

Title: Mutualism and invasion: Consequences of an invasive pollinator

Keywords: Pollination, bees, invasive species, Hawaiian Islands

Introduction: Escape from antagonistic interactions is the classic model for invasion success and underlies modern attempts at biological control. However, the potential role of mutualisms in invasions was largely neglected until a few years ago (11). Recent research has demonstrated the critical importance of mutualisms in invasions: ants on Christmas Island became invasive only after addition of an exotic mutualist scale insect (10), and pines are unable to invade areas lacking their mycorrhizal partners (11). Similarly, when plants are introduced into a new environment, their reproductive success can be limited by the lack of suitable pollinator (11). If there is no suitable native pollinator, then exotic plants may require the presence of exotic pollinators. These positive interactions between invasive species have been characterized as an invasional meltdown, and could lead to detrimental effects greater than the sum of their parts (12). The islands of Hawaii, where there are many invasive plants and only a single genus of native bees, provide an ideal location to test this theory. The European honey bee (*Apis mellifera*: Apidae), an invasive species which has become naturalized on all of the main islands, could now play a major role in pollinating both native and invasive plant species. My research will test the importance of facilitation in the biology of invasion. Specifically, I will assess 1) the role of native bees as pollinators, 2) the extent to which pollination webs have been infiltrated by invasive bees, and 3) most crucially, the importance of invasive bees for pollinating invasive plants.

Background: Very little is currently known about pollination ecology in Hawaii, despite a simplified native pollinator fauna and the attention devoted to native plant conservation. The native bees of Hawaii are composed of a single monophyletic lineage of *Hylaeus* (Colletidae) comprising 60 species. The genus has been recently revised (3), and a biogeographic analysis suggests that the genus may have been in Hawaii for < 1 m.y. (8). Many aspects of the ecology of *Hylaeus* remain to be investigated. In particular, these bees are believed to be important pollinators of native plants (8), but their pollination ecology is largely unknown.

Hylaeus bees have been observed to generally ignore exotic plants (8), suggesting that exotic plant species may rely solely on generalist pollinators such as the honey bee (9). This observation also suggests that although *Hylaeus* may be relatively recent in Hawaii, there has been sufficient time for the evolution of pollination interactions. Honey bees in other locations have previously been observed to visit and pollinate exotic plants which are ignored or unsuccessfully visited by native pollinators (5). In several cases, a synergistic effect between invasive honey bees and invasive plants has been suggested (1,4). Thus, honey bees in Hawaii may facilitate the invasion of exotic plant species not pollinated by native bees, and the invasive plants may benefit the honey bees in turn.

Hypotheses: In order to define the role of invasive pollinators and the potential role of facilitation in invasion biology, I will test the following three hypotheses:

1. Native pollinators only pollinate native plant species. I will test the prediction that *Hylaeus* species are restricted to indigenous plants.
2. Invasive pollinators pollinate both native and exotic plant species. This hypothesis will be tested by examining the pollination ecology of *Apis mellifera*. If *Apis* is found only associated with invasive plants, it suggests that their invasion has been facilitated by that of the plants.
3. Invasive plant species rely exclusively on invasive bees for pollination. This hypothesis will be tested by determining the pollinators of invasive plants in Hawaii. If *Apis* is the sole pollinator for exotic plants, this suggests that *Apis* is facilitating plant invasions.

Methods: At selected sites on the islands of Hawaii and Maui suggested by earlier collections (3,8), I will establish transects to quantify floral visitors and visitation rates. The foraging behavior of *Hylaeus* bees and honey bees will be observed in order to determine the range of plants (both native and exotic) that are utilized as food sources. At each site, all insect floral visitors will be recorded, and subsequent movement will be followed to see if they next visit a flower on the same plant (selfing), on a conspecific (outcrossing), or on a different species. The effectiveness of pollen transfer during cross-visitation can be determined through the use of fluorescent dye particles, which creates a record of pollen movement (2). I applied similar techniques in my previous research in Virginia. I will then construct pollination webs (see 9).

Next, hand-pollination and exclusion studies will be used to establish the extent of natural pollen limitation and the effectiveness of different pollinators. Hand-pollinating flowers ensures a full pollen load of conspecific, out-crossed pollen, and thus results in maximum seed set. The maximum seed set will then be compared with seed set under three different pollination regimes: honey bees only, honey bees excluded, and control (no pollinator exclusion). Since the native *Hylaeus* are significantly smaller than *Apis mellifera*, access to flowers can be restricted using mesh with the correct diameter openings (see 1). The tests of pollen-limitation under each pollination regime will be controlled for possible resource reallocation (for recommendations, 7). Plant species selected for these trials will be site-specific and selected from native and invasive species known to require biotic pollination. If plant invasion is facilitated by *Apis*, I predict that invasive plant species will be more pollen-limited than native plant species under honey bee exclusion, with full pollination of invasives recovered under honey bee-only treatments.

Conclusion and consequences: The long-term effects of species invasion have only recently begun to be considered (13), so although honey bees have long been established on the Hawaiian Islands, they may still be exerting strong community-level effects on both native and exotic species. If honey bees and exotic plant species are indeed facilitating each other, then the effect of honey bees may be increasing with the rising numbers of newly-introduced plants. As more and more resources are devoted towards combating invasive species, it becomes increasingly important that we determine the role of pollinators in facilitating plant invasions.

As a further consequence, the invasive bees may also be disrupting native reproductive mutualisms (14). Since eusocial honey bees are highly active and proficient foragers, there is a strong possibility that they may have detrimental effects on the solitary *Hylaeus* through resource competition (6). Honey bees may also be less efficient or effective pollinators of native plants than *Hylaeus*, or they may increase levels of selfing or hybridization (14). Thus, an important additional result of this research will be to establish the importance of *Hylaeus* as native plant pollinators, which would have important consequences for conservation planning.

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Statement: I attest that this is an original research proposal.