Competitive impacts of an invasive nectar thief on plant–pollinator mutualisms

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Abstract. Plant–pollinator mutualisms are disrupted by a variety of competitive interactions between introduced and native floral visitors. The invasive western yellowjacket wasp, *Vespula pensylvanica*, is an aggressive nectar thief of the dominant endemic Hawaiian tree species, *Metrosideros polymorpha*. We conducted a large-scale, multiyear manipulative experiment to investigate the impacts of *V. pensylvanica* on the structure and behavior of the *M. polymorpha* pollinator community, including competitive mechanisms related to resource availability. Our results demonstrate that *V. pensylvanica*, through both superior exploitative and interference competition, influences resource partitioning and displaces native and nonnative *M. polymorpha* pollinators. Furthermore, the restructuring of the pollinator community due to *V. pensylvanica* competition and predation results 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 pollinator community structure.

Key words: Apis mellifera, honey bee; bees; community structure; competition; Hawaii; Hylaeus spp.; invasive species; Metrosideros polymorpha; *mutualism; pollination; resource partitioning; Vespula pensylvanica.*

Introduction

Invasive species disrupt the structure and function of native ecosystems by displacing native species and establishing novel interactions (Hobbs et al. 2006). Competitively dominant invasive floral visitors are a threat to plant–pollinator mutualisms worldwide (Traveset and Richardson 2006), but an incomplete understanding of how they interact with native pollinators and how these interactions affect pollination services hinders the restoration of plant–pollinator mutualisms. To gain a better understanding of this pervasive threat, we performed a large-scale, multiyear 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). When exploitative and/or interference competitive mechanisms are predominantly asymmetrical, floral visitors are competitively displaced (Reitz and Trumble 2002). In a diverse floral landscape or during peak floral bloom, competition may be reduced due to resource abundance or potential for partitioning, whereas similar pollinator communities in simple floral landscapes or during off-peak portions of the season may not be able to partition

resources because of limited resources. 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 can override resource partitioning strategies, resulting in the competitive displacement of less dominant foragers (Gross and Mackay 1998, Lach 2008, Junker et al. 2010).

Invasive social insects alter the composition and functioning of plant–pollinator interactions in a variety of ways. They displace effective pollinators, replace extirpated native pollinators, or facilitate native or invasive plant–pollinator mutualisms (Traveset and Richardson 2006). The invasive western yellowjacket, *Vespula pensylvanica*, inhabits the Hawaiian Islands and its impacts on Hawaiian plant–pollinator mutualisms are multidimensional. *Vespula pensylvanica* is a generalist predator and scavenger that consumes native and introduced pollinators (Wilson and Holway 2010). Additionally, to satisfy the energy demand of adults and developing brood (Richter 2000), *Vespula* wasps both exploit (Moller et al. 1991) and aggressively defend (Thomson 1989, Grangier and Lester 2011) a variety of carbohydrate-rich resources (e.g., nectar, honeydew). Their competitive dominance and multiple impacts are augmented by the increased year-round population density that results from the formation of large perennial colonies (Wilson et al. 2009, Hanna et al.

2013a), 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 dominance 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 native bird (honeycreepers) and bee (*Hylaeus* spp.) floral visitors (Magnacca 2007, Banko and Banko 2009) may have granted *V. pensylvanica* access to the floral nectar of ʻōhiʻa lehua, *Metrosideros polymorpha*, the dominant endemic tree species across a diverse array of Hawaiian ecosystems. The native *M. polymorpha* floral visitors, in many areas, have been at least partially replaced by introduced bird (*Zosterops japonica*) and insect visitors (*Apis mellifera*, *V. pensylvanica*, and Formicidae).

To investigate the competitive mechanisms and impacts of *V. pensylvanica* on the plant–pollinator mutualisms of *M. polymorpha*, we experimentally removed *V. pensylvanica* populations in large multiyear 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 separate the effects of removing *Vespula* from the natural spatial and temporal variation in *Vespula* abundance. 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 asked 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 (Green 1979) to examine the competitive impacts of invasive *V. pensylvanica* on the pollinator community of *M. polymorpha* in 2009 and 2010. We haphazardly selected eight 9-ha study sites within seasonal submontane *M. polymorpha* woodland within Hawaii Volcanoes National Park between approximately 700 and 1100 m elevation (Hanna et al. 2011). The 9-ha study sites (300×300 m) were marked, and covered with a grid with cell sizes of 25×50 m. In the four removal sites, we used 0.1% fipronil chicken baits to reduce *V. pensylvanica* populations by 95% ± 1.2% (mean ± SE), and we maintained four sites as

experimental controls (Hanna et al. 2011). The suppression of the *V. pensylvanica* population within the removal sites actually extended beyond the 9-ha study site to ≥36 ha, as a result of the spatial extent of *V. pensylvanica* foraging (Hanna et al. 2011). We paired the removal and control sites to account for environmental variation (e.g., in 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 (i.e., biomass and nectar) important endemic Hawaiian tree species that has facultative interactions with a diverse array of species (Carpenter 1976, Gruner 2004). It occurs on all the main islands of the Hawaiian archipelago across a variety of climate zones and substrates from sea level to 2500 m elevation (Corn 1979). It flowers all year, with peak flowering from February to July (Ralph and Fancy 1995). Its open inflorescences 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 pollen limited (Carpenter 1976, Hanna et al. 2013b).

Phenology of M. polymorpha

We characterized the temporal and spatial variation of *M. polymorpha* phenology in 2009 and 2010 during the off-peak floral bloom (August–November) by recording and calculating the mean number of flowers per inflorescence ($N = 1114$), the number of inflorescences per tree ($N = 8417$), and the number of flowering trees within a 12.5 m radius of every 25×50 m study-grid intersection at each site per month.

Insect visitation

To determine how the behaviors and relative frequency of specific plant–pollinator mutualisms change through time in response to *V. pensylvanica* removal, we performed timed inflorescence observations ($N = 1869$) on randomly selected trees, simultaneously within the paired sites. Each observation round consisted of 10-min observations on 1–5 focal inflorescences on 5–8 trees for an average of 15.66 ± 0.9 observations per site (mean ± SE). In 2009, we conducted observation rounds at each site two weeks before (August) and six weeks after (October) *V. pensylvanica* removal. In 2010, to study *M. polymorpha* visitation patterns in more detail, we conducted observation rounds at each site during four time spans: 7:00–10:00, 10:00–12:00, 13:00–15:00, and 15:00–17:00 hours, two weeks before (August), and six weeks (October) and 10 weeks (November) after *V. pensylvanica* removal. Observations were only conducted during sunny or partly cloudy weather with wind speed < 2.5 m/s. For each visitor ($N = 5069$), we recorded: the species or lowest field-identifiable taxo-

nomic category, time on inflorescence, number of flowers visited, and behavior (pollen collection, nectar collection, and/or stigma contact) per flower. We calculated the mean visitation rate (visits/min) and floral behavior rate (behavior/min) per observation round per site for each taxonomic group. To compare the relative frequency of behaviors among visitors, we calculated the frequency per site with which each taxonomic group performed a specific behavior while visiting a flower.

Interference between Vespula and other floral visitors

To determine how the frequency and outcome of interference competition between *M. polymorpha* floral visitors changed through time in response to *V. pensylvanica* removal, we collected data on all observed interactions between floral visitors ($N = 447$) during the 10-min focal inflorescence observations. For each interaction, we recorded the taxonomic group of and outcome for each participant. We assigned each interaction to one of three outcomes: Winner (the visitor on the flower prevents an incoming visitor from occupying the flower or the incoming visitor remains on the flower after it makes the visitor occupying the flower leave); Neutral (both visitors remain on or leave the inflorescence); and Loser (the visitor leaves the inflorescence and the other visitor remains). To compare the frequency of interaction outcomes for each taxonomic group through time, we calculated the percentage of observed visits when each taxonomic group experienced an interaction outcome by site type per observation round (total number of a specific interaction outcome observed/total number of observed visits for that taxonomic group). We included the number of observed visits as a covariate to control for its potential effect on the likelihood of observing an interaction.

Resource exploitation

To determine how the *M. polymorpha* standing nectar crop and the proportion of unexploited nectar change through time in response to *V. pensylvanica* removal, 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 ($N = 222$), we randomly sampled five flowers within a randomly chosen open and bagged inflorescence ($N = 1114$) on the same tree. 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* removal. In 2010, we performed collection rounds coinciding with the four daily observation rounds conducted two weeks before and six and 10 weeks after *Vespula* removal. We measured the quantity of nectar within each flower using 1–50 µL fixed-capacity microcapillary tubes,

depending on the volume remaining, and the sucrose-equivalents of the nectar, using a handheld low-volume refractometer (Bellingham and Stanley, Lawrenceville, Georgia, USA). To calculate the energy value of the nectar (in joules), we calculated the amount of sucrose-equivalents (in mg) present per 1 µL of nectar, multiplied this value by the volume obtained, and assumed 16.736 J/mg sucrose (Carpenter 1976, Dafni et al. 2005). To compare the energy availability per flower within each site, we calculated the mean energy value of the standing nectar crop per flower, i.e., the number of joules present in an open flower at a given moment. To compare the energy consumption across sites, we calculated the mean percentage of unexploited nectar (energy value of the nectar remaining within open flower/energy value of bagged flower on the same inflorescence) ×100.

Simulations of M. polymorpha energetics

To estimate the site-level energy value of *M. polymorpha* nectar (J/ha) while accounting for the statistical error associated with each measured variable, we developed a Monte Carlo propagation of error simulation. The input to the simulation included the mean and variance for the following: (1) standing nectar crop per flower (J) or 24-h floral energy production (determined from diurnal and nocturnal nectar production data); (2) number of flowers per inflorescence; (3) number of inflorescences per tree; and (4) number of flowering trees per hectare within each site. The simulation randomly selected a number for each input variable from a normal distribution with a site-specific mean and variance for that variable and multiplied all of the input values to obtain a site-level estimate. We used normal probability distributions for all variables because none were significantly different from normal using goodness-of-fit tests; to prevent negative values, the distributions were bounded at their lower ends by zero. We ran the simulation for 10 000 repetitions per collection round at each site, both for standing nectar crop and 24-h energy production, which produced estimation errors of 4.28% ± 0.13% and 3.80% ± 0.07%, respectively (mean ± SE). Because output distributions were skewed, we used median instead of mean values for the corresponding analyses (Winfree et al. 2007). The simulations were performed in Microsoft Excel 2010.

Data analysis

We performed blocked repeated-measures ANOVAs to analyze the within- and between-year variation in four dependent variables: the mean standing nectar crop and percentage of unexploited nectar per flower, and the median standing nectar crop and 24-h production of J/ha from the Monte Carlo simulations. We used *V. pensylvanica* treatment (removal and control) as a fixed factor, month as the repeated-measures factor, and site pair as the blocking factor. To analyze the variation in

nectar availability and floral visitation at different discrete time periods throughout the day, we performed identical analyses for the mean floral standing nectar crop, percentage of unexploited nectar, total visitation rate, and the visitation rates for selected taxonomic groups at each daily collection/observation round in 2010. 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-measures factor.

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* J/ha data; and a (log + 1) transformation to normalize the visitation rate, stigma contact rate, and relative visitor behavior data. To correct for Type I errors, we used Bonferroni corrections for multiple comparisons. We conducted all statistical analyses in SYSTAT 11 (SYSTAT 2004).

RESULTS

Phenology of M. polymorpha

Across sites and monitoring months there were 11.82 ± 0.41 flowers per inflorescence ($N = 1114$), 14.08 ± 0.40 inflorescences per tree ($N = 222$), and 23.38 ± 2.23 flowering trees/ha ($N = 196$); all values are given as mean ± SE. There was a significant difference (criterion for significance throughout is $P < 0.05$) between the site pairs, the blocking factor, and monitoring months for the number of flowers per inflorescence and the number of flowering trees per hectare, but not for the number of inflorescences per tree (Appendix A). There was an interaction between site pair and monitoring month for all the dependent variables (Appendix A). There were no significant differences between the *Vespula* removal and control sites ($P \geq 0.351$ 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.

Interference between Vespula and other floral visitors

Participants in the interactions included introduced *V. pensylvanica*, *A. mellifera*, and Formicidae (*Anoplolepis gracilipes*, *Linepithema humile*, and *Pheidole megacephala*) and native *Hylaeus* spp. The winner and aggressor of all the observed interactions was either *V. pensylvanica* or Formicidae, both of which were also observed preying on floral visitors directly from *M. polymorpha* flowers. There were no significant differences between removal and control sites in the percentage of visits when each interaction occurred before *V. pensylvanica* removal (Fig. 1), but after *V. pensylvanica* removal, both *A. mellifera* and *Hylaeus* spp. encountered a significantly higher percentage of "neutral" and a significantly lower
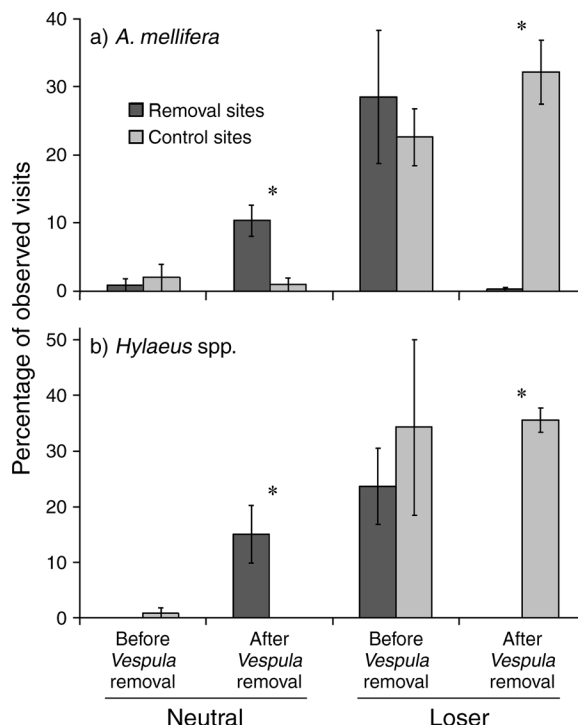

FIG. 1. Percentage of observed visits (mean ± SE) to *Metrosideros polymorpha* flowers at a study area in which (a) *Apis mellifera* and (b) *Hylaeus* spp. experienced a "neutral" or "loser" interaction outcome within the removal sites and control sites before and after removal of *Vespula pensylvanica*, the invasive western yellowjacket wasp. We used a Before–After, Control–Impact experimental design to examine the competitive impacts of invasive *V. pensylvanica* on the pollinator community of *Metrosideros polymorpha* in Hawaii Volcanoes National Park, Hawaii, USA.

* $P < 0.05$ (from the two-sample t tests).

percentage of "loser" outcomes in the removal sites compared to the control sites (Fig. 1). The change in the percentage of "neutral" and "loser" interaction outcomes was significantly different after *V. pensylvanica* removal, based on two-way ANCOVAs: fixed factors, *V. pensylvanica* treatment and time (pre- and post-*V. pensylvanica* removal); covariate, total number of observed visits; "neutral" interaction outcomes (for *A. mellifera*, $F_{1,11} = 5.713$, $P = 0.036$; for *Hylaeus*, $F_{1,11} = 12.596$, $P = 0.005$) and "loser" interaction outcomes (for *A. mellifera*, $F_{1,11} = 13.387$, $P = 0.004$; for *Hylaeus*, $F_{1,11} = 13.814$, $P = 0.003$). Prior to *V. pensylvanica* treatment, *A. mellifera* and *Hylaeus* encountered and lost an interspecific interaction during 25.56% ± 5.05% and 27.93% ± 6.74% of their observed visits, respectively (mean ± SE). Interactions with *Vespula* accounted for 96.88% ± 3.13% and 96.18% ± 4.07% of the interactions lost by *A. mellifera* and *Hylaeus*. Prior to *V. pensylvanica* treatment, *Vespula* wasps encountered and lost an interaction during 7.56% ± 1.16% of their observed visits, 78.91% ± 8.4% of which were to other *V. pensylvanica* and 21.09% ± 8.40% to Formicidae. All
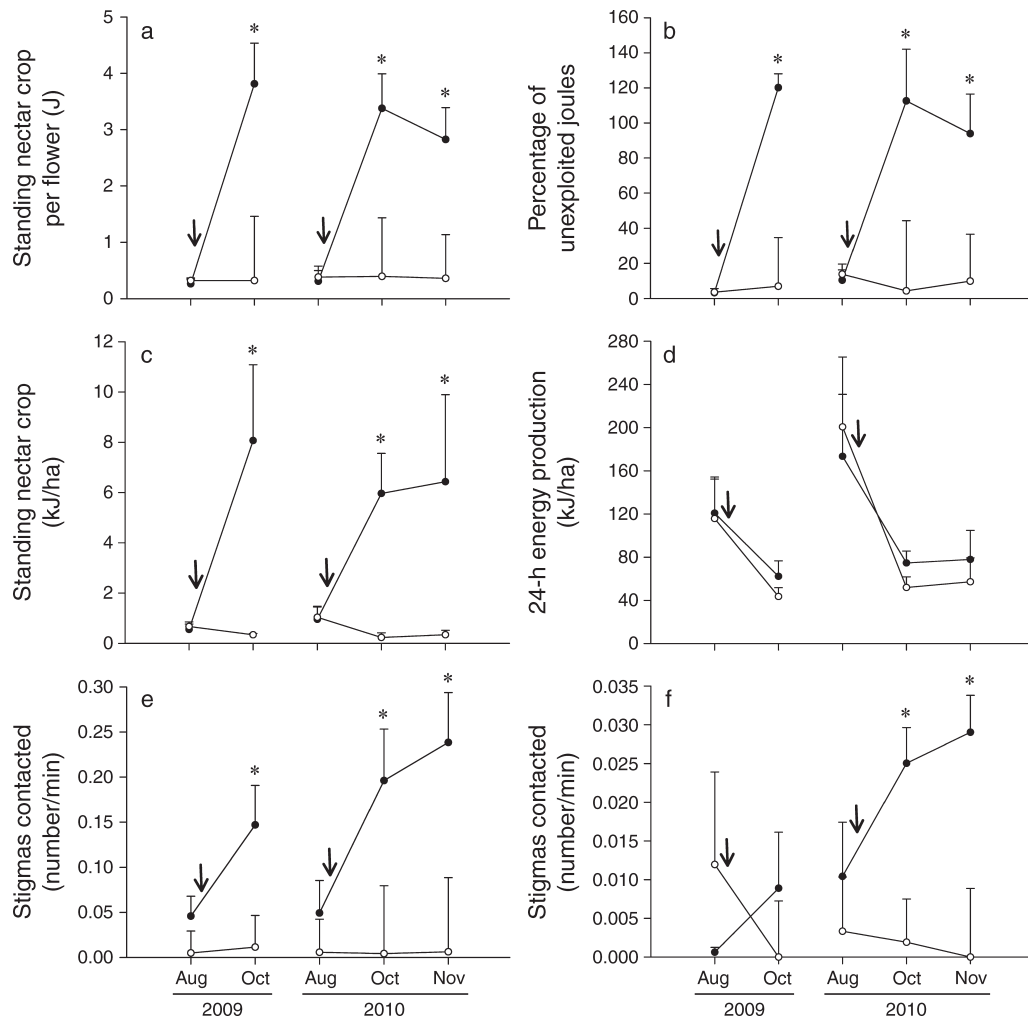
FIG. 2. For *Metrosideros polymorpha*, means for (a) standing nectar crop per flower and (b) percentage of unexploited joules per flower. From the Monte Carlo simulation, medians for (c) standing nectar crop and (d) 24-h energy production, and the mean number of stigmas contacted per minute for (e) *A. mellifera* and (f) *Hylaeus* spp. within the removal (solid circles) and control (open circles) study sites during each sampling month in 2009 and 2010. Arrows indicate the timing of the annual *V. pensylvanica* removal. Error bars are +SE.
* $P < 0.05$ (from the two-sample t tests).

neutral interactions among visitors observed prior to *V. pensylvanica* treatment were intraspecific.

Resource exploitation

Variation in the standing nectar crop and percentage of unexploited nectar significantly differed between the *V. pensylvanica* removal and control sites within and across years (Appendix B) and for each daily collection round, with the exception of the 15:00–17:00 hours collection round in 2010 (Appendix C). The post-removal standing nectar crop and percentage of unexploited nectar were significantly higher in the *V. pensylvanica* removal sites in 2009 and 2010 (Fig. 2a, b) and for each of the daily collection rounds in 2010, with the exception the 15:00–17:00 collection round (Fig. 3c, e). Prior to *V. pensylvanica* treatment, however, there

were no significant differences between the removal and control sites for any of the daily collection rounds (Fig. 3a).

Simulations of M. polymorpha *energetics*

Variation in the median standing nectar crop significantly differed between the removal and control sites within and across years (Fig. 2c; Appendix B). Prior to annual *V. pensylvanica* removal, there was no significant difference in the standing nectar crop, whereas it was significantly higher in the removal sites at all post-removal time periods (Fig. 2c). There was a significant difference between site pairs and monitoring months in the median 24-h energy production of *M. polymorpha* (Fig. 2d; Appendix A), but there was no significant difference between the *V. pensylvanica* removal and
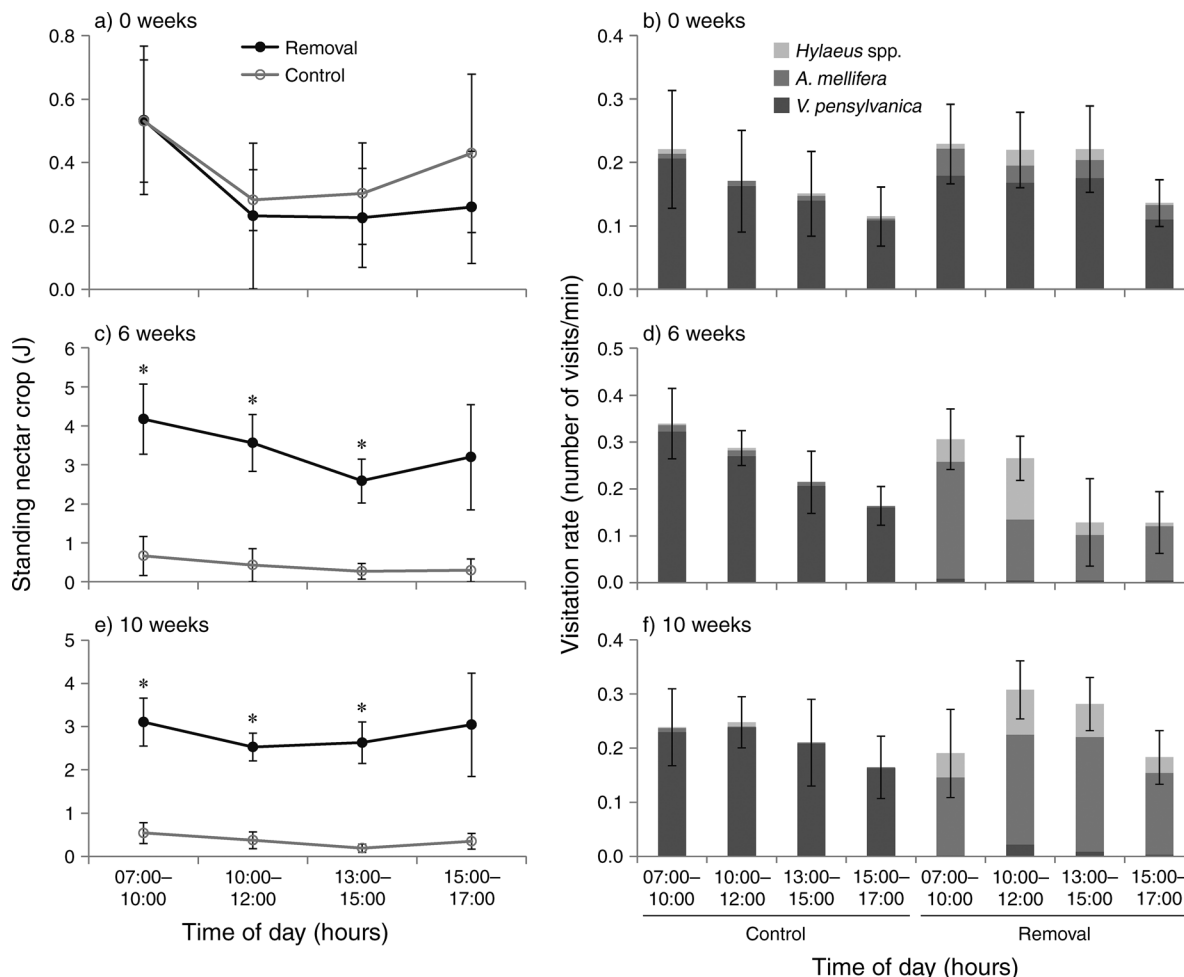
Fig. 3. The line graphs represent the standing nectar crop of *M. polymorpha* (means ± SE) from multiple collection rounds during each day in 2010 (a) pre-*V. pensylvanica* removal and at (c) 6 weeks and (e) 10 weeks post-*V. pensylvanica* removal within the removal (solid circles) and control (open circles) study sites. The corresponding stacked-bar histograms (b, d, f) show the individual visitation rates (means ± SE) of *V. pensylvanica*, *A. mellifera*, and *Hylaeus* spp. and the total visitation rate in the removal and control sites at each corresponding daily observation round.

* $P < 0.05$ (from the two-sample *t* tests).

control sites within and across years (Fig. 2d; Appendix B).

Insect visitation

Variation in the mean visitation rate for all visitors was not significantly different between the removal and control sites for any of the daily collection rounds within 2010, whereas variation in the mean visitation of *V. pensylvanica* was significantly different for all of the daily collection rounds (Appendix D). After *V. pensylvanica* removal, the visitation rates of *V. pensylvanica* dropped in the removal compared to the control sites by an average of 95.43% ± 1.99% (mean ± SE) in the daily collection rounds (Fig. 3d, f). Conversely, the visitation rates of *A. mellifera* and *Hylaeus* spp. increased in the removal sites by an average of 1611.13% ± 535.32% and 334.55% ± 86.11%, respectively (Fig. 3d, f). Correspondingly, the variation in the *A. mellifera* and *Hylaeus*

spp. mean visitation rates was significantly different between the removal and control sites for three and two of the daily collection rounds, respectively (Appendix D). 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* spp. ($y = 0.000324 - 0.0555x$, $P < 0.001$, $r^2_{adj} = 0.460$). The visitation rate of all visitors was affected by time within the day (RM-ANOVA, $F_{3, 198} = 8.547$, $P < 0.001$), but there were no differences in the daily activity patterns among different visitor groups (taxonomic group × time of day RM-ANOVA, $F_{6, 198} = 1.735$, $P = 0.115$) (Fig. 3).

Floral visitor behavior

The *M. polymorpha* visitors differed in the proportion of flowers at which they performed specific behaviors

(ANOVA: for pollen collection, $F_{2,84} = 86.005$, $P < 0.001$; for nectar collection, $F_{2,84} = 59.491$, $P < 0.001$; for stigma contact, $F_{2,84} = 14.426$, $P < 0.001$). *Vespula pensylvanica* collected nectar at a significantly higher proportion of flowers (post hoc Tukey test, $P < 0.001$ in both cases), whereas *A. mellifera* and *Hylaeus* spp. collected pollen ($P < 0.001$ in both cases) and contacted the stigma ($P < 0.038$ in both cases) at a significantly higher proportion of flowers. There was a significant interaction between *V. pensylvanica* treatment (removal and control) and month for the relative proportion of *A. mellifera* nectar- to pollen-foragers (proportion of flowers foraged for nectar/proportion of flowers foraged for pollen) in 2009 (two-way ANOVA, $F_{2,15} = 12.29$, $P = 0.001$) and 2010 (two-way ANOVA, $F_{2,15} = 12.29$, $P = 0.001$). There were no significant differences in the relative proportion of *A. mellifera* nectar- to pollen-foragers between the removal and control sites prior to *V. pensylvanica* removal, but the relative proportion of nectar- to pollen-foragers was significantly higher in the removal sites in all time periods after removal (two-sample t test, $P \leq 0.01$ 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 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% (mean ± SE) in the removal sites after *V. pensylvanica* removal, but there was no significant interaction between *V. pensylvanica* treatment (removal and control) and month (two-way ANOVA, $F_{2,11} = 1.425$, $P = 0.282$).

Pollen-foragers were more likely to contact the stigma than were nectar-foragers. *Apis mellifera* (Wilcoxon signed-rank test, $Z = 4.433$, $P < 0.001$) and *Hylaeus* (Wilcoxon signed-rank test, $Z = 3.463$, $P = 0.001$) pollen-foragers were significantly more likely to contact the stigma than were nectar-foragers. The rate of stigma contact increased in the removal sites following *V. pensylvanica* removal. The variation in the mean rate of stigma contact for *A. mellifera* and *Hylaeus* differed significantly between the *V. pensylvanica* removal and control sites within and across treatment years, except for *Hylaeus* in 2009 (Appendix E). Prior to annual *V. pensylvanica* removal, there were no significant differences between the removal and control sites in the mean rate of *A. mellifera* and *Hylaeus* stigma contact, whereas they were significantly higher in the removal sites at all post-removal periods, except for *Hylaeus* in 2009 (Fig. 3e, f).

DISCUSSION

The large-scale removal of *V. pensylvanica* significantly reduced levels of interference and resource exploitation that *M. polymorpha* visitors experienced and, as a consequence, directly impacted their foraging behavior and indirectly impacted the pollination of *M. polymor-*pha. The removal of *V. pensylvanica*, when compared to control sites, resulted in a significant increase in the visitation rates of effective bee pollinators (e.g., introduced *Apis mellifera* and native *Hylaeus* spp.) and in the fruit production of *M. polymorpha* (Hanna et al. 2013b). *Apis mellifera*, following the removal of *V. pensylvanica*, appears to be acting as a substitute pollinator for *M. polymorpha*, replacing extinct or threatened bird species and *Hylaeus* species in our study system.

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; see Plate 1). *Vespula* aggressively patrolled *M. polymorpha* floral nectar, physically removed and, during several observations, directly preyed upon *A. mellifera* and *Hylaeus* from *M. polymorpha* inflorescences. Interference (Primack and Howe 1975) and predation (see Romero et al. 2011) can result in the behavioral avoidance of flowers by foragers. Although *A. mellifera* and *Hylaeus* are known from the diets of *Vespula* in Hawaii (Wilson and Holway 2010), the significant increase in *A. mellifera* and *Hylaeus* visitation rates following the removal of *V. pensylvanica* was probably a behavioral response to removal, given that the time frame was shorter than the time required for populations of *A. mellifera* and *Hylaeus* to increase (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* also exerted a strong suppressive effect on *Apis* (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 energy profit for *V. pensylvanica*, but not for other species of insects (Willmer and Corbet 1981). *Vespula* systematically consumes nectar at the base of each floral cup within an inflorescence, leaving a negligible standing nectar crop at both the flower (<0.1 μL) and landscape level (<2510.4 J/ha). The removal of *V. pensylvanica*, at a scale equivalent to the perception of foragers, resulted in increases in nectar availability and 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 (Inouye 1978, Pleasants 1981, Brosi and Briggs 2013). Consequently, following *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 an ecosystem's susceptibility to invasion (Shea and Chesson 2002, Cleland et al. 2004) by impacting the strength of competitive processes (Schmitt and Holbrook 1986). The floral phenology of *M. polymorpha* resulted in a significant decrease in nectar

PLATE 1. *Vespula pensylvanica* at the base of a *M. polymorpha* flower. Photo credit: C. Hanna.

production (J/ha) from August to October 2009 and August to November 2010 (Fig. 2d). As a result, the standing nectar crop (J/ha) decreased in the control sites; however, in the removal sites the standing nectar crop significantly increased relative to pre-*Vespula* removal. Despite the natural decrease in nectar at this time due to *M. polymorpha* phenology, 26.70% ± 3.10% of the joules per flower (mean ± SE) in *M. polymorpha* was unexploited after *V. pensylvanica* wasps were removed. The unconsumed nectar could be a consequence of the inability of the remaining forager populations to reach equilibrium within the experimental time frame, or it could be due to the extinctions and/or declines of other important native Hawaiian pollinators that would have also exploited this nectar source, such as endemic Hawaiian honeycreepers (Scott et al. 1988). These results evoke a future avenue of research examining the lack of competition between *Apis mellifera* and *Hylaeus* for *M. polymorpha* nectar, and possibly nectar in general, when *V. pensylvanica* are absent.

The competitive impacts of *V. pensylvanica* on the *M. polymorpha* forager guild caused the species within the guild to partition their energy resources to minimize the overlap of their ecological niches (Schoener 1974).

Floral resource partitioning occurs 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) and intrinsic (e.g., competition, predation, resource availability) 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 largely responsible for the patterns of forager activity at the beginning of the day, whereas resource availability determines 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. 3a, 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 displaces native floral visitors (Roubik 1978, Gross and Mackay 1998, Dupont et al. 2004), but the population-level impacts have rarely been documented (Thomson 2004). The inability of the less competitive members of the *M. polymorpha* visitor guild to partition and acquire critical energy 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 probably results in a lower net energy return for *A. mellifera* and *Hylaeus* foragers and their developing larvae. Although our experimental study did not measure the impact of *V. pensylvanica* competition on *A. mellifera* and *Hylaeus* reproduction, experimental data on forager abundances 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 the wasps depleted nectar without contacting the floral stigma or contributing to floral pollination (Hanna et al. 2013b). 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 overall visitation rate; thus, the floral stigma contact rates of *A. mellifera* significantly increased. 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 et al. 2013b).

Introduced *Vespula*, ants, and bees 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* competitively displace legitimate *M. polymorpha* pollinators (Lach 2008, Junker et al. 2010, Wilson and Holway 2010). Invasive ants have a neutral impact (Junker et al. 2010) and *V. pensylvanica* has a negative impact on *M. polymorpha* pollination (Hanna et al. 2013b). The grouping of ant species in the analysis may have impacted our results regarding the competitive impact of introduced ants, because the three species of introduced ants within our study sites (*A. gracilipes*, *L. humile*, and *P. megacephala*) have contrasting effects on *M. polymorpha* pollinators, particularly *Hylaeus* (Lach 2005, 2008). Thus, future pollination studies should determine the species identity of all ants observed. In our study, invasive ants successfully defended *M. polymorpha* floral resources from *V. pensylvanica*, but the low frequency of ant encounters (e.g., ants were present on only 10.83% ± 1.84% of inflorescences; mean ± SE), their patchy distribution, and the superior mobility of *V. pensylvanica* enabled *V. pensylvanica* to compromise *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 substitute pollinator for *M. polymorpha*, possibly replacing extinct or threatened bird and *Hylaeus* species in our study system (Junker et al. 2010, Hanna et al. 2013b). Similarly, in other disturbed ecosystems that lack native pollinators, *A. mellifera* contributes positively to the pollination of native plants (Dick 2001), but its community-wide effects and modification to the evolutionary trajectory of plant–pollinator mutualisms need to be further examined because their impact on native flora and fauna varies depending on the ecological and evolutionary context (Butz Huryn 1997, Traveset and Richardson 2006). 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 removal (Zavaleta et al. 2001).

Our results demonstrated that *V. pensylvanica*, through both superior exploitative and interference competition, displaced native and nonnative *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 findings 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.

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SUPPLEMENTAL MATERIAL

Appendix A

Results of the two-way ANOVAs (fixed factors: site pair and month) for mean number of flowers per inflorescence, inflorescences per tree, flowering trees per hectare, and the Monte Carlo simulation median 24-h energy production (*Ecological Archives* E095-141-A1).

Appendix B

Results of within- and between-year blocked repeated-measures ANOVAs (fixed factor is treatment [removal vs. control], repeated-measures factor is month, blocking factor is site pair) for mean standing nectar crop and percentage of unexploited energy per flower and the Monte Carlo simulation median standing nectar crop and 24-h energy production (*Ecological Archives* E095-141-A2).

Appendix C

Results of the 2010 daily collection round blocked repeated-measures ANOVAs (fixed factor is treatment [removal vs. control], repeated-measures factor is month, blocking factor is site pair) for mean percentage of unexploited energy and standing nectar crop per flower (*Ecological Archives* E095-141-A3).

Appendix D

Results of the 2010 daily collection round blocked repeated-measures ANOVAs (fixed factor is treatment [removal vs. control], repeated-measures factor is month, blocking factor is site pair) for mean visitation rates of all visitors and individual taxonomic groups (*Vespula pensylvanica*, *Apis mellifera*, and *Hyleaus* spp.) (*Ecological Archives* E095-141-A4).

Appendix E

Results of the within- and between-year blocked repeated-measures ANOVAs (fixed factor is treatment [removal vs. control], repeated-measures factor is month, blocking factor is site pair) for mean stigma contact rate for *A. mellifera* and *Hyleaus* spp. (*Ecological Archives* E095-141-A5).