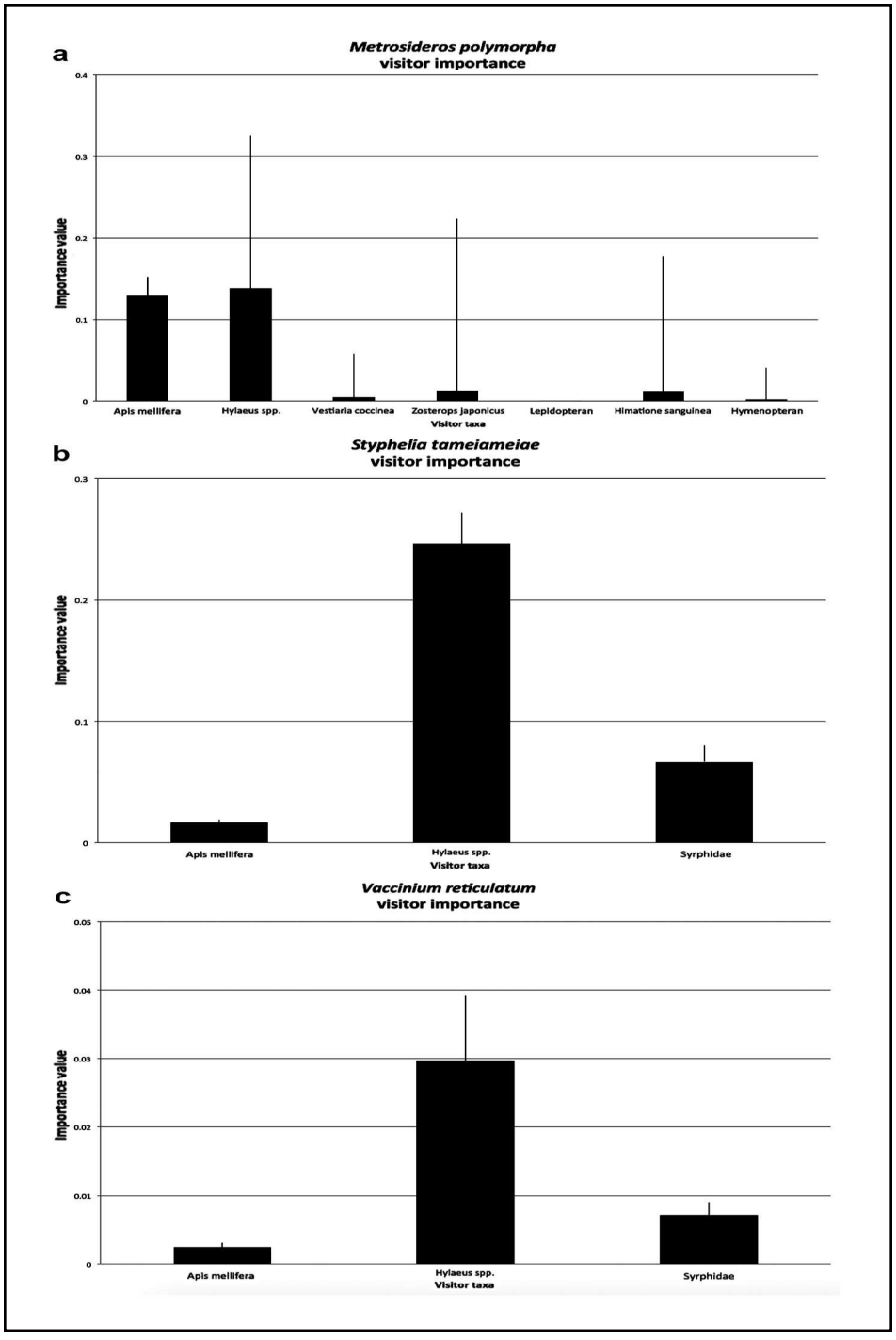

Figure 1. FPI of flower visitors to three native Hawaiian plant species, quantified via flower visitation observations recording visitor presence and behavior. (a) For *Metrosideros polymorpha*, the most important visitors were the native *Hylaeus* spp. bees, but *A. mellifera* was only marginally less important. (b) *Hylaeus* spp. bees were also the most important visitors for *Styphelia tameiameiae*, with much smaller importance attributed to *A. mellifera*. (c) Similarly, *Hylaeus* spp. bees were by far the most important visitors to *Vaccinium reticulatum*, with little visitation by *A. mellifera*. Bars represent mean importance ± standard error.

nomenon that could restructure interaction networks and ecological communities. The role of *A. mellifera* as a pollinator of rare or conservation-dependent plants depends on the floral characteristics of those plants and their communities as well as on the diversity of the extant native pollinator community.

Although its close ties to human agriculture have led to its successful spread around the globe, *A. mellifera* currently faces a number of emerging threats. Factors such as pesticide use, habitat loss, and disease and parasite introductions are likely culprits in current *A. mellifera* declines (Ball and Allen 1988; Genersch 2010; Johnson et al. 2010). Colony infestation by the *Varroa destructor* (Anderson & Trueman) mite reduces colony resource reserves during winter months and causes significant *A. mellifera* losses, especially in northern regions (Guzmán-Novoa et al. 2010), implying that in many cases *A. mellifera* will not persist in northern natural areas without active management. Extreme habitat loss is also correlated with significant declines in diversity and abundance of bees (Winfree et al. 2009; Abrol 2012; Goulson et al. 2015). The predominance of plant monocultures in agriculture and resulting lack of pollen and nectar diversity have also been identified as potential stressors for *A. mellifera* (Decourtye et al. 2010). Proximity of forest habitats to agricultural areas boosted bee diversity in Costa Rica (Brosi et al. 2007). Where *A. mellifera* is native, the presence of game reserves appears to increase the density of hives, perhaps bolstering bee populations (Vaudo et al. 2012). Network analysis implies that plant species with fewer pollinator species are most at risk of negative impact from pollination disruption resulting from loss of those pollinator species (Spira 2001). The presence of natural areas and diverse native species appears essential to conservation of pollination as a service, whether mediated by *A. mellifera* or native pollinators.

Maintaining large, structurally-diverse expanses of habitat may be key to sustaining maximum richness of pollinator species (Kearns et al. 1998; Spira 2001). Habitat can be maintained or increased by planting native host plants (Dumroese et al. 2016 this issue pps. 499-511), following best management practices with regard to nonnative plant species, forest conditions, and roadside and powerline corridors (Hanula et al. this issue pps. 427-439), and managing the timing and intensity of ungulate grazing (DeBano et al. 2016 this issue pps. 458-477). *Apis mellifera* is integrated into many natural areas and

interacts with hundreds of native plant species, but its generality makes it unlikely to replicate the function of diverse communities of native pollinators in natural areas. Natural area managers concerned about native plant reproduction should assess the effectiveness of *A. mellifera* as a pollinator of target plant species when determining how to manage *A. mellifera* populations. In many cases, management efforts to boost native pollinator communities threatened by habitat loss and environmental change may be critical.

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