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Restoring Ecological Function with Invasive Species Management

By

Cause Hanna

A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Claire Kremen, Chair

Professor Bruce G. Baldwin

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Spring 2012

Abstract

Restoring Ecological Function with Invasive Species Management

by

Cause Hanna

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor Claire Kremen, Chair

Mutually beneficial interactions between pollinators and flowering plants represent a critical but threatened component of ecosystem function that can underlie the success of ecological restoration. The management and removal of invasive species may give rise to unanticipated changes in plant-pollinator mutualisms because they can alter the composition and functioning of plant-pollinator interactions in a variety of ways. In an attempt to incorporate a functional framework into invasive species management, we conducted a large-scale manipulative experiment to examine the restoration of the plant-pollinator mutualisms and the pollination of a functionally important endemic tree species, *Metrosideros polymorpha*, following the removal of a competitively dominant invasive floral visitor and arthropod predator, *Vespula pensylvanica*. The invasive western yellowjacket wasp, *Vespula pensylvanica*, is an adept and aggressive nectar thief of the partially self-incompatible and pollen limited *M. polymorpha*. A management strategy utilizing 0.1% fipronil chicken bait with the addition of heptyl butyrate reduced the abundance of *V. pensylvanica* by $95 \pm 1.2\%$ during the 3 months following treatment and maintained a population reduction of $60.9 \pm 3.1\%$ a year after treatment in the managed sites when compared with unmanaged sites. The large-scale management of *V. pensylvanica* demonstrated that *V. pensylvanica* through both superior exploitative and interference competition inhibits resource partitioning and displaces native and non-native *M. polymorpha* pollinators. Correspondingly, the removal of *V. pensylvanica* resulted in the competitive release and restructuring of the pollinator community and the re-establishment of the plant-pollinator mutualisms and pollination of *M. polymorpha*. This research elucidates the competitive mechanisms and contrasting implications of introduced species on ecological function and provides a framework from which future invasive species management can preserve ecological function and maintain ecosystem resilience.

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ACKNOWLEDGEMENTS

CHAPTER 1

Short- and long-term control of *Vespula pensylvanica* in Hawaii by fipronil baiting

Cause Hanna,[a]* David Foote[b] and Claire Kremen[a]

Abstract

BACKGROUND: The invasive western yellowjacket wasp, *Vespula pensylvanica* (Saussure), has significantly impacted the ecological integrity and human welfare of Hawaii. The goals of the present study were (1) to evaluate the immediate and long-term efficacy of a 0.1% fipronil chicken bait on *V. pensylvanica* populations in Hawaii Volcanoes National Park, (2) to quantify gains in efficacy using the attractant heptyl butyrate in the bait stations and (3) to measure the benefits of this approach for minimizing non-target impacts to other arthropods.

RESULTS: The 0.1% fipronil chicken bait reduced the abundance of *V. pensylvanica* by $95 \pm 1.2\%$ during the 3 months following treatment and maintained a population reduction of $60.9 \pm 3.1\%$ a year after treatment in the fipronil-treated sites when compared with chicken-only sites. The addition of heptyl butyrate to the bait stations significantly increased *V. pensylvanica* forager visitation and bait take and significantly reduced the non-target impacts of fipronil baiting.

CONCLUSION: In this study, 0.1% fipronil chicken bait with the addition of heptyl butyrate was found to be an extremely effective large-scale management strategy and provided the first evidence of a wasp suppression program impacting *Vepsula* populations a year after treatment.
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Keywords: social wasps; *Vespula pensylvanica*; invasive species; fipronil; insecticidal bait; Hawaii

1 INTRODUCTION

Invasive species are widely recognized as one of the leading threats to global biodiversity, human health and ecosystem integrity.[1–4] Social insects rank among the most widespread and damaging of invasive organisms throughout the world.[5,6] In Hawaii, the high taxonomic endemism and extensive evolutionary adaptive radiations in the absence of eusocial insects[7] make native ecosystems highly vulnerable to the invasive social insects owing to their cooperation and foraging strategies.[8–10] First records of *Vespula pensylvanica* (Saussure) occurrence in Hawaii include Kauai, 1919,[11] Oahu, 1936,[12] and the easternmost Hawaiian Islands, 1976.[13] *Vespula* are generalist arthropod predators that also forage for nectar to subsidize their energy demands. The expansion and competitive advantages of invasive *V. pensylvanica* in Hawaii may lead to the extinction or reduction of native invertebrates[14,15] and endemic birds,[16] which in turn may have indirect effects on the reproduction of native plants.[14,17] In addition, the aggressive nature of *V. pensylvanica* and the propensity of stings to cause anaphylactic shock in hypersensitive individuals directly impacts human welfare and recreational activities.[18,19] The magnitude of these impacts is augmented relative to their effects on mainland habitats by the increased year-round population density resulting from the formation of perennial supercolonies observed among introduced *Vespula* populations.[15,20–22] In addition, the invaded region coincides with some of the remaining areas of high Hawaiian endemism.[23]

Vespula species are continuing to spread around the globe[24], and effective tools are needed potentially to manage their spread, as well as to reduce their current impact in areas where they are already problematic. Insecticidal baits currently offer the most effective method for suppressing wasp populations while minimizing effects on non-target arthropods.[14,25–30] In contrast, biological control attempts have not reduced wasp numbers,[31,24] and the time and labor intensity of locating nests makes insecticidal dusts an inefficient large-scale control strategy. Insecticidal baiting takes advantage of the tropholactic feeding, the transfer of food among workers and larvae within yellowjacket colonies,[32] thus killing the foragers that collect the bait and the larvae within the colony.[23] However, no insecticidal baits are currently registered in Hawaii for yellowjacket control. Current guidelines for control of *V. pensylvanica* in Hawaii specify the use of KnoxOut® 2FM (Cerexogri, PA), a microencapsulated formulation of the organophosphate insecticide diazinon, mixed with chicken meat, in bait stations.[14,18,26] However, KnoxOut® 2FM has not been manufactured since December 2000, and supplies are limited to stock in hand. The phenylpyrazole insecticide fipronil has been used successfully as a bait insect toxicant for *Vespula* wasp control in other countries, such as New Zealand[27] and Argentina.[28] Fipronil was more effective than diazinon in a shorter period of time (1–3 days instead of 6+ weeks),[33,34] and consequently

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the exposure of insecticidal baits to non-target species should be reduced with higher cost effectiveness. The addition of the chemical heptyl butyrate, one of multiple synthetic esters attractive to some species of yellowjackets, in bait stations could further reduce the exposure of non-target species to insecticidal baits by increasing the attraction of *Vespula* to bait stations.

The aim of the present study was to evaluate the efficacy of fipronil for *V. pensylvanica* control on a management scale in Hawaii by: (1) determining the short- and long-term efficacy of a 0.1% fipronil chicken bait for the control of *V. pensylvanica* populations over large treatment areas (9 ha); (2) measuring the effects of the addition of a long-range attractant heptyl butyrate, on the attraction of bait used for *V. pensylvanica* control; (3) quantifying the non-target exposure and attraction of treatments.

2 EXPERIMENTAL METHODS

2.1 Study design
A BACI (Before-After, Control-Impact) experimental design was used to determine the efficacy of fipronil as an insecticide for yellowjacket control in Hawaii Volcanoes National Park from 2008 to 2010. This paper reports the impact of 3 years of annual baiting on *V. pensylvanica* populations in Hawaii.

2.2 Study area
Ten 9 ha study sites were randomly selected within seasonal submontane ohia (*Metrosideros polymorpha*) woodland within Hawaii Volcanoes National Park (Fig. 1) between approximately 700 to 1100 m elevation, where the mean annual rainfall ranges from 1200 to 1900 mm and mean annual temperatures are 20–22 °C.[35,36] In five of the sites, 0.1% fipronil chicken bait was deployed annually, while the other five were kept as non-insecticide sites. The fipronil and non-insecticide sites were paired to control for environmental variables, treatment was allocated randomly within pairs and all sites were separated by ≥1 km to maintain site independence (95% of wasps travel ≤200 m from the nest when foraging).[37] The 9 ha study sites (300 × 300 m) were marked, and a 25 × 50 m flagged grid was constructed in each of them.

2.3 Bait application
The 0.1% fipronil chicken bait was composed of Frontline® Top Spot® for Dogs and Puppies (Merial Limited, GA), a product currently registered in Hawaii (65 331-3), and Valley Fresh Chicken Meat™ (Hormel Foods, MN). The fipronil concentration was chosen on the basis of previous lab and field tests,[27,28,31] and the type of protein bait was determined from previous bait choice experiments.[14,37–39] To increase the long-range attraction, a 1.5 mL microcentrifuge tube (USA Scientific, FL) filled with 1 mL of heptyl butyrate (98%; Aldrich, MO) absorbed within a paper towel wick was placed within each bait station.

In 2008 and 2009, fipronil bait was deployed in September under Hawaii Department of Agriculture experimental use permits on a 25 × 25 m grid within the center hectare of the study site (16 bait stations ha⁻¹) (Fig. 1). In 2010, bait was deployed in August, and the scale of the control effort under an EPA experimental use permit was increased by deploying fipronil bait on a 25 × 50 m grid covering the entire 9 ha study area (8 bait stations ha⁻¹). A quantity of 10 g of fipronil bait was placed in each bait station. Bait stations were hung from vegetation 1–2 m off the ground and made from 2 oz plastic portion cups (Solo Cup Co., IL) with lids attached, and with four 17 mm diameter holes in the sides of the cups for yellowjackets to enter and exit through.[33] In 2008 the fipronil bait was offered in bait stations for a 72 h deployment, whereas in 2009 and 2010 the fipronil bait was deployed for 24 h.

2.4 *Vespula* activity indices
Nest activity is an index of the resident wasp population in the study site.[40] The traffic rates of all known yellowjacket nests, observations of the number of *Vespula* flying in and out of nests per minute (mean of three counts each way), within the study sites were monitored weekly at a consistent time of day prior to and for 2–3 months following fipronil bait deployment.

Three additional *Vespula* activity measures were collected within each site during three monitoring rounds per year, once before and twice after annual fipronil baiting, to estimate indices of the total number of wasps (resident and non-resident visitors) in the study sites:

- *Instantaneous counts.* Non-insecticidal chicken bait was deployed at the same density as fipronil baits, and instantaneous counts of wasps at bait stations were completed every 1–3 h, 2–6 times daily at each bait station.
- *Bait take.* After surveyors had performed each instantaneous count, they estimated the amount of bait that had been removed from the bait cup and recorded the loss in 5% increments. The bait was replenished if ≤20% of the bait remained in the station. Surveyors were trained to account for desiccation, and their bait take estimates were calibrated.
- *Heptyl butyrate trapping.* Heptyl butyrate is a strong long-distance wasp attractant.[41–44] Thirteen Seabright yellowjacket wasp traps (Seabright Laboratories, CA) baited with 1.5 mL of heptyl butyrate were hung for 5 days per site during each monitoring round (see Fig. 1).

Variation in the mean pretreatment nest activity percentage data and the mean instantaneous count, bait take, and heptyl butyrate trap catch data per site was analyzed with a repeated-measures ANCOVA, using treatment as the fixed factor (fipronil versus non-insecticide), time as the repeated-measures factor and site pair as a covariate. Separate repeated-measures analyses were performed for individual years and across all years. The heptyl butyrate trap data were normalized using a lognormal transformation, whereas the nest activity, instantaneous count and bait take data were normalized using a ln $(x + 1)$ transformation to account for zeros in the dataset. Bonferroni corrections for multiple comparisons were used to correct for type I error. A simple linear regression analysis was performed to examine the relationship between the proportion of wasps caught in heptyl butyrate traps after treatment and the distance to the center of the study site. The heptyl butyrate trap proportion data were arcsine square-root transformed before analysis for normalization. To determine the relationship between pretreatment *Vespula* abundance and fipronil bait efficacy, a Spearman rank correlation was performed between pretreatment instantaneous count and percentage pre-treatment instantaneous count within the fipronil sites following treatment. All statistical analyses were performed with Systat 11.[45]

The change in *Vespula* activity indices after treatment within a site, relative to those before treatment, was calculated as follows:

$$\% \text{ Pretreatment} = \frac{\text{number of specimens post-treatment}}{\text{number of specimens pretreatment}} \times 100$$

The difference in *Vespula* activity indices between the paired fipronil and non-insecticide sites over time was calculated as
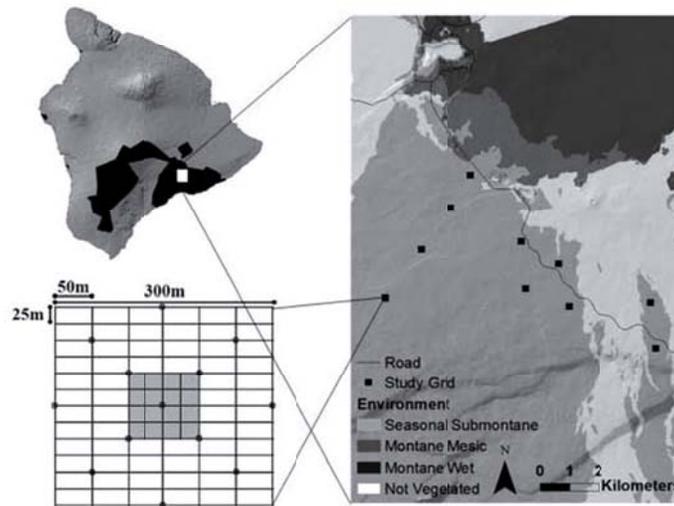
Figure 1. Locations of the ten study sites within Hawaii Volcanoes National Park and of the heptyl butyrate traps within the 9 ha (50 × 25 m) study grids. The shaded area in the study grid represents the 100 × 100 m plot used in 2008 and 2009 for small-scale application. Bait stations were placed at intersections of grid lines, and yellowjacket population monitoring trap locations are represented as circles.

follows:

$$\text{Abundance ratio}\% = \left(\frac{\% \text{ pretreatment in fipronil site}}{\% \text{ pretreatment in non-insecticide site}} - 1 \right) \times 100$$

When the abundance ratio % = 0, there is no difference between fipronil and non-insecticide sites.

2.5 Fipronil bait take

To determine the most critical time period for a successful fipronil baiting program, following fipronil bait deployment, instantaneous counts and bait take estimates were conducted 4–7 times daily at every bait station. Separate one-way ANOVA tests were performed to compare the variation in mean instantaneous count and bait take percentage per site between 2008 fipronil bait deployment days and between monitoring rounds conducted within the first 24 h of fipronil bait deployment for all years (2008–2010). The experimental groups for the deployment day analyses were defined as the number of days since bait deployment (1–3), whereas the experimental groups for the monitoring round analyses were defined as the number of hours since bait deployment (2, 4, 6 and 24). A Fisher LSD test was used for *a posteriori* comparisons.

2.6 Enhancement of bait attraction and acceptance

Heptyl butyrate is particularly useful for monitoring and managing the Hawaiian invasion of *Vespula* because it is effective at attracting *V. pensylvanica*, whereas it is weak or ineffective as a lure for other species of pestiferous social wasps.[46,47] Its effect on the amount of bait collected by wasps and the number of wasps visiting the bait stations was tested using two different experimental designs across five study sites separated by > 1 km from each other and the 9 ha study grids to maintain site independence.

2.6.1 Randomized complete block

Five complete blocks, 50 m apart, were established within each site. Each randomized complete block consisted of three treatments (no bait; chicken; chicken and heptyl butyrate), 5 m apart in a line. Instantaneous counts and bait take estimates were performed 3 times daily for three consecutive days.

2.6.2 Alternating transects

A different experimental design was implemented to reduce interactions between treatment groups, to establish more distance between bait stations and to monitor the most critical time period for a successful insecticidal baiting program, the first 6 h of bait deployment.[28] Within each site, two treatments (chicken; chicken and heptyl butyrate) were alternated along a 225 m transect every 25 m for a total of ten bait cups. Instantaneous counts and bait take estimates were performed every hour for 6 h.

Variation in mean instantaneous count and bait take percentage per site was analyzed with a one-way ANCOVA, using treatment as the main factor (chicken versus chicken and heptyl butyrate) and site as a covariate. A Fisher LSD test was used for *a posteriori* comparisons.

2.7 Non-target species monitoring

All non-target invertebrates observed at bait stations during non-insecticide and fipronil baiting were recorded and, when possible, collected. Laboratory identifications were attempted on all species collected and reported as part of the experiment. The non-target species data were used to examine the impact of the fipronil baiting program on non-target species and how changes to the fipronil bait program can reduce non-target exposure and attraction. Variations in the mean number of taxa (*Vespula* versus non-target) observed at each bait station per site, for the separate deployment days (1–3) in 2008, were determined from the taxa × day interaction term in a two-way ANOVA analysis. A two-tailed
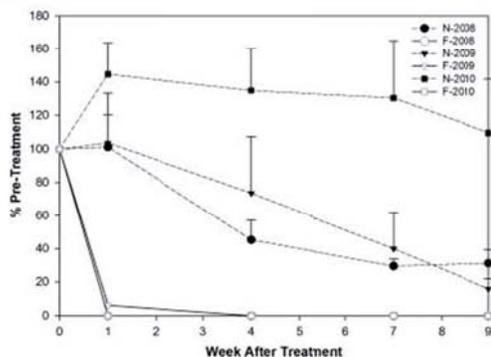
Figure 2. Mean % pretreatment [(number of specimens post-treatment/number of specimens pretreatment) × 100] nest activity within the five fipronil (F) and non-insecticide (N) study sites for each treatment year (2008–2010). Vertical bars show plus one standard error.

Table 1. Results of repeated-measures ANCOVA [fixed factor: treatment (fipronil versus non-insecticide); repeated-measures factor: year(s); covariate: site pair] for three *Vespula* activity indices (instantaneous counts, bait take and heptyl butyrate trap catch)

Dependent variable	Repeated-measures factor	Interaction (treatment and time)		
		df	F	P
Instantaneous counts	All years	7, 35	3.935	0.003
	2008	2, 10	9.307	0.005
	2009	1, 7	6.19	0.042
	2010	2, 14	2.11	0.015
Bait take (%)	All years	7, 35	6.387	< 0.001
	2008	2, 14	3.199	0.032
	2009	1, 7	40.702	< 0.001
	2010	2, 14	2.86	0.041
Heptyl butyrate trap catch	All years	10, 50	7.244	< 0.001
	2008	3, 15	5.935	0.007
	2009	2, 14	8.466	0.001
	2010	2, 14	19.037	< 0.001

t-test was used to compare differences, during the first 24 h of fipronil bait deployment, between the mean number of *Vespula* and all non-target taxa observed on each bait station per site. To determine the impact of heptyl butyrate on the attraction of the only observed native non-target organism, a two-tailed *t*-test was performed to compare differences in the mean number of *Dyscritomyia* spp. (Diptera: Calliphoridae) observed on each bait station per site between bait cups with and without heptyl butyrate.

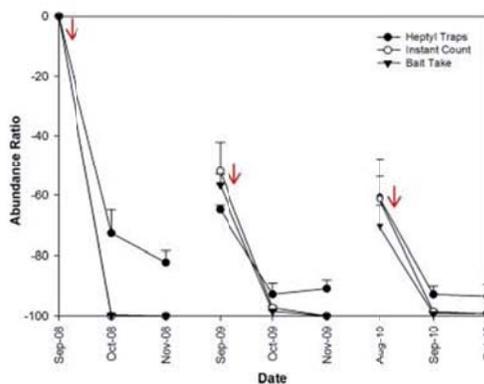## 3 RESULTS

3.1 *Vespula* activity indices

During the 3 years of annual treatment, 2008–2010, observations of traffic rates were collected from a total of 61 nests, with pretreatment traffic rates ranging from 2 to 257 min^{-1}. Within 4 h of 0.1% fipronil chicken bait deployment, foragers were seen removing dead wasps and larvae from the nest. Within a week of treatment, nest activity within the fipronil sites decreased by an average of 97.2 ± 2.8% compared with non-insecticide sites (Fig. 2). All the wasp colonies ($n = 27$) were inactive inside the fipronil sites within 2 weeks of treatment, whereas all the wasp colonies ($n = 34$) were active inside the non-insecticide sites within 9 weeks of the experiment (Fig. 2). The trends in yellowjacket traffic rates at nests over time differed significantly between the two treatments (fipronil and non-insecticide) ($F_{3,60} = 1912$, $P < 0.001$).

To determine the range of the fipronil bait effect, the activity of nests ($n = 16$) up to 150 m outside the systematic bait grids was monitored. All nests monitored outside the fipronil bait grids were inactive within 2 weeks, whereas there was no evidence that the activity of nests within 150 m of the non-insecticide sites but more than 1000 m from a fipronil bait station was affected.

The variation in the remaining *Vespula* activity indices (instantaneous counts, bait take and heptyl butyrate trapping) differed significantly between the two treatments (fipronil and non-insecticide) within and across treatment years (Table 1). The short-term efficacy of the 0.1% fipronil bait is demonstrated by the immediate and significant (Table 1) reduction in all *Vespula* activity indices within the fipronil sites when compared with the non-insecticide sites. The activity indices were reduced by an average of 95.02 ± 1.2% for the duration of the sampling period

Figure 3. Mean abundance ratio [% pretreatment in fipronil site/% pretreatment in non-insecticide site − 1) × 100] for three *Vespula* activity indices (instantaneous counts, bait take and heptyl butyrate trap catch) within the five paired sites once before and twice after annual insecticidal baiting for each treatment year (2008–2010). Arrows show the annual insecticidal baiting events. Vertical bars show plus one standard error.

following the annual treatments in the fipronil sites compared with the non-insecticide sites (Fig. 3). During the 2008 sampling period, the *Vespula* abundance indices were reduced by an average of 92.41 ± 1.66% following treatment in the fipronil sites compared with the non-insecticide sites (Fig. 3). During the subsequent treatment years, the carryover impacts of the previous treatments in addition to the current year's treatment may have further reduced *Vespula* abundance. The *Vespula* abundance indices were reduced by an average of 96.13 ± 1.72% in 2009 and 97.07 ± 0.21% in 2010 following treatment in the fipronil sites compared with the non-insecticide sites.

Prior to the initial fipronil bait treatment in 2008, all *Vespula* activity indices were equivalent in the non-insecticide and fipronil paired sites (Table 2). The long-term efficacy of the 0.1% fipronil

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Table 2. Results of one-way ANOVA tests [independent variable: treatment (fipronil and non-insecticide); dependent variable: activity index (instantaneous counts, bait take and heptyl butyrate trap catch)] measuring the difference between sites prior to insect toxic bait deployment in 2008

Dependent variable	df	F-ratio	P
Instant count	1,7	0.122	0.737
Bait take (%)	1,7	0.011	0.921
Heptyl butyrate trap catch	1,7	0.075	0.795

bait is demonstrated by the extended and significant reduction in all *Vespula* activity indices in the fipronil sites when compared with non-insecticide sites across treatment years (Table 1). The carryover impact of the previous year's treatment maintained a population reduction of $60.92 \pm 3.16\%$ prior to treatment in 2009 and 2010 in the fipronil compared with the non-insecticide sites. After the initial round of fipronil baiting in 2008, the wasp abundances never rebounded to pretreatment levels in the fipronil sites during the 3 years of *Vespula* activity monitoring.

Pretreatment instantaneous counts varied widely across sites and years (0.81–9.98 wasps count^{-1}), but a significant reduction (94.6–100%) in instantaneous counts was always obtained after fipronil baiting. A Spearman rank correlation test revealed no relationship between pretreatment instantaneous counts and the reduction in the instantaneous counts following fipronil baiting.

The heptyl butyrate trap catch was reduced by an average of $88.7 \pm 3.1\%$ for the duration of the sampling period following the annual treatments in the fipronil sites compared with the non-insecticide sites. Although there was a significant reduction in wasp presence within the fipronil sites, reinvasion of foragers did occur. To determine the distribution of the reinvasion of foragers into the study sites, the relationship between the proportion of wasps caught in heptyl traps after treatment and the distance to the center of the study site was examined. A simple linear regression revealed a significantly positive relationship between the proportion of trap catch (arcsine square-root transformed) and distance to the center of the study site at 1 month ($y = 0.264 + 0.00255x, F_{1,54} = 80.522, P = <0.001, r^2_{adj} = 0.591$) and 2 months ($y = 0.120 + 0.00353x, F_{1,54} = 24.885, P = <0.001, r^2_{adj} = 0.303$) after treatment.

3.2 Fipronil bait take

In 2008, an average of 4.6 ± 0.6 g of fipronil bait was consumed per bait station during the 3 days of fipronil bait deployment. An average of $91.9 \pm 3.4\%$ of the total bait take was removed from the bait stations within the first 6 h of deployment, and $96.8 \pm 8.6\%$ of the *Vespula* collecting bait during instantaneous counts were observed during the same period (Fig. 4). The average percentage bait take ($F_{2,33} = 9.279, P < 0.001$) and average instantaneous count ($F_{2,33} = 18.89, P < 0.001$) differed significantly among the three bait deployment days within the fipronil sites. Significantly more bait was consumed and more *Vespula* visited bait stations during the first day of fipronil bait deployment.

As the majority of the bait was consumed within the first 24 h of deployment in 2008, in an attempt to reduce non-target impacts the fipronil bait was only deployed for 24 h in 2009 and 2010. During the first 24 h of bait deployment in 2008–2010, an average of 2.4 ± 0.7 g was consumed per bait station within the fipronil sites. Within 2 h of deployment, an average of $52.3 \pm 7\%$ of the total
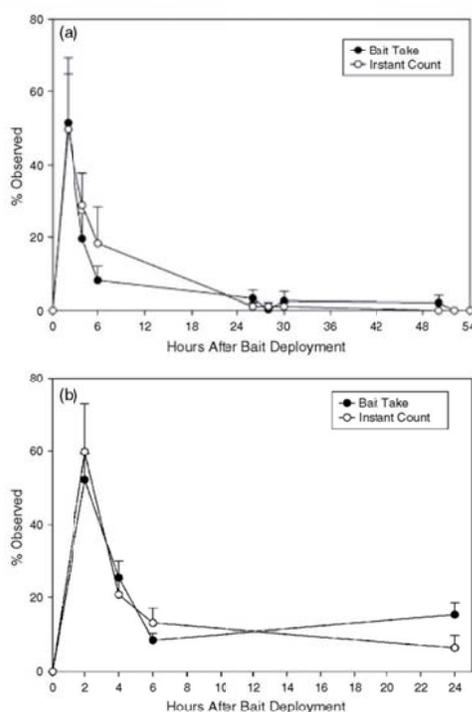
Figure 4. Mean percentage insecticidal bait take and instantaneous counts within the five fipronil study sites over (a) the first 54 h of bait deployment in 2008 and (b) the first 24 h of bait deployment in 2009 and 2010. Vertical bars show plus one standard error.

bait take was removed from bait stations, and $59.8 \pm 13.1\%$ of the *Vespula* collecting bait during the instantaneous counts were observed (Fig. 4). The average percentage bait take ($F_{3,44} = 17.87, P < 0.001$) and average instantaneous count ($F_{3,44} = 10.5, P < 0.001$) differed significantly among the four monitoring times (2, 4, 6 and 24 h after bait deployment) within the fipronil sites. Significantly more fipronil bait was consumed and more *Vespula* visited bait stations within 2 h of bait deployment.

3.3 Enhancement of bait attraction and acceptance
3.3.1 Randomized complete block

In a replicated complete block design, the addition of a heptyl butyrate wick increased the number of *Vespula* visiting the bait stations by $146.6 \pm 25.1\%$ and the bait take by $76.3 \pm 28.3\%$ when compared with bait stations with chicken only. Significantly more *Vespula* visited ($F_{2,11} = 59.7, P < 0.001$) and *Vespula* took significantly more bait ($F_{2,11} = 9.279, P < 0.001$) from stations with heptyl butyrate wicks.

3.3.2 Alternating transects

The addition of a heptyl butyrate wick to chicken bait stations increased the number of *Vespula* visiting the bait stations by $698.2 \pm 153\%$ and the bait take by $1067.1 \pm 228.1\%$ when compared with bait stations with chicken only. Significantly more

Vespula visited ($t_{1,5} = 22.195$, $P = 0.005$) and *Vespula* took significantly more bait ($t_{1,5} = 11.885$, $P = 0.018$) from stations with heptyl butyrate wicks.

3.4 Non-target analysis

In total, 1987 observations of non-target arthropods were made during 13 860 instantaneous count bait station observations. Non-target species on baits included flies (Diptera), ants (Formicidae), grasshoppers (Orthoptera), cockroaches (Blattodea) and beetles (Coleoptera).

In 2008, insecticidal bait was deployed in the fipronil sites for three consecutive days. A two-way ANOVA analysis revealed a significant interaction between deployment day (1–3) and taxa (*Vespula* and non-target) ($F_{2,18} = 9.981$, $P = <0.001$). This is a result of a significant decrease in *Vespula* visitation rates following the first day of fipronil baiting ($F_{2,9} = 18.89$, $P = 0.004$) and no significant change in non-target specimen visitation rates across days ($F_{2,9} = 0.203$, $P = 0.82$).

In an attempt to reduce the non-target impact of the fipronil bait program, fipronil bait was only deployed for 24 h in 2009 and 2010. A total of 1241 specimens were observed in 3325 fipronil bait station observations during the first 24 h of fipronil bait deployment. Significantly more *Vespula* were observed visiting the bait stations than all non-targets combined ($t_{1,24} = 14.603$, $P = 0.001$). *Vespula* accounted for 82.7%, invasive ants (Formicidae; *Pheidole megacephala*, *Linepithema humile*) for 14.9%, Diptera (Calliphoridae; *Drosophila suzukii*; Phoridae; Sacrophagidae) for 1.9% and Orthoptera (Tettigoniidae; *Conocephalus saltator*) for 0.6% of the observed visitors. Approximately 92% of all non-target visitors were adventive. All native non-target species identified were endemic calliphorids in the genus *Dyscritomyia*. One species, *D. fasciata*, was the most prevalent and accounted for 70.8% of all observed Diptera and 1.35% of all visitors. During the heptyl butyrate alternating transect experiment, the addition of a heptyl butyrate wick to the bait stations significantly decreased the number of *Dyscritomyia* ($t_{1,5} = 6.87$, $P = 0.011$) visiting bait stations.

4 DISCUSSION

The results of the study support previous findings[33] that indicate that 0.1% fipronil with chicken meat was effective for suppression of yellowjacket populations in Hawaii. The present results also showed that wasp populations remained low into the following year. In the fipronil sites, all monitored colonies were inactive and *Vespula* activity indices were reduced by an average of 95.02 ± 1.2% for the duration of the season and by 60.92 ± 3.16% the following year when compared with the non-insecticide sites.

The enhancement of bait attraction by heptyl butyrate, the small amount of fipronil bait needed to render a colony inactive[27] and the 50–600 m foraging distance capabilities of wasps[37,48] create an area of *Vespula* population suppression much larger than the treated area. All known nests within the treated area and at least 150 m outside the treated area were inactive. Therefore, the reinvasion of *Vespula* in the treated areas was the consequence of foragers traveling from nests further than 150 m away. Although reinvasion was extremely limited, a strong edge effect was observed within the 9 ha fipronil study sites. The addition of heptyl butyrate may increase the effective treatment area by increasing the long-range attraction of wasps and attract wasps that are foraging for alternative resources to the bait. It was

observed that, on average, individual foragers removed 0.03–0.2 g of bait per visit, and Harris and Etheridge[27] found that 0.2 g of 0.1% fipronil bait entering a *Vespula vulgaris* nest reduced traffic rate by 90%. Based on these estimates, approximately 1–7 visits are required to reduce nest activity significantly. The enhanced bait attraction attained with the addition of heptyl butyrate and the small number of visits required for the 0.1% fipronil bait to impact a nest may partially explain why the high levels of reinvasion described in previous studies[14,25–27,29] were not observed. To obtain a more precise estimate of the extent of the fipronil bait impact and subsequent reinvasion, the treated areas need to be expanded and nests from 100–1000 m from a fipronil bait station need to be monitored after a successful fipronil bait deployment.

The present study demonstrates that only a small amount of fipronil bait deployed for ≤24 h can result in area-wide control. In 2008, when the fipronil bait was deployed for three consecutive days, over 95% of the observed *Vespula* visits occurred within the first 6 h of the first day of deployment. Furthermore, during the first 24 h of fipronil bait deployment in 2008–2010, the majority of the bait take and observed *Vespula* visits occurred within the first 2 h. This emphasizes the importance of maximizing fipronil bait take during the first few hours of bait deployment and removing the fipronil bait when *Vespula* visitation significantly decreases (e.g. ≤24 h).

Increasing the evenness and density of deployed bait stations increases the likelihood that foragers will encounter the bait stations and take colony-lethal doses of bait back to a nest.[27] The 25 × 25 m spacing between bait stations in 2008 and 2009 (16 stations ha^{-1}) and the 25 × 50 m spacing in 2010 (8 stations ha^{-1}) may be more than needed. Insecticidal baiting with fipronil, without the addition of heptyl butyrate, was successful against *Vespula* species in New Zealand using a 50 × 100 m spacing (2 stations ha^{-1}).[27] The addition of heptyl butyrate probably increases the range of *Vespula* attraction, and thus fewer or more widely spaced bait stations may suffice and the variation associated with bait lines[27] may be reduced. Additional fipronil bait trials could determine the optimal bait station spacing and configuration to maximize efficacy while minimizing the effort per unit area.

The rapid attraction to, and small amount of, fipronil bait needed to effectively control *Vespula* also reduced non-target arthropod exposure. Deploying the fipronil bait for ≤24 h maximized *Vespula* visitation per unit time and minimized the attraction of flies, the main non-target group of arthropods that included native species (Foote D *et al.*, unpublished data) Diptera may be more attracted to more aged bait or simply less likely to visit bait when it is occupied by *Vespula*. The authors only have observations to support the former: more Diptera are found on experimentally aged chicken baits (Foote D *et al.*, unpublished data). However, given that *Vespula* prey on other arthropods, it seems likely that their presence on baits may also be a deterrent to visits from non-target arthropods, and *Vespula* have been observed actively to interfere with non-target ant visitation to bait stations.[49] Therefore, to reduce non-target effects, fipronil bait should be removed when *Vespula* visitation significantly diminishes.

It also bears mentioning that the impact of fipronil bait on non-target arthropods (with the exception of social ants) compared with *Vespula* is further differentiated at the population level because the impact of the fipronil bait is limited to the solitary dipteran individuals who visit the bait, whereas yellowjacket foragers carry bait to their colonies and further transmit its effects. The complete absence of honey bee visitation is likely

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a consequence of using a protein bait (chicken) to deliver fipronil to the wasps.

The goal of fipronil baiting in natural areas is primarily for conservation gains.[24] However, a major disadvantage identified in previous studies[25,28,29] is that baiting is not effective until a certain threshold of wasps visiting the bait stations is reached. The dependency of fipronil bait efficacy or wasp density enabled wasp nests to have a substantial impact prior to treatment, thus limiting conservation gains. In this study, pretreatment instantaneous counts varied widely across sites, but a significant reduction in wasp abundance was always achieved. No relationship was found between wasp density and fipronil bait efficacy. The use of heptyl butyrate with fipronil increases *Vespula* visitation and bait take and should therefore improve the efficacy of fipronil to suppress wasp populations sooner.

Annual fipronil baiting may not be required to reduce yellowjacket populations because of carryover wasp population reductions into the subsequent year. Reducing wasp numbers within the treated sites reduces intraspecific competition and increases the abundance of food; this could lead to a higher success rate of queens establishing nests in the treated areas the following year.[25] The potential increase in nest establishment success may be negated by a decreased number of queens dispersing into the treated site. Most *Vespula* queens do not fly more than a few hundred meters from their nests,[50,51] and the fipronil bait impact is hypothesized to extend to the upper foraging range of wasps (200–600 m).[37,48] Thus, the nests that have the potential to contribute the majority of queens are destroyed, so only queens dispersing long distances are able to reinvade the treated area the following year. The observed carryover impact of the preceding year's treatment is most likely the combined result of a reduced number of colonizing queens and the destruction of perennial nests.

The proven large-scale efficacy of fipronil bait could result in the localized suppression or removal of *V. pensylvanica* populations in areas of high endemic biodiversity. Hawaii Volcanoes National Park currently focuses on the management and restoration of Special Ecological Areas, a strategy designed to protect the biologically most unique and rich habitats in the park.[52,53] The fipronil baiting strategy reported in this study can provide resource managers with a cost-effective tool (e.g. maximum estimated cost of $US 21 ha^{-1}, including labor and materials) to minimize or eliminate the impacts of *Vespula* wasps within Special Ecological Areas, particularly kipukas. Kipukas are islands of denser vegetation that range in size from a few square meters to thousands of hectares, the surrounding areas of which having been covered by lava flows.[54] Kipukas are common landscape features in Hawaii, and three kipukas ranging from 33 to 150 ha are designated as Special Ecological Areas within Hawaii Volcanoes National Park.[52] Although a small quantity of fipronil bait is needed to effectively control *V. pensylvanica*, the environmental fate of fipronil needs to be examined if there is repeated exposure within an area.

In the present study, fipronil baiting immediately reduced *V. pensylvanica* populations by >90%, and the isolation provided by sparsely vegetated lava flows surrounding kipukas could further reduce the rate of reinvasion and permit the localized removal of most *V. pensylvanica*. Resource managers in Hawaii can utilize fipronil baiting to reduce seasonal irruptions of *Vespula* populations within these unique biological communities and integrate *Vespula* control with other alien predator management programs designed to protect natural areas in Hawaii.

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CHAPTER 2

Invasive Species Management Restores a Plant-Pollinator Mutualism in Hawaii

Abstract. Mutually beneficial interactions between pollinators and flowering plants represent a critical but threatened component of ecosystem function that can underlie the success of ecological restoration. The management and removal of invasive species may give rise to unanticipated changes in plant-pollinator mutualisms because they can alter the composition and functioning of plant-pollinator interactions in a variety of ways. In an attempt to incorporate a functional framework into invasive species management, we examined the restoration of the plant-pollinator mutualisms and the pollination of an endemic foundational tree species, *Metrosideros polymorpha*, following the large-scale removal of an invasive floral visitor and arthropod predator, *Vespula pensylvanica*. To integrate knowledge of the invader's behavior and the plant's mating system, we determined the efficacy of *V. pensylvanica* as a pollinator of *M. polymorpha* and quantified the dependence of *M. polymorpha* on animal pollination (e.g., self-compatibility and pollen-limitation). The reduction of *V. pensylvanica* in managed sites, when compared to unmanaged sites, resulted in a significant increase in the visitation rates of effective pollinators (e.g., *Apis mellifera* and *Hylaeus*) and in the fruit production of *M. polymorph*a. Furthermore, introduced *A. mellifera*, following the management of *V. pensylvanica*, acted as a substitute pollinator for *M. polymorpha*, replacing extinct or threatened bird species in our study system. The results of this study link the large-scale management of an ecologically damaging invader to the re-establishment of the plant-pollinator mutualisms and pollination of a functionally important endemic tree species. Consequently, this research demonstrates the contrasting impacts of introduced species on ecological function and provides a framework from which future invasive species management can preserve ecological function and maintain ecosystem resilience.

Key-words: *Apis*, ecosystem function, honeybee, interaction, *Metrosideros*, pollination, *Vespula*

Introduction

The accelerating loss of global biodiversity and rate of environmental degradation have concentrated conservation efforts on identifying the fundamental drivers of species loss. Isolation of factors responsible for the imperilment of species remains a prominent research focus, but ecologists increasingly recognize that species interactions also require attention because of their importance in maintaining biological diversity and underpinning ecosystem function (Kiers et al. 2010, Potts et al. 2010). An ongoing conservation challenge is to develop and implement management plans that maintain and restore essential interactions between species, particularly plant-pollinator mutualisms (Traveset and Richardson 2006, Stout and Morales 2009, Potts et al. 2010, Menz et al. 2011). In an attempt to confront this challenge, we examined the restoration of the plant-pollinator mutualisms and the pollination of a functionally important endemic tree species following the large-scale removal of an invasive floral visitor and arthropod predator.

Mutually beneficial interactions between pollinators and flowering plants represent a critical but threatened component of ecosystem function that can underlie the success of ecological restoration (Dixon 2009). Animal pollination occurs in virtually all terrestrial ecosystems, involving 87.5% of angiosperms (Ollerton et al. 2011), and is threatened worldwide

because of arthropogenic impacts (e.g., introduced species) on native pollinators (Kearns et al. 1998). The global threats to and importance of pollination to plant reproduction (Aguilar et al. 2006) make it critical to incorporate pollinator management into natural area conservation and restoration planning (Dixon 2009, Menz et al. 2010).

Introduced species can disrupt plant-pollinator mutualisms (Traveset and Richardson 2006) compromising the persistence of ecosystem functioning (Tylianakis et al. 2008), but the restoration of pollination following the removal of an invasive species remains largely unexplored (but see Wenner and Thorp 1994, Forup et al. 2008). Invasive floral visitors can alter the composition and functioning of plant-pollinator interactions in a variety of ways. They can displace effective pollinators, replace extirpated native pollinators, or facilitate native plant-pollinator mutualisms (Traveset and Richardson 2006, Stout and Morales 2009). For this reason, the management and removal of invasive species may give rise to unanticipated changes in plant-pollinator mutualisms (Burkle and Alarcon 2011). An incomplete understanding of these issues currently hinders the implementation and assessment of invasive species management.

Island plant-pollinator mutualisms are severely impacted by invasive species and are critical to the overall functioning of island ecosystems (Cox and Elmqvist 2000, Dupont et al. 2004). Island pollination systems appear vulnerable to invasive species because of their low taxonomic diversity and lack of coevolution with continental predators and competitors (Traveset and Richardson 2006). In Hawaii, the extensive adaptive radiations of endemic Hawaiian honeycreepers [Drepanididae (Cabanis)] (Banko et al. 2002), and bees [*Hylaeus* (Fabricius)] (Magnacca 2007) have occurred in the absence of social insects. The historic absence of social insects in Hawaii (Wilson 1996), which elsewhere are numerically and behaviorally dominant, has magnified the impacts of invasive social insects because endemic pollinators have not evolved appropriate competitive and defensive mechanisms (Zimmerman 1970, Wilson and Holway 2010). The extinctions and declines of important Hawaiian pollinator guilds, notably among honeycreepers (Scott et al. 1988, Banko et al. 2002) and *Hylaeus* (Magnacca 2007, 2011), and the continued presence of invasive species has made restoring plant-pollinator mutualisms critical to the long-term integrity of Hawaiian ecosystems.

The competitive and predatory dominance of invasive social insects is well known (Moller 1996), but the results of studies examining their impact on plant reproduction are highly variable and restricted to social bees and ants. Invasive social wasps in the genus *Vespula* are considered some of the world's most ecologically damaging invaders and are continuing to spread around the globe (Beggs et al. 2011). The potential impacts of the invasive western yellowjacket, *Vespula pensylvanica* (Saussure)*,* on Hawaiian plant-pollinator mutualisms are multi-dimensional. *Vespula* are generalist predators that have a direct impact on native and introduced pollinators including endemic *Hylaeus* and the introduced honey bee, *Apis mellifera* (Linnaeus) (Wilson and Holway 2010). To further subsidize their energy demand, *Vespula* consume copious amounts of carbohydrates and have been found to exploit (Moller et al. 1991, Hanna Chapter 3) and aggressively defend (Thomson 1989, Grangier and Lester 2011) critical carbohydrate resources (e.g., floral nectar and honeydew). In Hawaii, the impact of these direct and indirect effects on plant-pollinator mutualisms is augmented by the increased year round population density resulting from the formation of large perennial colonies by invasive *V. pensylvanica* populations (Wilson et al. 2009).

The impacts of invasive floral visitors on plant-pollinator mutualisms and plant reproduction have been thoroughly investigated in several systems (Traveset and Richardson 2006, Dohzono and Yokoyama 2010), but because of the limited spatial and temporal scales used

in these studies, our knowledge of the re-establishment of plant-pollinator mutualisms following the removal of an invasive floral visitor is limited (Stout and Morales 2009, Burkle and Alarcon 2011). To incorporate all the disruptive pathways and interactions and allow sufficient time for restoration to occur we reduced *V. pensylvanica* populations in large multi-year management plots (Hanna et al. 2011). The scale and design of our experiment enabled us to examine explicitly the response of the plant-pollinator interactions and the pollination of a functionally important Hawaiian tree species, *Metrosideros polymorpha* (Gaudich). We hypothesized that the frequency and diversity of plant-pollinator mutualisms and the pollination of *M. polymorpha* would increase after the large-scale management of invasive *V. pensylvanica*. To test this hypothesis, we investigated the invader's behavior, the plant's mating system, and the ecological context of the plant-pollinator interaction. Specifically, we (1) determined the efficacy of *V. pensylvanica* as a pollinator of *M. polymorpha*, (2) quantified the dependence of *M. polymorpha* on animal pollination (e.g., self-compatibility and pollen-limitation), and (3) compared the pollinator visitation rates, and the pollination of *M. polymorpha* in *V. pensylvanica* managed versus unmanaged plots through time.

Methods

Experimental design
We used a Before-After, Control-Impact experimental design to observe the effects of annual management of invasive *V. pensylvanica* on the plant-pollinator interactions and pollination of *M. polymorpha* in Hawaii Volcanoes National Park in 2009 and 2010.

Study sites
We randomly selected eight 9 ha study sites within seasonal submontane *M. polymorpha* woodland within Hawaii Volcanoes National Park between approximately 700 to 1100 m elevation. In the four managed 9 ha sites we used 0.1% fipronil chicken baits to annually reduce *V. pensylvanica* populations by 95 ± 1.2%, while we maintained the four unmanaged sites as experimental controls (Hanna et al. 2011). The actual *V. pensylvanica* population suppression within the managed sites extended beyond the 9 ha study area and encompassed ≥ 36 ha due to the foraging distance capabilities of *V. pensylvanica* (Hanna et al. 2011). We paired the managed and unmanaged sites to control for environmental variables (e.g., precipitation, elevation, and vegetation), randomly allocated treatment within pairs, and separated all sites by ≥ 1 km to maintain site independence (95% of wasps travel ≤ 200 m from the nest when foraging) (Edwards 1980).

Study plant
Metrosideros polymorpha, ʻōhiʻa lehua, is a functionally important endemic tree species that has facultative interactions with a diverse array of species, provides a critical nectar resource and habitat for a largely endemic biota, and contributes to the overall biomass and productivity of the ecosystem (Carpenter 1976, Raich et al. 1997, Gruner 2004). *Metrosideros polymorpha* is found on all the main islands and occurs in a variety of climate and substrate regimes from sea-level to 2500 m (Corn 1979). Peak flowering occurs from February to July, but flowers can be found at any time of the year (Ralph and Fancy 1995). *Metrosideros polymorpha* has open inflorescences, which were comprised of 11.82 ± 0.41 red flowers in our study sites, that attract native and introduced birds and insect visitors (Carpenter 1976, Corn 1979, Lach 2005, Junker et al. 2010).

The flowers are partially self-compatible and, when pollinated, the ovary develops into a green capsule containing thousands of wind-dispersed seeds that reach full size within a month of anthesis (Carpenter 1976).

Flower visitation by a single V. pensylvanica wasp
To quantify the effectiveness of *V. pensylvanica* as a pollinator, we monitored the fruit-set of flowers with a virgin stigma after a single *V. pensylvanica* visit. To generate virgin stigmas we placed fine mesh bags over inflorescences with advanced flower buds. We removed the bag and exposed the stigmas to *V. pensylvanica* visitation within 1-3 days of flowering, to ensure the stigmas were receptive (Carpenter 1976). We allowed the flowers (1-5 per inflorescence) to be visited by a single *V. pensylvanica* and recorded the visitor's behavior (e.g., pollen collection, nectar collection, and/or stigma touch) and time on each flower. Following the visitation event, we isolated the stigma with a plastic tube to prevent the stigma from receiving any additional pollination and monitored for fruit success 2-3 months later. To control for the possible self-pollination of flowers, we performed an identical methodology on flowers that received no visitation within the same inflorescence.

Metrosideros polymorpha mating system
To examine the self-compatibility and pollen limitation of *M. polymorpha* we compared the fruit set of three inflorescence treatments: (1) self-pollination - bagged with fine-mesh nylon bags to prevent cross-pollination and maximize self-pollination (Carpenter 1976), (2) supplemental cross-pollination - applied pollen from ≥ 5 pollen donors collected from synchronously blooming plants > 1 km away to all the stigmas within the inflorescence, and (3) open - received natural visits by pollinators. We used the index of self-incompatibility (ISI) to examine the variation of *M. polymorpha* self-incompatibility across sites and time. The ISI ranges from self-incompatible (0-0.2), partially self-compatible (0.2-1), and self-compatible (1) (Zapata and Arroyo 1978). The ISI provides a quantitative estimate of the frequency of self-fruit compared with that following supplemental cross-pollination (Zapata and Arroyo 1978). We calculated the mean ISI per site, before and after *V. pensylvanica* treatment, using the following equation: ISI = (mean self-pollinated fruit production/mean supplemental cross-pollinated fruit production).

Pollen limitation occurs when plants produce fewer fruits than they would with adequate pollen receipt. We used the index of pollen-limitation (PLI) to examine the variation of *M. polymorpha* pollen limitation across sites before and after *V. pensylvanica* treatment, using the following equation: PLI = [1–(mean open fruit production/mean supplemental cross-pollinated fruit production)]. The PLI ranges from 0, no pollen limitation, to 1, the highest pollen limitation (Larson and Barrett 2000).

Relative bird abundance
Due to infrequent observations of bird visits to *M. polymorpha*, we measured the impact of *V. pensylvanica* on passerine bird abundance by performing nine 8-min point counts within study sites once before and twice after (6 & 10 weeks) *V. pensylvanica* treatment in 2010. Station locations within sites were located 100 m apart and we conducted point counts simultaneously in the paired sites from 6:00-10:00 in good weather.

Insect Visitation Rates

To determine how the relative frequency of specific plant-pollinator mutualisms change through time in response to *V. pensylvanica* treatment we performed timed focal inflorescence observations. We conducted 10 min focal inflorescence observations for 1-5 inflorescences on 5-8 trees per observation round, simultaneously within the paired sites. To account for tree and inflorescence variation, we recorded the tree height and inflorescence abundance and the inflorescence height and flower abundance. We classified each observed floral visitor into one of six taxonomic groups: *V. pensylvanica*, *A. mellifera*, *Hylaeus*, Formicidae (Latreille), Diptera (Linnaeus), and Lepidoptera (Linnaeus). In 2009, we conducted a single observation round from 7:00-15:00 two weeks before and six weeks after *V. pensylvanica* treatment. In 2010, to examine *M. polymorpha* visitation in more detail we conducted four observation rounds per day from 7:00-17:00 two weeks before, and twice (6 & 10 weeks) after *V. pensylvanica* treatment. To determine the relative frequency of visitors, we calculated the mean site visitation rate (visits per min) for all visitors and for *V. pensylvanica*, *A. mellifera*, and *Hylaeus* because they represented > 85% of all visitors observed.

Metrosideros polymorpha pollination
Before and after *V. pensylvanica* treatment, we randomly selected 5-8 *M. polymorpha* trees with ≥ 3 inflorescences in the bud stage at all sites. On each study tree, we assigned an inflorescence to one of three treatments: "No Visitors" - bagging with fine-mesh nylon bags to prevent visitation; "Insects" - caging with 0.3×0.5 m cylinders made of 2.5 cm mesh chicken-wire to allow only insect visitation; and "All Visitors" - no bagging to allow bird and insect visitation (methods were adopted from Carpenter 1976). At least one complete trio of treatments was established in each tree. To account for tree and inflorescence variation, we recorded the tree height and inflorescence abundance and the inflorescence height and bud abundance. Three months after the inflorescence flowered we counted the number of swollen capsules and calculated the fruit production (percent of flowers setting fruit) for each inflorescence treatment within every study tree.

Vespula pensylvanica abundance and M. polymorpha fruit production
To inform future *V. pensylvanica* management decisions, we collected *Vespula* abundance data in conjunction with the *M. polymorpha* fruit production data. To estimate the total number of wasps (resident and non-resident visitors) in the study sites, we deployed thirteen Seabright yellowjacket wasp traps (Seabright Laboratories, Emeryville, USA) baited with 1.5 ml of heptyl butyrate (98%; Aldrich, MO), a strong wasp attractant (Davis et al. 1969), for five days per site during each monitoring round (See Hanna et al. 2011).

Statistical Analyses
To analyze variation in mean relative bird abundance and insect visitation per site, we performed repeated measures ANCOVAs, using *V. pensylvanica* treatment as the fixed factor, day as the repeated measures factor, and site pair as the covariate. We analyzed variation in mean insect visitation rate per site across and within years, with separate analyses for total visitation rate and visitation rates for the selected taxonomic groups.

To examine the restoration of *M. polymorpha* pollination (e.g., fruit production) resulting from annual *V. pensylvanica* management, we performed within and across year statistical analyses. To analyze variation in mean fruit production per site across years, we performed separate repeated measures ANCOVAs for each inflorescence treatment (No Visitors, Insects,

and All Visitors). The fixed factor was *V. pensylvanica* treatment and day was the repeated measures factor. We used a hierarchical nested ANOVA to analyze within year variation in fruit production. Inflorescence fruit production was nested within tree, tree was nested within site, and site was nested within *V. pensylvanica* treatment. The fixed factors included: *V. pensylvanica* treatment, inflorescence treatment, and time (pre & post *V. pensylvanica* treatment).

Prior to analysis we used an arcsine square root transformation to normalize the pollen limitation, self-incompatibility, and fruit production data; a log+1 transformation to normalize the visitation rate data; and a *ln* transformation to normalize the heptyl butyrate trap data. To correct for Type 1 errors we used Bonferroni corrections for multiple comparisons. We conducted all statistical analyses in Systat 11 (Systat 2004).

Results

Flower visitation by a single V. pensylvanica wasp
We collected *V. pensylvanica* single visitation fruit set data from 117 flowers in 34 inflorescences on 17 trees. *Vespula pensylvanica* was never observed contacting the stigma or collecting pollen, whereas they were observed collecting nectar from 93.6% of the flowers visited. No relationship was found between fruit production and the time *V. pensylvanica* spent on the flower (43.8 ± 3.7 s) (Spearman correlation, $r = 0.11$, $P = 0.253$). There was no significant difference between the fruit production of flowers visited by a single *V. pensylvanica* and flowers receiving no visitation (Wilcoxon signed rank test, $Z = 0.414$, $P = 0.679$) or between the fruit production of the first flower visited by *V. pensylvanica* and flowers receiving no visitation (Wilcoxon signed-rank test, $Z = 0.194$, $P = 0.846$). We conducted an additional Wilcoxon signed rank test using only the fruit production of the first flower visited by *V. pensylvanica* in the sequence, since flowers visited subsequently may mostly be receiving *V. pensylvanica* facilitated self-pollen, and this might weaken any positive effect of *Vespula* visits on fruit production.

Meterosideros polymorpha mating system
The ISI of *M. polymorpha* was not significantly different within sites before and after *V. pensylvanica* treatment (*V. pensylvanica* treatment x time ANOVA, $F_{1, 12} = 0$, $P = 0.997$) (Fig. 1). An average *M. polymorpha* ISI of 0.214 ± 0.013 across sites and time confirms that *M. polymorpha* is partially self-compatible, although weakly so.

The change in *M. polymorpha* PLI after *V. pensylvanica* treatment was significantly different between the managed and unmanaged sites (*V. pensylvanica* treatment x time ANOVA, $F_{1, 12} = 24.15$, $P < 0.001$). *Metrosideros polymorpha* PLI was significantly lower in the managed sites after annual *V. pensylvanica* treatment than in all other *V. pensylvanica* treatment x time categories (ANOVA, $F_{3, 12} = 25.341$, $P < 0.001$) (Fig. 1).

Relative bird abundance
We recorded 1,793 bird detections during 216 point counts in the eight study sites. The relative bird abundance increased by an average of $81 \pm 43\%$ six weeks and by an average of $140 \pm 52\%$ ten weeks after *Vespula* treatment in the managed compared to the unmanaged sites. The variation in relative bird abundance was significantly different through time between the *V. pensylvanica* treatments ($F_{2,10} = 14.350$, $P = 0.027$).

Insect visitation rates
We observed 5,069 visitors on 28,148 flowers in 1,869 inflorescences from 593 trees across the eight study sites, over the two years. Variation in mean total visitation rate was not significantly different between *V. pensylvanica* treatments across years and within 2010, but was significantly different within 2009 because six weeks after *V. pensylvanica* treatment the mean total visitation rate was significantly higher in unmanaged sites compared to managed sites (Table 1, Fig. 2a). Visitation rates of *V. pensylvanica* were reduced in managed sites compared to unmanaged sites by an average of 98.4 ± 0.9% in 2009 and 97.3 ± 2.1% in 2010 following the annual *V. pensylvanica* treatment (Fig. 2b). Mean visitation rates of *A. mellifera* and *Hylaeus* were increased by an average of 595.9 ± 150.5% and 162.6 ± 82.7% in 2009, and 1472.1 ± 406.4% and 763.5 ± 260.8% in 2010 following the annual *V. pensylvanica* treatment in managed sites, whereas visitation rates remained at or close to zero in unmanaged sites (Fig. 2c, d). Correspondingly, variation in mean visitation rate per site for all three taxonomic groups differed significantly between the *V. pensylvanica* managed and unmanaged sites within and across treatment years ($P \leq 0.016$ in all cases), except for *Hylaeus* in 2009 (Table 1, Fig. 2). There were no significant relationships between the tree and inflorescence characteristics and the insect visitation rates.

Metrosideros polymorpha pollination
We collected fruit set data from 32,351 flowers in 1,419 inflorescences from 172 trees across the eight study sites, over the two years. Fruit production was increased in "All Visitors" inflorescences by an average of 99.4 ± 17.4% in 2009 and 107.3 ± 44.1% in 2010 and in "Insects" inflorescences by 118.9 ± 18.6% in 2009 and 142 ± 37.1% in 2010 following *V. pensylvanica* treatment in the managed sites compared to the unmanaged sites (Fig. 3). The slightly lower increases for "All Visitors" are an artifact of the lower fruit production of "Insects" compared to "All Visitors" inflorescences in the unmanaged sites. Fruit production in "No Visitors" inflorescences remained unchanged between *V. pensylvanica* treatments within and across years (Fig. 3). Correspondingly, variation in mean fruit production per site differed significantly between the two *V. pensylvanica* treatments across years for "All Visitors" ($F_{3,18} = 16.81$, $P = < 0.001$) and "Insects" ($F_{3,18} = 14.964$, $P = < 0.001$) inflorescences, but not for "No Visitors" ($F_{3,18} = 0.036$, $P = 0.999$) inflorescences. In 2009 ($F_{2,617} = 5.471$, $P = 0.004$) and 2010 ($F_{2,638} = 3.366$, $P = 0.035$) there was a significant three-way interaction between *V. pensylvanica* treatment, inflorescence treatment, and time (pre versus post treatment), due to no significant differences in fruit production between *V. pensylvanica* treatments before treatment, but a significantly higher fruit production following treatment in managed sites for "All Visitors" and "Insects" inflorescences compared to unmanaged sites (Fig. 3).

Mean fruit production per site was significantly different between inflorescence treatments for all *V. pensylvanica* treatment × time categories (ANOVA, $P \leq 0.007$ in all cases, Table 2). Mean fruit production per site was significantly higher in all "All Visitors" and "Insects" inflorescences compared to "No Visitors" inflorescences across all categories (Tukey HSD tests, $P \leq 0.009$ in all cases), but there were no significant differences between "All Visitors" and "Insects" inflorescences (Table 3). There were no significant relationships between tree and inflorescence characteristics and fruit production.

Vespula Pensylvanica Abundance and M. Polymorpha Fruit Production

Simple linear regression analyses revealed significantly negative relationships between heptyl butyrate trap catch of *V. pensylvanica* and *M. polymorpha* fruit production for "All Visitors" (y = 1.076 - 0.108x, $F_{1, 54}$= 43.829, P < 0.001, r^2_{adj} = 0.580) and "Insects" (y = 1.036 - 0.108x, P < 0.001, r^2_{adj} = 0.589) inflorescences.

Discussion

Large-scale management of *V. pensylvanica* initiated pollinator behavioral changes leading to higher visitation rates and consequently *M. polymorpha* pollen limitation significantly decreased and fruit production significantly increased. A morphological mismatch with flowers of *M. polymorpha* enables *V. pensylvanica* to competitively exploit and antagonistically defend the nectar without contributing to flower pollination (e.g., obligatory nectar thieving) (Irwin et al. 2001). Additionally, we observed *V. pensylvanica* hunting directly from *M. polymorpha* flowers, and a substantial portion of the diet of Hawaiian *V. pensylvanica* consists of *A. mellifera* and *Hylaeus* (Wilson et al. 2009); however, the significant recovery of these effective pollinators within six weeks of *V. pensylvanica* management, on a time frame far shorter than the time needed for the populations to logistically increase, suggests a non-consumptive (altering pollinator behavior) effect (Wilson and Holway 2010). Behavior avoidance of flowers by pollinators has been caused by numerous predators (see Romero et al. 2011 and therein) and the behavioral changes of the pollinators following the reduction of *V. pensylvanica* could include the following: (1) moving into the area where *V. pensylvanica* is no longer present, which they may previously have avoided and (2) visiting *M. polymorpha* flowers in the absence of *V. pensylvanica* within an area of persistent occupation by pollinators.

Partial self-compatibility and pollen limitation of *M. polymorpha* is likely a consequence of past evolution and the current ecological context. *Metrosideros polymorpha* flowers were historically visited by native honeycreepers and the predominately red flower color, the dimensions of the floral parts, and the copious nectar secretion suggest this species is adapted to bird pollination (Carpenter 1976). Experimental evidence has revealed that flower-visiting birds transmit *M. polymorpha* pollen on their head feathers (Corn 1979) and are important pollinators (Carpenter 1976). However, presently most species of honeycreepers are absent at lower elevations (< 1,000 m) because of disease transmitting mosquitoes, introduced predators, and degraded habitat (Ralph and Fancy 1995, Banko et al. 2002). Native and introduced birds were observed visiting *M. polymorpha* in our study sites, but native and introduced insects were the most frequent and numerous visitors. Furthermore, the inflorescence exclusion experiment showed insects were responsible for the majority of *M. polymorpha* fruit production within our study sites (Fig. 5).

The ability of *M. polymorpha* to attract a diverse array of visitors makes it more vulnerable to invasive nectar thieves but more resistant to shifts in the local floral pollinator assemblage (Knight et al. 2005). Nectar and pollen are spatially separated by 1-3 cm (Carpenter 1976, Corn 1979), thus nectar thieving invasive ants (Lach 2005, 2008) and *V. pensylvanica* (Hanna Chapter 3) are able to deplete and defend the nectar resource, and reduce visitation rates of effective pollinators without contacting the reproductive organs (Lach 2008, Junker et al. 2010). Conversely, pollen collecting insects (e.g., *A. mellifera* and *Hylaeus*) are likely contributing to both cross-pollination and pollinator mediated self-pollination because self-pollination is limited by spatial separation of the anthers and central style (Corn 1979).

Visitation rates of endemic *Hylaeus* and introduced *A. mellifera* increased after *V. pensylvanica* management, but their relative contributions to the corresponding increase in fruit production of *M. polymorpha* differed. After *V. pensylvanica* management, *A. mellifera* represented $57.3 \pm 6.2\%$ of the total floral visitors, whereas *Hylaeus* represented $13.9 \pm 2.1\%$ (Fig. 3). Additionally, Junker et al. (2010) found that *A. mellifera* contacted the stigma more frequently and deposited significantly more pollen per stigma contact than did pollen collecting *Hylaeus*. Thus, the increased visitation rates and effective pollination of introduced *A. mellifera* was likely the main cause of the increased fruit production of *M. polymorpha* following *V. pensylvanica* management. *Apis mellifera* appears to be acting as a substitute pollinator for *M. polymorpha* by replacing extinct or threatened bird species in our study system, similar to the role of introduced Japanese white-eye (*Zosterops japonicus*) for the Hawaiian 'ie'ie vine (*Freycinetia arborea*) (Cox 1983).

In our study system and in some other degraded systems that lack native pollinators, *A. mellifera* contributes positively to the pollination of native plants (Dick 2001), but their community-wide effects need to be further examined because their impact on native flora and fauna varies depending on the ecological context (Butz Huryn 1997, Gross 2003). *Apis mellifera* was intentionally introduced to Hawaii in 1857 (Snelling 2003). Consequently, the original pollinator community, through competition with numerically dominant *A. mellifera*, may have already undergone displacement and local extinction (Paini 2004). Displacement of native pollinators has been observed on degraded oceanic islands (Wenner and Thorp 1994, Dupont et al. 2004) and in Hawaii nearly half of the native *Hylaeus* species are threatened or extinct (Magnacca 2007) and one third of the endemic Hawaiian birds are extinct (Cox and Elmqvist 2000).

The change from a diverse native bird and bee fauna to an *A. mellifera*-dominated pollinator fauna in Hawaii may differentially impact plant reproduction depending on the plant's pollinator specialization and mating system (Aguilar et al. 2006). *Apis mellifera* has a negative impact on the highly specialized and self-incompatible (< 1% autogamous fruit production) *Sesbania tomentosa* (Hooper 2002), whereas it has a positive impact on the highly generalized and partially self-compatible *M. polymorpha*. The lower functional redundancy of oceanic island pollinator systems makes them more vulnerable to extinction and range reduction of endemic pollinators. As a result, the abundance and general foraging strategy of *A. mellifera* may make it a critical pollinator substitute for endemic flora, but a subset of the flora may not receive any benefit or may be negatively impacted. In Hawaii, future research needs to further examine the potential benefits and risks of *A. mellifera* to pollination in order to formulate appropriate management plans aimed at preserving or restoring plant-pollinator mutualisms (Dixon 2009, Stout and Morales 2009).

Ecosystems are rapidly being transformed and novel ecosystems are being created because of species extinctions and introductions (Hobbs et al. 2006). As a consequence, the composition and function of many ecosystems have been altered and continue to change (Seastedt et al. 2008, Hobbs et al. 2009). However, the maintenance and restoration of key ecosystem functions is still possible (Hobbs et al. 2009). Our study presents a unique example in which the management of an introduced species (*V. pensylvanica*) that disrupts plant-pollinator mutualisms and decreases pollination of an endemic tree species enabled a different introduced species (*A. mellifera*) to facilitate the plant-pollinator mutualism and increase the pollination of the same endemic tree species. This result emphasizes the importance of utilizing a functional framework when planning and assessing invasive species management (Zavaleta et al. 2001).

We documented the recovery of plant-pollinator mutualisms and pollination of *M. polymorpha* following *V. pensylvanica* management, but the restoration implications are limited to a specific timeframe and management scale. To determine more accurately the demographic consequences of *V. pensylvanica* management, restoration of *M. polymorpha* pollination needs to be examined throughout the entire flowering season and the relative impact of fruit production on long-lived *M. polymorpha* needs to be compared to other vital rates such as adult survivorship (Knight et al. 2005). Logistically, the *V. pensylvanica* management strategy utilized in this study may not enable island-wide eradication, but it will enable managers to remove or suppress *V. pensylvanica* populations within naturally occurring and endemically diverse forest fragments (e.g., kipukas). Furthermore, the significant relationship between abundance of *V. pensylvanica* within monitoring traps and fruit production of *M. polymorpha* can be utilized to define a *V. pensylvanica* management threshold, based on the reproduction *M. polymorpha*. Thus, *V. pensylvanica* monitoring traps provide an economically efficient tool that incorporates ecological function in the ongoing implementation and assessment of invasive species management.

Conventional conservation and restoration approaches focus on species richness and population size, yet the ecological interactions that underlie habitat restoration are often incompletely understood. Given the importance of pollination, restoration projects cannot assume that plant-pollinator interactions re-establish themselves (Forup et al. 2008). The results of this study linked the large-scale management of an ecologically damaging invader to the reestablishment of plant-pollinator interactions (e.g., flower visitation rates) and pollination (e.g., fruit production) of a functionally important endemic tree species. Consequently, this research demonstrated the diverse impacts of introduced species and provided specific tools and a general framework from which future invasive species management can be performed in the context of ecosystem function.

Tables

Table 1. Results of repeated measures ANCOVA [fixed factor: treatment (managed vs. unmanaged), repeated measures factor: day(s), covariate: site pair] for the mean site visitation rate of all visitors and individual taxonomic groups (*Vespula pensylvanica*, *Apis mellifera*, *Hylaeus*).

Dependent Variable	Repeated Measures	Interaction (Treatment & Time)		
		df	F	P
All Visitors	All Years	4, 20	1.905	0.149
	2009	1, 5	13.369	0.015
	2010	2, 10	1.866	0.205
Vespula pensylvanica	All Years	4, 20	10.537	<0.001
	2009	1, 5	30.679	0.003
	2010	2, 10	31.019	<0.001
Apis mellifera	All Years	4, 20	7.278	<0.001
	2009	1, 5	12.703	0.016
	2010	2, 10	14.516	<0.001
Hylaeus	All Years	4, 20	13.532	<0.001
	2009	1, 5	3.064	0.140
	2010	2, 10	22.279	<0.001

Table 2. Results of 1-way ANOVA [fixed factor: inflorescence treatment (No Visitors, Insects, and All Visitors)] for mean fruit production per site of each *V. pensylvanica* treatment (managed and unmanaged) × time (pre & post treatment) category.

Year	*V. pensylvanica* Trt.	Time (Pre or Post Trt.)	df	F	P
2009	Managed	Pre	2, 9	76.865	<0.001
		Post	2, 9	125.729	<0.001
	Unmanaged	Pre	2, 9	20.874	<0.001
		Post	2, 9	130.175	<0.001
2010	Managed	Pre	2, 9	18.780	<0.001
		Post	2, 9	11.519	<0.001
	Unmanaged	Pre	2, 9	24.197	<0.001
		Post	2, 9	8.964	0.007

Table 3. Post-hoc test p-values of the 1-way ANOVA for mean fruit production per site of each *V. pensylvanica* treatment (managed and unmanaged) × time (pre & post treatment) category.

a. 2009 Pre-Managed

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0	-	
Insects	0.373	0	-

b. 2009 Post-Managed

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0	-	
Insects	0.848	0	-

c. 2009 Pre-Unmanaged

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0.001	-	
Insects	1	0.001	-

d. 2009 Post-Unmanaged

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0	-	
Insects	0.237	0	-

e. 2010 Pre-Managed

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0.001	-	
Insects	0.736	0.002	-

f. 2010 Post-Managed

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0.001	-	
Insects	0.703	0.004	-

g. 2010 Pre-Unmanaged

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0	-	
Insects	0.703	0	-

h. 2010 Post-Unmanaged

	All Visitors	No Visitors	Insects
All Visitors	-		
No Visitors	0.007	-	
Insects	0.393	0.009	-

Figures

Figure 1. Mean (±1 SE) ISI and PLI within the four managed and unmanaged study sites pre and post *V. pensylvanica* treatment. Bars representing each index (ISI and PLI) with different letters are significantly different (P < 0.05, post-hoc Tukey tests).
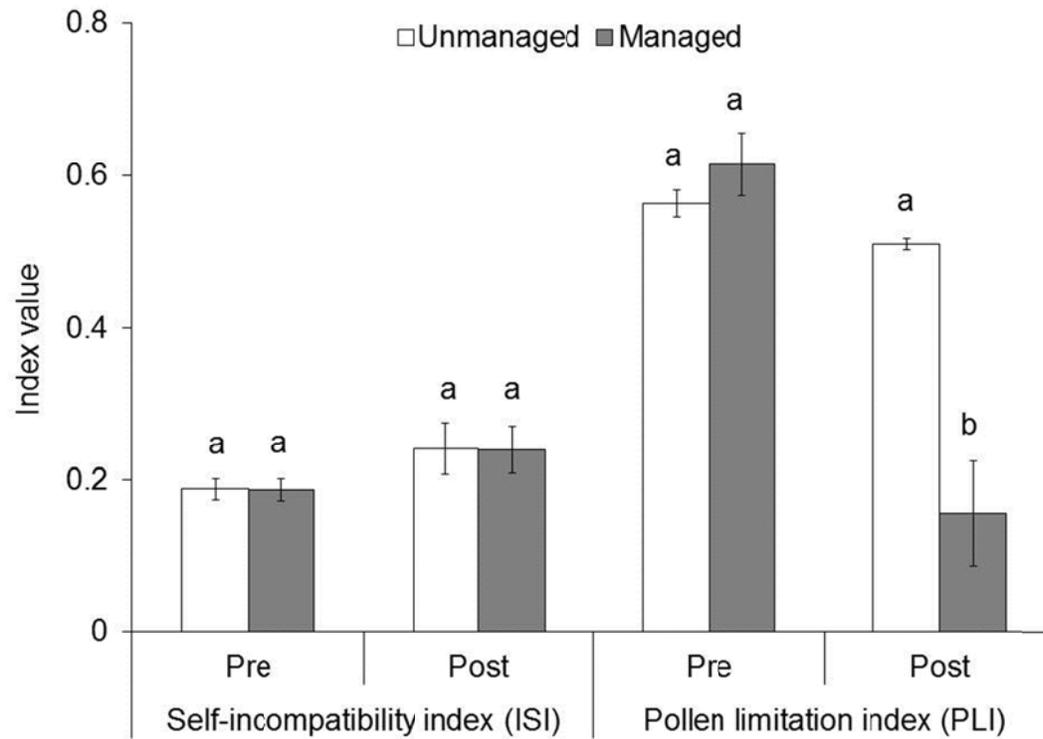
Figure 2. Mean (+1 SE) visitation rate for (a) all visitors, (b) *V. pensylvanica*, (c) *A. mellifera*, and (d) *Hylaeus* within the four managed (-●-) and unmanaged (-○-) study sites during each sampling month in 2009 and 2010. Arrows indicate the timing of the annual *V. pensylvanica* treatment.*P < 0.05 (from the two-sample t-tests)
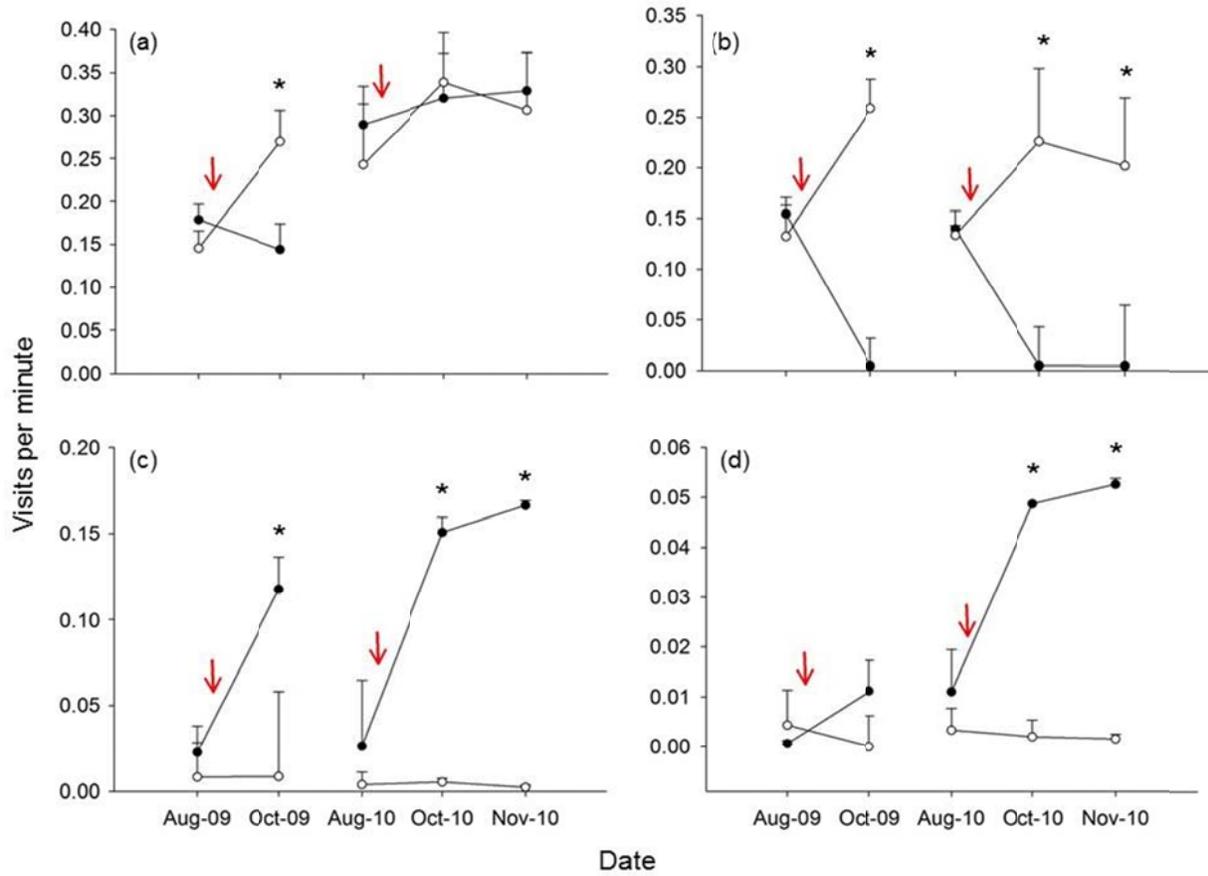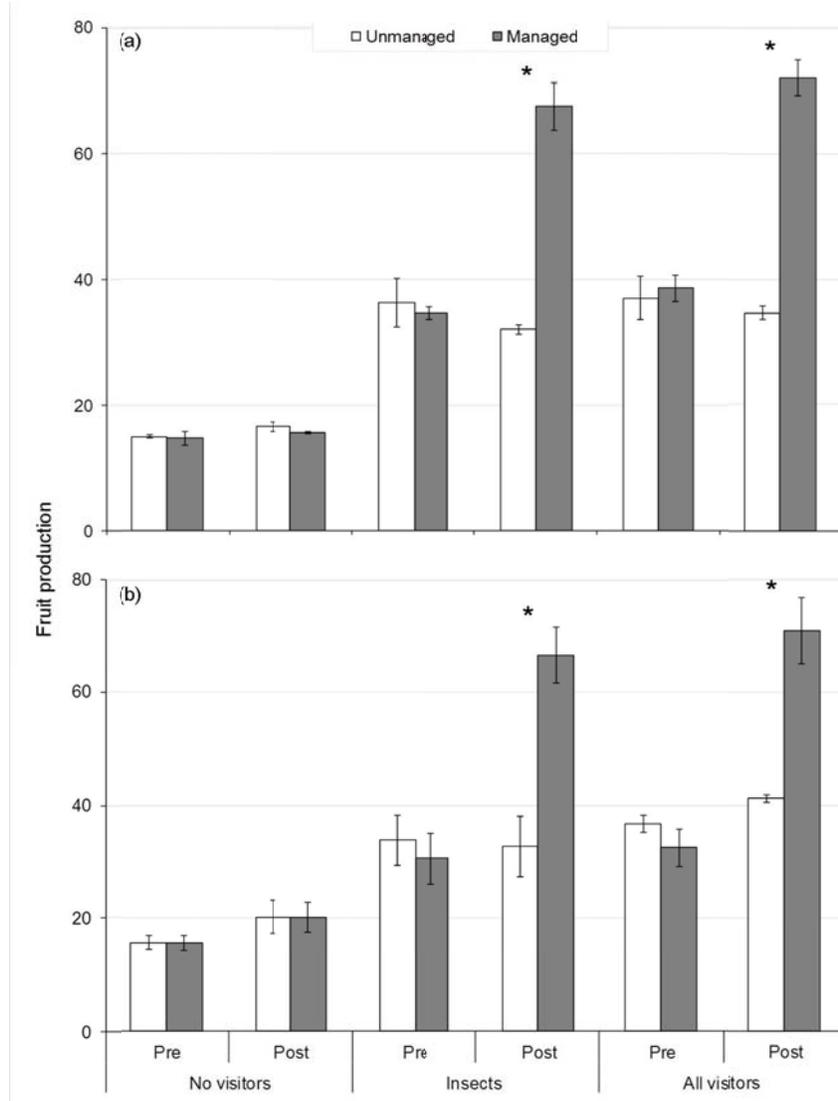
Figure 3. Mean (±1 SE) fruit production (percent of flowers setting fruit) within the managed and unmanaged sites for each inflorescence treatment (No Visitors, Insects, and All Visitors) pre and post *V. pensylvanica* treatment in (a) 2009 and (b) 2010. *P < 0.05 (from two-sample t-tests).

CHAPTER 3

Competitive Impacts of an Invasive Nectar Thief on Plant-Pollinator Mutualism

Abstract. Plant-pollinator mutualisms can be disrupted by a range of competitive interactions between invasive and native floral visitors. As the most abundant tree species in undisturbed Hawaiian forests, ʻōhiʻa lehua, *Metrosideros polymorpha*, is critical to the Hawaiian fauna and the energy flow through Hawaiian ecosystems. The invasive western yellowjacket wasp, *Vespula pensylvanica*, is an adept and aggressive nectar thief of the partially self-incompatible and pollen limited *M. polymorpha*. A multi-year, large-scale manipulative experiment was used to investigate the competitive mechanisms and impacts of *V. pensylvanica* on the structure and behavior of the *M. polymorpha* pollinator community relative to resource availability. The results demonstrated that *V. pensylvanica*, through both superior exploitative and interference competition, inhibits resource partitioning and displaces native and non-native *M. polymorpha* pollinators. Furthermore, the competitive restructuring of the pollinator community by *V. pensylvanica* resulted in a significant decrease in the overall pollinator effectiveness and fruit-set of *M. polymorpha*. This research highlights both the competitive mechanisms and contrasting effects of social insect invaders on plant-pollinator mutualisms and the role of competition in structuring pollinator communities.

Key-words: bees, Hawaii, pollination, resource partitioning, *Vespula*

Introduction

Invasive species disrupt the structure and function of native communities by displacing native species and establishing novel interactions (Mack et al. 2000, Hobbs et al. 2006). Competitively dominant invasive floral visitors are considered a threat to plant-pollinator mutualisms worldwide (Traveset and Richardson 2006, Bascompte and Jordano 2007), but an incomplete understanding of their competitive mechanisms and corresponding impacts currently hinders invasive species management and the restoration of plant-pollinator interactions. To gain a better understanding of this widespread threat, we performed a large-scale manipulative experiment to examine how an invasive floral visitor competes with and displaces effective pollinators.

Interspecific competition among floral visitors for critical, limited resources makes pollinator communities highly dynamic systems (Kevan and Baker 1983). Competitive mechanisms are generally categorized as either exploitative, in which an organism depletes a resource (i.e., nectar or pollen) below the minimum level required by another, or interference, when an organism physically limits or denies another access to a resource (i.e., displaces from flower or predates on flower). When one or both of these mechanisms are predominantly asymmetrical, floral visitors are competitively displaced (Reitz and Trumble 2002). Floral resource availability naturally fluctuates, creating variability in resource limitation and the strength of competitive displacement (Heinrich 1976, Pleasants 1981, Schmitt and Holbrook 1986). In a diverse floral landscape or during peak floral bloom, competition may be reduced due to resource abundance or partitioning, whereas in simple floral landscapes or during off-peak portions of the season, resources may be limiting and partitioning may not be possible. For floral visitors, temporal and spatial resource partitioning minimizes interspecific competition and enables the coexistence of species occupying similar niches (Heinrich 1976, Palmer et al. 2003).

However, invasive species tend to have broad ecological niches and efficient foraging strategies that result in the competitive displacement of subordinate foragers.

The competitive abilities of social insects have been the focus of research examining invasion theory (Moller 1996) and the role of resource competition in community structure (Heinrich 1976, Inouye 1978, Bowers 1985, Thomson 2006). Although the direct and indirect effects of invasive social insects have been thoroughly investigated (Moller 1996, Holway et al. 2002, Goulson 2003), considerable controversy remains regarding their impact on plant-pollinator mutualisms. In their invasive ranges they can compete with native pollinators (Roubik 1978, Thomson 2004, Lach 2005, Junker et al. 2010), reduce the fitness of native plant species (Gross and Mackay 1998, Dupont et al. 2004, Dohzono and Yokoyama 2010), and increase the fitness of invasive plant species (Barthell et al. 2001). These effects appear far from universal, however; other studies indicate little evidence for competition with native pollinators (Butz Huryn 1997, Roubik and Wolda 2001) or negative effects on native plant reproduction (Gross 2001, Junker et al. 2010). Furthermore, in some degraded systems that lack native pollinators, invasive species pollinate native plants and thus contribute positively to their fitness (Dick 2001, Madjidian et al. 2008).

Trade-offs between the exploitative (e.g., searching ability) and interference (e.g., defensive ability) competitive capabilities of species within floral visitor guilds can enable them to co-exist through resource partitioning (Nagamitsu and Inoue 1997). Due to their behavioral and numerical dominance, invasive bee and ant species have been found to uncouple the trade-off between these two forms of competition (Gross and Mackay 1998, Holway 1999). The same uncoupling may occur in invasive *Vespula*, considered as some of the world's most ecologically damaging invaders and rapidly spreading around the globe (Beggs et al. 2011). The invasive western yellowjacket, *Vespula pensylvanica*, inhabits the Hawaiian Islands and its impacts on Hawaiian plant-pollinator mutualisms are multi-dimensional. *Vespula pensylvanica* are generalist predators that directly consume native and introduced pollinators (Wilson and Holway 2010). Additionally, to satisfy the energy demand of adults and developing brood (Richter 2000), *Vespula* both exploit (Moller et al. 1991) and aggressively defend (Thomson 1989, Markwell et al. 1993, Grangier and Lester 2011) a variety of carbohydrate-rich resources (e.g., nectar, honeydew, etc.). The competitive dominance and multiple impacts of invasive *Vespula* populations are augmented by the increased year-round population density that results from the formation of large perennial colonies (Wilson et al. 2009), in a fashion similar to invasive ant species (Holway et al. 2002).

The insular characteristics of Hawaiian plant-pollinator mutualisms make them particularly susceptible to the competitive capabilities of *V. pensylvanica*. The historic absence of social insects in Hawaii (Wilson 1996) has prevented endemic pollinators and plants from evolving the appropriate competitive and defensive mechanisms (Wilson and Holway 2010, Junker et al. 2011). Furthermore, the generalized nature of island pollinator systems (Dupont et al. 2004) and the extinctions and declines of important Hawaiian pollinator guilds (Scott et al. 1988, Magnacca 2007) have granted *V. pensylvanica* access to the floral nectar of ʻōhiʻa lehua, *Metrosideros polymorpha*. *Meterosideros polymorpha* is the most prevalent tree species across a diverse array of Hawaiian ecosystems and provides a critical energetic resource and habitat for a diverse array of species (Carpenter 1976, Corn 1979, Gruner 2004).

To investigate the competitive mechanisms and impacts of *V. pensylvanica* on the plant-pollinator mutualisms of *M. polymorpha,* we experimentally reduced *V. pensylvanica* populations in large multi-year management plots (Hanna et al. 2011) and examined the

structural and behavioral changes of the pollinator community relative to resource availability. The scale and design of our experiment enabled us to discriminate the effects of removing *Vespula* from the natural spatial and temporal variation in *Vespula* abundance. We used this experimental design to reveal competition between *Vespula* and other floral visitors for nectar resources, elucidate the competitive mechanisms, and estimate the competitive effects on other floral visitors and on the pollination of the plant. We hypothesized that, in response to competitive release from the interference and exploitative impacts of *V. pensylvanica*, the remaining *M. polymorpha* visitors would change their foraging behavior and increase their utilization and pollination of *M. polymorpha*. To test this hypothesis we explored three questions: (1) Does *V. pensylvanica* competitively displace the floral visitors of *M. polymorpha*? (2) If so, what competitive mechanisms are responsible? (3) What impact does *V. pensylvanica* competition have on the foraging behavior and effectiveness of *M. polymorpha* pollinators?

Methods

Experimental design and field sites
We used a Before-After, Control-Impact experimental design to examine the competitive impacts of invasive *V. pensylvanica* on the pollinator community of *M. polymorpha* in 2009 and 2010. We randomly selected eight 9-hectare study sites within seasonal submontane *M. polymorpha* woodland within Hawaii Volcanoes National Park between approximately 700 to 1100 m (Hanna et al. 2011). In the four managed 9-hectare sites we used 0.1% fipronil chicken baits to reduce *V. pensylvanica* populations by 95 ± 1.2%, whereas we maintained the four unmanaged sites as experimental controls (Hanna et al. 2011). The actual *V. pensylvanica* population suppression within the managed sites encompassed ≥ 36-hectares, extending beyond the 9-hectare study area, as a result of the spatial extent of *V. pensylvanica* foraging (Hanna et al. 2011). We paired the managed and unmanaged sites to control for environmental variables (e.g., precipitation, elevation, vegetation, and substrate) and separated all sites by ≥ 1 km to maintain site independence (95% of wasps travel ≤ 200 m from the nest when foraging) (Edwards 1980).

Study plant
Metrosideros polymorpha is a functionally and energetically important and widespread endemic Hawaiian tree species that has facultative interactions with a diverse array of species (Carpenter 1976, Gruner 2004). *Metrosideros polymorpha* is found on all the main islands and occurs in a variety of climate and substrate regimes from sea-level to 2500 m elevation (Corn 1979). Peak flowering occurs from February to July, but flowers can be found at any time of the year (Ralph and Fancy 1995). *Meterosideros polymorpha* has open inflorescences that attract native and introduced birds and insect visitors (Carpenter 1976, Corn 1979, Lach 2005, Junker et al. 2010). The flowers are partially self-compatible (Carpenter 1976, Hanna Chapter 2) and pollen limited (Hanna Chapter 2).

Phenology of M. polymorpha
To examine the temporal and spatial variation of *M. polymorpha* phenology, we recorded and calculated the mean number of flowers per inflorescence, the number of inflorescences per tree, and the number of flowering trees within a 12.5 m radius of every 25 × 50 m study grid intersection at each site.

Nocturnal and diurnal energy production of M. polymorpha
We measured the diurnal energy production of *M. polymorpha,* in five random flowers within a bagged inflorescence, by emptying the nectar within an hour of dawn using filter paper, and then assessing the quantity and quality of nectar within each flower within an hour of dusk. We used the same methods for nocturnal energy production, but emptied the nectar from the flowers at dusk and measured the flower nectar at dawn. To compare the diurnal and nocturnal rates of energy production we calculated the mean number of cal h^{-1} produced by each flower per tree.

Insect visitation
To determine how the behaviors and relative frequency of specific plant-pollinator mutualisms change through time in response to *V. pensylvanica* treatment (managed or unmanaged), we performed timed inflorescence observations. Each observation round per site consisted of 15.66 ± 0.9 (SE) 10-min focal inflorescence observations for 1-5 inflorescences on 5-8 trees. Observation rounds were conducted simultaneously within the paired sites. In 2009, we conducted observation rounds at each site one time two weeks before and once six weeks after *V. pensylvanica* treatment. Whereas in 2010, in order to study *M. polymorpha* visitation patterns in more detail, we conducted observation rounds during each of the four following time spans: 7:00-10:00, 10:00-12:00, 13:00-15:00, and 15:00-17:00, two weeks before, and twice (6 and 10 weeks) after *V. pensylvanica* treatment. The 10-min observations were conducted during sunny or partly cloudy weather when wind speed was < 2.5 m s^{-1}. Prior to each 10-min observation we recorded the number of flowers within the inflorescence and open inflorescences on the tree. During the 10-min observation for each visitor we recorded: the species or lowest field identifiable taxonomic category, time on inflorescence, number of flowers visited, and behavior (pollen collection, nectar collection, and/or stigma contact) per flower. To determine the relative frequency of visitors and floral behaviors, we calculated the mean site visitation rate (visits min^{-1}) and floral behavior rate (behavior min^{-1}) per observation round for each taxonomic group. To compare the relative frequency of behaviors among visitors, we calculated the frequency with which each taxonomic group performed a specific behavior while visiting a flower.

Interference competition
To determine how the frequency and outcome of interference competition between *M. polymorpha* floral visitors change through time in response to *V. pensylvanica* treatment, we collected data on all observed interactions during the 10-min focal inflorescence observations (N = 1869). For each interaction we recorded the taxonomic identification of and outcome for each participant. We assigned each interaction to one of three outcomes: Winner – the visitor remains on the inflorescence and the other visitor leaves; Neutral – both visitors remain on or leave the inflorescence; and Loser – the visitor leaves the inflorescence and the other visitor remains. To compare the relative frequency of interaction outcomes for each taxonomic group through time, we calculated the percent of observed visits that the taxonomic group experienced each interaction outcome (total number of a specific interaction outcome observed/total number of observed visits for that taxon).

Exploitative competition
To determine how the *M. polymorpha* standing nectar crop and the proportion of unexploited nectar change through time in response to *V. pensylvanica* treatment, we collected nectar data immediately following each 10-min observation at an inflorescence. Within a half hour of dawn

we randomly assigned 1-5 inflorescences on each observation tree to remain open and a similar number to be bagged with fine nylon mesh. After each focal inflorescence observation on a given tree we randomly sampled five flowers within randomly chosen open and bagged inflorescence. In 2009, we performed one nectar collection round (5-8 trees) per day, simultaneously within the paired sites, coinciding with visitation observation rounds that occurred two weeks before and six weeks after *Vespula* treatment. Similarly in 2010, we performed collection rounds coinciding with the four daily observation rounds conducted two weeks before and six and ten weeks after *Vespula* treatment, to determine the effect of *Vespula* on the standing nectar crop and percent of unexploited nectar throughout the day. We measured the quantity of nectar within each flower with a 1-50 ul micro-capillary tube and the percent sucrose of the nectar with a hand-held refractometer. To calculate the energetic value of the nectar (cal), we calculated the amount of sucrose (mg) present per 1 ul of nectar, multiplied this value by the volume obtained, and assumed 4 cal mg^{-1} sucrose (Carpenter 1976, Dafni et al. 2005). To determine the energetic availability within each site we calculated the mean energetic value of the standing nectar crop per flower, i.e., the number of calories present in an open flower at a given moment. To compare the energetic consumption across sites, we calculated the mean percentage of unexploited nectar (energetic value of the nectar within open flower/energetic value of bagged flower on the same inflorescence) × 100.

Simulations of M. polymorpha energetics
To estimate the site level energetic value of *M. polymorpha* nectar (cal ha^{-1}) and account for the statistical error associated with each input we developed a Monte Carlo propagation of error simulation. The input to the simulation included the mean and variance for: i) standing nectar crop per flower (cal) or 24 h floral energy production (determined from diurnal and nocturnal nectar production data), ii) number of flowers per inflorescence, iii) number of inflorescences per tree, and iv) number of flowering trees ha^{-1} within each site. Prior to running these simulations, the fit of a normal distribution to the raw input data was assessed with goodness-of-fit tests. Normal probability distributions were used for all the input variables; to prevent negative values the distributions were bounded at their lower ends by zero. The simulation randomly selected a number for each input from a normal distribution having the site-specific input mean and variance for that variable and multiplied all the input values to obtain a site level estimate. When the standing nectar crop per flower was input as the initial step, each run of the simulation represented the cal ha^{-1} of available *M. polymorpha* nectar. When the 24 h floral energy production was input as the initial step, each run of the simulation represented the cal ha^{-1} produced by *M. polymorpha* over 24 h. We ran the simulation for 10,000 repetitions (runs) per collection round at each site which produced estimation errors of $4.28 \pm 0.13\%$ and $3.80 \pm 0.07\%$ for the standing nectar crop and 24 h energy production simulations. The distributions were skewed in some cases, so we used median instead of mean values for the corresponding analyses (Winfree et al. 2007). The simulations were performed with Microsoft Excel 2010.

Data analysis
To examine the temporal and spatial variation in the phenology of *M. polymorpha* and the interaction between the two, we conducted 2-way ANOVAs. The dependent variables were the mean number of *M. polymorpha* flowers per inflorescence, inflorescences per tree, and flowering trees ha^{-1}. The fixed variables were site pair and monitoring month. To compare the paired mean

nocturnal and diurnal energy production per tree (cal h^{-1}), we performed a Wilcoxon signed rank test.

To determine how the relative frequency of interaction outcomes for the most prominent *M. polymorpha* pollinators (*Apis mellifera* and *Hylaeus*) changed in response to *V. pensylvanica* treatment we performed 2-way ANCOVAs. We used *V. pensylvanica* treatment (managed and unmanaged) and time (pre and post *V. pensylvanica* treatment) as the fixed factors, the proportion of visits in which *A. mellifera* or *Hylaeus* experienced each interaction outcome as the dependent factor. We included the number of observed visits as a covariate to control for its potential effect on the likelihood of observing an interaction. We conducted two sample t-tests to compare the variation of the dependent factors within managed and unmanaged sites at each observation round.

We performed repeated measures ANCOVAs to analyze the within and between year variation in four dependent variables: the mean standing nectar crop and percent of unexploited nectar per flower, and the Monte Carlo simulation median standing nectar crop and 24 h production of cal ha^{-1}. We used *V. pensylvanica* treatment as the fixed factor, month as the repeated measures factor, and site pair as the covariate. To analyze the variation at different discrete time periods throughout the day, we performed identical analyses for the mean floral standing nectar crop, proportion of unexploited nectar, total visitation rate, and the visitation rates for selected taxonomic groups at each daily collection/observation round in 2010. We conducted two sample t-tests to compare the variation within *V. pensylvanica* between managed and unmanaged sites at each discrete time period. To compare the temporal influence on daily activity patterns among taxonomic groups, we performed a repeated measures ANOVA using taxonomic group as the fixed factor and daily collection round as the repeated factor. We performed simple linear regression analyses to examine the relationships between *M. polymorpha* standing nectar crop and the visitation rates and behaviors of floral visitors.

We compared the relative frequency with which each taxonomic group performed a specific floral behavior with 1-way ANOVAs and performed Tukey HSD tests for *a posteriori* comparisons. To compare the relative frequency of *A. mellifera* and *Hylaeus* nectar and pollen foragers (proportion of flowers foraged for nectar collected/proportion of flowers foraged for pollen) within sites before and after *V. pensylvanica* treatment we performed separate 2-way ANOVAs, using *V. pensylvanica* treatment and month as the fixed factors. To connect the changes in visitor behavior to the pollination of *M. polymorpha*, we performed a Wilcoxon signed rank test to compare how often *A. mellifera* and *Hylaeus* contacted the stigma while collecting pollen versus collecting nectar. To analyze the within and between year variation in the mean rate of *A. mellifera* and *Hylaeus* stigma contact (floral stigmas contacted min^{-1}) per site, we performed repeated measures ANCOVAs, using *V. pensylvanica* treatment as the fixed factor, month as the repeated measures factor, and site pair as the covariate. We conducted two sample t-tests to compare the variation within *V. pensylvanica* managed and unmanaged sites at each discrete time period.

Prior to analysis we used an arcsine square root transformation to normalize the proportion of unexploited nectar, interaction outcome, and proportion of daily visitation rate data; a log transformation to normalize the Monte Carlo simulation *M. polymorpha* cal ha^{-1} data; and a log+1 transformation to normalize the visitation rate, stigma contact rate, and relative visitor behavior data. To correct for Type 1 errors, we used Bonferroni corrections for multiple comparisons. We conducted all statistical analyses in Systat 11 (Systat 2004).

Results

Phenology of M. polymorpha
We collected phenological data from 1114 inflorescences and 8417 trees across 72 ha. Across sites and monitoring months there were 11.82 ± 0.41 flowers per inflorescence, 14.08 ± 0.40 inflorescences per tree, and 23.38 ± 2.23 flowering trees ha^{-1}. There was a significant difference between the site pairs, the blocking factor, and monitoring months for the number of flowers per inflorescence and the number of flowering trees ha^{-1}, but not for the number of inflorescences per tree (Table 1). There was an interaction between site pair and monitoring month for all the dependent variables (Table 1), whereas there were no significant differences between the managed and unmanaged members of site pairs ($P \geq 0.351$ in all cases). Due to the significant temporal and spatial variation of *M. polymorpha* phenology and the interaction between the two, we utilized site and month specific *M. polymorpha* data for all analyses and simulations.

Nocturnal and diurnal energy production of M. polymorpha
The average diurnal energy production of 0.465 ± 0.063 cal h^{-1} was higher than the average nocturnal energy production of 0.328 ± 0.027 cal h^{-1}, but not significantly different ($Z = -1.487$, $P = 0.138$). The energy production values may be underestimated because nectar was occasionally observed overflowing from floral nectar cups.

Interference competition
We observed and recorded the outcomes of 447 interactions during 1869, 10-min inflorescence observations. Participants in the interactions included *V. pensylvanica*, *A. mellifera*, *Hylaeus*, and Formicidae. The winner and aggressor of all the observed interactions was either *V. pensylvanica* or Formicidae, both of which were also observed predating floral visitors directly from *M. polymorpha* flowers. Prior to *V. pensylvanica* treatment, *A. mellifera* and *Hylaeus* encountered and lost an inter-specific interaction during $25.56 \pm 5.05\%$ and $27.93 \pm 6.74\%$ of their observed visits, respectively (Fig. 1). Interactions with *Vespula* accounted for $96.88 \pm 3.13\%$ and $96.18 \pm 4.07\%$ of the interactions lost by *A. mellifera* and *Hylaeus* (Fig. 1). Prior to *V. pensylvanica* treatment, *Vespula* encountered and lost an interaction during $7.56 \pm 1.16\%$ of their observed visits, $78.91 \pm 8.4\%$ of which were to other *V. pensylvanica* and $21.09 \pm 8.40\%$ to Formicidae (Fig. 1). All neutral interactions among visitors observed prior to *V. pensylvanica* treatment were intraspecific (Fig. 1). There were no significant interaction differences between managed and unmanaged sites before *V. pensylvanica* treatment, but after *V. pensylvanica* treatment both *A. mellifera* and *Hylaeus* encountered a significantly higher percent of "neutral" outcomes (*A. mellifera*: $F_{1, 11} = 5.713$, $P = 0.036$; *Hylaeus*: $F_{1, 11} = 12.596$, $P = 0.005$) and a significantly lower percent of "loser" (*A. mellifera*: $F_{1, 11} = 13.387$, $P = 0.004$; *Hylaeus*: $F_{1, 11} = 13.814$, $P = 0.003$) outcomes in the managed sites compared to the unmanaged sites (Fig. 2).

Exploitative competition
We collected nectar data from 3342 flowers in 1114 inflorescences from 222 trees across the eight study sites, over the two years. Prior to *V. pensylvanica* treatment in 2009 and 2010, $1.88 \pm 0.60\%$ of the nectar was unexploited within all sites, producing a standing nectar crop of 0.077 ± 0.150 cal per flower (Fig. 3a, b). After the annual *V. pensylvanica* treatments, $26.70 \pm 3.10\%$ of the nectar was unexploited in the managed sites, producing a standing nectar crop of 0.826 ± 0.108 cal per flower (Fig. 3a, b). Conversely, in the unmanaged sites the nectar continued to be

highly exploited (1.70 ± 0.42%) and the standing nectar crop remained low (0.084 ± 0.026 cal per flower) (Fig. 3a, b). Correspondingly, the variation in the standing nectar crop and percentage of unexploited nectar differed significantly between the two *V. pensylvanica* treatments within and across years (Table 2). Additionally, post-treatment, the variation in the standing nectar crop and percentage of unexploited nectar differed significantly between the two *V. pensylvanica* treatments for each of the daily collection rounds taken during the 2010 monitoring months, with the exception of the 3:00-5:00 collection round (Fig. 4c, e; Table 3). Prior to *V. pensylvanica* treatment there were no significant differences between the managed and unmanaged sites for any of the daily collection rounds (Fig. 4a).

Simulations of M. polymorpha energetics
Based on the flower and inflorescence abundance and flower tree data (see above) the median 24 h energetic value of *M. polymorpha* nectar production in August of 2009 and 2010 was 36490 ± 5766 cal ha^{-1}; whereas the median nectar production in October of 2009 and 2010 was 13895 ± 1385 cal ha^{-1} (Fig. 3d). There was a significant difference between site pairs and monitoring months in the median 24 h energy production of *M. polymorpha* (Table 1), but there was no significant difference between the two *V. pensylvanica* treatments within and across years (Table 2). Prior to *V. pensylvanica* treatment in 2009 and 2010, the median standing nectar crop across sites was 192.22 ± 40.26 cal ha^{-1} (Fig. 3c). After the annual *V. pensylvanica* treatments, the median standing nectar crop was 1234.10 ± 356.25 cal ha^{-1} within the managed sites, whereas it was 81.04 ± 23.39 cal ha^{-1} within the unmanaged sites. The variation in the median standing nectar crop differed significantly between the two *V. pensylvanica* treatments within and across years (Table 2). Prior to annual *V. pensylvanica* treatment there was no significant difference in the standing nectar crop, whereas it was significantly higher in the managed sites at all post-treatment time periods (Fig. 3c).

Insect visitation
We observed 5069 visitors on 28148 flowers in 1869 inflorescences from 593 trees across the eight study sites, over the two years. The variation in the mean visitation rate for all three taxonomic groups differed significantly between the *V. pensylvanica* managed and unmanaged sites within and across treatment years, with the exception of *Hylaeus* in 2009 (Hanna Chapter 2). The variation in the mean total visitation rate was not significantly different between the managed and unmanaged sites for any of the daily collection rounds within 2010, whereas the mean visitation of *V. pensylvanica* was significantly different for all the daily collection rounds (Table 4). After *V. pensylvanica* treatment the visitation rates of *V. pensylvanica* were reduced in the managed compared to the unmanaged sites by an average of 95.43 ± 1.99% within the daily collection rounds (Fig. 4d, f). Conversely, the visitation rates of *A. mellifera* and *Hylaeus* were increased in the managed sites by an average of 1611.13 ± 535.32% and 334.55 ± 86.11% (Fig. 4d, f). Correspondingly, the variation in the *A. mellifera* and *Hylaeus* mean visitation rates were significantly different between the managed and unmanaged sites for three and two of the daily collection rounds, respectively (Table 4). The standing nectar crop per flower was negatively related to the visitation rate of *V. pensylvanica* (y = 0.0772 – 0.284x, P = < 0.001, r^2_{adj} = 0.511), and positively related to the visitation rates of *A. mellifera* (y = 0.00305 – 0.180x, P = < 0.001, r^2_{adj} = 0.435) and *Hylaeus* (y = 0.000324 – 0.0555x, P = < 0.001, r^2_{adj} = 0.460). The total visitation rate of the *M. polymorpha* visitors was affected by time within the day ($F_{3, 198}$ = 8.547,

P = <0.001), but there was no differences in the daily activity patterns among the *M. polymorpha* visitors (taxonomic group × time of day, $F_{6, 198} = 1.735$, P = 0.115) (Fig. 4).

Insect behavior
The *M. polymorpha* visitors differed in the proportion of flowers at which they performed specific behaviors. *Vespula pensylvanica* collected nectar at a significantly higher proportion of flowers, whereas *A. mellifera* and *Hylaeus* collected pollen and contacted the stigma at significantly higher proportions of flowers (Fig. 5). There was a significant interaction between *V. pensylvanica* treatment and month for the relative proportion of *A. mellifera* nectar to pollen foragers in 2009 ($F_{2, 15} = 12.29$, P = 0.001) and 2010 ($F_{2, 15} = 12.29$, P = 0.001). There were no significant differences in the relative proportion of *A. mellifera* nectar to pollen foragers between the managed and unmanaged sites prior to the annual *V. pensylvanica* treatments, but the relative proportion of nectar to pollen foragers was significantly higher in the managed sites in all time periods after treatment (P ≤ 0.01 in all cases). The relative proportion of *A. mellifera* nectar to pollen foragers was positively related to the standing nectar crop per flower (y = 0.135 − 1.021x, P = < 0.001, $r^2_{adj} = 0.571$). Insufficient data prohibited the analysis of the relative proportion of *Hylaeus* nectar to pollen foragers in 2009. In 2010, the relative proportion of *Hylaeus* nectar to pollen foragers increased by 250.76 ± 31.78% in the managed sites after treatment, but there was no significant interaction between *V. pensylvanica* treatment and month ($F_{2, 11} = 1.425$, P = 0.282). *Apis mellifera* ($Z_{30} = 4.433$, P = <0.001) and *Hylaeus* ($Z_{18} = 3.463$, P = 0.001) pollen foragers were significantly more likely to contact the stigma than nectar foragers. However, the mean rate of stigma contact of *A. mellifera* increased by an average of 512.54 ± 177.41% in 2009 and 1037.71 ± 202.72% in 2010, and of *Hylaeus* by 392.5 ± 123.29% in 2010 following the annual *V. pensylvanica* treatment in the managed sites, whereas the rate of stigma contact remained at or close to zero in the unmanaged sites (Fig. 6a, b). Correspondingly, the variation in the mean rate of stigma contact for *A. mellifera* and *Hylaeus* differed significantly between the *V. pensylvanica* managed and unmanaged sites within and across treatment years, except for *Hylaeus* in 2009 (Table 5). No significant relationships were found between the number of flowers visited and time spent per flower by *A. mellifera* or *Hylaeus* and the visitation rate of *V. pensylvanica*.

Discussion

The large-scale management of *V. pensylvanica* significantly reduced the interference and exploitative competition *M. polymorpha* visitors experienced and, as a consequence, directly impacted their foraging behavior and indirectly impacted the pollination of *M. polymorpha*. A morphological mismatch with *M. polymorpha* enables *V. pensylvanica* to defend and competitively exploit the nectar without contributing to flower pollination (i.e., nectar thieving). *Vespula* aggressively patrolled *M. polymorpha* floral nectar, physically removed and, during several observations, directly predated *A. mellifera* and *Hylaeus* from *M. polymorpha* inflorescences. Interference competition (Primack and Howe 1975) and predation (see Romero et al. 2011 and therein) can result in the behavioral avoidance of flowers by foragers. The significant increase in *A. mellifera* and *Hylaeus* visitation rates following the reduced presence of *V. pensylvanica* was likely a behavioral response to *Vespula* removal because the timeframe was shorter than the time required for the populations to increase logistically (Wilson and Holway 2010).

The removal of *V. pensylvanica* was accompanied by a significant increase in the relative abundance of *A. mellifera* nectar foragers compared to pollen foragers. The behavioral shift in foraging strategy suggests that *V. pensylvanica* exerts both exploitative and interference competition (Thomson 1989). The inflorescence structure of *M. polymorpha* in conjunction with the foraging behavior of *V. pensylvanica* enables the exploitation of *M. polymorpha* nectar to a level that maintains a net energetic profit for *V. pensylvanica* but not for other foragers (Willmer and Corbet 1981, Tilman 1990). *Vespula* systematically consume nectar at the base of each floral cup within an inflorescence, leaving a negligible standing nectar crop at both the flower and landscape level. The removal of *V. pensylvanica,* at a scale equivalent to the perception of foragers (Kareiva and Wennergren 1995), resulted in the competitive release of both *A. mellifera* and *Hylaeus*. The flexible foraging behavior of bees enables them to respond quickly to shifts in the profitability of flowers (Pleasants 1981). Consequently, in an effort to maximize their energetic profits, after *V. pensylvanica* removal, *A. mellifera* and *Hylaeus* changed their foraging behavior by expanding their use of *M. polymorpha* as a nectar source.

Temporal variation in the availability of critical resources influences the prevalence of interspecific competition and a community's susceptibility to invasion (Shea and Cheeson 2002, Cleland et al. 2004) by impacting the strength of competitive processes (Schmitt 1986). The floral phenology of *M. polymorpha* resulted in a significant decrease in nectar production (cal ha^{-1}) in the months following the annual *V. pensylvanica* treatments (Fig. 3d). As a result, the standing nectar crop (cal ha^{-1}) decreased in the unmanaged sites after *V. pensylvanica* treatment; however, in the managed sites the standing nectar crop significantly increased relative to pre-*Vespula* treatment. Despite the natural decrease in nectar at this time due to *M. polymorpha* phenology, $26.70 \pm 3.10\%$ of *M. polymorpha* cal per flower was unexploited in the absence of *V. pensylvanica*. The unconsumed nectar could be a consequence of the inability of the remaining forager populations to reach equilibrium within the experimental timeframe or it could be due to the extinctions and/or declines of other important native Hawaiian pollinator guilds that would have also exploited this nectar source, such as birds and bees (Scott et al. 1988, Magnacca 2007). Due to avian malaria and other habitat disturbances, endemic Hawaiian honeycreepers, including *M. polymorpha* nectarivores such as the `i`iwi (*Vestiaria coccinea*) and `apapane (*Himatione sanguinea*) have been largely replaced at lower elevations by an introduced generalist, the Japanese white-eye (*Zosterops japonicus*) (Ralph and Fancy 1995). Accordingly, we infrequently observed birds visiting *M. polymorpha* even though the presence of birds significantly increased after *V. pensylvanica* treatment (Hanna Chapter 2). The reduced presence of endemic Hawaiian honeycreepers may have resulted in the increased quantity of unused resources, thus providing a niche opportunity for invasive *V. pensylvanica* (Shea and Cheeson 2002, Cleland et al. 2004) and reducing the strength of resource competition in the absence of *V. pensylvanica*.

The competitive impacts of *V. pensylvanica* on the *M. polymorpha* forager guild may have caused the species to partition their energetic resources to minimize the overlap of their ecological niches (Schoener 1974). Floral resource partitioning can occur at the spatial or temporal scale. The separation between the nectar and pollen rewards on *M. polymorpha* flowers and the exploitation of nectar by *V. pensylvanica* led to intra-floral resource partitioning. Similar to the competitive effects of invasive ants on *M. polymorpha* visitors (Junker et al. 2010), *V. pensylvanica* impacted the visitation rates of *M. polymorpha* nectar foragers to a greater extent than pollen foragers. The foraging activity of insect floral visitors is determined by extrinsic (e.g., ambient temperature, wind velocity, etc.) and intrinsic (e.g., competition, predation, resource availability, etc.) factors (Herrera 1990). These species-specific constraints on foraging

activity create an opportunity for diel resource partitioning among nectarivores (Heinrich 1976, Inouye 1978) and correspondingly a temporal pattern of daily nectar availability (Corbet et al. 1995). Thermal constraints on the flight activity of foragers are thought to be largely responsible for the patterns of forager activity at the beginning of the day, whereas resource availability is thought to determine forager activity later in the day (Willmer and Corbet 1981, Herrera 1990, Corbet et al. 1993). The early morning temperatures in our study sites were well above the flight thresholds of *A. mellifera* (Corbet et al. 1993) and *Vespula* (Spradbury 1973). Correspondingly, we found no evidence of diel resource partitioning among *M. polymorpha* floral visitors, and when *V. pensylvanica* were present the standing nectar crop was immediately reduced and remained at virtually zero over the course of the day (Fig. 4a, c, e). The period of peak *Vespula* forager activity is within 1-2 hours of colony awakening and coincides with their peak nectar collection (Spradbury 1973). These results and observations suggest that the strong demand, efficient foraging, and aggressive protection of *M. polymorpha* nectar by *V. pensylvanica* competitively displaces other members of the *M. polymorpha* forager guild. The utilization of secondary, less preferred floral resources could enable foragers to spatially partition resources. However, floral resources at the time of our study (late summer/fall) were scarce, and the exclusion of visitors on floral resources occupied by *V. pensylvanica* has been found to occur across plant species (Wilson and Holway 2010).

Exploitative and interference competition by introduced floral visitors has been documented to displace native floral visitors (Roubik 1978, Gross and Mackay 1998, Dupont et al. 2004), but the population level impacts have rarely been documented (Thomson 2004, Goulson 2009). The inability of the less competitive members of the *M. polymorpha* visitor guild to partition and acquire critical energetic resources in the presence of *V. pensylvanica* and their competitive release in the absence of *V. pensylvanica* indirectly suggests that invasive *V. pensylvanica* are impacting their fitness (Roubik 1978). In the presence of *V. pensylvanica, A. mellifera* and *Hylaeus* may be unable to compensate for their reduced visitation rates to *M. polymorpha* because of the absence of temporal partitioning in *M. polymorpha* forager activity and alternative floral resources that do not overlap with *V. pensylvanica* resource use (Wilson and Holway 2010). The reduced level of resource acquisition and the increased time and energy expended searching for resources likely results in a lower net energetic return for *A. mellifera* and *Hylaeus* foragers and their developing larvae (Roubik 1978, Bowers 1985). Although our experimental study did not measure the impact of *V. pensylvanica* competition on *A. mellifera* and *Hylaeus* reproduction, experimental data on forager abundances has been found to accurately estimate and possibly underestimate competitive effects on reproduction (Thomson 2006).

The removal of *V. pensylvanica* had contrasting impacts on the components of *A. mellifera* pollinator effectiveness; however, the overall pollinator effectiveness of *A. mellifera* significantly increased. Pollinator effectiveness, i.e., the contribution of a pollinator to plant fitness, is a product of the pollinator efficiency per visit multiplied by the visitation frequency (Herrera 1987). *Vespula pensylvanica* was the most frequent *M. polymorpha* visitor but had a negative impact on *M. polymorpha* reproduction because they depleted nectar without contacting the floral stigma or contributing to floral pollination (Hanna Chapter 2). The per visit pollinator efficacy of *A. mellifera* decreased in the absence of *V. pensylvanica* because the relative proportion of nectar foragers increased and nectar foragers are significantly less likely to contact the stigma. However, the decreased pollinator efficiency was overridden by the significant increase in visitation rate, thus the floral stigma contact rates of *A. mellifera* significantly increased (Hanna Chapter 2). The positive relationship between the interaction frequency and

overall effectiveness of *A. mellifera* in the absence of *V. pensylvanica* resulted in a significant decrease in the pollen limitation and a significant increase in fruit production of *M. polymorpha* (Hanna Chapter 2); other studies and meta-analyses have also found that the visitation rate is more important than the per visit effectiveness in determining impacts of pollinators on pollination (Vazquez et al. 2005, Madjidian et al. 2008).

Trade-offs in the interference (e.g., searching ability) and exploitative (e.g., defensive ability) competitive capabilities of species within floral visitor guilds can enable them to co-exist through resource partitioning (Nagamitsu and Inoue 1997, Nagamitsu et al. 2010). However, the numerical and behavioral dominance of invasive social insects, such as wasps, ants, and bees have been documented to break this trade-off and displace legitimate pollinators (Gross and Mackay 1998, Lach 2008, Junker et al. 2010, Wilson and Holway 2010). All three groups of introduced social insects collect and compete for *M. polymorpha* floral resources but have contrasting impacts on *M. polymorpha* plant-pollinator mutualisms and pollination. Nectar thieving invasive ants and *V. pensylvanica* have been documented to competitively displace legitimate *M. polymorpha* pollinators (Lach 2008, Junker et al. 2010, Wilson and Holway 2010) but invasive ants were found to have a neutral impact (Junker et al. 2010) and *V. pensylvanica* a negative impact on *M. polymorpha* pollination (Hanna Chapter 2). In our study, invasive ants successfully defended *M. polymorpha* floral resources from *V. pensylvanica,* but the patchy distribution of invasive ants (present on $10.83 \pm 1.84\%$ of inflorescences) and the superior mobility of *V. pensylvanica* enabled *V. pensylvanica* to impact *M. polymorpha* pollination at the landscape scale. *Apis mellifera* did not aggressively defend *M. polymorpha* resources and, in the absence of *V. pensylvanica*, was unable to competitively exploit *M. polymorpha* nectar. Furthermore, *A. mellifera* appears to be acting as a substitutive pollinator for *M. polymorpha*, replacing extinct or threatened bird species in our study system (Junker et al. 2010, Hanna Chapter 2). The variability of impacts among these introduced social insects demonstrates the challenge of estimating and predicting invasion impacts (Thomson 2006) and emphasizes the importance of utilizing a functional framework when planning and assessing invasive species management (Zavaleta et al. 2001).

In conclusion, our results demonstrated that *V. pensylvanica*, through both superior exploitative and interference competition, displaced native and non-native *M. polymorpha* pollinators. The competitive restructuring of the pollinator community led to a reduction in overall pollinator effectiveness, resulting in decreased *M. polymorpha* fruit-set. These finding highlight the competitive mechanisms and the varied competitive effects of social invaders on plant-pollinator mutualisms and the role of competition in the structure of pollinator communities.

Tables

Table 1. Results of the 2-way ANOVAs (fixed factors: site pair and month) for the mean number of flowers per inflorescence, inflorescences per tree, flowering tree per hectare and the Monte Carlo simulation median 24 h energy production (cal ha^{-1}).

Dependent Variable	Month			Site Pair			Interaction (Month x Pair)		
	df	F	P	df	F	P	df	F	P
Flowers per inflorescence	4, 20	3.25	0.033	3, 20	8.68	0.001	12, 20	3.58	0.006
Inflorescences per tree	4, 20	1.28	0.311	3, 20	0.92	0.451	12, 20	2.97	0.015
Flowering trees ha^{-1}	4, 20	102.35	<0.001	3, 20	177.80	<0.001	12, 20	24.81	<0.001
24 h energy production (cal ha^{-1})	4, 20	30.28	<0.001	3, 20	20.60	<0.001	12, 20	9.99	<0.001

Table 2. Results of the within and between year repeated measures ANCOVAs [fixed factor: treatment (managed vs. unmanaged), repeated measures factor: month, covariate: site pair] for the mean standing nectar crop (cal) and percent of unexploited energy (cal) per flower and the Monte Carlo simulation median standing nectar crop (cal ha^{-1}) and 24 h energy production (cal ha^{-1}).

Dependent Variable	Repeated Measures	Interaction (Treatment & Month)		
		df	F	P
Percent of unexploited energy per flower (cal)	All years	4, 20	16.958	<0.001
	2009	1, 5	276.959	<0.001
	2010	2, 10	12.900	0.007
Standing nectar crop per flower (cal)	All years	4, 20	13.630	<0.001
	2009	1, 5	20.826	0.006
	2010	2, 10	12.212	0.002
Standing nectar crop (cal ha^{-1})	All years	4, 20	7.644	0.001
	2009	1, 5	13.222	0.015
	2010	2, 10	8.361	0.007
24 h energy production (cal ha^{-1})	All years	4, 20	0.507	0.731
	2009	1, 5	0.296	0.610
	2010	2, 10	0.878	0.445

Table 3. Results of the 2010 daily collection round repeated measures ANCOVAs [fixed factor: treatment (managed vs. unmanaged), repeated measures factor: month, covariate: site pair] for the mean percent of unexploited energy (cal) and standing nectar crop (cal) per flower.

Dependent Variable	Daily Collection Round	Interaction (Treatment & Month)		
		df	F	P
Percent of unexploited energy	7:00-10:00	2, 10	9.39	0.005
	10:00-12:00	2, 10	21.540	0.000
	13:00-15:00	2, 10	5.777	0.021
	15:00-17:00	2, 10	4.343	0.044
Standing nectar crop (cal) per flower	7:00-10:00	2, 10	5.962	0.020
	10:00-12:00	2, 10	8.338	0.007
	13:00-15:00	2, 10	12.352	0.002
	15:00-17:00	2, 10	3.956	0.048

Table 4. Results of the 2010 daily collection round repeated measures ANCOVAs [fixed factor: treatment (managed vs. unmanaged), repeated measures factor: month, covariate: site pair] for the mean visitation rates of all visitors and individual taxonomic groups (V. *pensylvanica*, *A. Mellifera*, and *Hyleaus*).

Dependent Variable	Daily Collection Round	Interaction (Treatment & Time)		
		df	F	P
V. pensylvanica	7:00-10:00	2, 10	15.317	0.001
	10:00-12:00	2, 10	15.52	0.001
	13:00-15:00	2, 10	10.06	0.004
	15:00-17:00	2, 10	20.07	<0.001
A. Mellifera	7:00-10:00	2, 10	4.52	0.040
	10:00-12:00	2, 10	6.283	0.017
	13:00-15:00	2, 10	6.865	0.013
	15:00-17:00	2, 10	2.572	0.126
Hylaeus	7:00-10:00	2, 10	4.659	0.037
	10:00-12:00	2, 10	2.929	0.100
	13:00-15:00	2, 10	1.313	0.312
	15:00-17:00	2, 10	5.712	0.022
All Visitors	7:00-10:00	2, 10	1.037	0.390
	10:00-12:00	2, 10	1.336	0.306
	13:00-15:00	2, 10	1.935	0.195
	15:00-17:00	2, 10	0.9	0.437

Table 5. Results of the within and between year repeated measures ANCOVAs [fixed factor: treatment (managed vs. unmanaged), repeated measures factor: month, covariate: site pair] for the mean stigma contact rate for *A. mellifera* and *Hylaeus*.

Dependent Variable	Repeated Measures	Interaction (Treatment & Time)		
		df	F	P
A. mellifera	All Years	4, 20	10.102	<0.001
	2009	4, 20	9.374	0.028
	2010	4, 20	21.641	<0.001
Hylaeus	All Years	4, 20	4.207	0.012
	2009	4, 20	1.956	0.221
	2010	4, 20	4.765	0.035

Figures

Figure 1. Mean percent of observed visits at a site in which *V. pensylvanica*, *A. mellifera*, and *Hylaeus* experienced a given interaction outcome (W = winner, N = neutral, and L = loser) with a specific taxonomic group (*V. pensylvanica*, *A. mellifera, Hylaeus,* or Formicidae) prior to the annual *V. pensylvanica* treatments. The number of observed visits for each taxon are in parentheses. *Bars* means ± SE
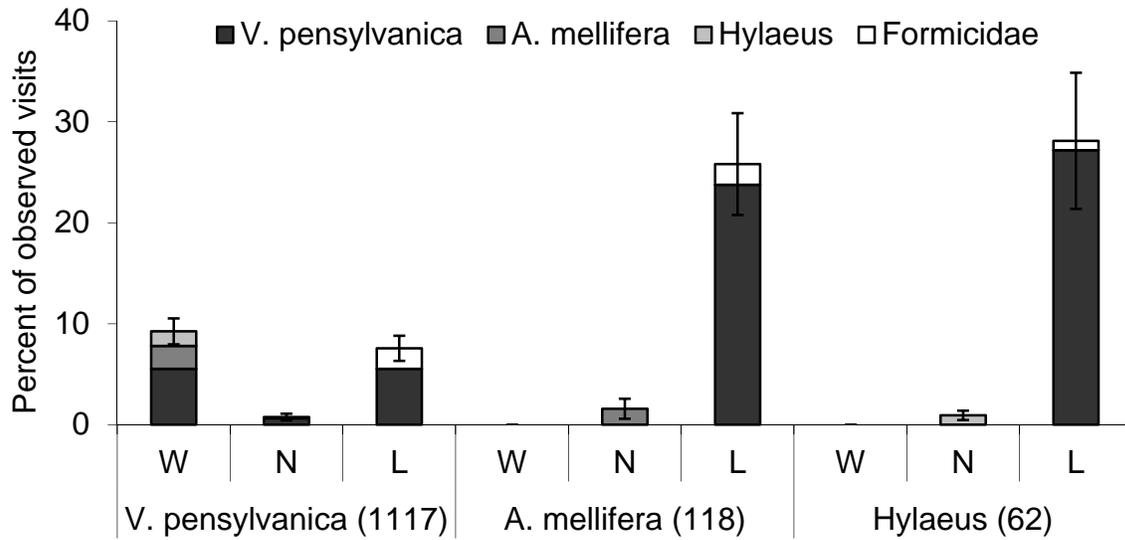
Figure 2. Percent of observed visits at a site in which (**a**) *A. mellifera* and (**b**) *Hylaeus* experienced a "loser" or "neutral" interaction outcome within the managed and unmanaged study sites pre and post the annual *V. pensylvanica* treatments. *Bars* means ± SE; *P < 0.05(from the two-sample t-tests)
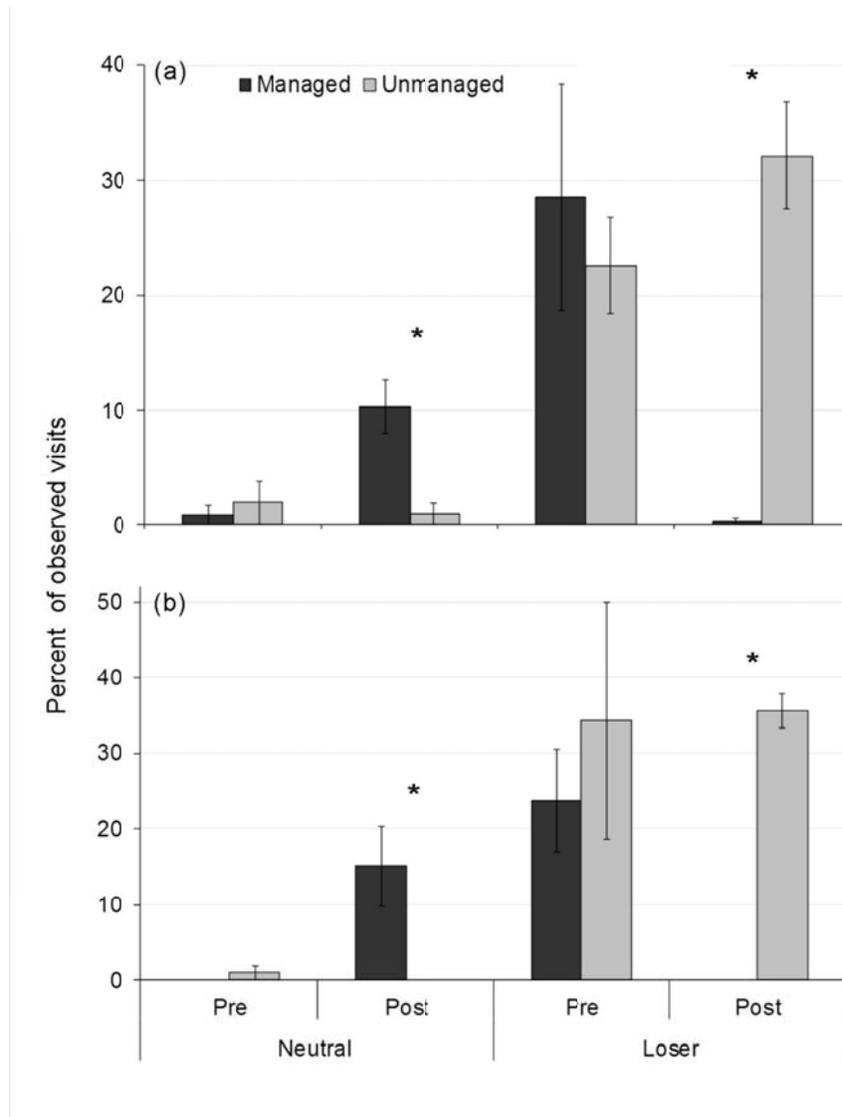
Figure 3. Mean (**a**) standing nectar crop (cal) and (**b**) percent of unexploited calories per flower, and the Monte Carlo simulation median for (**c**) standing nectar crop (cal ha^{-1}) and (**d**) 24-hr energy production (cal ha^{-1}) within the managed (-●-) and unmanaged (-○-) study sites during each sampling month in 2009 and 2010. Arrows indicate the timing of the annual *V. pensylvanica* treatment. *Bars* means + SE; *P < 0.05 (from the two-sample t-tests).
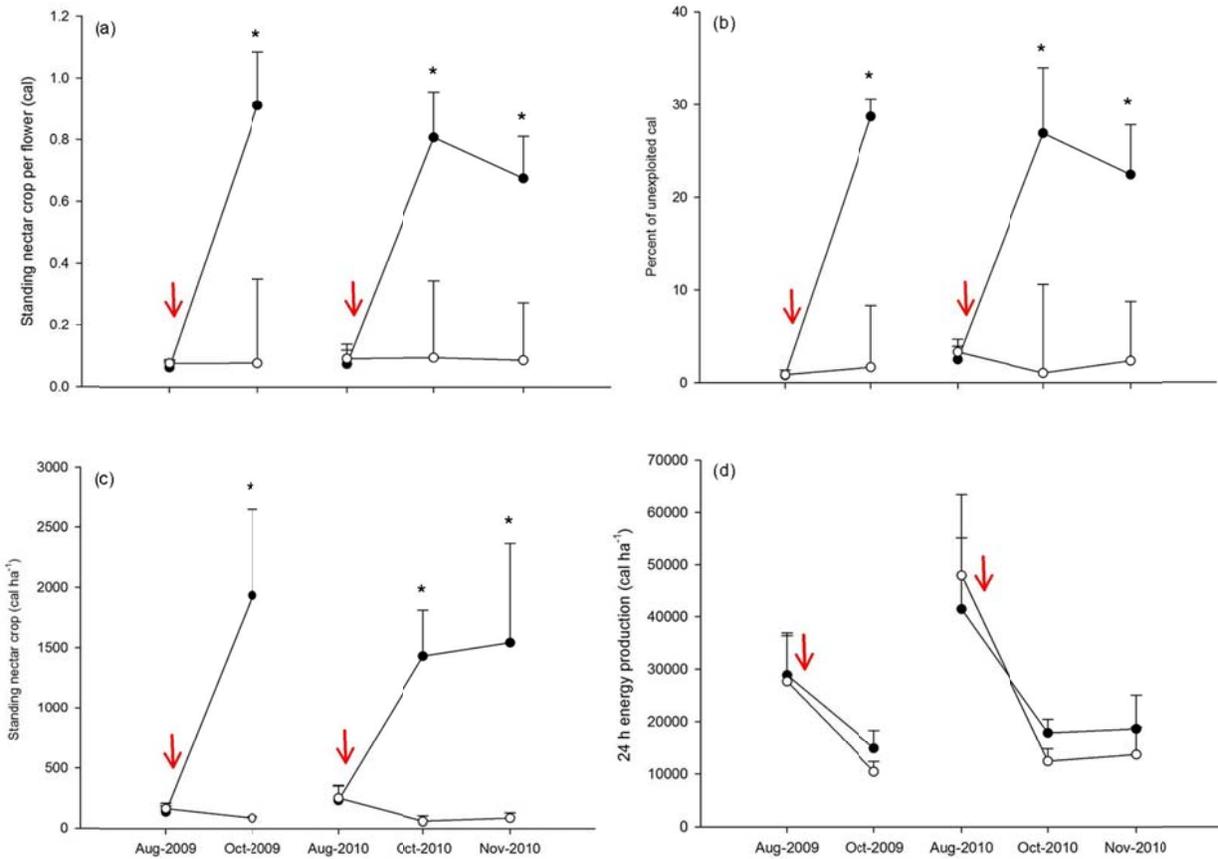
Figure 4. The line graphs represent the standing nectar crop at each daily collection rounds in 2010 (**a**) pre *V. pensylvanica* treatment, (**c**) 6 weeks and (**e**) 10 weeks post *V. pensylvanica* treatment within the managed (-●-) and unmanaged (-○-) study sites. The corresponding stacked-bar histograms (**b**, **d**, and **f**) show the individual visitation rates of *V. pensylvanica*, *A. mellifera*, and *Hylaeus* and the total visitation rate in the managed and unmanaged sites at each daily observation round. *Bars* means ± SE; *P < 0.05 (from the two-sample t-tests)
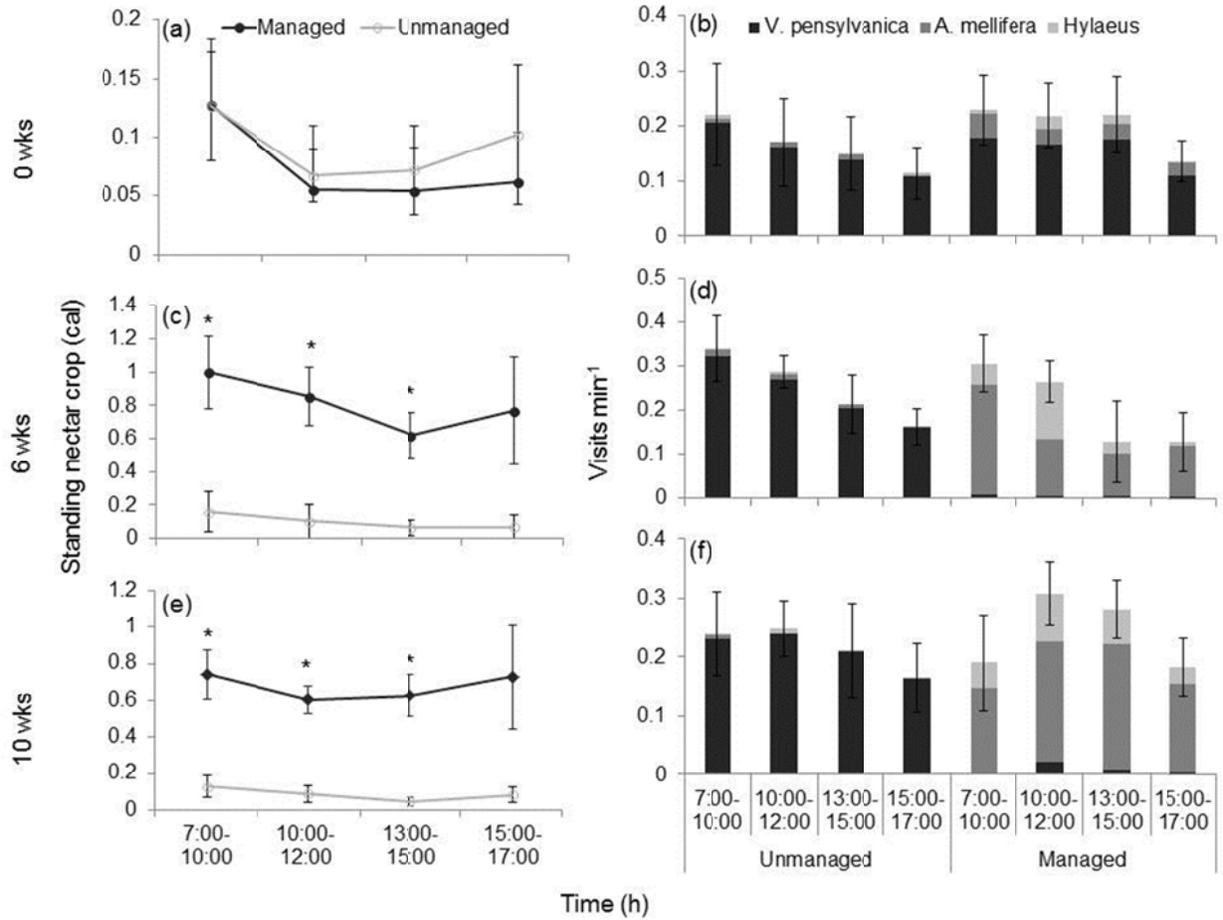
Figure 5. The mean percent of visited flowers at which each taxonomic group (*V. pensylvanica*, *A. mellifera*, and *Hylaeus*) collected nectar, collected pollen, and/or contacted the stigma. Letters denote significant differences between taxonomic groups for a given floral behavior (P < 0.05, post-hoc Tukey tests). *Bars* means ± SE
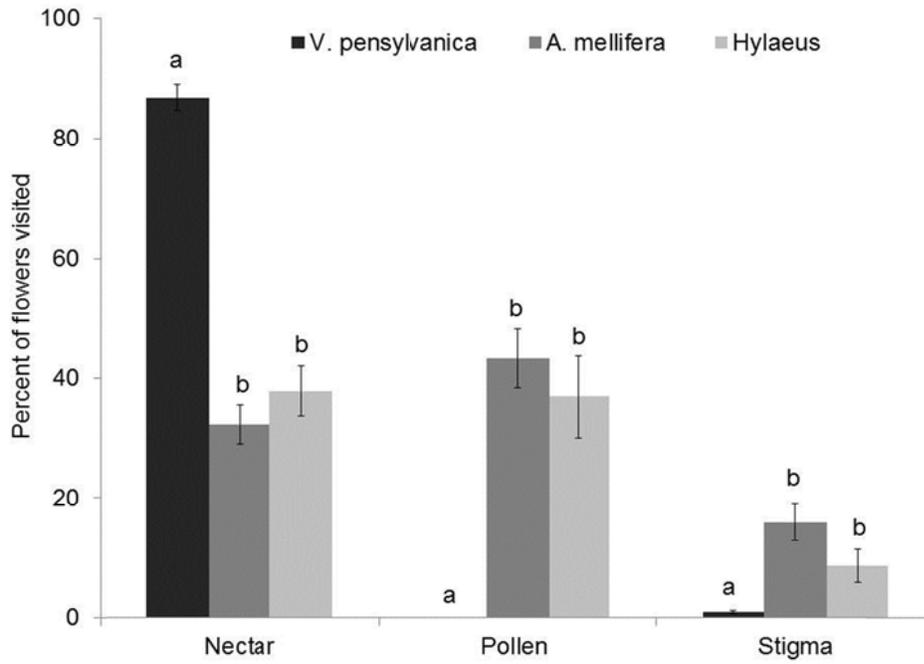
Figure 6. Mean stigmas contacted min^{-1} for (**a**) *A. mellifera* and (**b**) *Hylaeus* within the four managed (-●-) and unmanaged (-○-) study sites during each sampling month in 2009 and 2010. Arrows indicate the timing of the annual *V. pensylvanica* treatment. *Bars* means + SE; *$P < 0.05$ (from the two-sample t-tests)
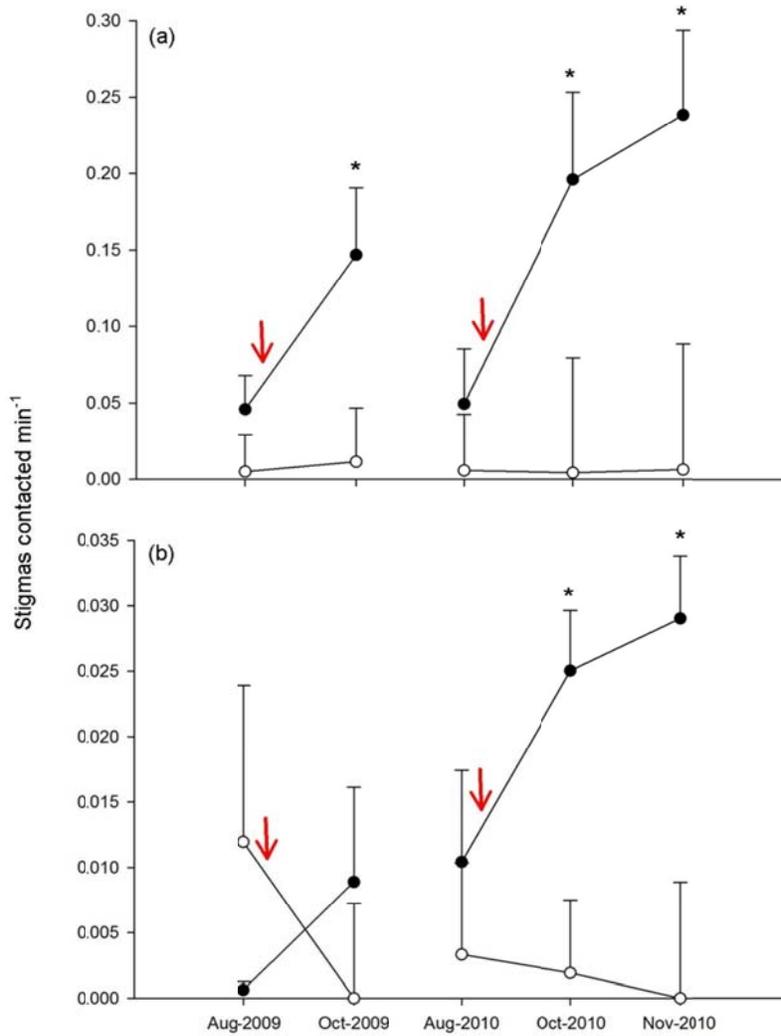
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