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Alien Insects Dominate the Plant-Pollinator Network of a Hawaiian Coastal Ecosystem¹

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Abstract: Little is known regarding pollination webs involving island coastal plants and pollinators, and roles that nonnative flower visitors may play in these interaction networks. Plant-pollinator observations made in March 2008 and 2009 were used to describe the pollination network for Ka'ena Point, one of Hawai'i's best-conserved coastal communities. The network includes 15 native plant species, two native bee species, and 26 nonnative insect taxa, forming 119 interactions. Network connectance is 29.4% and weighted nestedness is 17.9, which are similar to values of other dry-habitat, island networks. The network's structure has a core of generalized pollinators plus several more-specialized pollinators. Nearly all plant species interact with two or more generalist pollinators and a variable number of specialists. Small, nonnative bees (*Lasioglossum*, *Ceratina*), wasps (*Proconura*), and flies (mostly Tachinidae) were responsible for 72.7% of flower visits, and they visit five plant species not visited by native bees. The two native visitors were the bees *Hylaeus anthracinus* and *H. longiceps* (both proposed as endangered). *Hylaeus* spp. (especially females) provided 19.8% of flower visits, foraging at high visitation rates and on many species, including the endangered *Scaevola coriacea* and *Sesbania tomentosa*. In Hawai'i's coastal habitat, nonnative insects form novel interactions with native species and may maintain an ecosystem's function following loss of most of the original native pollinators. However, their high visitation rates suggest that the two remaining native *Hylaeus* species are potentially important pollinators for many of the native plants on which they rely for nectar and pollen resources.

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SPECIES INTERACTION networks have been described as "the architecture of biodiversity" because of their importance for community composition and dynamics (Jordano et al. 2006, Bascompte and Jordano 2007). Networks can be analyzed to identify keystone species (Christianou and Ebenman 2005), monitor biodiversity (Forup et al. 2008), and determine the functional roles of nonnative species (Kaiser-Bunbury et al. 2010, Tylianakis et al. 2010). Network analyses are increasingly being used to understand how communities are changing as a result of species invasions or extinctions (Memmott et al. 2004, Bjerknes et al. 2007, Kaiser-Bunbury and Muller 2009; Traveset, Heleno, et al. 2013; Traveset, Chamorro, et al. 2015).

Plant-pollinator networks on oceanic islands are of interest for a variety of reasons. Owing to their isolation, island biotas are often naturally disharmonic and relatively

species-poor (MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2007). As a result, their plant-pollinator networks commonly have generalized interactions [i.e., most species interact with many mutualists (Olesen et al. 2002, Dupont et al. 2003)] and taxonomic disharmony among the pollinators (Kaiser-Bunbury et al. 2010). This often translates into small network sizes, high connectance (i.e., a high proportion of potential plant-pollinator interactions being realized), and a super-generalist species that dominates interactions (Olesen et al. 2002, Dupont et al. 2003, Trøjelsgaard and Olesen 2013, Traveset et al. 2016). In addition, in many island systems, some native species have become rare or gone extinct, and one or more non-native species dominates interactions or visits (Dupont et al. 2003, Kaiser-Bunbury et al. 2010, Traveset et al. 2013). Nonnative species typically enter a network by interacting with generalist native species; this has been documented with nonnative plant invasions (Traveset and Richardson 2006, Bjerknes et al. 2007, Bartomeus et al. 2008) and the honey bee, *Apis mellifera* (Dupont et al. 2003, Kaiser-Bunbury et al. 2011). Once in the network, nonnative species have a large impact by interacting with many partners (Bartomeus et al. 2008, Padron et al. 2009) and affecting other species' interactions (Aizen et al. 2008, Kaiser-Bunbury et al. 2011, Traveset et al. 2013).

In Hawai'i, few studies have assessed relationships between plants and their insect pollinators (Medeiros et al. 2013). Hawai'i's native insect fauna is disharmonic because many pollinator taxa common in other ecosystems are underrepresented or absent. For example, Hawai'i has only two native butterfly species (Zimmerman 1958) and lacks native social insects altogether (Wilson and Taylor 1967). Hawai'i's only native bees are a radiation of >60 species of *Hylaeus* (Colletidae, yellow-faced bees) (Daly and Magnacca 2003). They have been found visiting flowers of native plants throughout Hawai'i (Magnacca 2007, Wilson et al. 2010, Koch and Sahli 2013, Krushelnicky 2014, Sahli et al. 2016). Unfortunately, lowland native insect communities have been devastated by a variety of factors,

including interactions with nonnative insects (Howarth 1985, Cole et al. 1992), novel predators (e.g., Kraus et al. 2012), and habitat loss (Asquith and Messing 1993). As a result, many insect pollinators, including many *Hylaeus* spp., are rare or extinct (Howarth 1985, Magnacca and King 2013).

Little is known about the original state of the coastal strand ecosystem of Hawai'i beyond general descriptions of vegetation and the physical environment, and the observation that these ecosystems have been severely impacted by development, recreation, and nonnative species (Richmond and Mueller-Dombois 1972, Cuddihy and Stone 1990, Warshawer et al. 2009). At least three coastal plant species require a pollinator for outcrossing or for transfer of self-pollen to the stigma for seed set: *Sesbania tomentosa* (Hopper 2002), *Sida fallax* (Yorkston and Daehler 2006), and *Jacquemontia sandwicensis* (Shay 2014). Observations of flower visitors of five coastal plant species have recorded two native and at least 19 nonnative insect taxa, mostly bees, ranging from likely pollinators to nectar thieves (Hopper 2002, Elmore 2008, Pleasants and Wendel 2010, Shay 2014). Authors of these studies have frequently postulated the importance of native *Hylaeus* species as likely pollinators. The objectives of the research reported here are to (1) describe a plant-pollinator network qualitatively and quantitatively, in a community of native Hawaiian coastal plants; and (2) determine the relative diversity and potential importance of native and alien insects in the network.

MATERIALS AND METHODS

The study was carried out at Ka'ena Point Natural Area Reserve on the northwest coast of O'ahu (Figure 1). Annual rainfall is approximately 650 mm/yr, concentrated mainly in the winter (Giambelluca et al. 2013), and mean annual temperature is 22.2°C–25.5°C (Richmond and Mueller-Dombois 1972, Giambelluca et al. 2014). Plant communities on the north shore of O'ahu experience strong solar radiation, strong and regular trade winds, and effects of salt spray (Richmond and Mueller-Dombois 1972, Alpha et al. 1996,

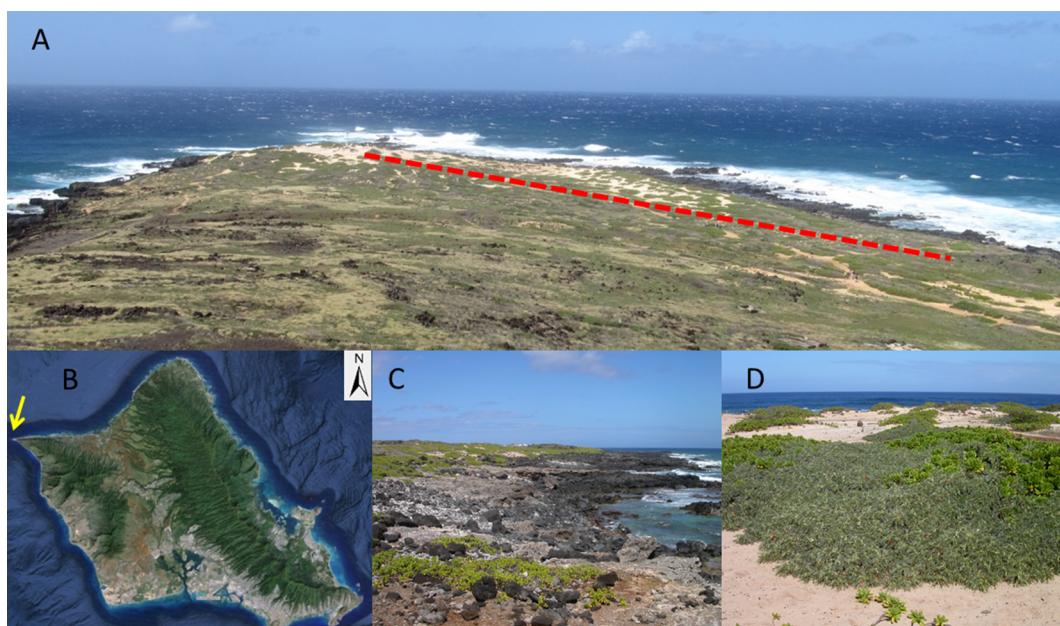


FIGURE 1. Ka'ena Point, O'ahu, Hawai'i. (A) Approximate transect through coastal habitat along the north shore of Ka'ena Point (dashed line). (B) Location of Ka'ena Point on O'ahu, Hawai'i (Google Earth, Landsat 2013). (C) Example of coastal strand vegetation. (D) Example of dune vegetation, including *Sesbania tomentosa* and *Scaevola taccada*.

Gagné and Cuddihy 1999). The study area contains protected native coastal strand (Young et al. 2013) and dune vegetation dominated by shrubs and low-growing plants.

Observations were made in March of 2008 and 2009. Ten observation points were placed 20–50 m from the shoreline, at approximately 100-m intervals from east to west along the north edge of the Natural Area Reserve (Figure 1). Alternate observation points were observed on every other day for 7 days in 2008 and 4 days in 2009.

Fifteen native dicot species flowered regularly during observations, including both common (*Jacquemontia sandwicensis*, *Sida fallax*, and *Scaevola taccada*) and endangered (*Scaevola coriacea* and *Sesbania tomentosa*) species (see Table 1). Grasses were ignored and nonnative dicots that were flowering in the area were uncommon and located outside the observation points. A representative of each plant species within 10 m of the observation point was randomly selected and observed for 15 min, if possible. For a plant species not

occurring within 10 m of the observation point, the closest flowering individual within 30 m was observed (or in rare cases additional plants at a different observation point were observed to obtain similar amounts of observation times for each species). Observations occurred from 0930 hours to 1700 hours and totaled 72.5 hr in 2008 and 56 hr in 2009. Observers recorded observation point; plant species; number of flowers observed; flower visitor; number of flowers visited by the visitor; duration of visit; whether reproductive structures of the flower were touched by the visitor; and whether the visitor foraged for nectar, pollen, or both. The flower visitors were identified in the field when possible; otherwise they were collected, when possible, for later identification. Collected insects were deposited in The University of Hawai'i at Mānoa Insect Museum after being resolved to the lowest possible taxonomic level by the museum's curator, Dr. Luc Leblanc.

In 2009, flower abundance (no./m²) was determined in a 20 by 20 m plot centered on

each observation point. For species having few or large flowers, all flowers in the plot were counted. For species having numerous or small flowers, flowers were counted in five parallel 0.5 by 20 m transects spaced 5 m apart. For plant species having small flowers borne in specialized inflorescences (*Boerhavia*, *Melanthera*), each inflorescence was counted as a single flower.

Overall, 2,072 observations of plant-flower visitor interactions were recorded. Visitors that were never observed contacting reproductive structures, those that were recorded visiting flowers only once (singletons), and visitors that could not be identified with certainty were removed from the network. These three groups accounted for 140 observed flower visits (6.8%) of the original observations. Although ants and thrips were frequent visitors (945 and 12 of the 2,072 observed flower visits, respectively), they were removed from the analysis (see Discussion). Removing singletons has little effect on most network indices (Dormann et al. 2009). Although we have data only for flower visitation, not pollination, we follow other studies in referring to the network as a plant-pollinator network (Jordano 1987), based on our criteria that flower visitors must visit more than once and must touch the reproductive structures on at least one of the visits (Dupont et al. 2003). Similarly, we refer to the flower visitors as (potential) pollinators based on the same criteria (see Table 2). We use the term “interaction” to indicate the presence of a pollinator taxon contacting a plant species.

Both binary and weighted bipartite interaction networks were created from the observation data. A bipartite network consists of two trophic levels, in this case plants and pollinators. In the binary network, interactions were recorded as present or absent, whereas in the weighted network, interactions were weighted by their frequency of occurrence. The observations from 2008 and 2009 were combined to build the binary network to create a more comprehensive estimate of interactions for the community (Nielson and Bascompte 2007, Hegland et al. 2010).

The appropriate weighting for a quantitative visitation network is the frequency of

visits by a given pollinator taxon to a particular plant species within a community: the number of visits per unit time within a study area. The stratified design of our observations did not directly yield estimates of these frequencies but instead gave frequencies of visits per flower per unit time. These then were multiplied by estimates of numbers of flowers in the study site to yield the desired weights, equivalent to weight M5 of Castro-Urgal et al. (2012). Because flower abundance data were collected only in 2009, the 2008 visitation data could not be used in the weighted network. For each observation session, the total number of visits to observed flowers by all visitors of a given pollinator taxon was divided by the number of flowers observed and the observation time, to give a rate of visits per flower per hour. Note that in this usage a “visit” is to a flower, not to the plant; a single visitor might visit several flowers on the plant and might even make more than one visit to the same flower. These rates, for a given plant-pollinator pair, were then averaged over all observation sessions at a given observation point. This average visitation rate for a plant-pollinator pair at an observation point then was multiplied by the number of flowers of that plant species at that point (i.e., in the 20 by 20 m plot) to give an estimate of the frequency of that interaction (as visits to flowers) for the entire plot. These rates were then averaged across the 10 observation points to give a measure of the community-wide frequency of visits by a given pollinator to flowers of a given plant species.

The bipartite package (version 2.04) (Dormann et al. 2009) in R 3.0.2 (R Core Team 2013) was used to calculate qualitative and quantitative network indices at the network level, trophic level, and at the species level to describe plant-pollinator interactions of this community.

In interaction networks, a nested pattern is present when relatively specialized species in one trophic level interact with a subset of those species in the other trophic level that interact with relatively generalist species (Bascompte et al. 2003). Nestedness was estimated with two indices: NODF and weighted nestedness. NODF is a measure of nestedness

in a binary network, based on decreasing fill and paired overlap (Almeida-Neto et al. 2008), where a value of 0 indicates nonnestedness and a value of 100 indicates perfect nestedness. Weighted nestedness (WNODF) is a quantitative measure of nestedness that is more robust to different patterns of species interactions than are other measures of nestedness in quantitative networks. It is based on overlap and decreasing number of interactions (Almeida-Neto and Ulrich 2011). Values range from 0 (not nested) to 100 (highly nested). The observed value of NODF in the 2008–2009 binary data set was compared by a z test to 1,000 null models with fixed row and column totals generated using NODF (Almeida-Neto et al. 2008). We could not perform a similar test using WNODF because null models for weighted networks are generated by shuffling individual visits, but the weights in our quantitative network were average frequencies rather than discrete visits. Modularity detects groups of species that interact more among themselves than with the rest of a quantitative network (Dormann et al. 2009, Dormann and Strauss 2014). The modularity index and modules were computed for the quantitative data set. The modularity index ranges from 0 to 1, where 0 indicates that the network has no more links within modules than expected by chance and 1 indicates the presence of modules in the network (Dormann and Strauss 2014). Interaction evenness, based on Shannon evenness, describes the distribution and uniformity of interactions between species in a community (Tylianakis et al. 2007, Kaiser-Bunbury et al. 2011); values range from 0 (uneven) to 1 (uniform).

Connectance is the realized proportions of links in the matrix (Dunne et al. 2002). Degree is the number of links, or interactions for a species (Dormann et al. 2009).

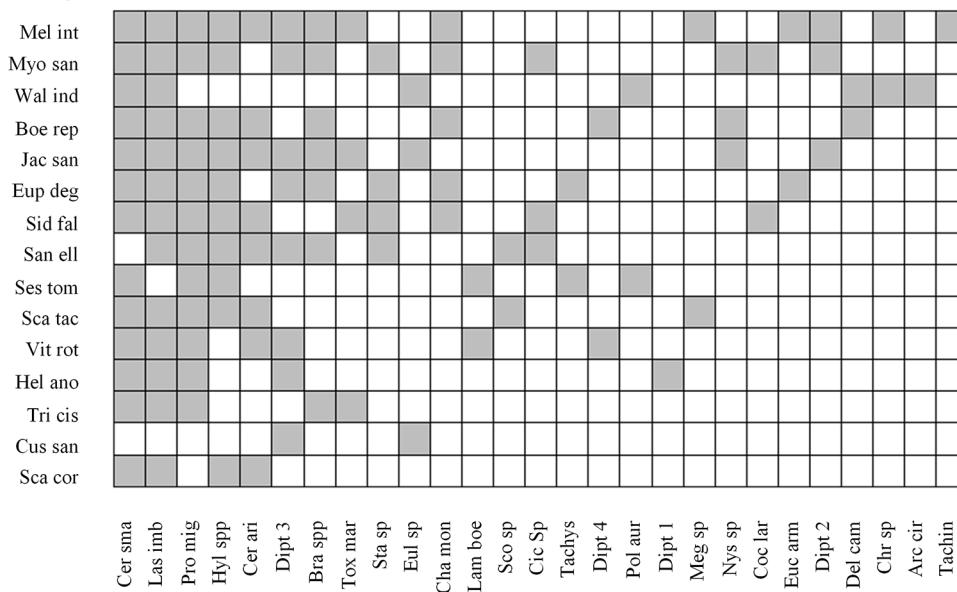
We use the terms “generalist/generalized” and “specialist/specialized” with respect to the number of interactions in which a species is involved. Generality is calculated for both trophic levels and is the weighted mean number of partners per species across a trophic level, using Shannon diversity for frequency of interactions by species (Bersier et al. 2002).

Network selectivity H2', based on Shannon entropy, measures the overall level of selectiveness within the network (Bluthgen et al. 2006); values range from 0 (highly opportunistic) to 1 (highly selective). Species selectiveness index d' is low when interactions of a species are proportional to the abundance of its partners, reflecting opportunistic interactions, and high when interactions of a species are not proportional to the abundances of potential partners (selective) (Bluthgen et al. 2006); values range from 0 (highly opportunistic) to 1 (highly selective).

RESULTS

The binary plant-pollinator network of 2008–2009 (Figure 2) includes 15 native plant species (Table 1), two native insect species (*Hylaeus* bees), and 26 nonnative insect taxa (Table 2) and has 119 interactions. Of the 119 interactions from the 2008 and 2009 data set, 44.5% of interactions were unique in 2008, 21.8% of interactions were unique in 2009, and 33.6% interactions were shared in both years. The quantitative network of 2009 (Figure 3) includes 12 plant species (Table 1), two native insect species, and 19 nonnative insect taxa (Table 2), with 51 interactions (Table 3). Because the females of the two native *Hylaeus* species are indistinguishable in the field, *Hylaeus* visitors were grouped together as one taxon in both networks (cf. Forup et al. 2008), yielding 27 pollinators in the binary data set and 20 in the quantitative data set (Table 3). In the binary data set, the most frequent generalist pollinators were the nonnative bees *Ceratina smaragdula* and *Lasioglossum imbrex* (13 interactions each), and *Myoporum sandwicense* was the most visited generalist plant (14 interactions) (Figure 3). The native *Hylaeus* spp. had 10 interactions (Figure 3). In the quantitative data set, *L. imbrex* (nine interactions) and *Jacquemontia sandwicensis* (eight interactions) were the most frequent generalist pollinator and visited plant, respectively (Figure 4). In the quantitative data set, Diptera 2 had the most visits to plants (27.3% of pollinator visits) (Figure 5), and *M. sandwicense* had the most visits from pollinators (42.8% of plant visits) (Figure 4). The native *Hylaeus*

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FIGURE 2. Binary plant-pollinator network of Ka‘ena Point, O‘ahu, Hawai‘i, 2008–2009. Each shaded cell represents an interaction between two species. Pollinators are represented in the columns, and plants are represented in the rows. Matrix rows and columns are sorted according to the “bimmatnests” algorithm in bipartite. See Table 1 for scientific names of plants and Table 2 for the most resolved names of taxa of pollinators.

TABLE 1
Plant Species in Pollination Networks at Ka‘ena Point, O‘ahu, Hawai‘i

Family	Species	Status ^a	Present in 2009 Quantitative Web
Asteraceae	<i>Melanthera integrifolia</i>	e	Yes
Boraginaceae	<i>Heliotropium anomalam</i>	i	Yes
Convolvulaceae	<i>Cuscuta sandwichiana</i>	e	Yes
	<i>Jacquemontia sandwicensis</i>	e	Yes
Euphorbiaceae	<i>Euphorbia degeneri</i>	e	No
Fabaceae	<i>Sesbania tomentosa</i>	e,*	Yes
Goodeniaceae	<i>Scaevola coriacea</i>	e,*	Yes
	<i>Scaevola taccada</i>	i	Yes
Lamiaceae	<i>Vitex rotundifolia</i>	i	Yes
Malvaceae	<i>Sida fallax</i>	i	Yes
	<i>Waltheria indica</i>	i	Yes
Nyctaginaceae	<i>Boerhavia repens</i>	i	Yes
Santalaceae	<i>Santalum ellipticum</i>	e	No
Scrophulariaceae	<i>Myoporum sandwicense</i>	i	Yes
Zygophyllaceae	<i>Tribulus cistoides</i>	i	No

^a e, endemic; i, indigenous; *, endangered.

TABLE 2
Pollinator Taxa in Pollination Networks at Ka‘ena Point, O‘ahu, Hawai‘i

Order	Family	Species	Present in 2009 Quantitative Web
Coleoptera	Bruchidae	<i>Stator</i> sp.	No
	Chrysomelidae	Chrysomelidae sp.	Yes
	Coccinellidae	Coccinellidae sp. larvae	Yes
	Scolytidae	Scolytidae sp.	Yes
	Syrphidae	<i>Toxomerus marginatus</i>	Yes
	Tachinidae	<i>Archytas cirphis</i>	Yes
		<i>Chaetogaeidia monticola</i>	Yes
		<i>Eucelatoria armigera</i>	No
		Tachinidae sp.	Yes
	Unknown	Diptera sp. 1	Yes
Diptera	Unknown	Diptera sp. 2	Yes
	Unknown	Diptera sp. 3	Yes
	Unknown	Diptera sp. 4	No
	Cicadellidae	Cicadellidae sp.	No
Hemiptera	Lygaeidae	<i>Nysius</i> sp.	Yes
	Apidae	<i>Ceratina arizonensis</i>	Yes
Hymenoptera	Braconidae	<i>Ceratina smaragdula</i>	Yes
	Chalcididae	Braconidae spp.	No
	Colletidae	<i>Proconura migratoria</i> ^a	Yes
	Crabronidae	<i>Hylaeus antbracinus</i> ^b	Yes
	Eulophidae	<i>Hylaeus longiceps</i> ^b	Yes
	Halictidae	<i>Tachysphex</i> sp.	No
	Megachilidae	Eulophidae sp.	Yes
	Vespidae	<i>LasioGLOSSUM imbrex</i>	Yes
		<i>Megachile</i> sp.	Yes
		<i>Delta campaniforme esuriens</i>	No
Lepidoptera	Lycaenidae	<i>Polistes aurifer</i>	Yes
		<i>Lamprodes boeticus</i>	Yes

^a *Proconura migratoria* is listed in an unpublished MS by Yoshimoto (L. Leblanc, pers. comm.).

^b Native species.

spp. interacted with seven plants and were responsible for 19.8% of visits in the quantitative data set (Figure 4).

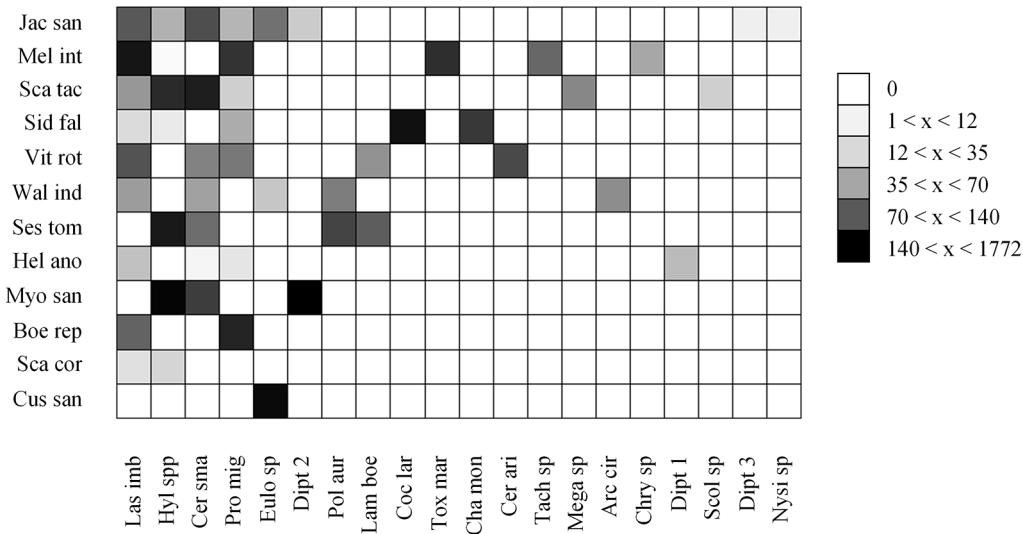
The binary data set had a connectance of 29.4% (Table 3). The NODF index (45.6) (Table 4) is significantly lower than the mean NODF of the randomized networks (47.9 ± 0.03 S.D., $z = -2.41$, $P < 0.01$), indicating a significantly anti-nested pattern in the observed network relative to null models.

The quantitative network's connectance was 21.3% (Table 3). WNODF was 17.9 (Table 4). The modularity index was 0.56, indicating a network with some division of modules. The modularity algorithm found five modules, where two modules include nine species or more and three modules include three species or less. This network lacks

compartments but does have a core block of generalists among which the majority of the interactions occur (Figure 2). Interaction evenness (IE) of the quantitative network was 0.52 (0 indicates uneven distribution of interactions and 1 indicates uniform distribution of interactions between species in the community). The H2' value of 0.73 indicates a selective network.

In both data sets, native bees (*Hylaeus*) and nonnative small bees (*LasioGLOSSUM*, *Ceratina*), wasps (*Proconura*), and flies (Tachinidae) were the most important pollinators both for presence/absence of interactions and rate of visitation (Table 5, Figure 4). Hymenoptera made up the largest proportion of taxa in the networks and were involved in more interactions and visits than other insect orders.

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FIGURE 3. Quantitative plant-pollinator network of Ka'ena Point, O'ahu, Hawai'i, 2009. Each cell is shaded from white (no interaction and no visits) to black (interaction present and visits very frequent), indicating the strength of the interaction between the plant and pollinator. Pollinators are represented in columns, and plants are represented in rows. Columns and rows are sorted according to the weighted interaction version of the NODF algorithm in bipartite. See Table 1 for scientific names of plants and Table 2 for the most resolved names of taxa of pollinators.

Diptera composed the second-largest proportion of taxa in the networks and in numbers of interactions and visits. Coleoptera, Hemiptera, and Lepidoptera made up minor proportions of the flower visitor community.

In both years, nonnative insects visited five plant species not visited by native *Hylaeus* bees (Figures 3 and 4, Table 6), and they provided 80.2% of visits in the quantitative network (Figure 5). The number of partners of native and nonnative pollinators ranged from 1 to 13 out of 15 possible plant species, with a mean degree of 4.4 ± 0.73 in the binary data set (Table 4). In the quantitative data set, nonnative insects visited from one to nine out of 12 possible plant species and had a mean degree of 2.6 ± 0.59 . This difference between data sets is due to the subset of data used for the quantitative analysis. Overall animal generality (weighted mean number of partners) was 2.4 in the 2009 quantitative data set.

The two native *Hylaeus* (*H. antibracinus* and *H. longiceps*) in aggregate visited many plant

species and foraged at high frequencies on multiple species, including the endangered *Scaevola coriacea* and *Sesbania tomentosa*. *Hylaeus* spp. visited 10 plant species in the overall data set (Figure 2), including seven plant species and 19.8% of the flower visits in the 2009 quantitative data set (Table 6). *Hylaeus* spp. provided large fractions of the visits to four plant species, including 50.4% for *S. coriacea*, 43.2% for *S. tomentosa*, and 33.0% for *Scaevola taccada*. Most *Hylaeus* spp. visits were to flowers of *Myoporum sandwicense*, *S. tomentosa*, and *S. taccada* (70.0%, 15.4%, and 11.3% of *Hylaeus* visits, respectively).

Generalized nonnative pollinators (*Lasiosiglossum imbrex*, *Ceratina smaragdula*, and *Procomura migratoria*) interacted with $\geq 80\%$ of the 15 species in the binary data set and $\geq 58\%$ of the 12 species in the quantitative data set (Figures 2 and 3). These three pollinators visited plants frequently, making up 23.1% of the visits in the quantitative network (Figure 4). Two specialized pollinators, Diptera sp. 2

TABLE 3
Network Metrics of the Binary and Quantitative
Pollination Networks of Ka'ena Point, O'ahu, Hawai'i

Network Parameter	2008–2009 Binary Data Set	2009 Quantitative Data Set
Number of plant species (P) ^a	15	12
Number of pollinator taxa (A) ^b	27	20
Total Interactions ^c	119	51
Number of visits ^d	975	138
A/P ^e	1.8	1.7
Network size ^f	405	240
Connectance ^g	29.4%	21.3%

^a The number of plant species is represented as P.

^b The number of pollinator taxa is represented as A.

^c Total interactions is the sum of all interactions in the network.

^d Number of visits is the total observations of pollinators visiting flowers.

^e A/P is the ratio of number of pollinator taxa to the number of plant species.

^f Network size is the number of pollinator taxa times the number of plant species (A*P).

^g Connectance is the realized proportions of links in the matrix (Dunne et al. 2002).

and Eulophidae sp., visited *Myoporum sandwicense* and *Cuscuta sandwichiana*, and accounted for 27.3% and 11.5% of the visits in the quantitative network, respectively. In the binary data set, *M. sandwicense* had 12 partners, but in the quantitative data set, it had only three. Of these three pollinators, Diptera sp. 2 provided 63.3% of the visits. This was the strongest interaction in the quantitative data set (accounting for 27.1% of visits in the network) due to the high abundance of *M. sandwicense* flowers in a plot (5,648 flowers). *Cuscuta sandwichiana* had two visitor species in the binary data set and one in the quantitative data set. Eulophidae sp. provided 100% of the visits to *C. sandwichiana*; the remaining 14 of the 20 pollinators (flies, wasps, beetles, true bugs, and a butterfly) interacted with relatively few plant species, ≤2 out of the 12, and did so relatively infrequently, accounting for 18.2% of the visits in the network (Figure 5).

In both data sets, most plant species interacted with several pollinators and thus appeared to be generalists (mean plant degree 7.9 ± 0.85 in the binary data set and 4.3 ± 0.58

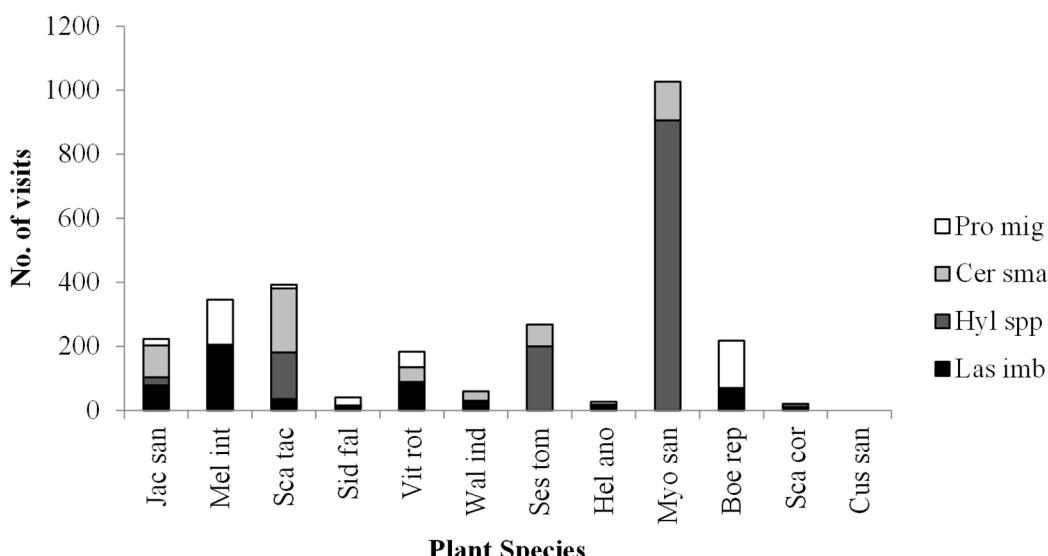


FIGURE 4. Distribution of visits of generalized pollinators to plant species from the quantitative network of Ka'ena Point, O'ahu, Hawai'i. The scientific name for plant species or most resolved name for pollinator taxa are shown in Table 1 for plants and Table 2 for pollinators. The percentage of visits by each taxon out of the total generalist pollinator visits is 46.1% for *Hylaeus* spp., 20.2% for *Ceratina smaragdula*, 19.4% for *Lasiglossum imbrex*, and 14.3% for *Proconura migratoria*.

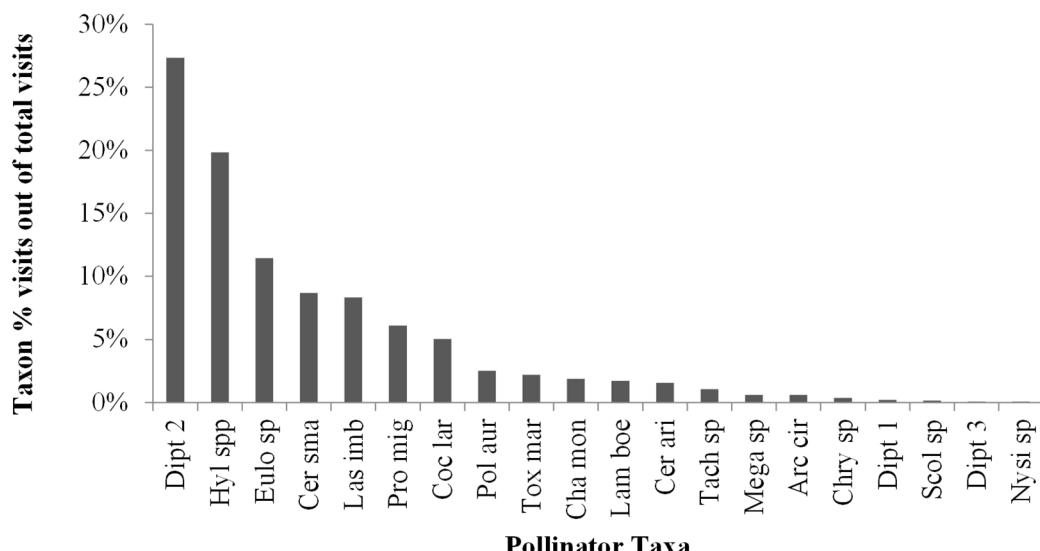


FIGURE 5. Proportion of visits by pollinator taxa in the quantitative network of Ka'ena Point, O'ahu, Hawai'i. The scientific name or most resolved name for taxa are given in Table 2 for pollinators.

in the quantitative data set) (Table 4). Plant generality (weighted mean of partners) for the quantitative data set was 2.8. In the quantitative data set, plants with the most visits included *Myoporum sandwicense* (42.8% of visits), *Cuscuta sandwichiana* (10.4%), and *Melanthera integrifolia* (9.0%) (Figure 6). Results for *S. coriacea* should be interpreted cautiously because only one individual was present at Ka'ena Point.

To assess species' selectivity, the d' index was evaluated in the quantitative network. Most plants and pollinators (42% and 50%, respectively) were categorized as selective (Figure 7) using the same four categories from Castro-Urgal and Traveset (2014).

DISCUSSION

In a Hawaiian coastal community consisting almost entirely of native flowering plants, the pollinator community is dominated by introduced insect species. This is an extreme example of novel interactions between natives and nonnatives within a community. Nonnative pollinators composed 96% of the pollinator taxa recorded over the 2 yr of observations

and were involved in 80.2% of flower visits in 2009. Unfortunately, the species composition of the original native pollinator community in the Hawaiian coastal habitat is unknown (Howarth 1985; L. Leblanc, pers. comm.), so there are no baseline data for comparison. Several studies have documented incorporation of nonnative plants (Traveset and Richardson 2006, Bjerknes et al. 2007, Bartomeus et al. 2008) and/or pollinators into plant-pollinator networks (Kaiser-Bunbury and Muller 2009, Traveset et al. 2015), but we are aware of none reporting such an extreme case of a native plant community interacting primarily with nonnative pollinators. A large shift in the pollinator assembly from natives to nonnatives has been reported on the Ogasawara (Bonin) Islands, Mauritius, and the Galápagos Islands (Abe 2006, Kaiser-Bunbury and Muller 2009, Traveset et al. 2013). Many native and endemic small bee taxa of the Ogasawara Islands have declined owing to predation by introduced lizards (Abe 2006, Abe et al. 2008). Nonnative taxa made up 22% of the observed pollinator taxa and 63% of the flower visits in heath vegetation in Mauritius (Kaiser-Bunbury and Muller 2009).

TABLE 4

Network Indices for the Binary and Quantitative
Pollination Networks of Ka'ena Point, O'ahu, Hawai'i

Network Index	2008–2009 Binary Data Set	2009 Quantitative Data Set
NODF ^a	45.6	—
Mean null model NODF	47.9 ± 0.0307	—
WNODF ^b	—	17.9
Mean degree A ^c	4.4 ± 0.73	2.6 ± 0.59
Mean degree P	7.9 ± 0.85	4.3 ± 0.58
Max degree A ^d	13	9
Max degree P	14	8
Generality A ^e	—	2.4
Generality P	—	2.8
Interaction evenness ^f	—	0.52
H2' ^g	—	0.73
Mean d'A ^b	—	0.57 ± 0.04
Mean d'P	—	0.58 ± 0.07

Note: Standard error of the means are reported for NODF, degree, and d'.

^a NODF determines nestedness based on decreasing fill and paired overlap, where a value of 0 indicates nonnestedness and 100 indicates perfect nestedness (Almeida-Neto et al. 2008).

^b WNODF is weighted nestedness, a quantitative nested measure that is based on overlap and decreasing number of interactions (Almeida-Neto and Ulrich 2011).

^c Mean degree is the mean number of links, or interactions of a species (Dormann et al. 2009).

^d Max degree is the species with the maximum number of links.

^e Generality is the mean number of partners per species from a trophic level weighted by their marginal totals (Bersier et al. 2002).

^f Interaction evenness, based on Shannon evenness, describes the distribution and uniformity of interactions between species in a community (Tylianakis et al. 2007).

^g H2' is the specialization of the network that is based on Shannon entropy (Bluthgen et al. 2006).

^b d' measures the level of specialization of a species (Bluthgen et al. 2006), based on Shannon entropy (Bluthgen et al. 2006).

In the Galápagos Islands lowlands, alien plants and pollinators made up 20% of the taxa and 38% of interactions (links) (Traveset et al. 2013). Pollination of native plants by nonnative pollinators may be either less efficient or more efficient than pollination by native pollinators (Ings et al. 2005, Kenta et al. 2007, Chamberlain and Schlising 2008).

As in our pollination network, nonnative species dominate various other arthropod assemblages in Hawai'i, including lowland insects (Asquith and Messing 1993), aquatic arthropods (Englund 2002), and parasitoids

of native moths feeding on native plants (Henneman and Memmott 2001). In addition, other systems in Hawai'i and on other islands include novel interactions between native and nonnative species, which in some cases appear to maintain ecosystem functions. In New Zealand, nonnative rats (*Rattus rattus*) and the recent colonist silveryeye (*Zosterops lateralis*) pollinate some native forest plants (Pattemore and Wilcove 2012). On Hawai'i Island, native and nonnative pollinators shared three native plants (*Clermontia parviflora*, *C. montis-loa*, and *C. hawaiiensis*), but the visits were dominated by the nonnative Japanese white-eye (*Zosterops japonicus*), which pollinated only *C. parviflora* and *C. montis-loa* effectively (Aslan et al. 2014). On Maui, in dry forest dominated by native plants but lacking native birds, the avian seed-disperser community consisted entirely of nonnative species, which disperse the seeds of most of the fleshy-fruited native and nonnative plants (Chimera and Drake 2010). Nonnative species have the potential to provide mutualistic services in the absence of native animals, though the quality and quantity of the services may differ from those provided by natives (Aslan et al. 2012).

In some plant-pollinator communities, native generalist species could provide a way for nonnative mutualists to enter the community (Bjerknes et al. 2007, Lopezaraiza-Mikel et al. 2007). Many insects can easily interact with the flowers of many coastal plants of Hawai'i, including most of those at Ka'ena Point, because the flowers are open and easily accessible, and at least some are available throughout much of the year (Hopper 2002). Our results support the idea that most plants interact with several partners [high mean plant degree (Table 4)]. Once involved in the network, nonnative species could replace native species (Olesen et al. 2002, Bartomeus et al. 2008, Padron et al. 2009) by usurping and disrupting the existing interactions and visits in the network (Aizen et al. 2008, Traveset et al. 2013). Alien plants have been reported to increase the visits received by other plants by attracting more pollinators to the plant community (Lopezaraiza-Mikel et al. 2007). Conversely, by dominating the interactions with pollinators, they can reduce visits to other

TABLE 5
Insect Orders Represented in Pollination Networks of Ka‘ena Point, O‘ahu, Hawai‘i

Insect Order	No. Taxa ^a		Taxa % ^b		Interaction % ^c		Visit % ^d
	B	Q	B	Q	B	Q	Q
Hymenoptera	11	8	40.7	40	62.2	72.5	59.2
Diptera	9	7	33.3	35	22.7	15.7	33.4
Coleoptera	4	3	14.8	15	8.4	5.9	5.6
Hemiptera	2	1	7.4	5	5.0	2.0	0.1
Lepidoptera	1	1	3.7	5	1.7	3.9	1.7

Note: The number of pollinator taxa or the proportion of that insect order involved in different degrees in the network are presented for the binary data set (B) and quantitative data set (Q). The full list of pollinator taxa and insect orders is in Table 2.

^a No. taxa is the number of pollinator taxa observed for the network that fall into that insect order.

^b Taxa % is the proportion of pollinator taxa of an insect order out of the total number of taxa observed.

^c Interaction % is the proportion of interactions an insect order was involved in out of the total interactions observed in the network.

^d Visit % is the proportion of visits an insect order was involved in out of the total visits in the network.

TABLE 6

Plant Species' Proportions of Visits from *Hylaeus* spp. from the Quantitative Pollination Network of Ka‘ena Point, O‘ahu, Hawai‘i

Plant	% Visits from <i>Hylaeus</i> spp. (Plant View)	% <i>Hylaeus</i> spp. Visits (<i>Hylaeus</i> View)
<i>Scaevola coriacea</i>	50.38	0.81
<i>Sesbania tomentosa</i>	43.22	15.44
<i>Scaevola taccada</i>	32.99	11.28
<i>Myoporum sandwicense</i>	32.38	69.96
<i>Jacquemontia sandwicensis</i>	8.27	1.92
<i>Sida fallax</i>	1.20	0.46
<i>Melanthera integrifolia</i>	0.29	0.13
<i>Vitex rotundifolia</i>	0.00	0.00
<i>Waltheria indica</i>	0.00	0.00
<i>Heliotropium anomalum</i>	0.00	0.00
<i>Boerhavia repens</i>	0.00	0.00
<i>Cuscuta sandwichiana</i>	0.00	0.00

plants (Bartomeus et al. 2008). Overall, integration of a nonnative species into a network appears to depend on the species involved and other undetermined factors (Vila et al. 2009).

In spite of the abundance of nonnative pollinators, the network was still similar to those of other insular ecosystems (Traveset, Héleno, et al. 2013; Traveset, Chamorro, et al. 2015; Traveset, Tur, et al. 2016; Trøjelsgaard and Olesen 2013, Castro-Urgal and Traveset

2014). Both the binary and quantitative network parameters are similar to those of other small networks on islands (Tables 7 and 8) (Olesen et al. 2002, Padron et al. 2009, Trøjelsgaard and Olesen 2013). Compared to other island networks (Table 7) (Trøjelsgaard and Olesen 2013), our networks have fewer species and higher connectance, which could be due to removing singletons. When compared to other island networks in dry ecosystems, however, the total number of taxa, connectance, ratio of animals to plants, and average degree of pollinators and of plants are broadly similar (Table 7) (Dupont et al. 2003, Philipp et al. 2006, Padron et al. 2009).

The Ka‘ena Point binary data set does not have a nested pattern based on the NODF index. This data set's NODF value (45.6) is higher than that of an average island network (26.9) (Trøjelsgaard and Olesen 2013). However, when the average island network included some of the more thoroughly surveyed networks, our NODF pattern is no longer higher. The quantitative data set has a WNODF value similar to those of other networks on islands (Table 8) (Traveset et al. 2013, Castro-Urgal and Traveset 2014), where number of plant species ranges from 18 to 25 and number of pollinator species ranges from 60 to 93. WNODF was not tested against null models because current quantitative null models are based on discrete numbers of visits and are inappropriate for our

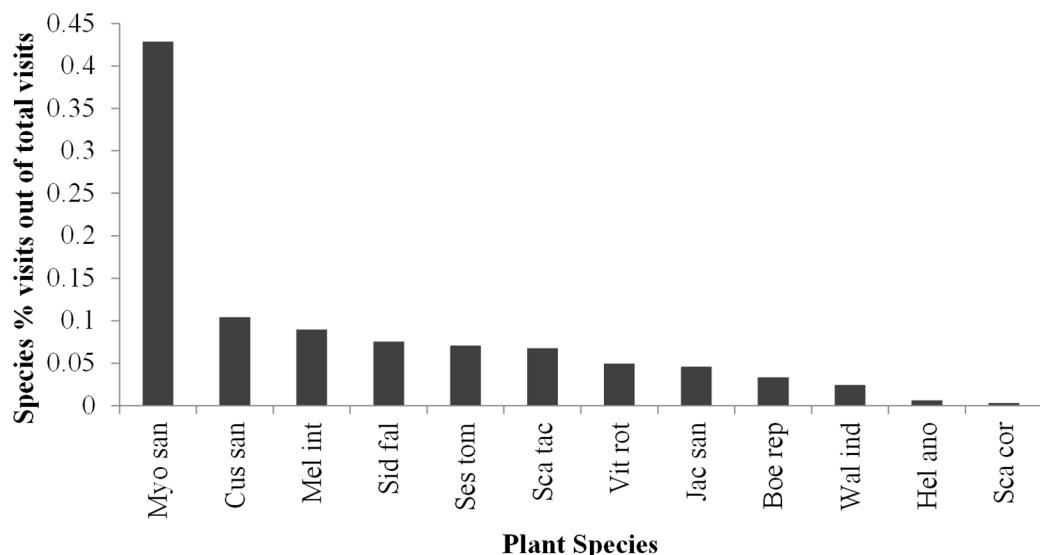


FIGURE 6. Proportion of visits to plant species in the quantitative network of Ka'ena Point, O'ahu, Hawai'i. Scientific names for plant species are given in Table 1.

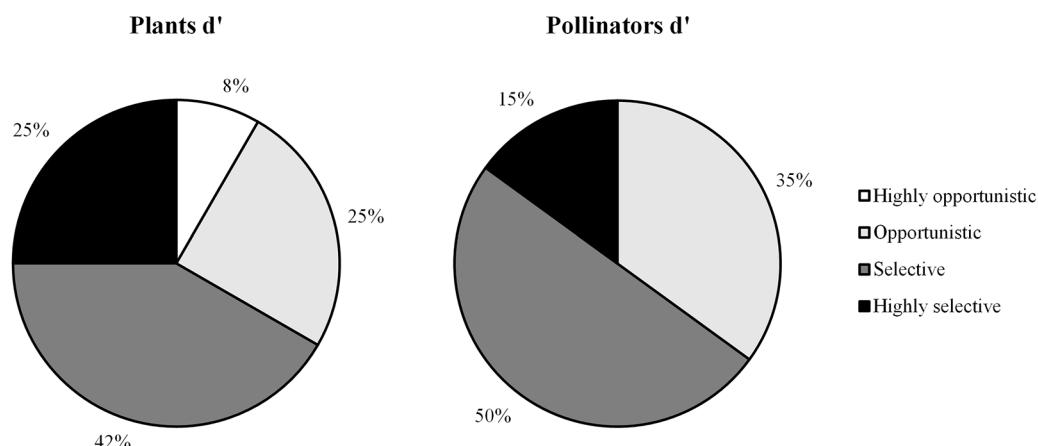


FIGURE 7. Categories of plant species or pollinator taxa d' values from the quantitative network of Ka'ena Point, O'ahu, Hawai'i. Species selectivity (d') index decreases when interactions of a species are proportionate to abundant partners (which is considered opportunistic), and the index increases when interactions of a species are disproportionately higher with a rare species (which is considered selective) (Bluthgen et al. 2006). d' categories (Castro-Urgal and Traveset 2014) are $0 \leq d' \leq 0.25$ (highly opportunistic), $0.25 < d' \leq 0.50$ (opportunistic), $0.50 < d' \leq 0.75$ (selective), and $0.75 < d' \leq 1.00$ (highly selective).

flower visitation rate (Ulrich et al. 2009, Gotelli and Ulrich 2011). Other studies have found mixed results when using different nestedness measures (Kratochwil et al. 2009, Ulrich et al. 2009), but most plant-pollinator

networks are nested (Bascompte et al. 2003). Our network had a core block of generalized plants interacting with generalized pollinators (Bascompte et al. 2003). Some studies report that the presence of nonnatives increases

TABLE 7
Pollination Network Metrics of Island Communities

Island	No. A ^a	No. P ^b	Connectance ^c	A/P ^d	Mean Degree (A) ^e	Mean Degree (P)	Study
O'ahu	27	15	29.4	1.8	4.4	7.9	This study
Average island	52	26	14.1	2	2.8	5.2	Trojelsgaard and Olesen (2013)
Flores	12	10	25	1.2	2.5	3	Olesen et al. (2002)
Ile aux Aigrettes	13	14	28.6	0.9	4	3.7	Olesen et al. (2002)
Tenerife (range of three subsets of data)	14–32	5–11	19.5–27.6	1.8–5.8	1.4–2.2	3.8–8.0	Padron et al. (2009)
Menorca (range of three subsets of data)	16–43	7–10	24.6–32.3	2.7–4.8	1.9–2.6	5.17–11.56	Padron et al. (2009)
Tenerife	38	11	25.8	3.5	2.8	9.82	Dupont et al. (2003)
Isabela	6	10	26.7	0.6	2.7	1.3	Philipp et al. (2006)
Son Bosc	143	69	2*	2.1	6.4	7.33	Castro-Urgal and Traveset (2014)
Cala Mesquida	131	42	3*	3.1	4.8	8.36	Castro-Urgal and Traveset (2014)
Caletón Blanco	62	18	6*	3.4	4.2	7.61	Castro-Urgal and Traveset (2014)
Las Conchas	62	25	5*	2.5	4.3	8.16	Castro-Urgal and Traveset (2014)
Mauritius restored site	135	74	13.2	1.8	5.5	10.2	Kaiser-Bunbury et al. (2009)
Mauritius control site	100	64	15.6	1.6	5.4	8.34	Kaiser-Bunbury et al. (2009)
All islands, Galápagos Islands	220	60	6	3.7	3.5	12.63	Traveset et al. (2013)

^a The number of pollinator taxa is represented as A.

^b The number of plant species is represented as P.

^c Connectance is the realized proportions of links in the matrix (Dunne et al. 2002).

^d A/P is the ratio of the number of pollinator taxa to the number of plant species.

^e Mean degree is the mean number of links, or interactions of a species (Dormann et al. 2009).

* Indicates this index was calculated differently than our methods.

nestedness (Bartomeus et al. 2008, Traveset et al. 2013), but this likely depends on the specific system.

The interaction evenness (IE) of the quantitative network was slightly lower than that of most other island networks (Table 8) (Kaiser-Bunbury et al. 2009; Traveset, Helleno, et al. 2013; Traveset, Tur, et al. 2016; Castro-Urgal and Traveset 2014). IE declined with invasion of nonnative plants in sites in Mauritius (Kaiser-Bunbury et al. 2011). Our network has mostly nonnative pollinators, and the lower IE value could reflect invasion by nonnatives.

Few plant-pollinator network studies report H2' and d' values, but the values observed

in our network fall in the upper range of values for other island pollinator networks (Table 8) for which these indices have been calculated (Traveset et al. 2013, Castro-Urgal and Traveset 2014). The observed values indicate a selective network (Bluthgen et al. 2006).

Nonnative flower visitors in this study were mostly bees, wasps, and flies, and they also provided most of the flower visits. The most generalized nonnative pollinators (*Ceratina smaragdula*, *LasioGLOSSUM imbrex*, and *Proconura migratoria*) interacted with the same plants, had similar degree, and provided many visits overall in the network, as did the native *Hylaeus* spp. However, the three nonnatives

TABLE 8
Quantitative Pollination Network Indices of Island Communities

Island	WNODF ^a	IE ^b	H2 ^c	d'A ^d	d'P	Study
O'ahu	17.9	0.52	0.73	0.57	0.58	This study
Son Bosc	10.41	0.42	0.73	0.54	0.56	Castro-Urgal and Traveset (2014)
Cala Mesquida	11.66	0.73	0.61	0.45	0.57	Castro-Urgal and Traveset (2014)
Caletón Blanco	19.91	0.79	0.46	0.37	0.41	Castro-Urgal and Traveset (2014)
Las Conchas	21.73	0.71	0.52	0.37	0.46	Castro-Urgal and Traveset (2014)
All islands, Galápagos Islands	11.87	0.67	0.57	0.42	0.52	Traveset et al. (2013)
Mauritius restored site	—	0.70 ± 0.027	—	—	—	Kaiser-Bunbury et al. (2009)
Mauritius control site	—	0.070 ± 0.026	—	—	—	Kaiser-Bunbury et al. (2009)

^a WNODF is weighted nestedness, a quantitative nested measure that is based on overlap and decreasing number of interactions (Almeida-Neto and Ulrich 2011).

^b Interaction evenness, based on Shannon evenness, describes the distribution and uniformity of interactions between species in a community (Tylianakis et al. 2007).

^c H2' is the specialization of the network that is based on Shannon entropy (Bluthgen et al. 2006).

^d d' measures the level of specialization of a species (Bluthgen et al. 2006), based on Shannon entropy (Bluthgen et al. 2006), by pollinator taxa (A) and by plant species (P).

distributed their visits among plant species differently than *Hylaeus* spp. These four pollinators may dominate in visits and share plant species as partners, but different plant species received varying numbers of visits from these frequent pollinators.

The only native pollinator taxon was *Hylaeus* spp. The two native *Hylaeus* species are probably important pollinators because of the high frequency of their visits. The *Hylaeus* taxon represented 3.7% of the pollinator taxa in the 2008–2009 binary data set and 5% of the pollinator taxa in the 2009 quantitative data set but interacted with many partners (10 out of 15 species in the binary network and seven out of 12 plant species in the quantitative network) and made many visits (19.8% of the total visitation rate in the 2009 quantitative data set). *Hylaeus* spp. are recognized across the Hawaiian Islands as potentially important pollinators for native plants (Hopper 2002, Magnacca 2007, Koch and Sahli 2013, Krushelnicky 2014, Sahli et al. 2016). Since this study was conducted in 2008 and 2009, *Hylaeus* populations appear to have declined throughout Hawai'i, and *Hylaeus anthracinus* and *H. longiceps* have been proposed as endangered (Magnacca and King 2013). *Hylaeus* bees have rarely been observed at Ka'ena Point since 2012 (Magnacca and King 2013;

K. N. Magnacca, pers. comm.; K.S., pers. obs.), which suggests that Ka'ena Point may become a coastal dune plant community in which all insect-pollinated plants are native and all pollinators are nonnative.

An unusual case in our network is the strong interaction between native *Cuscuta sandwichiana* and a nonnative wasp, Eulophidae sp., in 2009. Eulophidae sp. interacts with *C. sandwichiana*, *Jacquemontia sandwicensis*, and *Waltheria indica*. *Cuscuta sandwichiana* had one other partner in 2008, Diptera 3, which had eight partners in 2008. This appears to be a native specialist plant interacting with few nonnative partners. However, *C. sandwichiana* may have other pollinators at other seasons, or they may be lost from the system. Other species of *Cuscuta* have a variety of pollinators (Wright et al. 2012).

Another interesting change since 2008–2009 is the presence of the honey bee, *Apis mellifera*, which was not observed in 2008 or 2009 [probably because of a local decline caused by the *Varroa* mite (State of Hawai'i, Department of Agriculture 2007)]. Honey bees were quite noticeable in previous years (A.D.T., pers. obs.) and visited many flowers in spring 2014 (K.S., pers. obs.). Studies show that *A. mellifera* integrates into other island and native networks and dominates partners

and visits (Butz Huryn 1997). They dominated pollinator abundance and performed 43.8% of the visits in Mauritius (Kaiser-Bunbury et al. 2011), including 95% of the visits to the endemic shrub *Bertiera zaluzania* (Kaiser-Bunbury and Muller 2009). Honey bees visited 50% of the plant species in Canary Islands (Dupont et al. 2003).

Not all flower visitors are effective pollinators (Popic et al. 2013). One in particular that may rarely be a legitimate pollinator of *Sesbania tomentosa* was the nonnative butterfly *Lampides boeticus*. *Lampides boeticus* visited both *Vitex rotundifolia* and *S. tomentosa*, but contacted reproductive structures of only *V. rotundifolia*. *Lampides boeticus* may oviposit on *S. tomentosa* (Hopper 2002, Pratt et al. 2011).

Ants are an important component of this community, but one whose effects we were unable to determine. Impacts of ants on floral resources and plant reproduction in Hawai‘i range from negative to neutral or even beneficial for native flower visitors and native plants, but they are often regarded as nectar thieves (Junker et al. 2010, Bleil et al. 2011, Junker et al. 2011). Ants visited all plant species and were recorded 945 times out of 2,072 observations of flower visitors across both years. Ants were removed from the analysis because they are rarely pollinators (Junker et al. 2010, Beattie et al. 1984). However, other insect interactions in the community could be affected by ants. Ants could be removing floral resources or physically interfering with pollinators on flowers (Lach 2008, Junker et al. 2011, LeVan et al. 2014) and could decrease pollinator populations in the habitat (Cole et al. 1992, Krushelnicky and Gillespie 2008, Junker et al. 2011).

This description of plant-pollinator interactions can assist efforts to restore and conserve the native coastal ecosystem of Hawai‘i (Medeiros et al. 2013, Young et al. 2013). Restoration plans should consider assessing the status of remaining native pollinators, such as *Hylaeus* spp., and nonnative pollinators, because both are involved in many interactions and visits in the community (Magnacca 2007, Medeiros et al. 2013). This study and other examples (Aslan et al. 2012) describe how nonnative species form novel

interactions with native species and can potentially maintain an ecosystem’s function after it has lost most of its original native species.

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