



# Island Invasions by Introduced Honey Bees: What Can Be Expected for Puerto Rico and the Caribbean?

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*Apis* species are a major component of pollinator faunas in their native and introduced habitats. A widespread concern is that non-native *Apis mellifera* may have negative effects on native pollinators and on plant reproduction. This is based on the assumptions that natural communities are at capacity, resource competition structures communities, native pollinators are more effective pollinators of native species, yet *A. mellifera* are superior competitors. The latter two assumptions are often true, but evidence from the Neotropics indicates that tropical communities are not tightly structured, and the foraging flexibilities of native bees maintain their populations. However, the less diverse and disharmonic biotas of islands may limit the buffering capacity of flexible behaviors. While few studies address these assumptions or the ecological and evolutionary consequences of *A. mellifera* to the flora and fauna of tropical islands, an accumulation of taxon-specific studies are suggesting that such effects run the spectrum from subtle and indirect to obvious and direct. A concerted research effort is needed to address the multitude of issues to develop strategies to ameliorate or enhance honey bee effects, or just let nature take its course.

**Keywords:** competition, loose niches, invasional meltdown, biological invasion, Island biology, *Apis mellifera*, Africanized honey bees, pollinator services

## OPEN ACCESS

### Edited by:

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### Specialty section:

This article was submitted to  
Population and Evolutionary  
Dynamics,  
a section of the journal  
Frontiers in Ecology and Evolution

**Received:** 28 April 2020

**Accepted:** 22 December 2020

**Published:** 21 January 2021

### Citation:

Ackerman JD (2021) Island Invasions  
by Introduced Honey Bees: What Can  
Be Expected for Puerto Rico and the  
Caribbean?  
*Front. Ecol. Evol.* 8:556744.  
doi: 10.3389/fevo.2020.556744

## INTRODUCTION

Native island biotas are depauperate compared to areas of similar size on continents, a phenomenon driven by immigration, extinction, isolation, area, habitat diversity, among other factors (MacArthur and Wilson, 1967; Whittaker et al., 2017). Island biotas also tend to be phylogenetically and functionally disharmonic since some taxa are more likely than others to arrive, survive and reproduce on an island (Taylor et al., 2019; König et al., 2020). This often leaves functional gaps on islands, such as predators, or certain taxa such as ants and palms (Weigelt et al., 2015). Given the lower diversity and disharmony of island biotas, we expect interaction networks to be loosely structured (Traveset et al., 2015).

Islands, especially in the tropics, are also disproportionately subject to human-assisted biological invasions (Rejmánek, 1996; Sax et al., 2002). Among the possible reasons for this are low biotic resistance, high resource availability, and high propagule pressure (e.g., Loope and Mueller-Dombois, 1989; Simberloff, 1995, 2009; Denslow, 2003). Consequently, local biotas have become a novel but functioning mix of native and introduced species (Lugo et al., 2018). Here I review the role of non-indigenous honey bees, *Apis mellifera* (HB) in these novel systems of tropical and subtropical islands, and what we can expect of HB interactions for the Caribbean and Puerto Rico in particular.

## BEES AS INVADERS

Bees are among the most notable invasive insects. There are at least 80 species of bees recorded as non-indigenous invaders, many of them recorded in just the last 25 years (Russo, 2016). Bees are appreciated for their pollinator services in both natural and managed ecosystems, but there are costs. For all but two genera (*Apis* and *Bombus*), impacts are largely speculative as few studies have been published. However, the literature is replete with studies of invasive *Bombus* and *Apis*, and yet much more work needs to be done. Thus far, the negative impacts include competition with native species for floral resources and nest sites; displacement of native pollinators; transmission of pathogens and parasites; reduced reproductive success for native plants; disruption of plant-pollinator networks; hybridization with native species; and pollination services for invasive plants (Goulson, 2003; Thomson, 2004; Aizen et al., 2009; Abrol, 2012; Russo, 2016). The only negative impact that is unequivocally and consistently demonstrated is the transmission of pathogens and parasites to native bees (Paini, 2004; Russo, 2016).

### Bees as Tropical and Subtropical Island Invaders

Nearly half the invasive bee species records are for islands, a third of these are exclusively island invaders, and most accidentally introduced. HB are one of the few notable exceptions (Russo, 2016). While islands may be susceptible to invasions because of “open niches,” the relative frequency of floral visits by HB in island plant-pollinator networks generally do not attain the same level as they do in continental regions (Hung et al., 2018). Nevertheless, direct and indirect ecological impacts of non-indigenous bees through exploitative competition can be substantial.

### Impacts of Invasive Honey Bees

What impacts do invasive HB have on the native flora and fauna? There is evidence that invasive HB can deplete pollen and nectar supplies available to native pollinators. If just one strong colony collects enough pollen in a single season to support 100,000 progeny of an “average” native bee, then this should have an impact (Cane and Tepedino, 2017). Competition for resources is suggested when resource niches overlap, visitation frequencies or resource use changes when HB arrive, and negative relationships between *Apis* abundance and native bees occur (Aizen and Feinsinger, 1994; Roubik and Villanueva-Gutiérrez, 2009; Thomson, 2016). HB pathogens can spread to native bees when resource use overlaps, a problem most evident with managed colonies (Fürst et al., 2014; Graystock et al., 2016; Grupe and Quandt, 2020). To understand HB impacts on native bee abundance and diversity, populations need to be monitored and experiments designed to test for resource competition as well as parasite/pathogen spillover with sufficient replication and duration. This is not often done (Paini, 2004).

The Neotropical invasion of Africanized Honey Bees (AHB) have displaced native bees from floral resources through their highly efficient foraging behavior (Moritz et al., 2005; Roubik, 2009), which could be demographically catastrophic for native bees (Minckley et al., 2003; Roulston and Goodell, 2011). Thus

far, most continental studies of AHB show little or no negative demographic consequences for native solitary or social bees (Roubik, 1978, 1983, 1986, 2009; Roubik and Ackerman, 1987; Roubik and Wolda, 2001; Roubik and Villanueva-Gutiérrez, 2009). Native bees have the behavioral flexibility to shift to alternative food resources, which implies that floral resources are not limiting, and the bees have “loose niches” (Roubik, 1992), an idea supported by a global meta-analysis of pollination networks that revealed specialization decreases toward the tropics (Schleuning et al., 2012).

### Impacts of Invasive Honey Bees on Tropical and Subtropical Islands

If islands with their disharmonic biotas have unfilled niches, then their native bee fauna may also have the capacity to shift to alternative resources when confronted by competition with non-indigenous species. On the other hand, the lower floral diversity on islands may leave fewer options when favored resources are usurped (Valido et al., 2019). Thus far, responses of native pollinators to invasions of generalist bees on tropical and subtropical islands are varied. Sometimes they appear to co-exist. Fiji has an endemic generalist bee, *Homalictus fijiensis* (Halictidae), which has been joined by three invasive generalist bees: HB, *Amegilla pulchra*, and *Braunsapis puangensis* (Apidae). All four species share resources and forage heavily from a broad range of non-native plants resulting in the endemic generalist being as connected as the three invasive species (Groutsch et al., 2019; Hayes et al., 2019). Such exploitation of alien plants by a native generalist is fairly typical of other islands (Olesen et al., 2002). In Hawai'i, *Metrosideros polymorpha*, the dominant native forest tree is visited at all elevations by both native and non-indigenous nectar feeders, with relative frequencies elevation-dependent. HB were most frequent at low and high elevations whereas the native bee, *Hylaeus* sp. (Colletidae) dominated at mid-elevations (Cortina et al., 2019). The drivers of these shifts are unknown.

Evidence for resource competition has been seen more clearly on other islands. Hansen et al. (2002) found that introduced HB on Mauritius competed with native birds for nectar resources with a likely net loss of seed production and possible demographic consequences to the birds. On Ogasawara Islands, Kato et al. (2018) found that outcomes are dependent on the degree of human disturbance. HB are the primary visitors to both native and non-native plants on islands with the most severe human impacts, whereas native bees dominate on islands with well-preserved floras. New Caledonia is particularly species-rich with high levels of endemism. In a survey of floral visitors to 95 native species, nearly half of the species were mellitophilous and these were visited predominantly by alien HB. As native bees do exist, the inference is that their populations have been reduced through competitive interactions (Kato and Kawakita, 2004). Thus, case histories show a broad spectrum of potential outcomes.

A surge in HB abundance through seasonal placement of apiaries can have strong negative impacts on biodiversity (Geslin et al., 2017). High-density beekeeping in natural areas of the Canary Islands has led to a drop in wild pollinator frequencies and fewer interaction links in pollination networks. Furthermore,

reproductive success of native plants can decrease when heavily visited by HB, often a less effective pollinator (Valido et al., 2019). On islands where HB and non-native plants dominate, networks become more fragile. In the Seychelles and Hawai'i, networks with higher numbers of invasive plants have increased interspecific pollinations, and metrics such as connectivity, pollinator diversity and network redundancy are lower (Kaiser-Bunbury et al., 2011, 2017; Johnson and Ashman, 2019).

## APIS MELLIFERA IN THE CARIBBEAN

The Caribbean is comprised of both oceanic and long-isolated continental islands. Surprisingly, our knowledge of HB interactions in the region is sparse. HB pathogens and parasites are present in the region (Rangel et al., 2018) but disease transmission dynamics and pathogen/parasite loads of wild bees are unknown. Hung et al. (2018) did a global meta-analysis of HB importance as pollinators in natural habitats and showed that the proportion of floral visits by HB was higher on continents than on islands. They had two examples from Caribbean islands: HB on both Jamaica and Dominica accounted for roughly 10% of the floral visits in the pollination networks studied (inferred from Hung et al., 2018, **Figure 1**, data from Ingversen, 2006). On the other hand, a comprehensive survey of bees and their host plants in the French West Indies revealed that HB visited 78% of the flora visited by bees (Meurgey, 2016). The consequences of HB activities in the Caribbean remain largely unknown, but studies from Puerto Rico indicate the dynamics that may exist.

### *Apis mellifera* in Puerto Rico

The European honey bee (EHB) was established on Puerto Rico about 200 years ago (Mari Mut, 2018). In 1994, the Africanized honey bee (AHB) was unintentionally introduced and in a very short time fully supplanted EHB. Within 10 years AHB lost their aggressive defensive behavior resulting in bees that behave similarly to the original EHB populations (Cox, 1994; Rivera-Marchand et al., 2012). The change from EHB to AHB may have hidden consequences since AHB places greater emphasis on pollen foraging than EHB (Schneider et al., 2004); however, we have no means to determine whether a shift in pollinator services or any other interaction occurred since few studies of HB exist prior to the arrival of AHB. Nevertheless, we may expect that after 200 years, the flora and fauna of Puerto Rico have adjusted to the ubiquitous presence of HB (Moritz et al., 2005).

### Effects on the Fauna of Puerto Rico

Snyder et al. (1987) noted an overlap in tree hole characteristics favored by EHB and the highly endangered Puerto Rican Parrot (*Amazona vittata*) and speculated "there can be little doubt that honey bees have been a significant factor in limiting the availability of good nest sites." While EHB may have had a role in the decline of the parrot, it likely pales in comparison to 150 years of deforestation, which left only 5% of original forest cover uncut by the 1940s (Wadsworth, 1950). Since then, forest cover has risen to 55%, making the outlook brighter for the parrot (Brandeis and Turner, 2013) and perhaps for feral AHB.



**FIGURE 1** | Invasional meltdown in Puerto Rico. Africanized Honey Bees provides pollinator services for the bamboo orchid, *Arundina graminifolia*, thereby facilitating establishment and spread of the species across the island. Photo: James D. Ackerman.

Community assessments of plant-pollinator interactions in Puerto Rico where individual interactions can be extracted have not been published (e.g., Martín González et al., 2009, 2010). As in other islands worldwide (Crichton et al., 2018), Puerto Rico has at least one native super-generalist pollinator, *Xylocopa mordax* (Apidae), which uses at minimum 375 plant species for food and provides pollinator services for 43 fruit and seed crops (Jackson and Woodbury, 1976; Jackson, 1985). While there are ~42 bee species among islands of the Puerto Rican Bank (Genaro and Franz, 2008; Genaro, 2016; Gibbs, 2018), their floral resources are largely unknown. Without knowledge of plant-pollinator communities prior to HB introduction, we can only speculate what impact HB have had on native bees (Paini, 2004; Stout and Morales, 2009), and it may not have been negative as discovered in Fiji (Crichton et al., 2018).

Despite lacking knowledge of native bee populations in Puerto Rico before the arrival of either EHB or AHB, indirect evidence suggests HB may have had significant competitive effects. Fumero-Cabán (2019) conducted a 3-year study of the floral visitors to populations of a dry forest tree, *Guaiacum sanctum* (Zygophyllaceae) in Guánica, Puerto Rico, and nearby Mona Island, where HB do not occur. Frequencies of floral visitors were much higher in Guánica, but nearly all visits were



by AHB (98%). Whereas, on Mona Island, *G. sanctum* had twice the diversity of flower visitors as seen in Guánica, and it took the 10 most frequent visitors to reach 98% of the total visits. If these data reflect pollinator diversity and abundance at each site, then *Apis* may have affected the native flower-visiting fauna of Puerto Rico's dry forests.

## Effects on Pollinator Services in Puerto Rico

AHB are widespread across Puerto Rico, and because HB have been present for about two centuries, they should be fully integrated into local pollination networks. The following six case histories illustrate how AHB can have positive to neutral or even negative effects on the flora of the island, just as they have had on a global scale (Agüero et al., 2018).

HB have had a positive effect on the pollination of *Pitcairnia angustifolia* (Bromeliaceae), flowers of which fit the hummingbird pollination syndrome (Fumero-Cabán and Meléndez-Ackerman, 2007). As expected, the long-billed Green Mango (*Anthracothorax viridis*, Trochilidae) is a pollinator, but nectar-robbing Bananaquits (*Coereba flaveola*, Thraupidae) and pollen foraging HB also provide pollinator services despite their role differences. HB performed about 1/3 of the pollinations adding some redundancy which may buffer effects of catastrophic events.

In Guánica, AHB dominates the pollinator pool of the partially self-incompatible *G. sanctum*, but most visits were among flowers of the same tree, possibly resulting in reduced reproductive success due to inbreeding depression. However, AHB visitation frequencies were high, so that fruit and seed production were similar to populations where AHB did not occur (Fumero-Cabán, 2019).

The Sierra Palm (*Prestoea montana*) in Puerto Rico is a rainforest dominant and flowers abundantly from June to September. When the palms are in flower, numerous AHB forage over the inflorescences. Honey bees and small flies are presumed to be pollinators, but the frequency and effectiveness of floral visitors to this monoecious palm have yet to be quantified (Bannister, 1970). Fruit production is ~3,800–5,000 per palm each year (Bannister, 1970; Gregory and Sabat, 1996) so pollinators are effective. If HB are the primary pollinators, then their role is critical for maintaining the structure and function of the rainforest.

Honey bees forage pollen from the hummingbird-pollinated cactus, *Melocactus intortus*. Flowers are self-compatible, but fruit set is lower when selfing occurs. Fagua and Ackerman (2011) found that AHB performed about 10% of the pollinations, yet when they calculated pollinator effectiveness taking into account seed viability, AHB did not affect reproductive success of the cactus. Here the role of AHB may be as inconsequential pollen thieves.

The role of HB as pollinators of the endangered tree, *Goetzea elegans* (Solanaceae), is equivocal. They often visit numerous flowers on a tree and are as effective at transferring pollen as the native pollinator, the Bananaquit, but flowers are self-incompatible and most AHB visits, unlike

those of the bird, are within a tree (Caraballo-Ortiz and Santiago-Valentín, 2011; Caraballo-Ortiz et al., 2011). While AHB do perform some pollination services, many of them are incompatible pollinations, resulting in pollen wastage and perhaps stigma clogging, interfering with subsequent outcross pollinations.

Invasion of super-generalist pollinators such as HB has the potential to alter pollinator services and facilitate the invasion of alien plants by providing pollinator services that local pollinator would not otherwise perform (e.g., Morales and Aizen, 2006; **Figure 1**). The presence of HB in Puerto Rico has done this for several non-indigenous species, including the pigeon orchid (*Dendrobium crumenatum*, Orchidaceae). This epiphytic plant has escaped cultivation and has been spreading rapidly across moist and wet regions of the island. The nectar-rich flowers are pollinated by *Apis cerana* and *A. dorsata* in their native range (Brooks and Hewitt, 1909; Leong and Wee, 2013), but in the Caribbean, alien HB serve as a surrogate (Meurgey, 2016; Ackerman, 2017). While orchid enthusiasts may applaud orchid invasions, they serve as hosts to a native orchid-specialist weevil (*Stethobaris polita*, Curculionidae), whose populations have grown due to the increased food supply, resulting in reduced fruit set in native orchids (Recart et al., 2013).

## WHAT WE NEED TO KNOW

HB presence in the Caribbean is likely permanent, but populations are expected to fluctuate. Aside from catastrophic losses and recovery from diseases, droughts, and hurricanes, resource availability should also change as forests mature from the height of deforestation, and non-indigenous species proliferate (Abelleira Martínez et al., 2015; Rojas-Sandoval and Acevedo-Rodríguez, 2015). HB studies have revealed loose niches on the species-rich continent, but has the lower diversity of islands been as forgiving? Will plant invasions, so severe on islands, exacerbate the problem or relieve it? Answers to these questions are uncertain since current evidence from tropical islands is sparse and mixed. The following lines of inquiry should be addressed: (1) *Basic bee diversity and dynamics*—What are the bee diversities among and within islands? How do abundances and population dynamics of native and feral HB vary across the landscape? What are the pathogen and parasite loads? When these are answered, then HB densities may be manipulated while local bee populations are monitored for responses. (2) *Community dynamics and resource availability*—What role does HB have in the structure, function, and stability of pollination networks across environmental conditions, vegetation types, forest-urban gradients, and agroecosystems? Do network metrics indicate a high potential for competitive interactions involving HB? Are niches loose enough to accommodate HB and native pollinators? (3) *Pollinator services*—Do HB have a detrimental or supplemental role in plant reproductive success, for native and non-indigenous species? Are native pollinators more or less efficient/effective pollinators in the island's agroecosystems than HB?

## CONCLUSIONS

HB have been present in the Caribbean for at least 200 years and currently perform pollinator services for native plants, albeit imperfectly. Effects on native bee faunas are not clear, but the less diverse, disharmonic biotas of islands may limit the buffering capacity of loose niches against the competitive abilities HB. As the Caribbean has become a hotspot for biological invasions, the role of HB may become amplified resulting in further biological reorganization. This complicates the development of strategies to effectively foster local bee industries while minimizing negative consequences to natural and agro-ecosystems (e.g., Goulson and Hughes, 2015; Henry and Rodet, 2020). However, lessons learned

from Caribbean studies will certainly inform dynamics seen in other tropical island systems.

## AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

## ACKNOWLEDGMENTS

The author would like to thank Elvia J. Meléndez-Ackerman and Frontiers reviewers for constructive critiques of the manuscript.

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**Conflict of Interest:** The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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