

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA Wildlife Services - Staff Publications

U.S. Department of Agriculture: Animal and
Plant Health Inspection Service

2022

Invasive predators affect community-wide pollinator visitation

Christina T. Liang

USDA FS, Hilo, HI, christina.liang@usda.gov

Aaron B. Shiels

USDA, APHIS, Wildlife Services, aaron.b.shiels@usda.gov

William P. Haines

University of Hawai'i, Honolulu

Manette E. Sandor

Northern Arizona University

Clare E. Aslan

USDA FS, Nevada City, CA

Follow this and additional works at: https://digitalcommons.unl.edu/icwdm_usdanwrc



Part of the [Natural Resources and Conservation Commons](#), [Natural Resources Management and Policy Commons](#), [Other Environmental Sciences Commons](#), [Other Veterinary Medicine Commons](#), [Population Biology Commons](#), [Terrestrial and Aquatic Ecology Commons](#), [Veterinary Infectious Diseases Commons](#), [Veterinary Microbiology and Immunobiology Commons](#), [Veterinary Preventive Medicine, Epidemiology, and Public Health Commons](#), and the [Zoology Commons](#)

Liang, Christina T.; Shiels, Aaron B.; Haines, William P.; Sandor, Manette E.; and Aslan, Clare E., "Invasive predators affect community-wide pollinator visitation" (2022). *USDA Wildlife Services - Staff Publications*. 2576.

https://digitalcommons.unl.edu/icwdm_usdanwrc/2576

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Animal and Plant Health Inspection Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA Wildlife Services - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

ARTICLE

Invasive predators affect community-wide pollinator visitation

Christina T. Liang^{1,6}  | Aaron B. Shiels²  | William P. Haines³ |
Manette E. Sandor⁴  | Clare E. Aslan^{4,5}

¹Pacific Southwest Research Station,
USDA Forest Service, Hilo, Hawai'i, USA

²National Wildlife Research Center,
USDA APHIS, Fort Collins,
Colorado, USA

³Center for Conservation Research and
Training, University of Hawai'i,
Honolulu, Hawai'i, USA

⁴Landscape Conservation Initiative,
Northern Arizona University, Flagstaff,
Arizona, USA

⁵Conservation Science Partners, Flagstaff,
Arizona, USA

⁶USDA Forest Service Tahoe National
Forest Supervisors Office, Nevada City,
California, USA

Correspondence

Christina T. Liang
Email: christina.liang@usda.gov

Funding information

U.S. Department of Defense, Grant/Award
Number: SERDP RC-2432; Department of
Agriculture; Strategic Environmental
Research and Development Program,
Grant/Award Number: RC-2432;
Department of Defense

Handling Editor: Alison K. Brody

Abstract

Disruption of plant–pollinator interactions by invasive predators is poorly understood but may pose a critical threat for native ecosystems. In a multiyear field experiment in Hawai'i, we suppressed abundances of globally invasive predators and then observed insect visitation to flowers of six native plant species. Three plant species are federally endangered (*Haplostachys haplostachya*, *Silene lanceolata*, *Tetramolopium arenarium*) and three are common throughout their range (*Bidens menziesii*, *Dubautia linearis*, *Sida fallax*). Insect visitors were primarily generalist pollinators, including taxa that occur worldwide such as solitary bees (e.g., *Lasioglossum impavidum*), social bees (e.g., *Apis mellifera*), and syrphid flies (e.g., *Allograpta exotica*). We found that suppressing invasive rats (*Rattus rattus*), mice (*Mus musculus*), ants (*Linepithema humile*, *Tapinoma melanocephalum*), and yellowjacket wasps (*Vespa pensylvanica*) had positive effects on pollinator visitation to plants in 16 of 19 significant predator–pollinator–plant interactions. We found only positive effects of suppressing rats and ants, and both positive and negative effects of suppressing mice and yellowjacket wasps, on the frequency of interactions between pollinators and plants. Model results predicted that predator eradication could increase the frequency of insect visitation to flowering species, in some cases by more than 90%. Previous results from the system showed that these flowering species produced significantly more seed when flowers were allowed to outcross than when flowers were bagged to exclude pollinators, indicating limited autogamy. Our findings highlight the potential benefits of suppression or eradication of invasive rodents, ants, and yellowjackets to reverse pollination disruption, particularly in locations with high numbers of at-risk plant species or already imperiled pollinator populations.

KEYWORDS

community ecology, insect pollinators, invasion biology, invasive predators, invasive species suppression, plant–animal interactions, pollination disruption

INTRODUCTION

An estimated 87.5% of flowering plant species worldwide are pollinated by animals (Ollerton et al., 2011). Animal pollinators may be critical for facilitating reproduction, gene flow, and adaptive capacity in these plant species; loss of pollinators can impact plant fitness and genetic diversity as well as wider ecosystem stability (Biesmeijer et al., 2006; Neuschulz et al., 2016; Potts et al., 2010). Pollinator declines have been observed across a wide range of geographic areas and ecosystem types (Kluser & Peduzzi, 2007), and causes of declines include habitat loss, disease, climate change, and pesticides (Bailes et al., 2018; Byers, 2017; Christmann, 2019; López-Osorio & Wurm, 2020; Tonietto & Larkin, 2018). Although their role has been less explored, invasive predators could negatively impact pollinators, thereby driving declines of pollinator-dependent plant species in invaded communities worldwide.

Predators, both native and introduced, may affect pollinators by eliciting numerical and/or behavioral responses, and therefore can impact plants through either density-mediated (e.g., numerical) or trait-mediated (e.g., behavioral) effects (reviewed by Benoit & Kalisz, 2020). The review by Benoit and Kalisz (2020) shows that predators generally reduce both the frequency and duration of pollinator visitation to flowers, but their top-down effect can be variable and dependent on the specific predator–pollinator–plant combination of traits. Temporal and spatial heterogeneity in any level of the tritrophic interaction could also affect the outcome, for example if pollinators are able to evade predators by becoming active at different times of the day or in different seasons or by escaping predators in space (e.g., Huey & Nieh, 2017). Empirical observations of predator–pollinator interactions have largely been restricted to highly simplified interaction pathways (e.g., between single predator species and one or a few affected pollinator species) and mainly focused on flower-dwelling ambush predators such as crab spiders (Chittka, 2001; Théry & Casas, 2002; Rodríguez-Gironés, 2012). Results have shown that pollinators seek cover and exhibit avoidance behaviors when ambush predators are present, diminishing the frequency and duration of flower visitation as well as pollen transfer (Gonçalves-Souza et al., 2008; Romero et al., 2011). Studies of interactions between focal predators and individual pollinator species (mainly economically important social bees used in agricultural production) have also shown that direct predation can reduce pollinator densities and disrupt pollination of plants with high dependence on those pollinators (Dukas, 2005; Knight et al., 2006). A predator species can be relatively rare in the system and have low

prey–capture rates, yet still significantly affect pollinator populations, particularly if the predator preferentially hunts on flowers (Cresswell, 2017; Rodríguez-Gironés, 2012).

Globally, invasive predators have been major causes of species extinctions and endangerment in ecosystems (Baxter et al., 2008; Doherty et al., 2015, 2016). Furthermore, invasive predators have led to ecosystem-level transformations such as altered nutrient flow regimes via elimination of seabirds (Maron et al., 2006), altered arthropod communities via competition with native predators (Cole et al., 1992), and modified vegetation cover via reductions in herbivore populations (Snyder & Evans, 2006). Invasive predators have reduced or eliminated bird populations on islands, for example, resulting in disrupted seed dispersal with consequent changes in vegetation patterns (Medina et al., 2014; Rogers et al., 2017). In addition to preying on dispersers, invasive rats have disrupted seed dispersal for diverse plant communities by depreying the seeds themselves, potentially transforming island floras (Harper & Bunbury, 2015). These examples illustrate the capacity of invasive predators to disrupt fundamental ecological processes in systems worldwide. Some studies have acknowledged that nonnative species may impact pollination of native plants (e.g., Traveset & Richardson, 2006), but only a few studies have directly investigated or quantified pollination disruption by invasive predators. The impacts of co-occurring, wide-ranging, and generalist predator suites on interacting communities of pollinators and plants have not been previously explored.

We examined the relationship between abundances of five invasive predator species and flower visitation by insects to a suite of six native Hawaiian plant species. Focal predators in this study are the black rat, *Rattus rattus*; house mouse, *Mus musculus*; Argentine and ghost ants, *Linepithema humile* and *Tapinoma melanocephalum*, respectively; and yellowjacket wasp, *Vespula pensylvanica*, all of which are globally invasive and have been introduced to island and continental ecosystems worldwide. These generalist and aggressive predators are known to consume insects including effective pollinators such as native bees, introduced European honey bee, and moths and butterflies (Hanna et al., 2015; Shiels et al., 2013; Wilson & Holway, 2010), and could therefore disrupt pollination for a broad spectrum of plants worldwide. Although rodents are well known seed eaters, they also consume adult and larval stages of insects and other small arthropods that commonly make up an important component of rodent diets. Stomach content analyses have revealed that more than 80% of black rat and house mouse diets in Hawai'i and elsewhere contain insects and other small arthropods (Shiels et al., 2013 and references therein). Insects in the rodent stomach contents

included known pollinator groups such as dipterans, lepidopterans, and hymenopterans. Therefore, invasive rat and mouse feeding behaviors, such as those of yellowjacket wasps and ants, may reduce populations of insect pollinators and subsequent pollination services through direct predation on larvae and adults. To better direct the management of pollinator-dependent plants, we carried out a large-scale field experiment testing the hypothesis that suppression of invasive predators would increase pollinator visitation to a diverse community of native plants.

METHODS

Study site, species, and timeline

Our study site on Hawai'i island was in a subalpine tropical dryland ecosystem at 1675 m elevation with two main habitat types: grassland–shrubland and *Metrosideros polymorpha* ('ōhi'a)-dominated woodland. We established 20 2.25-ha experimental plots within a 794-ha fenced unit to experimentally assess the effects of suppressing predators on insect pollinator visitation to a community of native Hawaiian plants. The fencing was previously installed to exclude nonnative invasive ungulates (primarily goat and sheep) from consuming vegetation and exerting negative effects on native plants within the unit, which contains many federally threatened and endangered plant species.

Focal study species included both nonnative predators and native plants. Nonnative predators were *R. rattus*, *M. musculus*, *L. humile*, *T. melanocephalum*, and *V. pensylvanica*. Focal plants included three federally endangered species (*Haplostachys haplostachya*, Lamiaceae; *Silene lanceolata*, Caryophyllaceae; *Tetramolopium arena-rium*, Asteraceae) and three common species (*Bidens menziesii*, Asteraceae; *Dubautia linearis*, Asteraceae; and *Sida fallax*, Malvaceae). We selected these six species of native Hawaiian plants for study because they can grow and flower within 1 year in cultivation (permitting us to place potted plants within experimental plots), are insect pollinated, and have diverse floral traits (to maximize the breadth of the relevant community of pollinators for this study).

Prior to the experimental suppression of predators, we conducted baseline monitoring of predator abundances in experimental plots from March 2015 through March 2016 to assess spatial and temporal variability in predator populations among plots. We simultaneously assessed the baseline pollination regime of focal plant species from March 2015 through February 2016. We used flower visitation observations to determine the

identity of current flower visitors (all of which were insects) for each of our focal native plant species, as well as the rate of visitation exhibited by each insect taxon. Our observations occurred on focal plant species, when in flower, that were already established within and adjacent to our 20 plots.

We initiated treatments to suppress focal predators in our experimental plots in April 2016 and all treatments were fully implemented by July 2016; we ceased all treatments in January 2018. From August 2016 through November 2017, we assessed pollinator visitation to potted individuals of our focal plant species placed within our experimental plots. We also monitored predator abundances in plots throughout the experimental suppression period and for 3 months after the treatments ended, using the same methods as in our baseline monitoring period. Predator abundance monitoring and pollinator visitation observations occurred at regular intervals through the experimental period. However, monitoring and visitation observations did not occur simultaneously within all plots nor across all predators, due to the number of plots, difficulty of traversing the terrain, and the fact that pollinator visitation observations could be performed only when potted plants were flowering.

Experimental plots

We suppressed predators in 16 plots (four Rodent treatment; four Ant treatment; four Yellowjacket treatment; four Combined treatment for rodent + ant + yellowjacket) and left four plots Untreated for reference (i.e., experimental control plots). Each of the 20 plots consisted of a 50 m × 50 m (0.25 ha) central core area nested within a 150 m × 150 m (2.25 ha) treatment area (Figure 1). Plot size was selected to protect the central 0.25-ha core area from predator intrusion, based on previous research on movements of these predators in Hawai'i (Hanna et al., 2013; Krushelnycky et al., 2011; Shiels, 2010). We placed potted plants of our focal plant species at the center of the core area, where we expected the effects of predator treatments to be maximized, during the experimental period. In total, 25 predator monitoring stations, spaced 25 m apart along a grid, were placed within each 2.25-ha plot in transects radiating outward from the plot center, to assess relative predator abundances in the plots.

We arranged our experimental plots into four blocks of five plots, with two blocks located in a grassland–shrubland habitat and two blocks in a woodland habitat (Figure 1). Locations of blocks within these habitats were arranged to occur within current distributions of ant colonies. Two species of ants existed within our

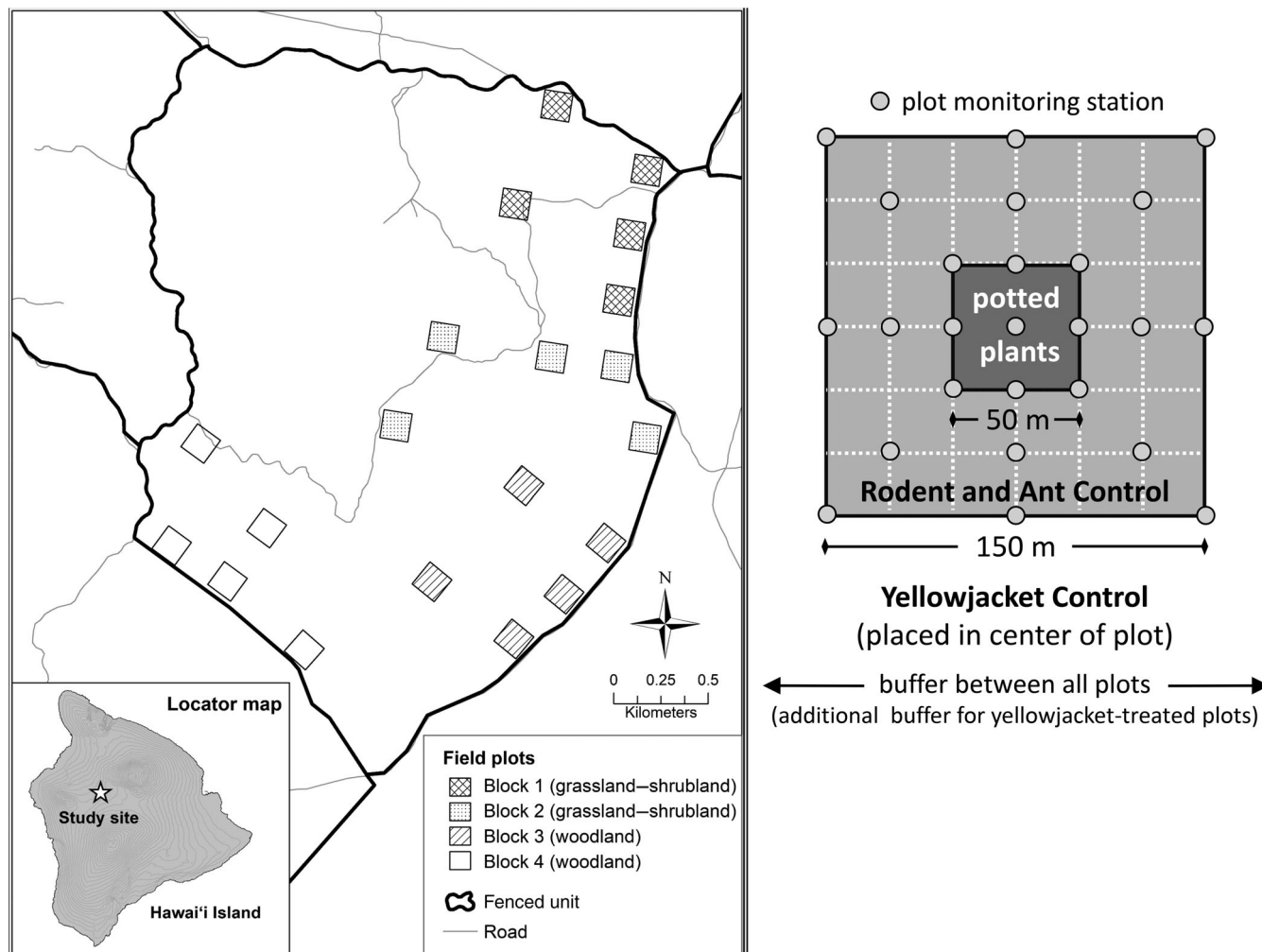


FIGURE 1 Experimental plots and layout within fenced 794-ha study site on Hawai'i island

experimental blocks: Argentine ants were in blocks 1–3, and ghost ants were in block 4. Each block included a Rodent treatment plot, Ant treatment plot, Yellowjacket treatment plot, Combined treatment plot, and Untreated plot. Plots were spaced at least 200 m apart with a wider buffer of at least 400 m around Yellowjacket and Combined treatment plots, to account for treatment effects on predator abundance. Once we arranged the plots, including buffers within the landscape, we randomly assigned the treatments, one randomization for the Yellowjacket and Combined treatment plots and a second randomization for the Rodent, Ant, and Untreated treatment plots. The double randomization was performed to compensate for the differences in buffer distances between plots.

Predator suppression and monitoring

Predator suppression methods included snap-traps for rodents, granular formicide for ants, and insecticide-laced

bait for yellowjackets. Rodent snap-trapping was performed continuously throughout the experimental suppression period, whereas ant and yellowjacket treatments were applied separately at intervals throughout the suppression period (see below). We monitored ants and yellowjackets immediately before and after their respective treatments to assess the efficacy of treatments, in the treated and untreated plots. We also monitored all predators regularly in the experimental plots. In each plot, predators were monitored at all or a subset of the monitoring stations situated along transects radiating outward from the center of the plot. Effectiveness of predator treatments was assessed by comparing treated and untreated plots, with the expectation that treatment effect would decrease with greater distance from the center of each plot due to predator influx from outside the plots.

For rodent suppression, we used two types of snap-traps to account for body size difference between rats and mice. Based on daily movements of rodents (Shiels, 2010), mouse snap-traps were spaced approximately 12.5 m apart in a grid

across the 2.25-ha experimental plot and rat traps were placed along the same grid but spaced every 25 m. There were 169 mouse traps and 49 rat traps in each plot receiving rodent treatment. Traps in each plot receiving rodent treatment were checked and re-baited every 2 weeks for the duration of our experimental suppression period.

For ant and yellowjacket suppression, we conducted regular applications of insecticides separately targeting the two predator groups. To reduce ant populations, granular formicide bait was applied by hand using “whirlybird” spreaders throughout the 2.25-ha plot every 3–5 months. Yellowjackets were targeted with fipronil insecticide, with bait applied twice each calendar year. Nine bait stations were placed in the 0.25-ha central core area in each yellowjacket treatment plot, and were constructed to allow yellowjacket workers to access the fipronil-laced bait inside the station through entry and exit holes. Canned chicken was used as the bait and fipronil was mixed into the meat, which was taken back to the yellowjacket nest by the workers. Bait stations were set up in the morning and taken down in the afternoon after approximately 8 h. Heptyl butyrate was used to attract the workers to the bait stations and stations were monitored throughout the day to assess yellowjacket activity. Application of formicide or fipronil treatments was conducted when there was an increase in predator abundance, determined through the regular predator monitoring conducted in the plots.

Rodent activity (an index of population abundance) was monitored using plastic tracking tunnels (50 cm × 10 cm × 10 cm) (as described in Pender et al., 2013). Tracking tunnels consisted of ink cards that were baited and placed inside plastic tunnels. When a rodent investigated the bait inside the tunnel, the ink was transferred onto the rodent’s foot, resulting in a footprint left on the card that could be identified to genus. Ant abundance was monitored using 7.6 cm × 6.4 cm index cards baited with a 40%:60% tuna:corn syrup mixture. Cards were set on the ground in a shaded location and left in place for approximately 1 h, after which they were photographed and collected (after Krushelnycky et al., 2011). Foraging ants attracted to the cards were identified in the field and later verified and counted in the office from the photographs. Yellowjacket abundance was monitored using heptyl butyrate traps left out for 4-day periods (after Foote et al., 2011). Individual yellowjackets in each trap were counted in the field on the fourth day.

Pollinator visitation assessment

In the year prior to our experimental manipulations, we evaluated plant reproductive dependence on insect

pollinators, quantified flower visitation rate and pollen transport by various insect groups, and measured predator populations across the study site. During this baseline year, we determined that most flower visitation in the system was performed by generalist insect taxa (e.g., *Apis mellifera*, Syrphidae, *Lasioglossum* sp.) that are found globally (Aslan et al., 2019; GBIF, 2020; Ollerton, 2017); we used these baseline data to determine which flower visitors carried pollen and interacted regularly with the reproductive structures of the focal plants, in order to group the visitor taxa and parameterize the tritrophic networks analyzed here (as described in the section on *Data synthesis*).

We grew our focal plant species in a greenhouse from seeds or cuttings collected from our field site for use as potted individuals in our experimental plots. Potted flowering plants were distributed among the 20 study plots, with the aim of placing eight flowering plant individuals of each species in each plot. When numbers of flowering individuals were limited, we distributed plants evenly among plots so that each plot received the same number of flowering individuals of a given species, ranging from 2 to 8. These densities were typical of those of wild plants in the broader landscape, which contains small patches of each focal plant species, distributed over the full study area. Potted plants were left in place within the plots for the duration of the experiment but were replaced if the plant died. Once pots were left in place within a plot, plants flowered on a rolling basis within those pots. Over the course of the experimental period, there were times when all potted species were flowering and times when only a subset was flowering.

We used a community-scale approach to pollinator visitation assessment for the potted plants, whereby an observer watched the flowers of up to three flowering potted plant species simultaneously while in an experimental plot. If more than three potted plant species were in flower during a given observation period, the observer performed an additional observation period to ensure that all flowering species were observed. Potential pollinators were recorded as flower visitors observed to contact the reproductive structures of a focal plant species, and pollen transport was later confirmed (see below). Rate of visitation was calculated as the product of the frequency of visits by a given visitor group (number of visits per observation period, standardized by the number of open flowers during that period) and the number of flowers visited by each individual during a visit, for each plant; observation effort was used to calculate rate variance for each flowering plant species. To obtain these data, observations followed a systematic protocol combining flower scans and focal individual observations (after Aslan et al., 2014, 2019; Farwig et al., 2017; Renne

et al., 2000). Each observation lasted 180 min, divided into 10-min blocks. The first minute of each observation block was devoted to scan sampling, in which the observer scanned all visible flowering plant individuals from a fixed observation point approximately 1 m from the potted plants. All visitors interacting with flowers in any way were recorded during this scan. For the remaining 9 min of the observation block, the observer conducted focal individual observations, following individual visitors for as long as they were present and visible or until 180 s had elapsed. During focal individual observations, the recorder noted the number of flowers and number of plants visited, as well as whether visitors contacted flower reproductive structures (i.e., made legitimate visits). If a visitor moved from one plant species to another, the move was recorded as the beginning of a separate visitation event. All flowering individuals and numbers of open flowers visible from a fixed observation point were counted and recorded during each observation period so that rates of visitation could be calculated based on number of available flowers of each focal plant species for each plot treatment.

We collected at least the first 10 available individuals of each visitor taxon that were recorded contacting reproductive structures of each plant species and swabbed collected individuals with cubes of fuchsin gel (Kearns & Inouye, 1993). Gel cubes were melted onto microscope slides in the field and later returned to the laboratory, where they were examined under a Reichert Microstar IV microscope (Reichert Technologies, Depew, New York, USA) at $\times 200$ magnification to determine whether they carried pollen grains. We matched pollen grain morphotypes to voucher pollen specimens taken directly from the anthers of focal plant species. These protocols permitted the calculation of the frequency of interactions between legitimate visitor taxa and flowers of each focal species. Visitors were considered to be likely effective pollinators if they were confirmed to contact flower reproductive structures in observations and if any collected individuals carried pollen (in any amount). Visitors collected directly from focal plants and carrying pollen morphotypes that matched those plants were considered to be likely effective pollinators of those plants; visitors carrying pollen in other contexts but for which we were not able to confirm transport of the specific morphotypes were considered to be likely pollinators and included in models (below) but their efficacy for those plants specifically remained unconfirmed (starred linkages in Figure 2).

Observations were conducted for all flowering potted plants in each plot at least once per month throughout the experimental period, such that all blocks were observed five times per month. Observers selected the order of plots for observation in an opportunistic fashion

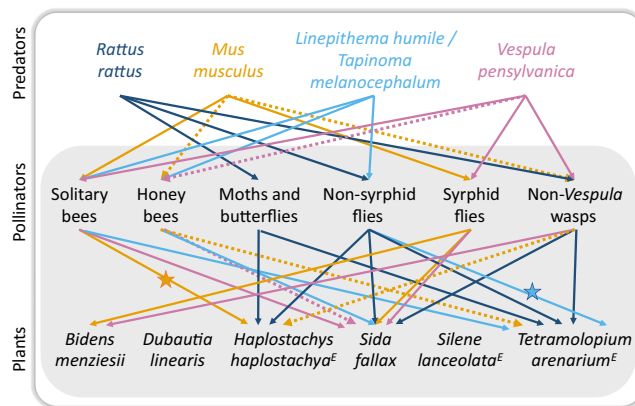


FIGURE 2 Interaction network linking invasive predators, pollinators, and native plants. Pollinator–plant relationships in gray box are affected by (a) rat (green lines), (b) mouse (orange lines), (c) ants (blue lines), and (d) yellowjacket wasp (red lines). Negative relationships between invasive predators and pollinator–plant pairs are indicated by solid lines, positive relationships are indicated by dotted lines. For example, mice negatively affect Syphidae visitation to *Sida fallax* and *Bidens menziesii* (solid orange lines), and positively affect *Apis mellifera* visitation to *Tetramolopium arenarium* (dotted orange lines). All insect–plant linkages in the network are confirmed as effective pollination, based on pollen transport, except for those linkages with stars which remain unconfirmed. ^E, federally endangered plant species

and observed all plots at all times of day. These observations allowed us to calculate the rate of visitation by each of the primary pollinator groups (described later) in the system to each focal plant species. We verified that these insect taxa transported the pollen of the focal plants, as described above. Although flower visitation does not equate to pollination, our prior work with breeding system floral treatments (e.g., bagging of flowers) found that flowers of each of the species in this experiment produced increased seed set when exposed to the visitor community, relative to flowers that were bagged to prevent outcrossing (Aslan et al., 2019); note that this increase was significant for all plant species except *S. lanceolata*.

Data synthesis

To capture seasonal and treatment-induced variation in predators and pollinators across our experiment, we divided the analysis period into three approximately half-year periods: August 2016 to January 2017, February 2017 to June 2017, and July 2017 to November 2017. This was necessary because pollinator visitor observations, invasive predator reduction treatments, and invasive predator surveys did not occur simultaneously within the

plots during the course of our experiment. By dividing our experiment into these half-year periods, for every plot we were able to capture a similar number of pollinator observations, applications of treatment for each invasive predator, and invasive predator surveys, while taking into account seasonal variations in weather that could affect flower, pollinator, and predator abundance. To achieve sufficient replication within pollinator groups for analysis, we classified six pollinator functional groups from the flower visitation data: solitary bees (primarily *Hylaeus* spp. and *Lasioglossum* spp.), European honey bee (*Apis mellifera*), moths and butterflies (Lepidoptera; primarily Crambidae spp., *Lampides boeticus*, *Orthomecyna* spp., *Pieris rapae*, and *Udara blackburni*), non-syrphid flies (primarily Tephritidae and Muscidae), syrphid flies (*Allograpta* spp.), and wasps excluding *Vespula pensylvanica* (primarily *Pachodynerus nasidens* and *Polistes aurifer*; from this point forwards, “non-*Vespula* wasps”). Flower visitors within these groups were all found during our baseline year of observations to perform frequent, legitimate (i.e., contacting reproductive structures) flower visitation (Aslan et al., 2019).

Values of predators within a plot for a time period were treated as relative abundances, in keeping with our data collection methods. We calculated a presence/absence-based relative abundance measure for rat and mice based on tracking tunnel data, with the observation unit at the level of the plot. To match the rat and mouse data, we converted ant and yellowjacket wasp abundances to their proportion of the maximum abundance recorded for the species. For ant and wasp data, the observation unit was at the level of the monitoring station. Rodent tracking tunnel data were collected only in the Rodent treatment, Combined treatment, and Untreated plots; in the statistical analyses, we used rodent relative abundance from the Untreated plot as the value for Ant treatment and Yellowjacket treatment plots, within the same block and time period (Appendix S1: Figures S1 and S2).

Statistical analysis

For our statistical modeling, we transformed pollinator observation data into presence/absence data by converting any observed interaction into “1” and any lack of interaction between a pollinator group and plant species into a “0” (from this point forwards referred to as “visitation frequency”). We performed this transformation on the pollinator observation data for every 180-min observation period within each half-year period within each plot.

We used Bayesian hierarchical models to determine the tritrophic relationships among our focal native plant

species, insect pollinators, and predator species. Our Synthesized Hawai'i Ecosystem-Level Observation-Based model contained two levels. Level one estimated the relationships between predators (independent variables) and the visitation frequency of pollinator groups with our focal plant species (dependent variables). Level two estimated predator relative abundances at each plot during each time period (20 plots over three time periods).

In level one of our model, we performed binomial regression with a logit link on each pollinator group for each plant species, using mean relative abundances of rats, mice, ants, and wasps as independent variables. Therefore, for each combination of pollinator group and plant species, we estimated the relationships with rat, mouse, ant, and yellowjacket abundances. The number of trials in the binomial distribution for each pollinator species was the number of 180-min observation periods for each plot within each half-year period. Most of the plant–pollinator group interactions were highly infrequent across the entire experimental period so, without the data transformation of pollinator observations described above, the zero-inflation component of the model was very large, causing severe convergence issues.

In level two, we modeled relative abundances of predators within each plot for each of the three half-year periods with a binomial distribution, in which the number of trials for the binomial distribution was the total number of monitoring stations within a plot (rodents) or the maximum number of ants or wasps found across all plots. Although treatments were effective at reducing predators within plots, stochasticity of predators across the landscape resulted in abundances of predators in treated plots that were at times higher than in untreated plots. Rather than using plot treatment as a categorical variable, we therefore modeled predator relative abundances as continuous variables across all plot/block combinations to take into account this natural variability in predator populations.

We fit the analyses in JAGS (Plummer, 2003) via the R packages *rjags* version 4-8 (Plummer et al., 2018) and *R2jags* (Su & Yajima, 2015). We used uninformative priors for all stochastic nodes. We ran three Markov chain Monte Carlo (MCMC) chains for each analysis, for 500,000 iterations, and we used the Gelman–Rubin convergence statistic to check for convergence between and within all chains by ensuring that its values were at least 1 and less than 1.1 (Gelman & Rubin, 1992). We fit all parameters within a single, hierarchical model, therefore negating any need for significance corrections such as Bonferroni corrections (Gelman et al., 2012). From our models, we then calculated the predicted changes in pollinator visitation, which quantified how much the insect

TABLE 1 Effective pollinators based on specimen collection. Values indicate the number of insect individuals carrying pollen of each plant species out of the total number of insect individuals captured when visiting the respective plant species. Insects were captured during periods when each plant species was flowering

	Solitary bees	Honey bees	Moths and butterflies	Non-syrphid flies	Syrphid flies	Non- <i>Vespula</i> wasps
<i>Bidens menziesii</i>	10/10	20/20	8/17	5/15	10/10	18/18
<i>Dubautia linearis</i>	3/10	10/10	2/10	5/10	10/10	2/10
<i>Haplostachys haplostachya</i>	NA	13/15	4/10	3/10	8/10	11/16
<i>Sida fallax</i>	10/10	10/10	4/10	2/10	7/10	3/10
<i>Silene lanceolata</i>	12/12	9/10	5/10	10/10	10/12	3/10
<i>Tetramolopium arenarium</i>	8/10	10/10	3/11	NA	9/10	2/10

Abbreviation: NA, data not available.

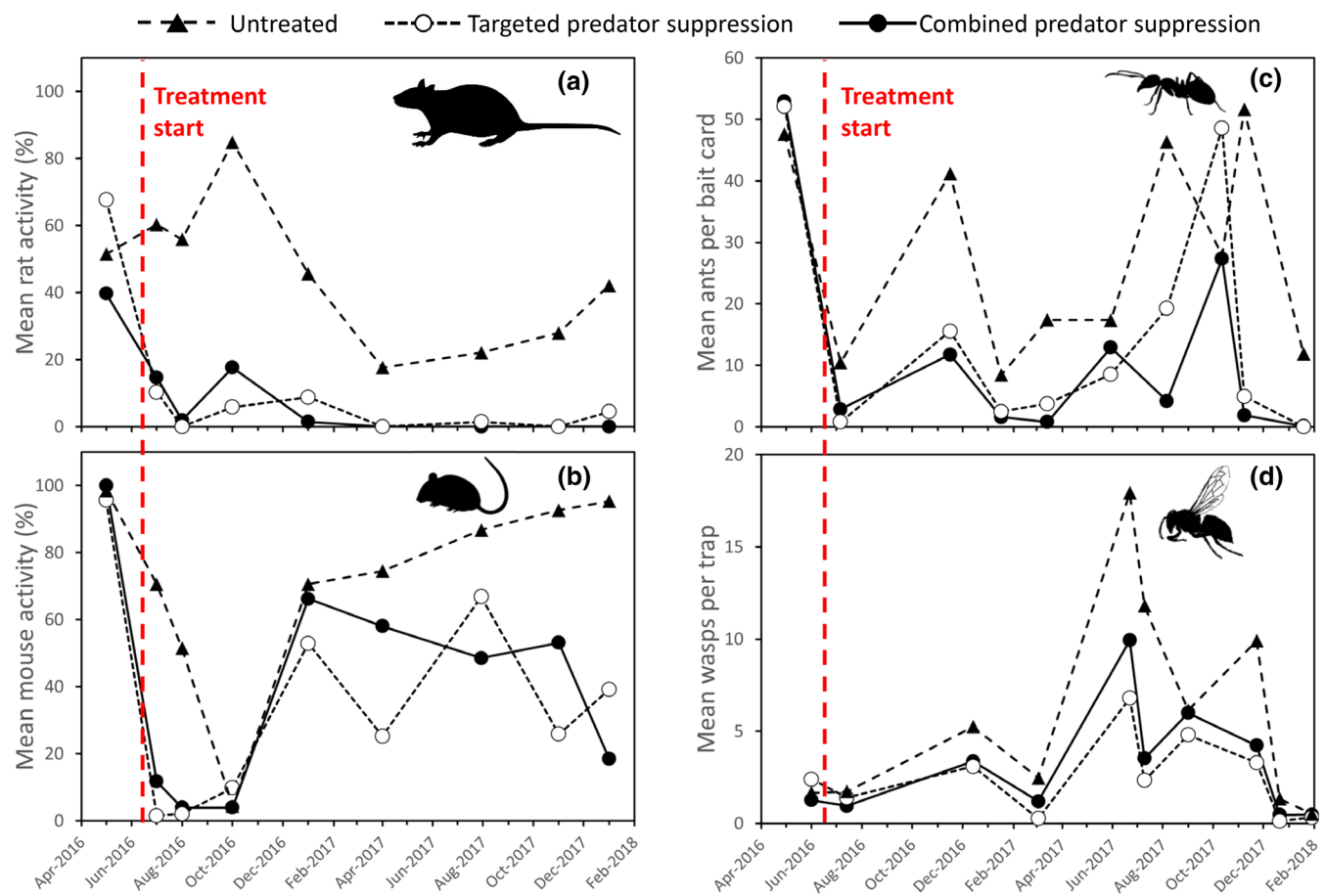


FIGURE 3 Dynamics of focal predators, with experimental treatments installed by July 2016 (red dashed line). Panels show (a) relative abundance of rat (*Rattus rattus*) and (b) mouse (*Mus musculus*) on tracking cards, (c) abundance of ants (*Linepithema humile*, *Tapinoma melanocephalum*) on baited cards, and (d) abundance of yellowjackets (*Vespula pensylvanica*) in heptyl butyrate traps. Lines depict predator suppression treatments: Untreated (solid triangle), suppression of single predator taxon (open circle), and suppression of combined predator taxa (solid circle)

visitation frequency would change if we were to decrease predator abundance from the untreated average (abundance of 0.6) to an abundance of 0, representing predator eradication.

RESULTS

In our models, only the visitor groups that were confirmed in structured observations to contact flower

TABLE 2 Predator relationships with insect visitation to flowering plants. For each pollinator group, upper and lower credible intervals (rows) are listed for the relationship between predator abundance and pollinator visitation to each plant species (columns). Emboldened numbers indicate a significant relationship (credible intervals do not overlap zero)

Plant species and pollinator group		Mouse	Rats	Ants	Yellowjacket
<i>Bidens menziesii</i>					
Solitary bees	CI (upper)	2.829	3.549	0.392	5.893
	CI (lower)	-2.831	-4.635	-23.049	-16.393
Honey bees	CI (upper)	1.689	4.269	1.572	7.763
	CI (lower)	-1.690	-0.176	-6.136	-1.286
Moths and butterflies	CI (upper)	3.391	3.991	0.884	0.279
	CI (lower)	-1.117	-2.030	-7.919	-16.863
Non-syrphid flies	CI (upper)	2.468	4.198	6.103	7.617
	CI (lower)	-3.563	-3.426	-2.283	-6.169
Syrphid flies	CI (upper)	-0.202	2.466	0.777	2.131
	CI (lower)	-4.024	-1.988	-5.825	-7.236
Non- <i>Vespula</i> wasps	CI (upper)	2.760	2.740	0.407	-3.086
	CI (lower)	-0.773	-2.516	-7.334	-20.935
<i>Dubautia linearis</i>					
Solitary bees	CI (upper)	5.420	5.425	6.830	26.232
	CI (lower)	-4.617	-30.219	-30.017	-24.114
Honey bees	CI (upper)	7.378	5.431	12.293	21.718
	CI (lower)	-1.818	-41.049	-4.925	-16.972
Moths and butterflies	CI (upper)	3.789	2.897	0.366	11.187
	CI (lower)	-5.014	-36.927	-26.185	-27.765
Non-syrphid flies	CI (upper)	7.165	8.716	13.409	26.194
	CI (lower)	-3.600	-45.467	-4.083	-25.564
Syrphid flies	CI (upper)	1.015	11.381	10.750	13.123
	CI (lower)	-5.383	-6.604	-4.803	-23.147
Non- <i>Vespula</i> wasps	CI (upper)	16.448	3.383	6.053	20.650
	CI (lower)	-1.500	-64.770	-13.122	-37.290
<i>Haplostachys haplostachya</i>					
Solitary bees	CI (upper)	-4.196	7.033	32.984	70.217
	CI (lower)	-74.556	-66.558	-56.643	-42.268
Honey bees	CI (upper)	2.546	3.767	6.805	23.480
	CI (lower)	-10.907	-23.882	-34.807	-44.010
Moths and butterflies	CI (upper)	8.810	-0.667	6.256	16.248
	CI (lower)	-2.283	-34.771	-16.663	-47.285
Non-syrphid flies	CI (upper)	22.628	-2.554	2.846	34.885
	CI (lower)	-2.712	-80.711	-70.129	-56.874
Syrphid flies	CI (upper)	3.072	4.135	2.977	12.111
	CI (lower)	-1.511	-3.681	-12.652	-18.454
Non- <i>Vespula</i> wasps	CI (upper)	52.772	8.564	4.185	33.422
	CI (lower)	2.582	-71.476	-69.791	-71.691

(Continues)

TABLE 2 (Continued)

Plant species and pollinator group		Mouse	Rats	Ants	Yellowjacket
<i>Sida fallax</i>					
Solitary bees	CI (upper)	1.620	1.940	1.293	-0.599
	CI (lower)	-3.024	-3.802	-11.278	-25.825
Honey bees	CI (upper)	0.606	1.002	-0.359	9.536
	CI (lower)	-2.457	-2.456	-10.059	0.109
Moths and butterflies	CI (upper)	2.549	1.580	4.653	6.287
	CI (lower)	-1.648	-4.343	-3.026	-6.009
Non-syrphid flies	CI (upper)	6.537	-3.471	4.817	14.817
	CI (lower)	-0.057	-34.321	-5.468	-3.527
Syrphid flies	CI (upper)	-0.333	2.388	1.037	-4.103
	CI (lower)	-3.755	-1.190	-5.963	-20.084
Non- <i>Vespula</i> wasps	CI (upper)	1.340	-1.283	1.570	4.822
	CI (lower)	-2.497	-11.056	-10.672	-10.479
<i>Silene lanceolata</i>					
Solitary bees	CI (upper)	17.384	5.456	3.536	8.530
	CI (lower)	-5.025	-56.921	-36.668	-80.122
Honey bees	CI (upper)	NA	NA	NA	NA
	CI (lower)	NA	NA	NA	NA
Moths and butterflies	CI (upper)	13.711	0.404	0.264	26.739
	CI (lower)	-10.985	-67.622	-78.282	-56.008
Non-syrphid flies	CI (upper)	NA	NA	NA	NA
	CI (lower)	NA	NA	NA	NA
Syrphid flies	CI (upper)	7.748	1.022	2.719	7.508
	CI (lower)	-1.737	-26.142	-9.527	-27.983
Non- <i>Vespula</i> wasps	CI (upper)	NA	NA	NA	NA
	CI (lower)	NA	NA	NA	NA
<i>Tetramolopium arenarium</i>					
Solitary bees	CI (upper)	13.326	3.667	-0.870	37.009
	CI (lower)	-2.717	-44.782	-81.065	-24.968
Honey bees	CI (upper)	52.006	38.153	14.222	88.484
	CI (lower)	3.560	-35.611	-75.134	-6.572
Moths and butterflies	CI (upper)	16.734	-11.968	10.455	29.825
	CI (lower)	-0.722	-79.321	-4.890	-35.342
Non-syrphid flies	CI (upper)	8.175	-0.359	-0.226	29.583
	CI (lower)	-2.102	-32.646	-42.763	-15.620
Syrphid flies	CI (upper)	1.582	0.567	4.812	13.820
	CI (lower)	-4.281	-8.210	-6.279	-14.338
Non- <i>Vespula</i> wasps	CI (upper)	14.223	-4.474	2.377	23.579
	CI (lower)	-4.875	-69.360	-26.601	-47.620

reproductive structures and via specimen collection to transport pollen were considered to be likely effective pollinators (Table 1). We did not successfully capture

non-syrphid flies from *T. arenarium* or solitary bees from *H. haplostachya*, so we were unable to confirm whether those visitors were likely to be effective

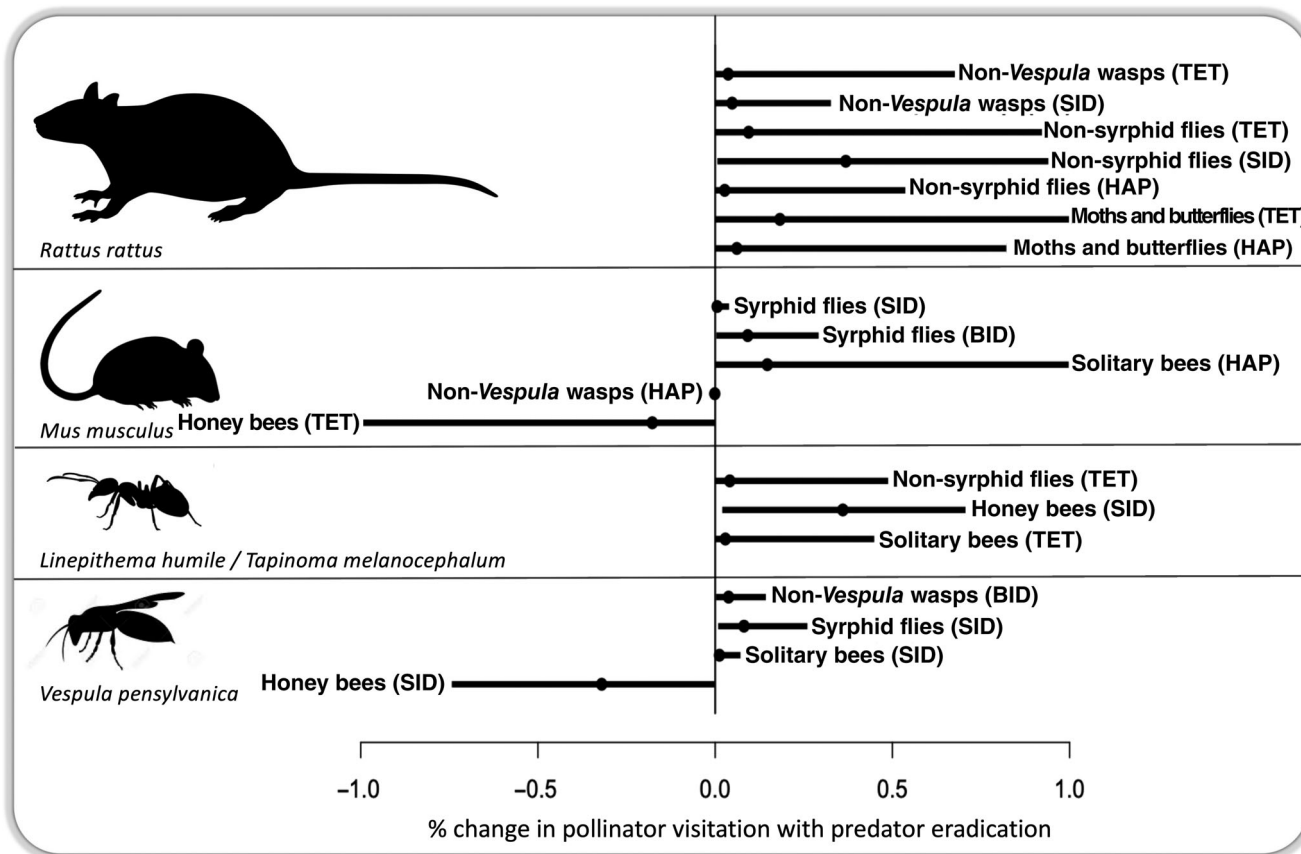


FIGURE 4 Modeled effects of predator eradication on pollinator–plant interactions. Predicted changes in pollinator visitation were calculated as the change in pollinator frequency on a given plant species when a predator abundance was reduced from 0.6 to 0. Positive predicted changes in pollinator visitation are increases in pollinator visitation frequency with reduced predator abundance, and negative predicted changes in pollinator visitation are decreases in pollinator visitation frequency with predator eradication. Dots are mean % change in pollination visitation with predator eradication and bars are 95% confidence intervals. Larger predicted changes in pollinator visitation mean a larger predicted impact of predator eradication. Plant codes: BID, *Bidens menziesii*; DUB, *Dubautia linearis*; HAP, *Haplostachya haplostachya*; SID, *Sida fallax*; TET, *Tetramolopium arenarium*

pollinators for those plants (starred linkages in Figure 2).

Predator treatments suppressed our target predator taxa measurably, even with inherent variability in predator populations (Figure 3). Overall, predator suppression had positive effects on interaction frequency (i.e., number of flowers visited per minute of observation) for 16 of 19 significant pollinator–plant interactions (Figure 2; Table 2). Rats and ants showed negative relationships with insect visitation to flowers (credible intervals do not overlap 0). Rat abundance was negatively associated with pollinator visitation to *H. haplostachya*, *S. fallax*, and *T. arenarium*, and ant abundance was negatively associated with pollinator visitation to *S. fallax* and *T. arenarium* (Figure 2; Table 2). Mice and yellowjackets exhibited both negative and positive relationships with flower visitation (credible intervals do not overlap 0). Mouse abundance was negatively linked to pollinator

visitation to *B. menziesii*, *H. haplostachya*, and *S. fallax* and positively associated with pollinator visitation to *H. haplostachya* and *T. arenarium* (Figure 2; Table 2). Yellowjacket abundance was negatively associated with pollinator visitation to *B. menziesii* and *S. fallax* and positively associated with pollinator visitation by one taxon (the honey bee) to *S. fallax* (Figure 2; Table 2). For four of six plant species, there were significant negative relationships between predator abundance and flower visitation frequency by at least one of their pollinator groups.

Our predicted change in pollinator visitation calculations illustrated the magnitude of the relationship between a predator and a pollinator visitation interaction with a plant species. These calculations predicted increased insect visitation frequency for many plant species (Figure 4; Table 3), including solitary bees visiting *H. haplostachya* following mouse eradication; Lepidoptera visiting *T. arenarium* following rat eradication; and

TABLE 3 Predicted changes in pollinator visitation frequency (mean and 95% confidence intervals) on a given plant species, when an invasive predator abundance was reduced from 0.6 to 0. Lower confidence intervals (CI) that are <0.001 are positive and do not overlap zero

Invasive predator	Mean	Lower CI	Upper CI	Pollinator group	Plant species
Rat	0.037	<0.001	0.676	Non- <i>Vespula</i> wasps	<i>Tetramolopium arenarium</i>
	0.048	<0.001	0.326	Non- <i>Vespula</i> wasps	<i>Sida fallax</i>
	0.095	<0.001	0.922	Non-syrphid flies	<i>Tetramolopium arenarium</i>
	0.368	0.006	0.940	Non-syrphid flies	<i>Sida fallax</i>
	0.027	<0.001	0.536	Non-syrphid flies	<i>Haplostachys haplostachya</i>
	0.183	<0.001	0.998	Moths and butterflies	<i>Tetramolopium arenarium</i>
	0.061	<0.001	0.821	Moths and butterflies	<i>Haplostachys haplostachya</i>
Mouse	0.005	<0.001	0.039	Syrphid flies	<i>Sida fallax</i>
	0.092	0.003	0.292	Syrphid flies	<i>Bidens menziesii</i>
	0.147	<0.001	0.998	Solitary bees	<i>Haplostachys haplostachya</i>
	<-0.001	<-0.001	<-0.001	Non- <i>Vespula</i> wasps	<i>Haplostachys haplostachya</i>
	-0.177	-0.995	<-0.001	Honey bees	<i>Tetramolopium arenarium</i>
Ant	0.041	<0.001	0.488	Non-syrphid flies	<i>Tetramolopium arenarium</i>
	0.360	0.020	0.706	Honey bees	<i>Sida fallax</i>
	0.029	<0.001	0.449	Solitary bees	<i>Tetramolopium arenarium</i>
Yellowjacket	0.038	<0.001	0.451	Non- <i>Vespula</i> wasps	<i>Bidens menziesii</i>
	0.081	0.008	0.260	Syrphid flies	<i>Sida fallax</i>
	0.012	<0.001	0.072	Solitary bees	<i>Sida fallax</i>
	-0.320	-0.743	-0.002	Honey bees	<i>Sida fallax</i>

non-syrphid flies visiting *S. fallax* and *T. arenarium* following rat eradication. (Figure 4; Table 3). The model predicted that eradication of mice or rats could increase visitation frequency by more than 90% for these plant-insect combinations, meaning, for example, that the probability of Lepidoptera visiting *T. arenarium* during an 180-min observation period would increase from 5% to more than 95%. Other plant-insect combinations were also predicted to receive increased visitation frequency with the eradication of mice, rats, ants, or yellowjackets, although by a smaller percentage (Figure 4; Table 3).

The largest mean positive predicted change in pollinator visitation was the increase in non-syrphid fly visitation to *S. fallax* following rat eradication (mean predicted change in pollinator visitation = 0.368, 95% confidence intervals [CI]: 0.006, 0.940) and the increase in honey bee visitation to *S. fallax* following ant eradication (mean predicted change in pollinator visitation = 0.360, 95% CI: 0.020, 0.706). Other eradications were predicted to produce increases in flower visitation frequency of up to approximately 50% and included solitary bees visiting *T. arenarium* following ant eradication; non-syrphid flies visiting *H. haplostachya* and *T. arenarium* following rat and ant eradication, respectively; and non-*Vespula* wasps visiting *T. arenarium*

following rat eradication. Positive but smaller maximum predicted changes in pollinator visitation were found for syrphid flies visiting *B. menziesii* and *S. fallax* following mouse eradication; non-*Vespula* wasps visiting *B. menziesii* after yellowjacket eradication; non-*Vespula* wasps visiting *S. fallax* following rat eradication; and syrphid flies visiting *S. fallax* following mouse and yellowjacket eradication (Figure 4; Table 3).

Our model predicted decreased insect visitation frequency after predator eradication for 3 of 19 significant pollinator-plant interactions: non-*Vespula* wasps visiting *H. haplostachya* following mouse eradication, honey bees visiting *T. arenarium* following mouse eradication, and honey bees visiting *S. fallax* following yellowjacket eradication (Figure 2; Table 2). The largest mean negative predicted change in pollinator visitation, for which decreasing a predator was predicted to result in a decrease in flower visitation frequency, was the reduction in honey bee visitation to *S. fallax* after eradication of yellowjackets (mean predicted change in pollinator visitation = -0.320, 95% CI: -0.743, -0.002). The predicted change in pollinator visitation for non-*Vespula* wasps visiting *H. haplostachya* following mouse eradication was extremely small (mean predicted change in pollinator visitation \leq -0.001, 95% CI: <-0.001, <-0.001).

DISCUSSION

Our community-wide investigation of plant–pollinator interactions revealed measurable effects of invasive predators on these critical interactions. Frequency of flower visitation by confirmed important pollinator groups was significantly related to landscape-level predator abundances. Top-down effects of predators on plant–pollinator interactions were not uniform, underscoring the importance of investigating each predator–pollinator–plant relationship individually. However, across multiple plant species and multiple pollinator groups, we found consistent community-scale patterns. Notably, rats and ants exerted only negative impacts on pollinator–plant visitation, with increased abundance of these predators associated with decreased visitation by various pollinator groups. Model outputs suggested that removing these invasive predators would increase the frequency of pollinator visitation and plant outcrossing, including for the endangered species *H. haplostachya* and *T. arenarium*. Such empirical and modeled effects can help to inform managers when selecting approaches to benefit native and endangered plant reproduction.

The positive predicted changes in frequency of pollinator visitation as a result of predator treatment (in 16 of 19 significant predator–pollinator–plant relationships) supported our initial hypothesis that suppression of invasive predators increases pollinator visitation. Predators could disrupt pollination through direct density-mediated (i.e., direct predation) or indirect trait-mediated (i.e., modifying pollinator behavior) interactions. Invasive vertebrate predators such as rats and mice that do not spend much time on flowers are likely to elicit density-mediated responses in some groups, whereas invasive invertebrate predators such as yellowjackets and ants may elicit both density-mediated responses through predation and trait-mediated responses through deterring other insects from visiting flowers (Benoit & Kalisz, 2020). Predator effects have been shown to be particularly strong in oceanic island ecosystems, where communities often lack certain predator guilds and pollinators can lack predation defenses (Doherty et al., 2016). Island ecosystems therefore allow the study of important ecological patterns and processes that may otherwise be difficult to discern or obscured by complex community responses or compensatory mechanisms.

Larger predicted changes in pollinator visitation are likely to be more ecologically meaningful and also dependent on the specific predator–pollinator–plant combination of traits (Benoit & Kalisz, 2020). The largest predicted changes in pollinator visitation benefited *S. fallax*, which was widely distributed and abundant throughout the study site, through increased visitation of

non-syrphid flies (with rat eradication) and honey bees (with ant eradication). These two pollinator groups were themselves widely distributed and abundant throughout the study site. Generalist traits and high abundances of all three species in each tritrophic relationship could be contributing factors in the strong top-down effects for these particular predator–pollinator–plant interactions.

Reproduction of our focal plant species is likely to be negatively affected by decreased pollinator interactions, based on our previous work in the system. Both common and endangered plant species are pollen limited, and flower treatment experiments showed that open-pollinated flowers produced significantly more seed than bagged flowers for all of our focal plant species except *S. lanceolata* (Aslan et al., 2019). In general, then, these focal plants have limited autogamy, or self-fertilization, and are dependent to some degree on pollinators for reproductive fitness. Our results showed that invasive predators reduced visitation by the primary pollinators of these plants, including solitary and social bees, moths, and non-*Vespula* wasps.

For our focal endangered plant species, rats reduced visitation to *H. haplostachya* by the key pollinator group Lepidoptera. Rats also reduced visitation to *T. arenarium* by the key pollinator groups Lepidoptera and non-*Vespula* wasps. In any system with generalist pollinators that are themselves below carrying capacity, endangered plant species may be less likely to compete successfully for flower visitors due to their rarity; that is, because the rare plants are less apparent as a resource, pollinators may fail to visit them and instead focus on more common plant flowers (Revilla & Křivan, 2016). Our previous work in this system demonstrated that the endangered plant species in this study demonstrated greater pollen limitation and interacted with a lower richness of flower visitor species compared with common plant species (Aslan et al., 2019). Therefore, the effects of predation on flower visitation to rare species detected in this study appear likely to disrupt pollination systems that are already vulnerable. Our results demonstrated that rat suppression is one tactic that managers can add to their toolboxes to conserve endangered endemic plant species within invaded island systems, particularly if these plant species are pollen limited.

Contrary to our initial hypothesis, we detected a few negative predicted changes in pollinator visitation as a result of predator treatment, whereby suppression of invasive predators decreased pollinator visitation. Such negative effects of predator suppression were infrequent (3 of 19 significant predator–pollinator–plant interactions; Table 2) and probably stemmed from the specific traits of the predator and pollinator taxa. The higher house mouse abundances associated with higher

visitation frequencies by non-*Vespula* wasps to *H. haplostachya* and by honey bees to *T. arenarium* could be the result of all three animal groups responding to shared seasonally high resources, or to other environmental factors that enabled these already abundant groups to thrive simultaneously. It should be noted, however, that the magnitude of relationship between house mouse abundances and non-*Vespula* wasps was extremely small and likely to be ecologically irrelevant or due entirely to chance. The largest mean negative predicted change in pollinator visitation occurred for the interaction between yellowjackets and honey bee visitation to *S. fallax*, perhaps due to a general positive association between yellowjackets and honey bees. Honey bee nests are known important resources for yellowjackets, which raid them for honey and bee larvae. Previous work has suggested that honey bee colonies enable yellowjackets to reach higher densities, increasing their negative impacts on native insects (Wilson & Holway, 2010). Negative predicted changes in pollinator visitation as a result of predator suppression could also stem from competitive relationships among flower visitors (Benoit & Kalisz, 2020), although research on these relationships is limited; decreased predation pressure on some flower-visiting taxa, and corresponding population increases in those taxa, could lead to the suppression of other flower-visiting taxa due to competition.

The European honey bee (*A. mellifera*), which is not native to the Hawaiian Islands, was the most frequently observed flower visitor detected at our study site, where it exists exclusively in unmanaged, feral colonies. The honey bee is considered by many to be an invasive species across its introduced range, and it has been implicated in the disruption of plant–pollinator interactions through competition with native bees and other pollinators in island and continental ecosystems (Thomson, 2004; Traveset & Richardson, 2006). In Hawai'i, where the honey bee has been established since the 1850s, its role in native ecosystems is complex and poorly understood. Although there is some evidence that honey bees provide valuable pollination services to some native plants and transfer more pollen than native solitary bees (Junker et al., 2010), individual honey bees also visit a higher diversity of plant taxa and a higher proportion of nonnative plants than do native bees (Miller et al., 2015), which may make them less efficient pollinators of native plants. We found that the honey bee visited all six of our focal plant species, and carried pollen for all them, strongly suggesting that they are important pollinators in our study system. Our results also suggested that the honey bee is relatively resilient to the impacts of invasive predators, compared with other pollinators in the study; the only

significant negative association between a predator and honey bees was with ants on *S. fallax* (Figure 4).

Indirect effects caused by target predators on insect pollinators are possible outcomes throughout our study. For example, the reduced flower visitation by solitary bees and syrphid flies that was attributed to predatory effects of yellowjacket wasps could have also led to simultaneous increases in honey bees, as solitary bees and syrphid flies are likely competitors with honey bees. However, honey bees are generally considered to be a stronger competitor than other pollinator taxa (Thomson, 2004; Traveset & Richardson, 2006) and so a more likely scenario is that the reduction in honey bees due to predators would have led to simultaneous increases in other pollinators. We did not find this in our study, however, as the only reduction in flower visitation by honey bees was attributed to ants and there were no simultaneous increases in flower visitation by other pollinator groups. In addition, correlation analyses between frequency of honey bee visitation with the other pollinator functional groups, by plot and across all plant species, showed no large correlations (honey bees & solitary bees: $r = 0.006$, honey bees & non-syrphid flies: $r = -0.176$, honey bees & syrphid flies: $r = 0.129$, honey bees & Lepidoptera, $r = -0.153$, honey bees & non-*Vespula* wasps: $r = -0.166$).

Environmental factors could account for both negative and positive impacts of predator effects on pollination, and we probably would find correlations if we had only followed population dynamics of both predators and pollinators over time. For example, if the predator population decreased due to environmental factors, some pollinator groups may also have decreased due to the same environmental factors. However, the decreased predator populations could also lead to increases in some pollinator groups through density-mediated or trait-mediated effects. Our experimental study, in which we collected predator abundance data in treated and untreated plots, allowed us to track the natural variability in predator populations and to account for some, but not all, of this variability in our statistical models to analyze top-down effects of each predator group on pollinator–plant interactions.

Our study experimentally demonstrated that invasive predators impact the most important pollinator groups previously identified in this system, specifically native and nonnative bees, Lepidoptera, wasps, and syrphid flies (Aslan et al., 2019). These dominant pollinators are themselves highly generalist (Martín González et al., 2010; Olesen et al., 2002). As a result, the community-scale effects documented here are also likely to occur in other systems, as these invasive predators exhibit broad diets that enable them to spread readily and consume pollinators following introduction. For example, more than 70%

of analyzed stomachs of *M. musculus* and *R. rattus* from other Hawaiian study sites contained insects (Shiels et al., 2013). Lepidoptera, primarily as larvae, occurred in 34% of *R. rattus* stomach contents and more than 80% of *M. musculus* stomach contents in those sites (Shiels et al., 2013). The Argentine ant, *L. humile*, has been implicated in both direct predation on native pollinators and reduced pollinator visitation to flowers as a result of aggressive competition for resources (Cole et al., 1992; Hanna et al., 2015; Sahli et al., 2016).

The invasive predators in this system are of global importance and concern, having become naturalized and invasive in systems worldwide, spanning large elevational and latitudinal ranges and occurring across continents and islands alike. Although some of their impacts on native ecosystems have been well documented (Cole et al., 1992; Doherty et al., 2016; Lester & Beggs, 2019; Towns, 2009), their potential to disrupt pollination has been understudied. Our experimental results elucidated the complex, community-scale impacts of these predators on plant-pollinator interactions and demonstrated the top-down effects across trophic levels. Underscoring their strength and importance, these effects emerged in spite of the spatial and temporal variability in predator populations within the system. Furthermore, the flower visitors in this system, which responded to the abundance of these predators, included many generalist, cosmopolitan taxa. As a result, the interacting predator and pollinator species in our study system are likely also to interact in many other systems where they co-occur around the world. These predator-pollinator relationships are therefore liable to influence pollination and pollinator communities in invaded systems worldwide.

Conservation or restoration of disrupted pollination requires an awareness of both plant and pollinator requirements as well as the threats they face. Rodents, ants, and wasps are probably reshaping global ecological communities and pollination networks in ways that might not be immediately obvious, but could have major impacts on native plant species and communities (Hanna et al., 2013; Kaiser-Bunbury et al., 2017). Although complete eradication of these invasive predators is not always feasible using current technology and resources, our findings suggest that even localized suppression or eradication will benefit native plant communities through increased pollination and may be especially beneficial when at-risk, pollinator-dependent plants are present. Policies and practices aimed at local reduction or eradication of these invasive predators are becoming more common and are often successful, particularly with the use of traps and toxicants (Boser et al., 2017; Duron et al., 2017; Lester & Beggs, 2019). Such efforts require significant investment of time and resources and have been the focus of extensive invasion biology research

aiming to inform managers about their barriers and benefits (e.g., Hoffmann et al., 2016; Jones et al., 2016; Peltzer et al., 2019). Furthermore, the effects of eradication efforts must be monitored over the long term. Removal of an influential predator species from an ecosystem may produce positive responses of pollinator populations over the short term, such as those we found in this study, but other predators or competitors may increase in number and eventually inherit the role of exerting regulatory forces on pollinator communities (Bode et al., 2015; Doherty & Ritchie, 2017). Because invasive predators can exert whole-ecosystem impacts (Doherty et al., 2016), managers aiming to support native communities must therefore consider and track non-target effects of predator management. Nevertheless, our findings that predator eradication is likely to bolster visitation to our focal plant species suggested that invasive predator treatments should be implemented when feasible, to reverse native plant pollination disruption within ecosystems that have been invaded by nonnative rodents, ants, or yellowjackets.

ACKNOWLEDGMENTS

We thank all field personnel for their work and the Pōhakuloa Training Area Natural Resources Office for logistical support and assistance. This study was funded by the Department of Defense Strategic Environmental Research and Development Program (grant no. RC-2432). Work was performed under USFWS Native Endangered Species Recovery Permit TE-28360B-0; Hawai'i DLNR-DOFAW Permit for Threatened & Endangered Plant Species P-201; and Hawai'i DLNR-DOFAW Permit for Native Invertebrate Research FHM17-428. Rodent methods were approved under the USDA NWRC Institutional Animal Care and Use Committee Study Protocol number QA-2452. Yellowjacket methods were approved under the Hawai'i Department of Agriculture Experimental Use Permit number EUP-16-010. Mention of a company or commercial product does not mean endorsement by the US government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.


DATA AVAILABILITY STATEMENT

Data (Liang et al., 2021) are available in Dryad: <https://doi.org/10.5061/dryad.02v6wwq40>.

ORCID

Christina T. Liang  <https://orcid.org/0000-0002-5386-2865>

Aaron B. Shiels  <https://orcid.org/0000-0002-6774-4560>

Manette E. Sandor  <https://orcid.org/0000-0002-3665-4837>

REFERENCES

- Aslan, C.E., A.B. Shiels, W. Haines, and C.T. Liang. 2019. "Non-native Insects Dominate Daytime Pollination in a High-Elevation Hawaiian Dryland Ecosystem." *American Journal of Botany* 106: 313–24.
- Aslan, C.E., E.S. Zavaleta, B. Tershy, D.O.N. Croll, and R.H. Robichaux. 2014. "Imperfect Replacement of Native Species by Non-native Species as Pollinators of Endemic Hawaiian Plants." *Conservation Biology* 28: 478–88.
- Bailes, E.J., K.R. Deutsch, J. Bagi, L. Rondissone, M.J. Brown, and O.T. Lewis. 2018. "First Detection of Bee Viruses in Hoverfly (Syrphid) Pollinators." *Biology Letters* 14: 20180001.
- Baxter, P.W., J.L. Sabo, C. Wilcox, M.A. McCarthy, and H. P. Possingham. 2008. "Cost-Effective Suppression and Eradication of Invasive Predators." *Conservation Biology* 22: 89–98.
- Benoit, A.D., and S. Kalisz. 2020. "Predator Effects on Plant-Pollinator Interactions, Plant Reproduction, Mating Systems, and Evolution." *Annual Review of Ecology, Evolution, and Systematics* 51: 319–40.
- Biesmeijer, J.C., S.P.M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, et al. 2006. "Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and The Netherlands." *Science* 313: 351–4.
- Bode, M., C.M. Baker, and M. Plein. 2015. "Eradicating down the Food Chain: Optimal Multispecies Eradication Schedules for a Commonly Encountered Invaded Island Ecosystem." *Journal of Applied Ecology* 52: 571–9.
- Boser, C.L., C. Hanna, D.A. Holway, K.R. Faulkner, I. Naughton, K. Merrill, J.M. Randall, C. Cory, D.-H. Choe, and S.A. Morrison. 2017. "Protocols for Argentine Ant Eradication in Natural Areas." *Journal of Applied Entomology* 141: 540–50.
- Byers, D.L. 2017. "Studying Plant–Pollinator Interactions in a Changing Climate: A Review of Approaches." *Applications in Plant Sciences* 5: 1700012.
- Chittka, L. 2001. "Camouflage of Predatory Crab Spiders on Flowers and the Colour Perception of Bees (Aranida: Thomisidae/Hymenoptera: Apidae)." *Entomologia Generalis* 25: 181–7.
- Christmann, S. 2019. "Do we Realize the Full Impact of Pollinator Loss on Other Ecosystem Services and the Challenges for any Restoration in Terrestrial Areas?" *Restoration Ecology* 27: 720–5.
- Cole, F.R., A.C. Medeiros, L.L. Loope, C.E. Howe, and W.W. Zuehlke. 1992. "Effects of the Argentine Ant on Arthropod Fauna of Hawaiian High-Elevation Shrubland." *Ecology* 73: 1313–22.
- Cresswell, J.E. 2017. "A Demographic Approach to Evaluating the Impact of Stressors on Bumble Bee Colonies." *Ecological Entomology* 42: 221–9.
- Doherty, T.S., C.R. Dickman, D.G. Nimmo, and E.G. Ritchie. 2015. "Multiple Threats, or Multiplying the Threats? Interactions between Invasive Predators and Other Ecological Disturbances." *Biological Conservation* 190: 60–8.
- Doherty, T.S., A.S. Glen, D.G. Nimmo, E.G. Ritchie, and C.R. Dickman. 2016. "Invasive Predators and Global Biodiversity Loss." *Proceedings of the National Academy of Sciences of the United States of America* 113: 11261–5.
- Doherty, T.S., and E.G. Ritchie. 2017. "Stop Jumping the Gun: A Call for Evidence-Based Invasive Predator Management." *Conservation Letters* 10: 15–22.
- Dukas, R. 2005. "Bumble Bee Predators Reduce Pollinator Density and Plant Fitness." *Ecology* 86: 1401–6.
- Duron, Q., A.B. Shiels, and E. Vidal. 2017. "Control of Invasive Rats on Islands and Priorities for Future Action." *Conservation Biology* 31: 761–71.
- Farwig, N., D.G. Schabo, and J. Albrecht. 2017. "Trait-Associated Loss of Frugivores in Fragmented Forest Does Not Affect Seed Removal Rates." *Journal of Ecology* 105: 20–8.
- Foote, D., C. Hanna, C. King, and E. B. Spurr. 2011. "Efficacy of Fipronil for Suppression of Invasive Yellowjacket Wasps in Hawaii Volcanoes National Park." Tech. Rep. HCSU-028. Hilo, HI: University of Hawaii at Hilo.
- GBIF. 2020. "Global Biodiversity Information Facility," March 2, 2020 <https://www.gbif.org>.
- Gelman, A., J. Hill, and M. Yajima. 2012. "Why We (Usually) Don't Have to Worry about Multiple Comparisons." *Journal of Research on Educational Effectiveness* 5: 189–211.
- Gelman, A., and D.B. Rubin. 1992. "Inference from Iterative Simulation Using Multiple Sequences." *Statistical Science* 7: 457–72.
- Gonçalves-Souza, T., P.M. Omena, J.C. Souza, and G.Q. Romero. 2008. "Trait-Mediated Effects on Flowers: Artificial Spiders Deceive Pollinators and Decrease Plant Fitness." *Ecology* 89: 2407–13.
- Hanna, C., D. Foote, and C. Kremen. 2013. "Invasive Species Management Restores a Plant–Pollinator Mutualism in Hawaii." *Journal of Applied Ecology* 50: 147–55.
- Hanna, C., I. Naughton, C. Boser, R. Alarcón, K.-L.J. Hung, and D. Holway. 2015. "Floral Visitation by the Argentine Ant Reduces Bee Visitation and Plant Seed Set." *Ecology* 96: 222–30.
- Harper, G.A., and N. Bunbury. 2015. "Invasive Rats on Tropical Islands: Their Population Biology and Impacts on Native Species." *Global Ecology and Conservation* 3: 607–27.
- Hoffmann, B.D., G.M. Luque, C. Bellard, N.D. Holmes, and C.J. Donlan. 2016. "Improving Invasive Ant Eradication as a Conservation Tool: A Review." *Biological Conservation* 198: 37–49.
- Huey, S., and J.C. Nieh. 2017. "Foraging at a Safe Distance: Crab Spider Effects on Pollinators." *Ecological Entomology* 42: 469–76.
- Jones, H.P., N.D. Holmes, S.H. Butchart, B.R. Tershy, P.J. Kappes, I. Corkery, A. Aguirre-Muñoz, et al. 2016. "Invasive Mammal Eradication on Islands Results in Substantial Conservation Gains." *Proceedings of the National Academy of Sciences of the United States of America* 113: 4033–8.
- Junker, R.R., R. Bleil, C.C. Daehler, and N. Blüthgen. 2010. "Intra-Floral Resource Partitioning between Endemic and Invasive Flower Visitors: Consequences for Pollinator Effectiveness." *Ecological Entomology* 35: 760–7.
- Kaiser-Bunbury, C., J. Mougil, A. Whittington, T. Valentin, R. Gabriel, J.M. Olesen, and N. Blüthgen. 2017. "Ecosystem Restoration Strengthens Pollination Network Resilience and Function." *Nature* 542: 223–7.
- Kearns, C.A., and D.W. Inouye. 1993. *Techniques for Pollination Biologists*. Niwot: University Press of Colorado.
- Kluser, S., and P. Peduzzi. 2007. *Global Pollinator Decline: A Literature Review*. Geneva, Switzerland: United Nations Environment Programme.

- Knight, T.M., J.M. Chase, H. Hillebrand, and R.D. Holt. 2006. "Predation on Mutualists Can Reduce the Strength of Trophic Cascades." *Ecology Letters* 9: 1173–8.
- Krushelnycky, P., W. Haines, L. Loope, and E. Van Gelder. 2011. *The Haleakala Argentine Ant Project: A Synthesis of Past Research and Prospects for the Future. Tech. Rep.* Honolulu, HI: Pacific Cooperative Studies Unit, University of Hawaii at Manoa.
- Lester, P.J., and J.R. Beggs. 2019. "Invasion Success and Management Strategies for Social *Vespula* Wasps." *Annual Review of Entomology* 64: 51–71.
- Liang, Christina, Aaron B. Shiels, William P. Haines, Manette E. Sandor, Clare E. Aslan. 2021. Invasive Predators Affect Community-Wide Pollinator Visitation, *Dryad*, Dataset. <https://doi.org/10.5061/dryad.02v6wwq40>
- López-Osorio, F., and Y. Wurm. 2020. "Healthy Pollinators: Evaluating Pesticides with Molecular Medicine Approaches." *Trends in Ecology and Evolution* 35: 380–3.
- Maron, J.L., J.A. Estes, D.A. Croll, E.M. Danner, S.C. Elmendorf, and S.L. Buckelew. 2006. "An Introduced Predator Alters Aleutian Island Plant Communities by Thwarting Nutrient Subsidies." *Ecological Monographs* 76: 3–24.
- Martín González, A.M., B. Dalsgaard, and J.M. Olesen. 2010. "Centrality Measures and the Importance of Generalist Species in Pollination Networks." *Ecological Complexity* 7: 36–43.
- Medina, F.M., E. Bonnaud, E. Vidal, and M. Nogales. 2014. "Underlying Impacts of Invasive Cats on Islands: Not Only a Question of Predation." *Biodiversity and Conservation* 23: 327–42.
- Miller, A.E., B.J. Brosi, K. Magnacca, G.C. Daily, and L. Pejchar. 2015. "Pollen Carried by Native and Nonnative Bees in the Large-Scale Reforestation of Pastureland in Hawai'i: Implications for Pollination." *Pacific Science* 69: 67–79.
- Neuschulz, E.L., T. Mueller, M. Schleuning, and K. Böhning-Gaese. 2016. "Pollination and Seed Dispersal Are the most Threatened Processes of Plant Regeneration." *Scientific Reports* 6: 29839.
- Olesen, J.M., L.I. Eskildsen, and S. Venkatasamy. 2002. "Invasion of Pollination Networks on Oceanic Islands: Importance of Invader Complexes and Endemic Super Generalists." *Diversity and Distributions* 8: 181–92.
- Ollerton, J. 2017. "Pollinator Diversity: Distribution, Ecological Function, and Conservation." *Annual Review of Ecology and Systematics* 48: 353–76.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. "How Many Flowering Plants Are Pollinated by Animals?" *Oikos* 120: 321–6.
- Peltzer, D.A., P.J. Bellingham, I.A. Dickie, G. Houlston, P.E. Hulme, P.O.B. Lyver, M. McGlone, S.J. Richardson, and J. Wood. 2019. "Scale and Complexity Implications of Making New Zealand Predator-Free by 2050." *Journal of the Royal Society of New Zealand* 49: 412–39.
- Pender, R.J., A.B. Shiels, L. Bialic-Murphy, and S.M. Mosher. 2013. "Large-Scale Rodent Control Reduces Pre- and Post-Dispersal Seed Predation of the Endangered Hawaiian Lobeliad, *Cyanea Superba* Subsp. *Superba* (Campanulaceae)." *Biological Invasions* 15: 213–23.
- Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models using Gibbs Sampling." *Proceedings of the 3rd International Workshop on Distributed Statistical Computer (DSC 2003) March* 124: 1–10.
- Plummer, M., A. Stukalov, and M. Denwood, 2018. "Rjags: Bayesian graphical models using MCMC." R package version 4-8. <https://CRAN.R-project.org/package=rjags>.
- Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. "Global Pollinator Declines: Trends, Impacts and Drivers." *Trends in Ecology and Evolution* 25: 345–53.
- Renne, I.J., S.A. Gauthreaux, Jr., and C.A. Gresham. 2000. "Seed Dispersal of the Chinese Tallow Tree (*Sapium Sebiferum* [L.] Roxb.) by Birds in Coastal South Carolina." *The American Midland Naturalist* 144: 202–15.
- Revilla, T.A., and V. Křivan. 2016. "Pollinator Foraging Adaptation and Coexistence of Competing Plants." *PLoS One* 11: e0160076.
- Rodríguez-Gironés, M.A. 2012. "Possible Top-Down Control of Solitary Bee Populations by Ambush Predators." *Behavioral Ecology* 23: 559–65.
- Rogers, H.S., E.R. Buhle, J. HilleRisLambers, E.C. Fricke, R.H. Miller, and J.J. Tewksbury. 2017. "Effects of an Invasive Predator Cascade to Plants Via Mutualism Disruption." *Nature Communications* 8: 1–8.
- Romero, G.Q., P.A.P. Antiqueira, and J. Koricheva. 2011. "A Meta-Analysis of Predation Risk Effects on Pollinator Behaviour." *PLoS One* 6: e20689.
- Sahli, H.F., P.D. Krushelnycky, D.R. Drake, and A.D. Taylor. 2016. "Patterns of Floral Visitation to Native Hawaiian Plants in Presence and Absence of Invasive Argentine Ants." *Pacific Science* 70: 309–22.
- Shiels, A. B. 2010. Ecology and Impacts of Introduced Rodents (*Rattus* Spp. and *Mus Musculus*) in the Hawaiian Islands. *Dissertation*, University of Hawaii at Manoa, Honolulu, Hawaii.
- Shiels, A.B., C.A. Flores, A. Khamsing, P.D. Krushelnycky, S.M. Mosher, and D.R. Drake. 2013. "Dietary Niche Differentiation among Three Species of Invasive Rodents (*Rattus Rattus*, *R. Exulans*, *Mus Musculus*)." *Biological Invasions* 15: 1037–48.
- Snyder, W.E., and E.W. Evans. 2006. "Ecological Effects of Invasive Arthropod Generalist Predators." *Annual Review of Ecology, Evolution, and Systematics* 37: 95–122.
- Su, Y.-S., and M. Yajima. 2015. "R2jags: Using R to Run 'JAGS'." R package version 0.5–7. CRAN. R-project. Org/package=R2jags.
- Théry, M., and J. Casas. 2002. "Predator and Prey Views of Spider Camouflage." *Nature* 415: 133–3.
- Thomson, D. 2004. "Competitive Interactions between the Invasive European Honey Bee and Native Bumble Bees." *Ecology* 85: 458–70.
- Tonietto, R.K., and D.J. Larkin. 2018. "Habitat Restoration Benefits Wild Bees: A Meta-Analysis." *Journal of Applied Ecology* 55: 582–90.
- Towns, D.R. 2009. "Rodents." In *Encyclopedia of Islands*, edited by R.G. Gillespie and D.A. Clague, 792–6. Berkeley, CA: University of California Press.
- Traveset, A., and D.M. Richardson. 2006. "Biological Invasions as Disruptors of Plant Reproductive Mutualisms." *Trends in Ecology and Evolution* 21: 208–16.

Wilson, E.E., and D.A. Holway. 2010. "Multiple Mechanisms Underlie Displacement of Solitary Hawaiian Hymenoptera by an Invasive Social Wasp." *Ecology* 91: 3294–302.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Liang, Christina T., Aaron B. Shiels, William P. Haines, Manette E. Sandor, and Clare E. Aslan. 2022. "Invasive Predators Affect Community-Wide Pollinator Visitation." *Ecological Applications* 32(2): e2522. <https://doi.org/10.1002/eap.2522>