

AN INDEPENDENTLY EVOLVED MUTUALISM AMONG ANTS (MYRMICINAE *PHEIDOLE TERRAMORIUM* AND *PARATRECHINA LONGICORNIS*), SEA HIBISCUS (*HIBISCUS TILIACEUS*) AND HEMIPTERA: AN INVADER-INVADER MUTUALISM AND INVASION MELTDOWN

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Abstract. The role of mutualisms among invasive species in facilitating invasions remains relatively unexplored. Yet such interactions have high potential to alter intact community composition and function due to their positive fitness effects on the species involved. The following study explores an interaction that evolved independently among naturalized hibiscus and invasive ants and Hemiptera that colonized the island of Mo'orea, French Polynesia centuries apart. For this study, a geographic survey was conducted across 7 plots, which revealed the relationship to be present across a broad range of habitats. Manipulative field experiments were also ran in order to classify the association as a mutualism, parasitism or commensalism. These experiments quantified changes in abundances and behaviors of ants and Hemiptera in response to different availabilities of sugar resources to ants. Results from these field experiments support the hypothesis that the relationship is indeed a mutualism, where all players receive a net benefit from their association with one another. The resultant finding that this is a geographically widespread mutualism among invasive species contributes to the study of invasion meltdowns. The discovery of the success of this invader-invader mutualism in an intact ecosystem contributes to a growing body of research on the role of synergistic effects of multiple species invasions in invasion meltdowns.

Key words: *mutualism; arthropods; Myrmicinae Pheidole terramorium; Paratrechina longicornis; Hibiscus tiliaceus; facilitation; invasion meltdown; Mo'orea; French Polynesia*

INTRODUCTION

Mutualist relationships are geographically prevalent and evolutionarily persistent interactions that have historically enjoyed the dedicated focus of the scientific community (Douglas 2008; Bronstein 1998). They can be defined by cooperation among species that results in increased inclusive fitness for all species involved (Bronstein 1998; Leigh 2010). These interactions are ecologically and evolutionarily important as they have the potential to impact species richness, abundance, and relationships at the community level (Byk and Del-Claro 2011). The prevalence of ant-plant mutualisms makes them particularly important in this respect, as up to one third of all woody plant species in a given habitat tend to be involved in an interaction with ants (Bronstein et al. 2006). In the context of the ecology of tropical food webs and communities, ant-plant mutualisms have been shown to have a significant impact as an important structuring force (Heil and McKey 2003). This is especially true when ant-plant interactions

impact resource allocation and consumption, making them influential in driving species interactions and biodiversity in their communities (Byk and Del-Claro 2011). In the current study, I aimed to evaluate the geographic extent of an ant-plant interaction on the island of Mo'orea, French Polynesia and assess whether this interaction may qualify as a mutualism.

In this study, I examined an interaction that involves ants (*Myrmicinae Pheidole terramorium* and *Paratrechina longicornis*), sea hibiscus (*Hibiscus tiliaceus*) and various species of sap-sucking, honeydew producing Hemiptera. The relationship among these species has often been described as a mutualism in other geographic regions (Styrsky and Eubanks 2007). In these cases, the plant provides the ant with carbohydrate-rich nectar secreted from extrafloral nectaries (EFNs) (Martinez et al. 2011), located on the underside of plant leaves, in exchange for defense against herbivores (Bronstein 1998; Pringle et al. 2011). However, the ant also defends Hemiptera herbivores feeding on these plant leaves from predators, increases

their reproductive output by caring for their offspring, and prevents growth of black sooty mold through removal of sugar-rich honeydew produced by Hemiptera (Bach 1991). The ant thus increases Hemiptera inclusive fitness through these behaviors, which are collectively referred to as Hemiptera tending. The ants' harvest of carbohydrate-rich honeydew from Hemiptera provides nutritional supplements to the ants, which increase colony fitness (Byk and Del-Claro 2011). The plant may receive indirect benefits from the interaction between ants and Hemiptera, as Hemiptera presence tends to promote increased ant defense against more harmful herbivores (Styrsky and Eubanks 2007; Hembry et al. 2006) (Fig. 1). The interaction among these three players may thus qualify as a mutualism structured by a set of competing costs and benefits that is vulnerable to exploitation by any one of the players. Though the presence of these three players on Mo'orea suggests a similar interspecies interaction is at work, no studies have yet been conducted to assess the characteristics of this relationship.

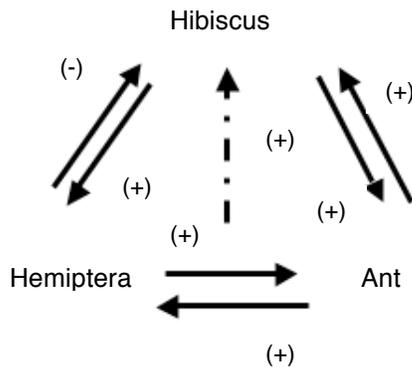


FIG. 1. Illustration of the network of competing costs and benefits that structure the ant-*Hibiscus*-Hemiptera mutualism. Arrows point to player receiving effect. Solid arrows represent a direct effect and dashed arrows represent an indirect effect. Plus signs (+) represent a positive fitness effect; minus signs (-) represent a negative fitness effect.

There is a unique opportunity in studying this relationship on Mo'orea because it may be the product of coevolution among naturalized *Hibiscus* and two invasive insects that arrived centuries apart. This could provide support for the ecological strength of this interaction despite variation in environmental conditions or time of colonizations. Furthermore, it could provide the opportunity to study the impact

of a mutualism among different invasive species on the species' ability to spread through a novel habitat. Ants were introduced to Mo'orea no earlier than the time of Captain Cook's first voyage between 1768 and 1771 (Wilson and Taylor 1967). *Hibiscus*, however, was likely introduced by Polynesians, who colonized the Society Islands between 1025 and 1120 (Wilmshurst et al. 2011). Thus, a temporally and spatially ubiquitous relationship (Bronstein 1998) may have independently evolved again among species introduced approximately 600 years apart. It has been suggested that understanding how mutualisms evolve independently in novel environments might facilitate understanding of how they will react to global changes (Hembry et al. 2011). Furthermore, the ability of mutualisms to improve habitat suitability and attractiveness means establishment of one nonnative player may facilitate invasion by subsequent players, in a phenomenon referred to as invasion meltdown (Green et al. 2011). This is a relatively unexplored issue in regards to invader-invader interactions. The effects of this process may also intensify with climate change (Altieri et al. 2010), making it increasingly important to understand.

In the current study, I evaluated the following aspects of this ant-Hemiptera interaction on Mo'orea by (1) sampling different habitats in order to determine the geographic prevalence of this interaction on the island and (2) implementing field experiments to assess the balance of costs and benefits that underlie this interaction so that it may be characterized as a mutualism, commensalism or parasitism. Geographic range of the interaction is important to examine as invasions are considered successful only once they have spread throughout a novel habitat (Mack et al. 2007). The interaction would therefore only be relevant to the study of facilitation if it had established throughout a geographically widespread region. I hypothesized that the relationship is widespread across a variety of habitats on Mo'orea, regardless of environmental conditions. The co-occurrence of these species in a variety of habitats would not, however, constitute sufficient evidence that their relationship is a mutualism. I therefore conducted field experiments to evaluate the extent to which the species are linked by a reciprocal exchange of services that increase one another's fitness. I hypothesized that the removal of services such

as nectar provisioning would push ants to exploit the relationship, thereby providing support for the classification of this interaction as a mutualism. In contrast, I hypothesized that increasing nectar availability to ants should enhance anti-herbivore defense provided by the ant for hibiscus. Results from this study would provide evidence for the prevalence of this interaction and its characterization as a mutualism on the island of Mo'orea. The qualification of the aforementioned relationship as a mutualism, on Mo'orea may allow it to serve as a model system for research on the impacts of invader-invader mutualisms on invasion facilitation and meltdowns.

METHODS

Study site

I selected plots in three spots along the Belvedere trail (plots 1-3 at 17°32'19.89"S 149°49'36.65"W, 17°32'20.70"S 149°49'35.88"W, 17°32'21.93"S 149°49'35.84"W, respectively), at three spots along the road up to the Belvedere trailhead (plots 4-6, at 17°31'11.92"S 149°50'47.36"W, 17°31'26.07"S 149°50'23.99"W, 17°30'54.68"S 149°51'15.98"W, respectively), and at one spot on Cook's Bay (plot 7, 17°29'28.27"S 149°49'40.68"W) on the island of Mo'orea in French Polynesia. Each plot contained 15 branches. I used plots on the Belvedere trail in manipulative nectar availability studies. The other plots I used in conjunction with the field experiment plots to assess the geographic range of the association. I selected plots in areas with open canopy and stands of young branches of hibiscus. Branches within plots originated from the same hibiscus plant and were of roughly the same height (height and width at 10 cm served as a proxy for branch age). This was done in the interest of minimizing variability between plants, as different plants within a species may exhibit different investment in EFNs (Byk and Del Claro 2011). I selected branches with ants and Hemiptera present for use in experiments. I assigned branches sprouting from the main trunk of the hibiscus plant as a control or to one of the treatments at random. Fieldwork at these sites was conducted from October 2011 to November 2011

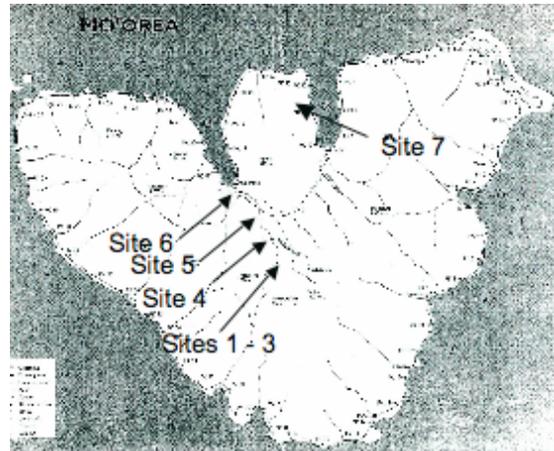


FIG. 2. Geographic locations of study sites 1 through 7, sampled in this study.

Sugar fed and deprived treatments

I manipulated availability of carbohydrate resources to ants to assess effects of plant and Hemiptera investment in carbohydrate production on the mutualism. To increase availability of carbohydrates to ants for the sugar-fed treatments, I filled a microvial with 30% vol/vol sugar solution and stopped it with a small piece of cotton ball. I then attached the vial upside-down to the branch stem near its tip using a cable tie. The vial thus allowed a small amount of sugar water to be administered to ants over time. I regularly refilled the vial so that it was never empty during the experimental period. To decrease availability of carbohydrates to ants for the sugar-deprived treatment, I sealed each EFN on each leaf of the branch using nail polish. For control branches, I attached empty vials to stems and painted nail polish alongside but not covering EFNs. I regularly monitored ant and Hemiptera abundances on all treatment and control plants (see following section).

Abundances of ants, Hemiptera and non-Hemiptera herbivores

I used visual observations to quantify the total number of ants, Hemiptera, and non-Hemiptera herbivores on hibiscus branches. Every two to four days, I conducted a 60-second timed search for each branch in which I examined the entire stem and every leaf for ants, Hemiptera and non-Hemiptera herbivores. I collected ants from different branches and took them back to the lab and identified them as *Myrmicinae* *Pheidole*

terrarium and *Paratrechina longicornis* using a dissecting microscope. I did not identify Hemiptera and non-Hemiptera herbivores any further but kept them in these rough categories. I analyzed data on differences in insect abundances among treatments and control using one-way ANOVA and Tukey-Kramer HSD. I conducted all statistical analyses of data by using the software JMP, 9.

Ant behaviors and distribution on plant

I recorded various ant behaviors, as well as distribution of ants on branches to assess services received and rendered by ants. I quantified ant tending of Hemiptera by counting how many ants were engaged in Hemiptera tending behavior during a two minute timed search. Hemiptera tending was defined as ants touching and/or standing over Hemiptera for at least ten seconds. I recorded the number of ants at EFNs and at the periphery of branches to account for ant distribution on the branch. This was done as a part of the 60-second timed search mentioned in the previous section. I then punctured leaves by hand to mimic leaf chewing by a non-Hemiptera herbivore and counted the number of ants that remained at EFNs ten seconds following the disturbance. I analyzed data on differences in ant behaviors and distributions among treatments and control using one-way ANOVA and Tukey-Kramer HSD.

Hemiptera population demography

I quantified changes in the age structure of Hemiptera populations in order to assess any changes in Hemiptera lifespan and/or reproductive rate in response to treatment and control. For each branch, I counted the numbers of early and late instar Hemiptera on the stem and every leaf. I repeated this count twice. If the counts were different, I repeated the process until I obtained the same count twice in a row. It was possible to do this as opposed to a timed search since Hemiptera are much more sessile than ants and did not move significantly during counts. I analyzed data on differences in Hemiptera population demography among treatments and control using one-way ANOVA and Tukey-Kramer HSD.

Effects of treatments on herbivory

To monitor differences in herbivory among treatments, I took photographs of three randomly selected leaves of each branch in each plot. I photographed leaves against a white backdrop with a centimeter scale drawn on it. For field experiment plots, I took photographs before treatments were applied and at the end of the study. I marked leaves whose photographs I took for field experiments with flagging tape so that they could be photographed again at the end of the study. I then used these photographs to determine amount of leaf area lost to herbivory. I compared differences in mean leaf area lost for the three leaves at the beginning and end of the study to serve as a proxy for herbivore action on the plant. I conducted all leaf image analysis with the software program ImageJ. I analyzed data on differences in leaf area lost to herbivory among treatments and control using one-way ANOVA and Tukey-Kramer HSD. I analyzed data on differences in leaf area lost to herbivory as a function of ant and Hemiptera abundances using regression.

RESULTS

Results indicate the interaction was present at all sites and that the treatments had effects on behaviors and abundances of ants, Hemiptera and non-Hemiptera herbivores.

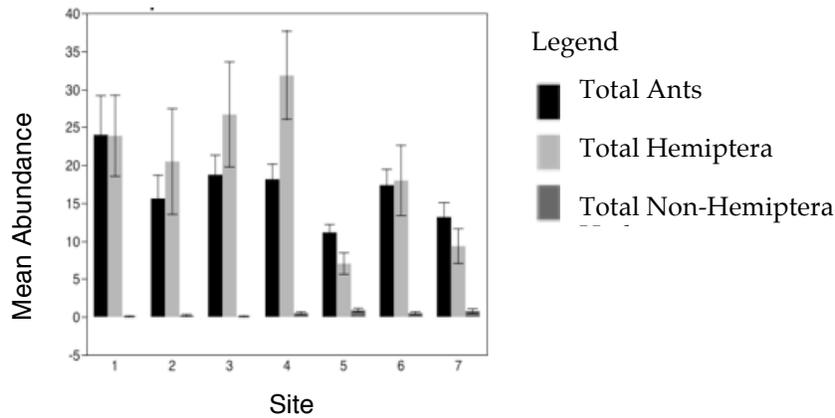


FIG. 3. Mean abundances of ants, Hemiptera, and non-Hemiptera herbivores at study sites. Error bars represent standard error. Black bars represent mean of total ant abundance, light grey bars represent mean of total Hemiptera abundance and dark grey bars represent mean of total non-Hemiptera herbivore abundance.

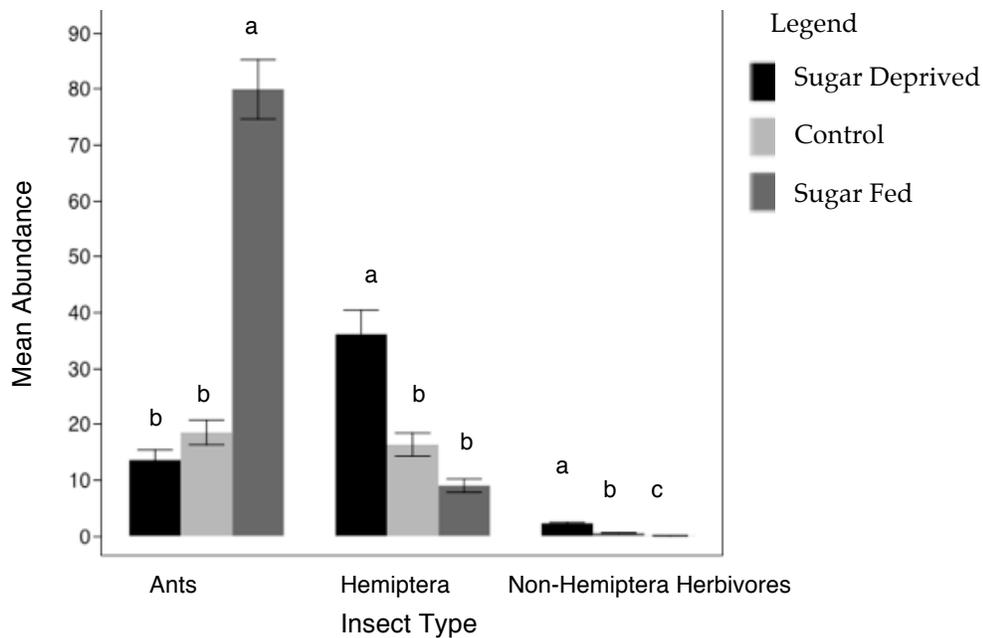


FIG. 4. Mean abundances of ants, Hemiptera and Non-Hemiptera herbivores in response to treatment. Bars are grouped according to the insect type they represent. Black bars represent mean total abundance of insect type in sugar deprived treatment, light grey bars represent mean total abundance of insect type in control and dark grey bars represent mean total abundance of insect type in sugar fed treatment. Columns representing abundance of same insect type with same letter are not significantly different. Error bars represent standard error.

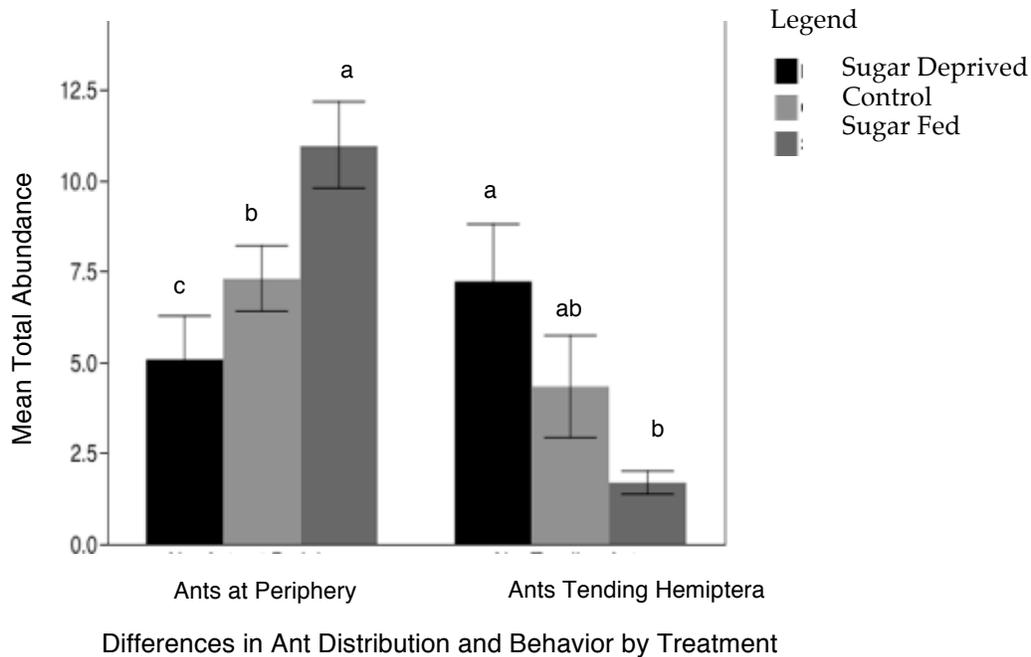


FIG. 5. Changes in ant tending of Hemiptera and ant distribution on plant branches in response to treatment. Columns grouped together represent ant distribution or Hemiptera tending behavior. Black bars represent the mean total number of ants at the branch periphery or tending Hemiptera in the sugar deprived treatment. Light grey bars represent the mean total number of ants found at the branch periphery or tending Hemiptera in the control. Dark grey bars represent the mean total abundance of ants at the periphery of branches or tending Hemiptera in the sugar fed treatment. Columns of same group (i.e. ants at periphery) with the same letter above are not significantly different. Error bars represent standard error.

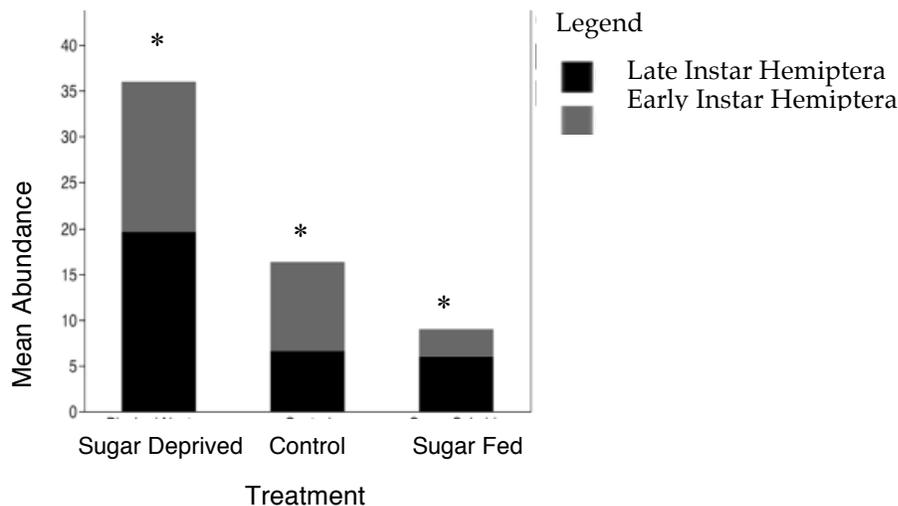


FIG. 6. Changes in Hemiptera population demography in response to treatment. Black bars represent mean of the total abundance of late instar Hemiptera and grey bars represent mean of the total abundance of early instar Hemiptera. The stacked black and grey bar together represent total abundance of Hemiptera by treatment. Total and late instar Hemiptera abundances were significantly greater in the sugar deprived treatment than in control or sugar fed treatment. Early instar Hemiptera abundance was significantly greater in the sugar deprived treatment compared with the sugar fed treatment

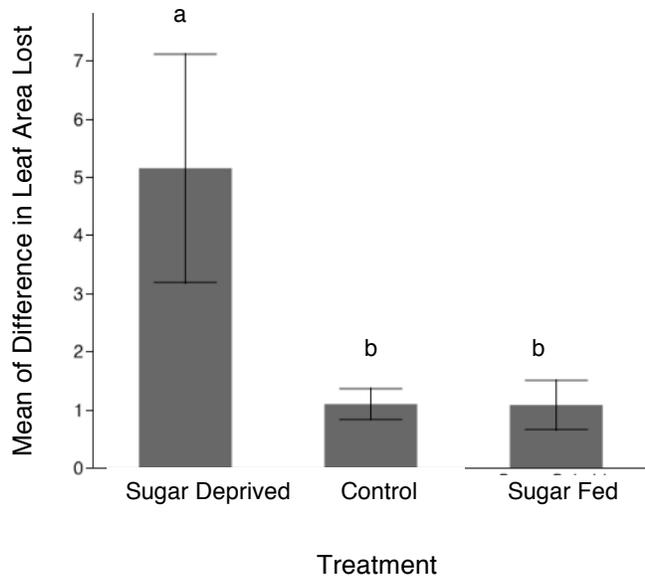


FIG. 7 Average of difference in amount of leaf area lost in response to sugar-deprived treatment, sugar-fed treatment, and control. Error bars represent standard error. Columns with same letter above them are not significantly different.

Geographic distribution of interaction

The three players involved in the interaction were present at all seven sites (Fig. 3), regardless of changes in elevation, temperature or other abiotic factors (Fig. 2).

Abundance of ants, hemiptera and non-hemiptera herbivores

Abundances of ants, Hemiptera and non-Hemiptera herbivores fluctuated in response to treatment. Ant abundance increased when sugar resource availability was increased in the sugar-fed treatment (one-way ANOVA, $F_{2,267}=113.11$, $P<.0001$). Hemiptera abundance increased as sugar resource availability to ants decreased in the sugar-deprived treatment (one-way ANOVA, $F_{2,267}=24.15$, $P<.0001$). Non-Hemiptera herbivore abundance increased when availability of sugar resources to ants decreased in the sugar-deprived treatment and decreased as availability of sugar to ants increased in the sugar-fed treatment. In short, non-Hemiptera herbivore abundance was lowest in sugar-fed treatment and highest in sugar-deprived treatment (one-way ANOVA, $F_{2,267}=129.25$, $P<.0001$) (Fig. 4).

Ant behaviors and distribution on plant

Hemiptera tending behavior exhibited by ants and ant distribution on plant

changed as a function of sugar availability according to treatment. When availability of sugar resources to ants increased in the sugar-fed treatment, ant abundance increased at the periphery of branches (one-way ANOVA, $F_{2,177}=36.02$, $P<.0001$). There were more ants tending Hemiptera in the sugar-deprived treatment compared with the sugar-fed treatment (one-way ANOVA, $F_{2,177}=5.51$, $P=.0048$) (Fig. 5).

Hemiptera population demography

Age structure of Hemiptera populations changed in response to treatment. When ants were not allowed access to sugar resources in the sugar-deprived treatment, total Hemiptera abundance increased (one-way ANOVA, $F_{2,267}=24.15$, $P<.0001$). Abundance of early instar Hemiptera decreased when ants were provided with a sugar subsidy in the sugar-fed treatment (one-way ANOVA, $F_{2,267}=8.25$, $P=.0003$). Late instar Hemiptera abundance increased in the sugar-deprived treatment (one-way ANOVA, $F_{2,267}=20.35$, $P<.0001$) (Fig. 6).

Effects of treatments on herbivory

There was no significant relationship between ant abundances and leaf area lost to herbivory (linear regression, $R^2=-.01$, $P=0.55$)

or between Hemiptera abundances and leaf area lost to herbivory (linear regression, $R^2 = .02$, $P = 0.58$). Leaf area lost to herbivory was higher in the sugar-deprived treatment compared with the sugar-fed treatment and control, with no difference between the sugar-fed treatment and the control (one-way ANOVA, $F_{2,42} = 4.03$, $P = .0251$) (Fig. 7).

DISCUSSION

The association among ants, Hemiptera and hibiscus was present at all sites sampled, regardless of variations in elevation, temperature or canopy cover. This suggests the interaction occurs throughout a broad range of habitats on the island. This is consistent with research that describes symbioses as being geographically widespread and temporally persistent interactions (Douglas 2008, Hembry et al. 2011). The wide geographic prevalence of the association provides evidence for its evolutionary and ecological strength as a mutualism. It also suggests that presence of any one of the players may facilitate the spread of the others, potentially leading to an invasional meltdown (Lach et al. 2010). These results suggest this system is an important one for understanding the effects of invader-invader interactions such as mutualisms on the spread of the invasive species involved.

The observed effects of the sugar-deprived and sugar-fed treatments on ant abundance and distribution on hibiscus provide support for the hypothesis that both hibiscus and ants benefit from their association. The increased abundance of ants on branches in the sugar-fed treatment suggests that nectar serves as an incentive provided by hibiscus to attract and sustain larger ant populations. This result is consistent with a study by Byk and Del Claro (2011), which showed that EFNs can positively influence survivorship, growth and reproduction of ants. These conclusions suggest that the mere presence of carbohydrate producers such as hibiscus and/or Hemiptera could facilitate the spread of invasive ants throughout a given habitat, thereby leading to an invasional meltdown. This is supported by another study by Blüthgen et al. (2000), which found Hemiptera tending ants to be the most dominant ants in tropical rainforest canopies. Ant distribution on hibiscus may also impact the quality of defensive services

provided, as presence of ants at the plant periphery in addition to at EFNs allows for better defense against non-Hemiptera herbivores. The increased presence of ants at the periphery caused by sugar-fed treatments suggests quality of defense provided by ants to hibiscus may improve with greater availability of nectar. The lower abundance of non-Hemiptera herbivores on hibiscus supports this idea, though more research should be done to better understand the mechanisms driving this interaction.

The impacts of treatments on herbivore abundance provide further support for the qualification of the ant-hibiscus association as a mutualism. There appears to be an inverse relationship between number of herbivores and amount of sugar available to ants, where the most herbivores were present when no sugar was available in the sugar-deprived treatment and the fewest were present when extra sugar was provided in the sugar-fed treatment. Assuming ants are responsible for excluding herbivores, this effect could be related to the higher abundance of ants that resulted from increased sugar availability in the sugar-fed treatment. It could result from a physiologically-driven change in ant behavior due to a higher sugar diet. This is supported by findings that carbohydrates serve as fuel for workers engaged in defense activity (Byk and Del Claro 2011) and have been shown to influence worker activity rates and territory (i.e. hibiscus) defense (Davidson 2008). Either way, this effect suggests that an increase in sugar content in ant diet would result in reduced herbivore action on the host plant. This provides further support for the hypothesis of EFNs as an incentive provided to the ant by the plant in exchange for defense against herbivores. This is consistent with other work that has shown ants to provide EFN-bearing plants with defense services (Bronstein 1998, Martinez et al. 2011). This also suggests that presence of both EFNs and Hemiptera benefit the plant as they increase carbohydrate content of the ant diet, thereby improving anti-herbivore defense provided by the ant. This is supported by the results that changes in leaf area loss to herbivory were highest in the sugar-deprived treatment. Other studies have shown that through their anti-herbivore defense, ants can reduce leaf area lost to herbivory (Byk and Del Claro 2011).

There was no relationship in the current study between ant abundances and leaf area lost to herbivory. This is likely due to the fact that other factors, such as fungi, can cause loss of leaf tissue in tropical forests. As area loss was not categorized according to cause, these methods were likely not fine-tuned enough to detect differences in herbivore action as a function of insect abundances. This effect should be explored further as all other results from this study suggest invasive capabilities of the three players could improve as they derive mutual fitness benefits from the ants' higher carbohydrate diet.

The changes in ant tending of Hemiptera and Hemiptera abundances in response to treatment suggest that there is a context-dependent mutualist interaction between ants and Hemiptera. Though the mechanism driving the change in Hemiptera abundance is unclear, the results suggest it is likely linked to changes in ant abundance and/or behaviors. I hypothesize that Hemiptera abundance increased as ants heightened the level of care for Hemiptera offspring in response to loss of EFN access in the sugar-deprived treatment, thereby improving the fitness of the Hemiptera. The higher number of tending ants and early instar Hemiptera in sugar-deprived treatment supports this hypothesis. The lack of a difference in Hemiptera abundance and ant tending behavior between the control and sugar-fed treatment suggests that plants may not be able to induce ants to abandon Hemiptera tending by increasing nectar production. This is consistent with another study by Helms et al. (2010), which found that ant symbionts of plants still required Hemiptera tending as plants alone were unable to provide sufficient dietary supplements. This could mean that presence of ants on hibiscus will lead to an invasional meltdown, as these ants will invariably tend Hemiptera and thereby facilitate Hemiptera spread as well as their own. Alternatively, it may be that it takes the ants longer to allow a decrease than an increase in Hemiptera abundance. If this is true, then experiments would need to be run for a longer time period in order to see an effect of increased sugar on Hemiptera abundance. This may be unlikely to happen, however, as hibiscus appears to benefit indirectly from Hemiptera tending by ants (Styrsky and Eubanks 2007; Hembry et al. 2006). Furthermore, these outcomes may

change in accordance to context, as the balance of costs and benefits that structure these relationships may fluctuate in response to environmental change. The contextual nature of this mutualism is supported by other studies which have also found ant tending does not always benefit Hemiptera (Styrsky and Eubanks 2007, Bronstein 1998) nor does it necessarily harm the host plant (Lach et al. 2010). It would therefore be interesting to see a study on the mechanisms driving this interaction. Results from a study such as this could provide insight on how mutualisms might be manipulated in order to prevent or mitigate invasions.

The results from this study suggest that a mutualism has independently evolved among invasive ants, hibiscus and Hemiptera on Mo'orea, which has enhanced their respective abilities to invade by increasing their fitness and thereby facilitating their geographic spread. These results imply that mutualist interactions among invaders may improve their success in novel habitats. This is important as few studies have examined the interactions among invader species that lead to invasional meltdowns, despite the potential importance of this dynamic in facilitating invasions (Green et al. 2011). The relationship between mutualisms and facilitation could have broad implications for invasion biology (Bronstein 2009) and this association in particular could provide an illuminating model system for future research in this area. Mutualisms among plants and animals that lead to habitat modification have been cited in particular as playing an important role in invasion facilitation (Simberloff and Von Holle 1999). Thus, as a mutualism among invasive habitat-modifying species, this interaction has the potential to contribute greatly to our understanding of invasional meltdowns and how they might be mitigated. The findings of this study have revealed a mutualist dynamic among three independently established invasive players, thereby illuminating a system where an invader-invader mutualism has facilitated the successful establishment of two important invasive insects and thereby altered a unique island ecosystem.

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