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Protection and reliability: an examination of the quality and quantity of ant protection in the food-for-protection mutualism between *Ferocactus viridescens*, *Crematogaster californica* and the invasive *Linepithema humile*

A thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Biology

by

John T. Ludka

Committee in charge:

Professor David A. Holway, Chair
Professor Joshua R. Kohn
Professor David Woodruff

2009

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Chair

University of California, San Diego

2009

DEDICATION

This thesis is dedicated to

my beloved wife

Colleen

... and to the insects.

EPIGRAPH

To see things in the seed, that is genius.

Lao Tsu

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ABSTRACT OF THE THESIS

Protection and reliability: an examination of the quality and quantity of ant protection in the food-

for-protection mutualism between

Ferocactus viridescens, *Crematogaster californica* and the invasive

Linepithema humile

by

John T. Ludka

Master of Science in Biology

University of California, San Diego 2009

Professor David A. Holway, Chair

In this study we investigate the effects of the invasive Argentine ant (*Linepithema humile*) on the food-for-protection mutualism between native ant species and the San Diego Barrel Cactus (*Ferocactus viridescens*). Mutualistic interactions may be disrupted by non-native species with possible detrimental effects for one or both partners. In the presence of *L. humile*, plant protection may be enhanced in the short term as a consequence of the Argentine ant's aggressive nature, yet may be compromised by pollinator harassment and abandonment of the cactus. Consequently, in the long term, this invasion may decrease the fitness of cacti by shifting the net effects of the interaction from a mutualism to one that is detrimental.

To quantify ant protection, we used an established surrogate herbivore assay to compare protective services offered by Argentine ants with those offered by a common native ant *C. californica*. Our results support the existence of a mutualism between ants and *F. viridescens*. Ant presence discouraged leaf-footed bugs, the most commonly observed herbivores, from feeding on

plant reproductive structures. Herbivory reduced mass per individual seed and seed mass per plant.

This study adds to a growing body of work concerning the variation found in mutualistic interactions, allows for predictive measures of plant benefits with respect to partner identity, and examines how these interactions are affected by a behaviorally dominant and aggressive invasive ant. Furthermore, it explores the consequences of reduced ant richness, and the impacts that result from the loss of functional redundancy in the *F. viridescens* food-for-protection mutualism.

INTRODUCTION

Mutualisms are often conceived as reciprocally beneficial interactions but are increasingly understood to involve mutual exploitation and to encompass a high degree of dynamical behavior and context dependency (Bronstein 1994). Cases of mutual exploitation involve partners vying for maximum gain at minimal cost. These conflicts of interest appear responsible for variation in the costs and benefits conferred to each partner species (Bronstein 2001). Mutualisms often depend on stage-specific phenomena such as the size or age of partner species (as in the case of many plant partners), the abiotic and biotic background in which interactions occur, fluctuations in the local abundance of the mutualists themselves, and increasingly the presence of non-native species (Bronstein 1994, Lach 2003, Morris et al. 2005, Miller 2007, Ness and Bronstein 2004, Stanton et al. 1999).

A common class of defensive mutualisms involves the exchange of food in return for protection from one's enemies. This type of mutualism commonly involves protective services provided by ants, which are abundant, aggressive, and form large colonies with social recruitment (Beattie 1985). To attract ants, many plant species produce extra-floral nectaries (EFNs), other nutritive rewards, and domatia. Food-for-protection mutualisms between ants and plants vary in their specificity with most systems featuring multiple species of ant partners, which may affect host plants quite differently (Stanton et al. 1999, Ness et al. 2006). An important and largely unresolved question concerns how invasive ants disrupt this type of defensive mutualism.

In this study we investigate food-for-protection mutualisms between the San Diego Barrel Cactus (*Ferocactus viridescens*) and different species of ants including both native species and the invasive Argentine ant (*Linepithema humile*). Interactions between cacti and ants have recently received considerable attention and provide a useful system to investigate how the identity of ant partners affects the reproductive success of cacti (Morris et al. 2005, Ness et al.

2006, Miller 2007). In a Sonoran desert barrel cactus system involving the fish-hook barrel cactus (*Ferocactus wislizeni*), Ness et al. (2006), for example, demonstrated that interspecific differences in the quality and quantity of ant protection predicted reproductive variables linked to cactus fitness. Interestingly, follow up studies further demonstrated that the most aggressive ant defenders also interfered with cactus pollination (Ness 2006).

Like the system involving *F. wislizeni*, the San Diego barrel cactus produces EFNs attractive to a variety of ant species. *Ferocactus viridescens* is restricted to coastal sage scrub on rocky well-drained slopes from coastal San Diego County to northwestern Baja California (Ingram 2008). Cacti bloom from May to June and produce small yellowish fruits (~1.5-4 cm in length) by late summer. EFNs are formed from areoles at the apical meristem and are most active during the bud phase of cactus development.

In contrast to the system involving *F. wislizeni*, the San Diego barrel cactus system now features an aggressive and invasive ant partner, the Argentine ant. How these mutualistic interactions are altered in the context of ant invasions is a largely unexplored area of research. EFN-bearing plants may generally benefit from invasive ant tending; however, few data are available to evaluate this hypothesis (Ness and Bronstein 2004). In coastal southern California, Argentine ants largely displace a diverse native ant fauna (Suarez et al. 1998, Holway et al. 2005, Glenn and Holway 2008), including native ants in areas occupied by *F. viridescens*. Argentine ants might differ from native ants in their ability to provide protective services to cacti in several respects. Argentine ants are aggressive and often enter into food-for-protection mutualisms involving carbohydrate rewards (Holway et al. 2002, Lach 2003, Ness and Bronstein 2004). For these reasons, one might expect that Argentine ants would effectively protect cacti from herbivores but that they may also interfere with pollination (Lach 2008). In contrast to many of the native ants common in areas where *F. viridescens* occur, Argentine ants undergo seasonal movements corresponding to abiotic variability. In seasonally dry areas where *F. viridescens* is

common, Argentine ants occur with cacti in winter and spring but retreat from these areas in summer and fall when soil moisture levels become too low to support this species (Holway and Suarez 2006). As a consequence and unlike in areas with native ants, areas invaded by Argentine ants are often only seasonally occupied by ants. From the perspective of *F. viridescens* an important consequence of this dynamic is that the level of protection may vary seasonally and could fluctuate from one in which ants are present at high numbers in winter and spring but are absent in summer and fall.

In this study we combine observational and experimental approaches in an attempt to quantify how ant invasions affect the San Diego Barrel Cactus. First we quantified the extent to which known herbivores effect fitness variables of reproducing cacti. Second, we compared native ants and invasive ants with respect to the quality and quantity of protective services offered. Lastly, we determined the extent to which interspecific differences in protective services translated into measurable effects on the cactus fitness. This study builds on a previous body of work addressing interactions between ants and barrel cacti (Ness et al. 2006, Morris et al. 2005) by explicitly considering how an aggressive invader affects cactus fitness. More generally, our study provides a detailed example of how novel species interactions can change the dynamics of mutualisms and in particular how the diversity of partners can influence the outcome of the interactions considered.

MATERIALS AND METHODS

Study system and area

We studied interactions between ants and cacti in protected areas along the immediate coast of San Diego County, CA between La Jolla and Del Mar (Figure A.1-A.4). Focal cacti grew in coastal sage scrub on rocky, well-drained soils (Figure 1.1; Ingram 2008). The most prevalent herbivore in both years of the study was *Narnia wilsoni* (Hemiptera: Coreidae), which occurred commonly on cacti especially in late summer and early fall (Figure 1.7). We also observed a species of *Leptoglossis* (Hemiptera: Coreidae) that occurred much less commonly. Herbivorous Hemiptera such as the Coreids that occurred on *F. viridescens* feed by penetrating the epidermal layer of plant tissues (e.g. floral buds) using their beak-like proboscis.

The study area is presently a mosaic of areas occupied by native ants, areas where these species have been displaced by Argentine ants (Figure 1.2) and areas where no ants are present (presumed native ant displacement followed by Argentine ant retreat) (Zee and Holway 2006, Glenn and Holway 2008). While 19 ant species occurred on cacti in areas not invaded by Argentine ants, the most common species was *Crematogaster californica* (Figure 1.3, Table 1.1). In invaded areas Argentine ants occurred commonly on cacti and were typically the only ant species present.

Because the distribution of Argentine ants on our study sites was approximately static during the period of study and because Argentine ants displace the majority of native ant species in this area (Glenn and Holway 2008), it was possible to designate sites as either invaded or un-invaded. To reduce problems caused by confounding environmental variation among sites, we interspersed cacti in invaded and uninvaded areas to the fullest extent possible within the study area (Figure A.1). Ants collected from cacti are deposited in the Bohart Museum of Entomology,

University of California, Davis (UCDC). Coreid herbivores are deposited in the entomology collection at the California Department of Food and Agriculture.

Observational surveys

In 2007 and 2008, we conducted weekly surveys of cacti to census ants, herbivores and pollinators, and to assess the production of buds, flowers, and fruits. The survey included 80 cacti in 2007 and 113 cacti in 2008 (Table A.1). Surveys were conducted when ambient temperatures were approximately 30°C (± 4.4), a temperature at which nearly all of the common ant species were active. We used a digital thermometer to record the temperature in the crown of each cactus.

During each visit to each cactus, we identified the ant species visiting EFNs and recorded the number and identity of herbivores present. Any pollinators visiting cactus flowers were noted as well as the presence of ants within the flowers themselves. Because EFNs are concentrated around the apex of the plant, ants could be easily counted and identified in the field. Asymmetrical competitive abilities and differences in environmental tolerances among ant species resulted in cacti that were generally tended by only one ant species at a time.

In order to quantify female reproductive output of all focal cacti, we measured six characteristics: total number of flowers/fruits produced, the ratio of buds surviving to mature fruits, seed set, mean number of seeds per fruit, mean seed mass per fruit, and mean mass per individual seed (Ness et al. 2006, Ness 2006). After fruits were dried, we separated the seeds from each fruit and measured fruit dry weight. A subsample of seeds from each fruit ($n = 100$) was counted and weighed in bulk, and the estimated mass of an individual seed was used to approximate the number of seeds per fruit by dividing total seed biomass per fruit by the estimated mass of an individual seed. Fruits ($n = 1-3$) were haphazardly selected off cacti and average values used for these measurements. The average reproductive output of cacti from invaded and uninvaded areas is listed in Table 1.2.

Data from the observational survey were used to assess seasonal trends in ant occurrence on cacti, to measure the effects of herbivory by coreid bugs, and to estimate plant reproductive variables used in *Quantification of ant protective services*. Finally, we examine the observations between leaf-footed bug activity, ant activity, and cactus fitness components.

Quantification of ant protective services

Data from the observational survey were used to quantify how plant reproductive variables vary as a function of the ant species present. Because uninvaded sites were numerically dominated by *C. californica*, we compare cacti dominated by this ant species in uninvaded areas with cacti dominated by Argentine ants in invaded areas. Cacti were designated as dominated by a particular species when it was present during at least fifty percent of visits to that cactus.

We quantified the quality of protection conferred to a subset of focal cacti by introducing surrogate herbivores, *Manduca sexta* (Lepidoptera: Sphingidae) caterpillars, using methods developed by Ness et al. (2006). This method allowed us to standardize herbivore threat to cacti across ant species under similar environmental conditions. Laboratory reared caterpillars (c. 1-2 cm) were introduced in April-May 2008 during the bud and flower phase and in July-August 2008 during the fruit phase. During each trial, we introduced ten *Manduca* caterpillars to focal cacti dominated by either *L. humile* ($n = 12$) or *C. californica* ($n = 17$). Caterpillars incapacitated by interactions with ants were counted during each 30-min trial along with the number of ants present at the beginning and at the end of the 30-min trial period. The number of ants present prior to caterpillar introduction is used to estimate the magnitude of recruitment that may take place during the trial. The maximum number of ants observed during the course of each trial is used as an estimate of the ant's capacity to kill caterpillars.

As in Ness et al. (2006), the Michelis-Menten statistic (Eq. 1) was used to estimate the fraction of caterpillars expected to be incapacitated (F) as a result of ant protection:

$$(F=A/(b+A)) \quad (1)$$

We first fit the data to Eq. 1 for *L. humile* and *C. californica* separately and used maximum likelihood estimates that assumed binomially distributed errors to estimate b , the number of ants required to incapacitate half of the caterpillars within the 30-min trial. Equation 1 describes the per capita ant effectiveness at incapacitating caterpillars ($1/b$) as well as any recruitment (A) that may take place during the 30-min trial (Ness et al. 2006). When ant numbers are low (e.g., 1), the fraction of caterpillars expected to be incapacitated is the reciprocal of b ($F=1/b*A$). As A increases, F approaches 1 as ant protection is saturated at high ant densities. We used a likelihood-ratio test to examine the null hypothesis that ant protective services did not differ between *L. humile* and *C. californica*. First, we pooled the herbivore introduction data for both species and computed the log likelihood of Eq. 1, estimating the parameter b assuming no difference in ant protective services. We then calculated twice the difference between this log likelihood and the sum of the log likelihoods for the data fit with different b values. The resulting values were then compared using a chi-square test with 2 degrees of freedom (Ness et al. 2006).

Combining quality and quantity of ant protection

After quantifying the quality of protective services provided by *L. humile* and *C. californica*, we then estimated the protective services offered to *F. viridescens* in 2007 and 2008. For survey data collected in these years, we substituted the maximum likelihood estimate of b into Eq. 1 for each ant species to estimate the level of potential herbivore removal. We averaged F values for each ant species across surveys to get a measure of annual protection. We also compared both conspecific and interspecific differences in protection offered by ants for cacti dominated by *L. humile* or by *C. californica* during bud/flower and fruit development. Finally, we

directly tested ant protection, F , on leaf-footed bug activity using linear regression. This analysis was repeated for multiple plant fitness variables (Table 1.2).

Pollinator harassment

To address how interference between ant bodyguards and pollinators could affect plant fitness, we compared the reproductive traits of cacti dominated by *L. humile* and *C. californica*. We restricted this analysis to periods of maximum pollinator visitation and only used those cacti that were consistently occupied by *L. humile* or by *C. californica* during the survey period. After controlling for flower number, we compared residual numbers of ants within flowers between cacti dominated by *L. humile* and *C. californica*. We also examined residual values of total seed set (controlling for any effect of fruitset) as well as the number of seeds per fruit (removing any effect of fruit size).

RESULTS

Observational survey: ant frequency and abundance

Patterns of ant activity varied strongly from season to season (Figure 1.4). Within both survey years, *L. humile* activity on cacti declined in summer, a period when *F. viridescens* fruits mature. Comparisons of mean Argentine ant presence between the floral-bud phase and the fruit phase, revealed that ant activity declined in both years (Figure 1.5; 2007 floral-bud phase versus fruit phase: paired t-test = 9.65, df = 51, p < 0.0001; 2008 floral-bud phase versus fruit phase paired t-test = 6.35, df = 75, p < 0.0001). In contrast, *C. californica* declined in 2008 but not in 2007 (Figure 1.6; 2008 floral-bud phase versus fruit phase paired t-test = 3.45, df = 35, p = 0.0015). Other native ants exhibited individualistic responses to seasonal variation but also tended to decline in summer (Figure 1.6). While turnovers occurred commonly in areas with native ants, in invaded areas, where *L. humile* was the most numerically dominant ant species, turnovers were rare.

The two survey years differed strongly in precipitation (4.64 inch: 2007, 7.39 inch: 2008; Del Mar) and also in levels of herbivore abundance on cacti (Figure A.5). During the springs of both years (April-June), a period of peak ant activity, the average proportion of cacti occupied by *L. humile* decreased by 24% (Figure A.6; 2007 bud phase versus 2008 bud phase, paired t-test: t = 2.37, df = 51, p = 0.0213). In uninvaded areas the average proportion of cacti occupied by native ants also declined in 2008. Native ant activity decreased by 26% between the two years during the bud phase (Figure A.7; 2007 bud phase versus 2008 bud phase, paired t-test: t = 5.27, df = 26, p < 0.0001). Individual native ant species exhibited idiosyncratic differences in between-year activity during the spring with some species being more active in one year versus the next (Figure 1.6). The proportion of cacti occupied by the most common native ant, *C. californica*, did

not change between years during the spring (Figure 1.6; 2007 bud phase versus 2008 bud phase, paired t-test: $t = 0.11$, $df = 26$, $p = 0.911$).

*Observational survey: leaf-footed bug herbivory on *F. viridescens**

On average, during the two years of the survey, the proportion of cacti occupied by leaf-footed bugs did not differ between invaded and uninvaded areas (Figure A5: average annual assignment: t-test = 0.631, $df = 111$, $p = 0.5292$). Across all cacti, leaf-footed bugs occurred on a greater proportion of cacti in 2008 than in 2007 (annual assignments across surveys paired t-test $t = 3.09$, $df = 17$, $p = 0.0066$). During the bud/floral phase in 2008, *N. wilsoni* increased by 6.6% in invaded areas (Figure A6; bud phase 2007-2008 paired t-test: $t = 2.38$, $df = 51$, $p = 0.0210$) and by 9.7% in uninvaded areas (Figure A7; bud phase 2007-2008 paired t-test: $t = 3.47$, $df = 26$, $p = 0.0018$) relative to 2007.

The results of the observational survey revealed that herbivory by leaf-footed bugs (and possibly other undetected herbivores) measurably affected cactus reproductive variables. Because bug presence increased with cactus volume (linear regression: $F_{1,192} = 54.2$, $p < 0.0001$), analyses pertaining to the effects of herbivory controlled for cactus volume. We detected effects of leaf-footed bug herbivory in invaded areas. The most conspicuous effect of herbivory was a negative relationship between mass per seed and the fraction of surveys occupied by leaf-footed bugs (Figure 1.8; linear regression: $F_{1,78} = 6.57$, $p = 0.0125$). The pattern illustrated in Figure 1.8 occurred in both years of the study (2007; residuals linear regression: $F_{1,27} = 23.19$, $p < .0001$; 2008; residuals linear regression: $F_{1,34} = 8.08$, $p = 0.0086$). After controlling for seed set, the total plant seed biomass was also lower for plants with higher leaf-footed bug occupation during the bud versus floral stage of 2007 (average annual values linear regression: $F_{1,41} = 10.51$, $p = 0.0024$) but not in 2008. Similar analyses conducted for uninvaded areas revealed no effects of herbivory (residuals mass per seed by seed number per fruit on the proportion of cacti occupied by leaf-

footed bugs, linear regression for 2007 data: $F_{1,14} = 0.0115$, $p = 0.9162$; linear regression for 2008 data: $F_{1,29} = 1.30$, $p = 0.2623$). Evidence that invaded areas and uninvaded areas included similar growing environments was reflected by similarities of mass per seed in invaded and uninvaded areas in the absence of leaf-footed bug herbivory (Figure A.8).

In invaded areas in 2007, we observed an inverse relationship between Argentine ant abundance and leaf-footed bug presence (Figure 1.9a). This relationship did not hold for invaded areas in 2008, nor did it hold for uninvaded areas in either year (Figure 1.9b).

Quantification of ant protective services

To quantify how the presence of ants influences plant reproductive variables we first estimated ant protective services for the two most common ant species, *L. humile* and *C. californica*. Interspecific comparisons of the number of ants required to kill 5 caterpillars in 30 minutes, b , differed for *L. humile* and *C. californica* (Figure 1.10). These differences held when we estimated b either using pretreatment ant abundance (log likelihood ratio (X^2) = 6.83, $df = 2$, $p < 0.05$) or maximum ant abundance (log likelihood ratio (X^2) = 9.27, $df = 2$, $p < 0.01$). Therefore, the quality of protection (or the per capita effectiveness $1/b$) offered by *L. humile* ($1/b = 0.0166$) was less than it was for *C. californica* ($1/b = 0.0483$). Although *L. humile* and *C. californica* both increased in abundance upon the addition of caterpillars, there was no interspecific difference in the magnitude of the increase (Figure 1.11; $t = -0.55$, $df = 29$, $p = 0.5847$).

Combining quantity and quality of ant protection

Protective services offered by ants exhibited both seasonal and inter-annual differences. In both years of the study, average ant protection (F) offered by Argentine ants declined from the bud phase (spring) to the fruit phase (summer). In contrast *C. californica* exhibited declines in

protection only in 2008 (Figure 1.12). Based on b and F values, Argentine ants offered cacti less protection both within and between years (Figure 1.12, Figure 1.13, Table A.2).

Argentine ants and *C. californica* exhibited divergent effects on protected cacti. Despite the lower estimated values of b and F for Argentine ants, compared to those for *C. californica* cacti controlled by *L. humile* exhibited a significant negative relationship between bug prevalence and the degree of protection offered by Argentine ants in the bud phase in 2007 (Figure 1.14) but not in 2008. Increased Argentine ant activity in the spring of 2007 was reflected in higher values of mass per seed (Figure 1.15). The presence of *C. californica* had no effect on plant fitness, however, the presence of this native ant did negatively affect leaf-footed bug presence in the spring of 2008 (2008 bud phase: Residuals: proportion of surveys cacti were occupied by leaf-footed bugs on ant protection: Linear regression: $F_{1,19} = 11.38$, $p = 0.0036$). Overall, unintended cacti in both invaded and uninvaded areas were associated with lower values of mass per seed presumably because of higher levels of herbivore activity (Figure A.9).

Pollinator Harassment

Compared to *C. californica*, Argentine ants occurred more often in cactus flowers (Figure 1.16). Based on ant activity during the bud/floral stage, cacti tended by Argentine ants produced fewer seeds overall compared to those tended by *C. californica* (Figure 1.17; bud phase 2007: $F_{1,34} = 3.93$, $p = 0.0558$; bud phase 2008: $F_{1,39} = 6.72$, $p = 0.0134$;). Moreover, in 2007 Argentine ant tended cacti produced fewer seeds per fruit (controlling for fruit dry weight) than did *C. californica* tended cacti (Figure A.10: bud phase 2007: $t = 2.05$, $df = 33$, $p = 0.0477$).

Ant Richness

From the observational survey data the number of ants present on cacti was related to the reproductive success of *F. viridescens*. While cacti in both invaded and uninvaded areas exhibited

different trends with respect to ant protection (Figures 1.14, 1.15), increasing ant richness was negatively associated with leaf-footed bug presence and positively associated with seed weight (Figures 1.18, 1.19). Therefore, in contrast to cacti tended primarily by one ant species, cacti with multiple ant partners suffered on average less herbivore damage caused by herbivory. Overall, invaded areas had less ant richness than uninvaded areas (Table 1.1, Figure A.11).

DISCUSSION

The results of the study are consistent with the existence of a food-for-protection mutualism between ants and *F. viridescens*, but we did not obtain evidence of a reciprocally positive interaction in both years of the study. Both native ants and the invasive Argentine ant visited cactus nectaries during the spring and summer, the one time of year when cacti are undergoing reproduction. The presence of ants at this time effectively discouraged leaf-footed bugs from feeding on plant reproductive structures. Leaf-footed bugs damaged *F. viridescens* by extracting resources allocated to floral buds and fruits; this herbivory reduced mass per individual seed and seed mass per plant. Interspecific comparisons of protective services offered by *C. californica* and by the Argentine ant revealed disparities in the per capita effectiveness at deterring surrogate herbivores. Differences in protective services offered by ants in invaded and uninvaded areas produced complex effects on reproductive variables effected by herbivory.

Ant abundance during the floral bud phase directly influenced important reproductive variables (e.g., mass per seed, seed mass per fruit, and seed number per fruit). Observed herbivores (*Narnia wilsoni* and *Leptoglossis*) fed primarily on buds and immature fruits. Herbivore damage consistently reduced the mass of individual cactus seeds; this form of herbivore damage is known to affect recruitment success during droughts in other species of cacti, including barrel cacti (Bowers and Pierson 2001). In numerous plant species in California, plants exposed to drought conditions produce heavier seeds (Baker 1972). Because southern California frequently experiences prolonged droughts, seed mass variation may be an important factor determining recruitment for *F. viridescens*.

The results of the present study provide an interesting basis for comparison with the Sonoran desert barrel cactus system (Ness et al. 2006, Ness 2006, Morris et al. 2005). A key difference between these systems concerns seasonal patterns of precipitation and their resulting

effects on when and how often cacti reproduce. The winter and summer rains of the Sonoran desert permit barrel cacti to bloom twice a year (McIntosh 2002), whereas in southern California winter rains are followed by a long summer drought, which presumably limits *F. viridescens* reproduction to the spring time. Differences in the seasonality of rainfall and the reproductive phenology of the cacti appear to be reflected in the seasonality of EFN activity. The nectaries of *F. wislizeni* remain active all year while those of *F. viridescens* in contrast produce extra floral nectar only during the spring and summer months when ant protection would be most valuable. Despite these climatic and phenological differences, both the Arizona system and the California system were numerically dominated by outwardly similar species of *Crematogaster*, which exhibited strikingly congruent per capita measures of protection ($b = 18.8$ for *C. opuntiae* in Arizona (Ness et al. 2006) versus 20.7 for *C. californica* (Figure 1.10)).

An additional salient difference between the Arizona and California barrel cactus systems results from the invasion of a non-native ant in southern California that displaces nearly all native ants. Interestingly, Argentine ants exhibit qualities quite different from those described for the Arizona barrel cactus system. Argentine ants had the highest b value ($b = 60.3$) of any ant species in either system, suggesting that at least on a per capita basis this species would provide inferior protective services. Argentine ants are a highly aggressive species but their workers are relatively small and may be able to deter herbivores only when their numbers exceed a threshold density. In spite of the Argentine ant's high b value, cacti growing in areas where *L. humile* occurred consistently had low herbivore presence and reduced herbivore damage. It thus appears that Argentine ants provide adequate or possibly even superior herbivore protection but only in sites where the ants remain consistently abundant.

Another key difference between the Argentine ant and the native ants it displaces in this system concerns the semi-nomadic behavior of *L. humile* and its intolerance of dry conditions (Ward 1987, Holway 2005). In southern California Argentine ants exhibit seasonal movements

corresponding to the availability of soil moisture and can abandon areas in summer and fall that they occupied in winter (Menke and Holway 2006, Menke et al. 2007). With respect to barrel cacti, this type of environmental forcing results in intermittent protection. For example, in both years of the study, Argentine ants abandoned cacti in invaded areas earlier in the season than did native ants in uninvaded areas. Cacti in invaded areas where Argentine ant densities were low, or where they were not observed on cacti, were sites where bug numbers and herbivore damage were high.

Pollinator harassment

The negative impacts of invasive species on plant reproductive mutualisms are well documented (Traveset and Richardson 2006). While invasive ants such as *L. humile* might be expected to benefit ant-tended plants like *F. viridescens* by offering superior protection, Argentine ants may also interfere with pollination (Lach 2003, Lach 2008), possibly leading to pollen limitation. In the context of ant-cactus interactions, pollinator harassment has been associated with increasing ant protection (Ness 2006). In the present study Argentine ants occurred more often in cactus flowers, which appear to have resulted in lower seed set. Thus, although high densities of Argentine ants were effective in deterring herbivores, an additional consequence of Argentine ant protection may include pollinator harassment.

Ant Richness

The observational survey revealed that the number of ants seasonally present on individual cacti was associated with both the presence of known herbivores and the degree of herbivore damage. Because the native ant species visiting barrel cacti differ in their environmental tolerances (e.g., Schilman et al. 2005), it may be the case that multiple ant species present at a site provide more consistent protection compared to that found at sites with just a

single species. At uninvaded sites we observed strong between year differences in the ant species present at particular cacti; this pattern presumably resulted from strong inter-annual differences in precipitation. For example, *Tapinoma sessile*, a common species in 2007, was effectively replaced in the relatively dry 2008 by *Dorymyrmex insanus* a more thermophilic species. Another strong pattern in this system concerns the ability of Argentine ants to reduce native diversity (Holway and Suarez 2006). While cacti growing along the invasion front may be visited by persisting native ant colonies during summer drought conditions, in the absence of *L. humile*, many cacti in invaded areas simply remained undefended for much of the year. These results potentially provide an example of how multiple species perform overlapping functional roles that provide insurance against declines in any one species (Winfree et al. 2007). Therefore, in the San Diego barrel cactus system, the functional integrity of the multi-species system has largely been replaced, at least in invaded areas, by an intermittently present single species system. Future studies should address how invasion and environmental forcing affect the quality and quantity of protective services offered by ants in this system.



Figure 1.1 A reproductively mature *Ferocactus viridescens* with floral buds, open flowers, and immature fruits.



Figure 1.2 Argentine ants visiting extra-floral nectaries of *Ferocactus viridescens*.



Figure 1.3 *Crematogaster californica* visiting extra-floral nectaries of *F. viridescens*.

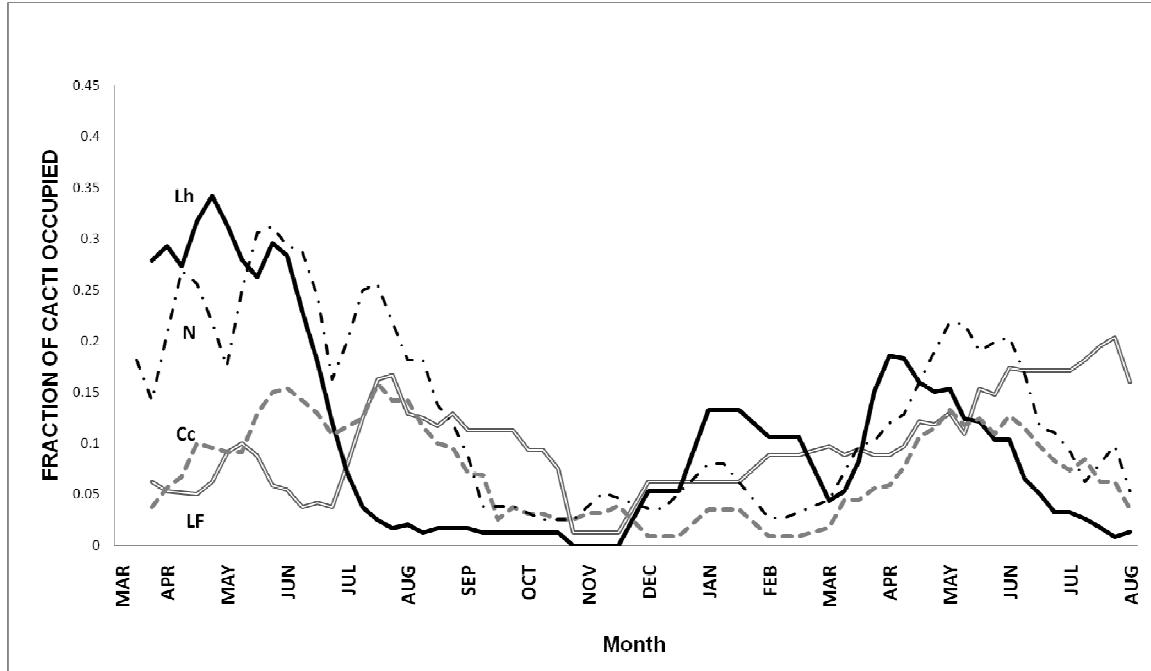
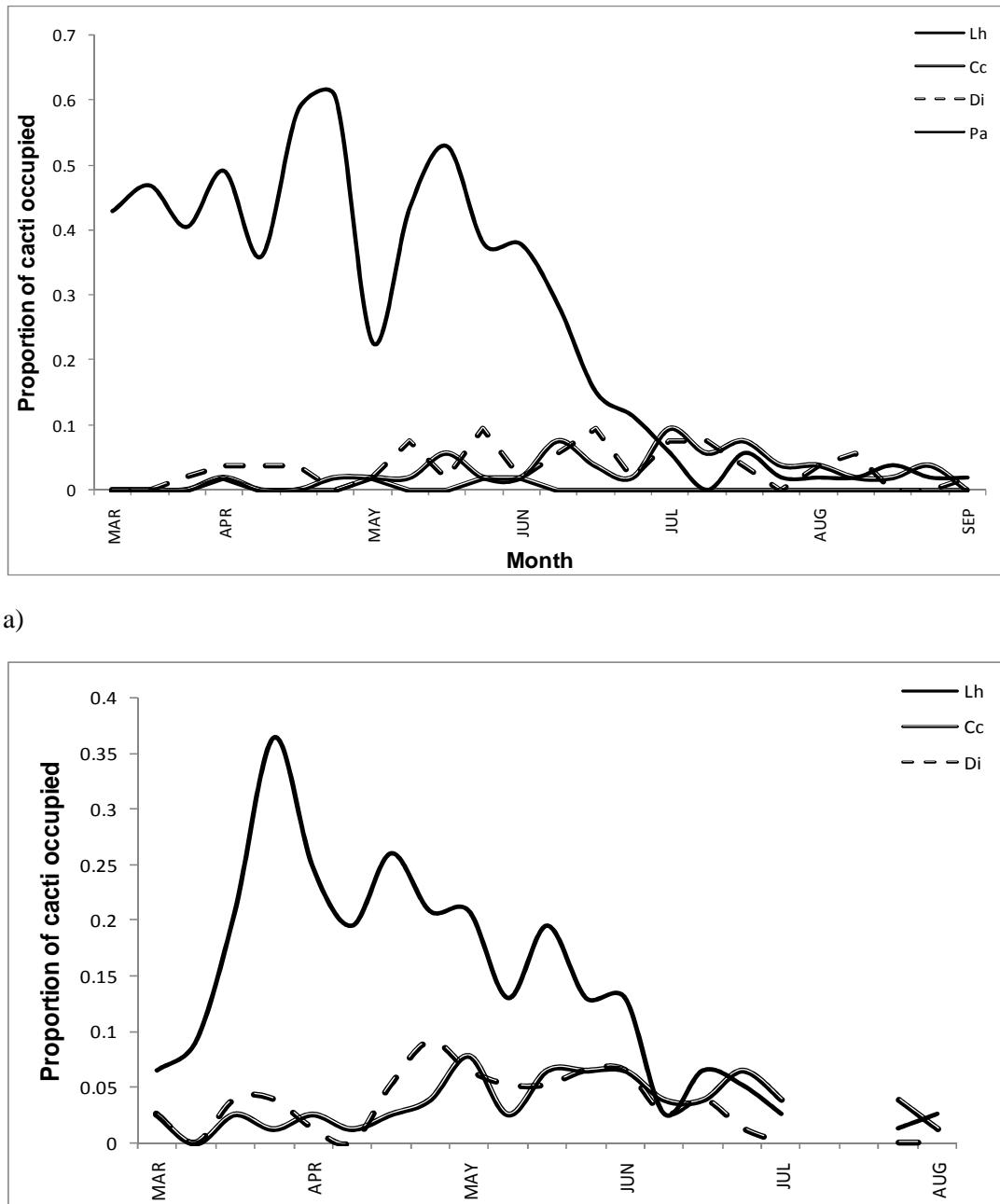


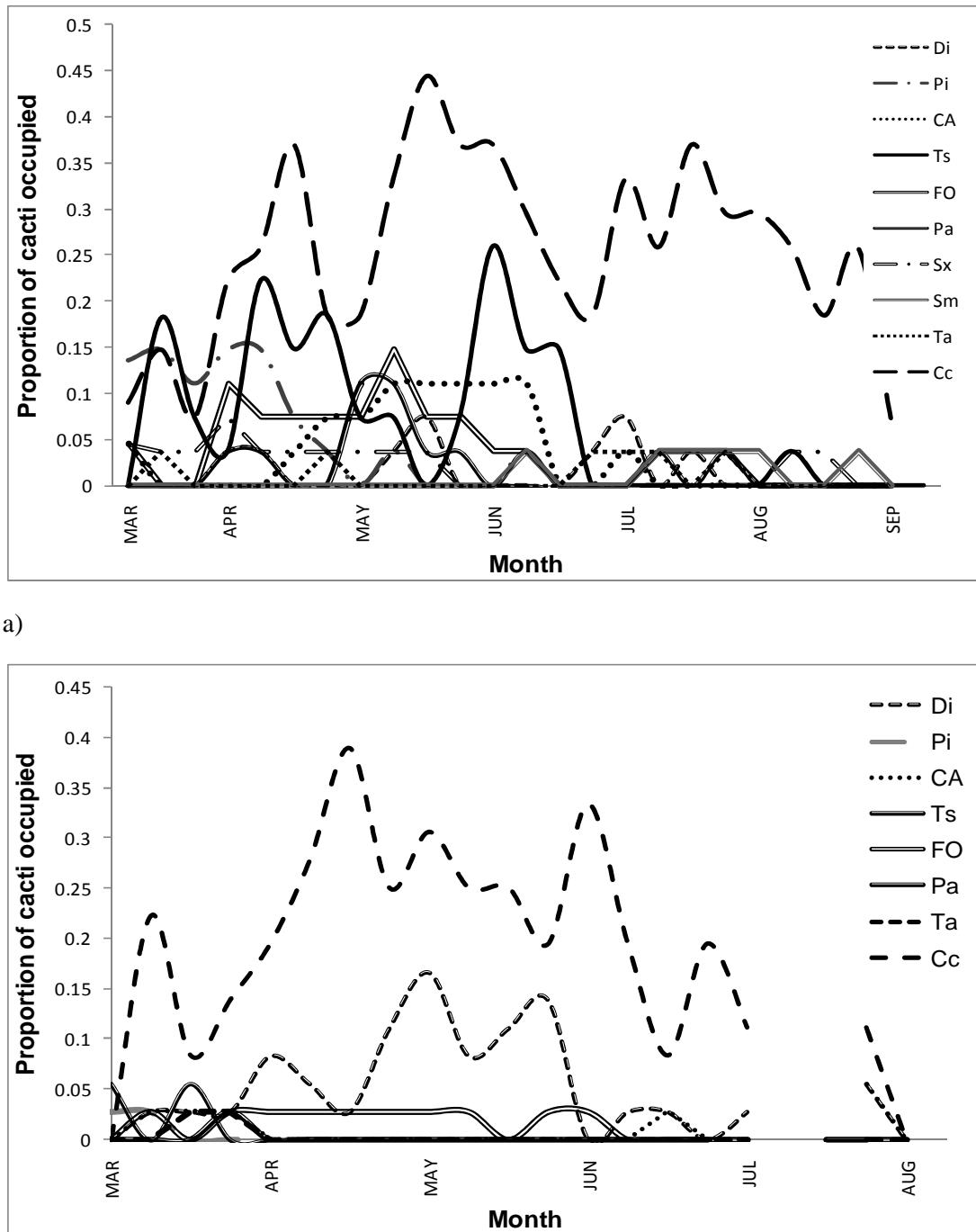
Figure 1.4 The proportion of focal cacti in the observational survey that were occupied by *Linepithema humile* (Lh), Native ants combined (N), *Crematogaster californica* (Cc), and leaf-footed bugs (LF) from March 2007 to August 2008.



a)

b)

Figure 1.5 The proportion of cacti occupied by ants in invaded areas in a) 2007, and b) 2008. Lh = *L. humile*, Cc = *Crematogaster californica*, Di = *Dorymyrmex insanus*, Pa = *Pseudomyrmex apache*.



b)

Figure 1.6 The proportion of cacti occupied by ants in uninvaded areas in a) 2007, and b) 2008.
 CA = *Camponotus* sp., Cc = *Crematogaster californica*, Di = *Dorymyrmex insanus*, FO = *Formica* sp., Pi = *Prenolepis imparis*, Pa = *Pseudomyrmex apache*, Sm = *Solenopsis molesta*, Sx = *Solenopsis xyloni*, Tn = *Temnothorax nevadensis*.



a)



b)



c)

Figure 1.7 *Narnia wilsoni* on *Ferocactus viridescens*: a) feeding on buds, b) feeding on immature fruits, and c) and in the central disk of cactus during fruit development.

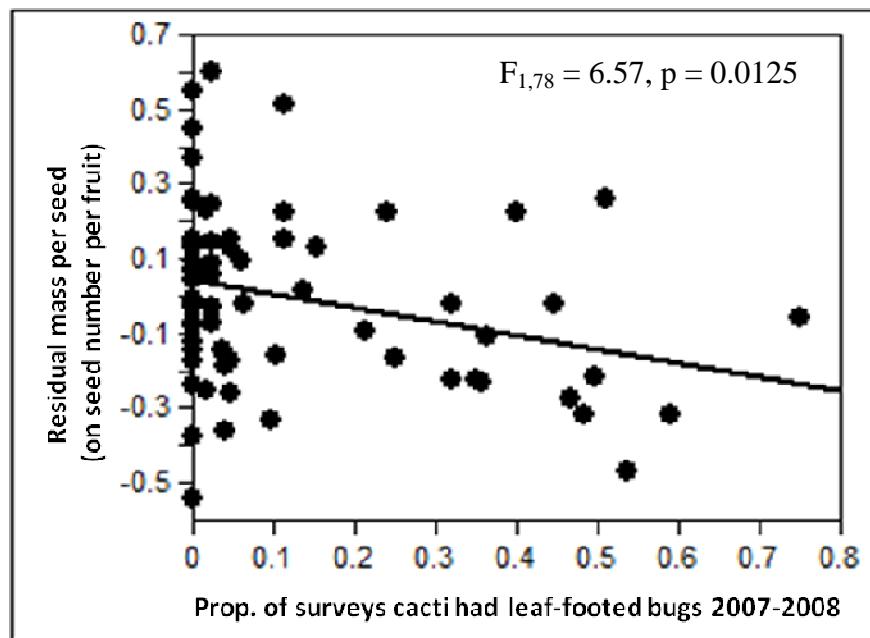
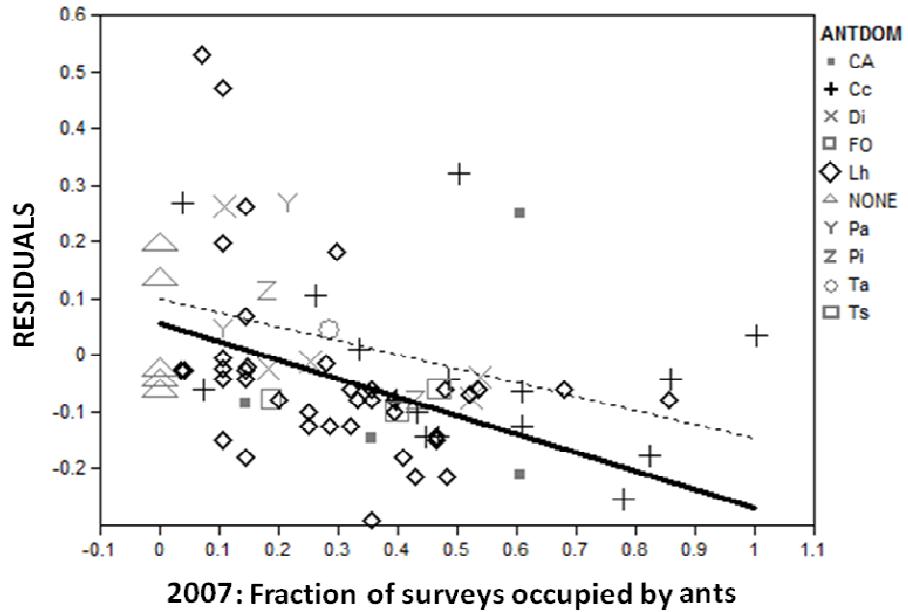


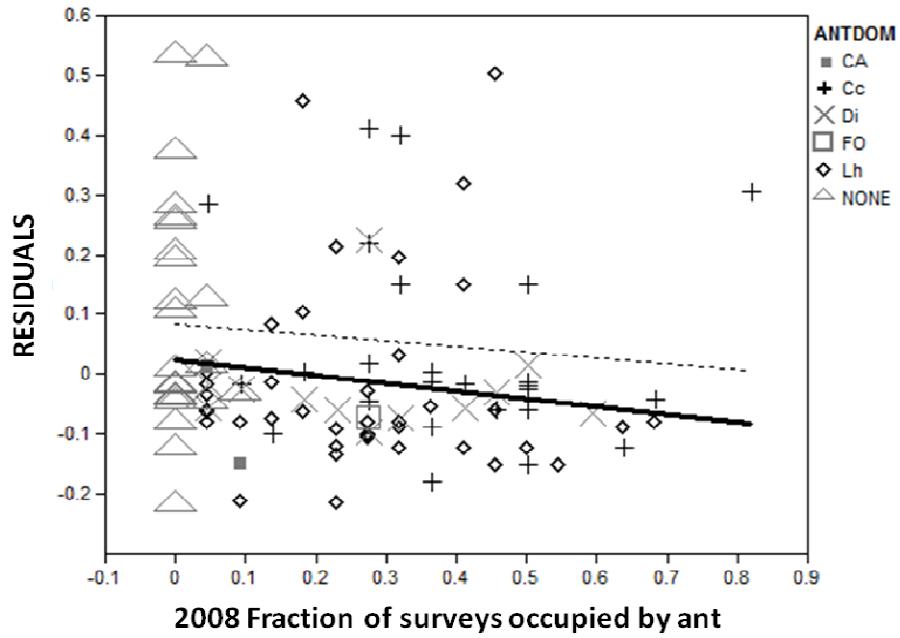
Figure 1.8 Leaf-footed bugs affect seed weight: individual seed mass was inversely related to the proportion of surveys occupied by leaf-footed bugs (residuals of average annual values: mass per seed controlling for seed number per fruit versus proportion of surveys occupied by leaf-footed bugs controlling for cactus volume: $F_{1,78} = 6.57, p = 0.0125$).



a)

Figure 1.9 Ants effect leaf-footed bugs: residual leaf-footed bug occupation (controlling cactus volume (cm^3)) on the proportion of cacti occupied by ants in invaded (solid black line) and uninvaded areas (dashed line). Cacti are individually marked according the most frequent ant occurring on the cacti in a) 2007 and b) 2008. See figure 1.6 for ant abbreviations.

a) 2007 regression model: $F_{2,79} = 5.44$, $p = 0.0019$, parameter estimate: invasion status[in] = -0.034, $p = 0.0491$, parameter estimate: proportion cacti occupied by any ant = -0.287, $p = 0.0002$, interaction: ants*invasion status [in] = -0.0387 $p = 0.6007$.



b)

Figure 1.9 Cont. b) 2008 regression model: $F_{2,112} = 2.12$, $p = 0.1011$, parameter estimate: invaded-uninvaded[in] = -0.034, $p = 0.0389$, parameter estimate: proportion cacti occupied by any ant : -0.110, $p = 0.1734$, interaction: ants*invasion status = -0.0167 $p = 0.8362$.

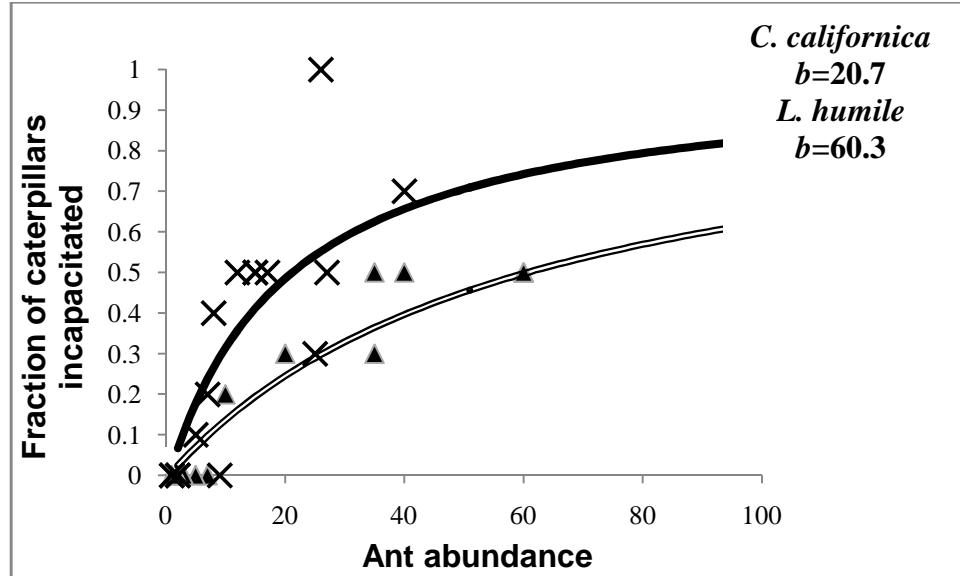


Figure 1.10 Michelis-Menten equation: estimated ant protective services provided by the two most common ant species: solid line = *C. californica*, open line = *L. humile*. For each ant species, b represents the value at which half of the caterpillars were incapacitated within 30 minutes.

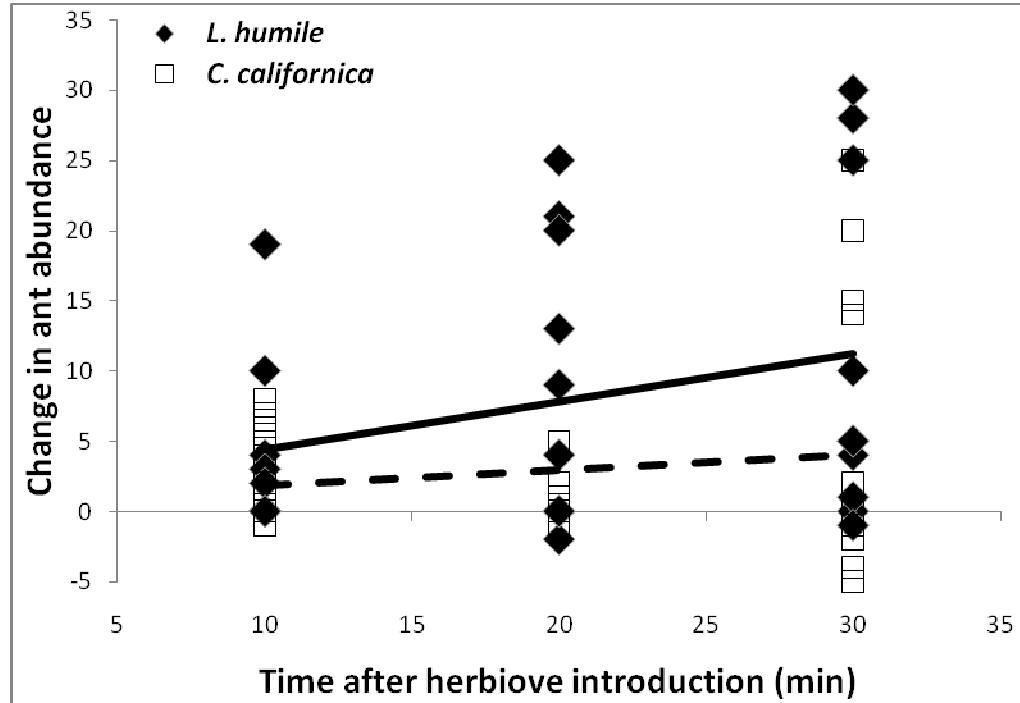
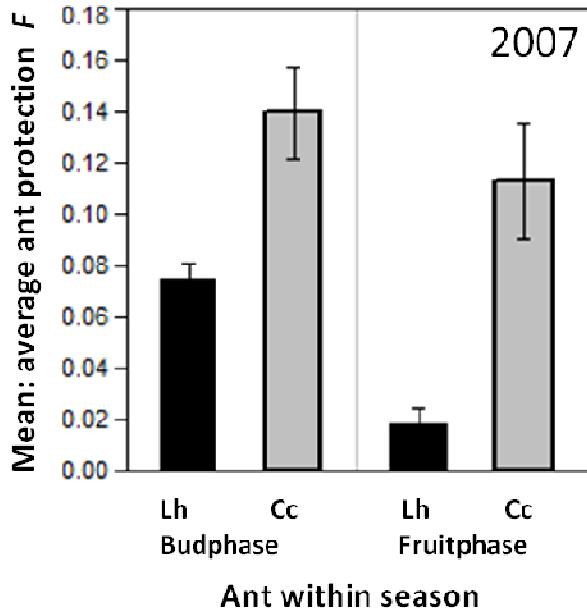
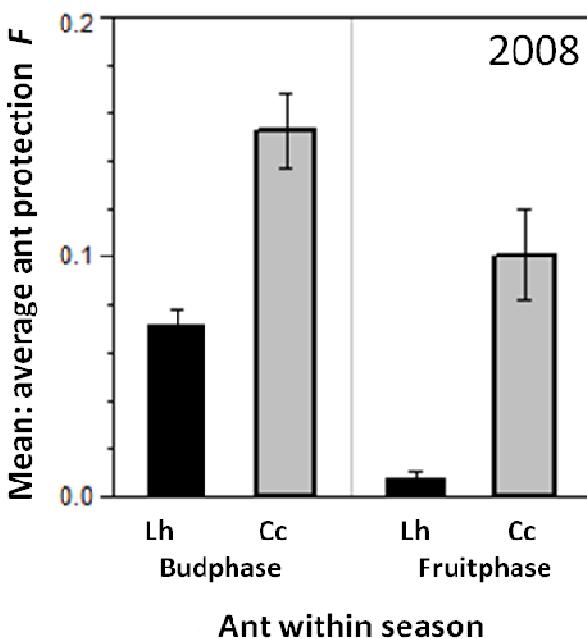


Figure 1.11 Ant recruitment ability: the change in ant abundance on *F. viridescens* when 10 *Manduca sexta* caterpillars were added to the central disk of each cactus. Both ants increased in magnitude upon the addition of caterpillars (comparison of ant abundance at time 0 min and time 30 min, *L. humile* paired t-test: $t = 3.36$, $df = 12$, $p = 0.0056$ and *C. californica* paired t-test: 2.77 , $df = 17$, $p = 0.0131$) There was no interspecific difference in the magnitude of the increase of ant recruitment during the *Manduca* introductions (ant abundance at time 30: t-test 0.56 , $df = 29$, $p = 0.5744$).



a)



b)

Figure 1.12 Seasonal declines in ant protection (F) for cacti assigned as either occupied by *L. humile* (Lh) or by *C. californica* (Cc) averaged across surveys during a) 2007 and b) 2008. In contrast to protection provided by *C. californica*, Argentine ant protection declined both years during the summer (2007 bud phase versus fruit phase Lh: $t = 6.78$, $df = 89$, $p < 0.0001$; and 2008: $t = 7.97$, $df = 85$, $p < 0.0001$). Ant protection for *C. californica* declined in 2008 (2008 bud phase versus fruit phase: $t = 2.15$, $df = 53$, $p = 0.0361$). Expected ant protection differed between these two ant species (two-way ANOVA: $F_{2, 247} = 76.3$, $p < 0.0001$).

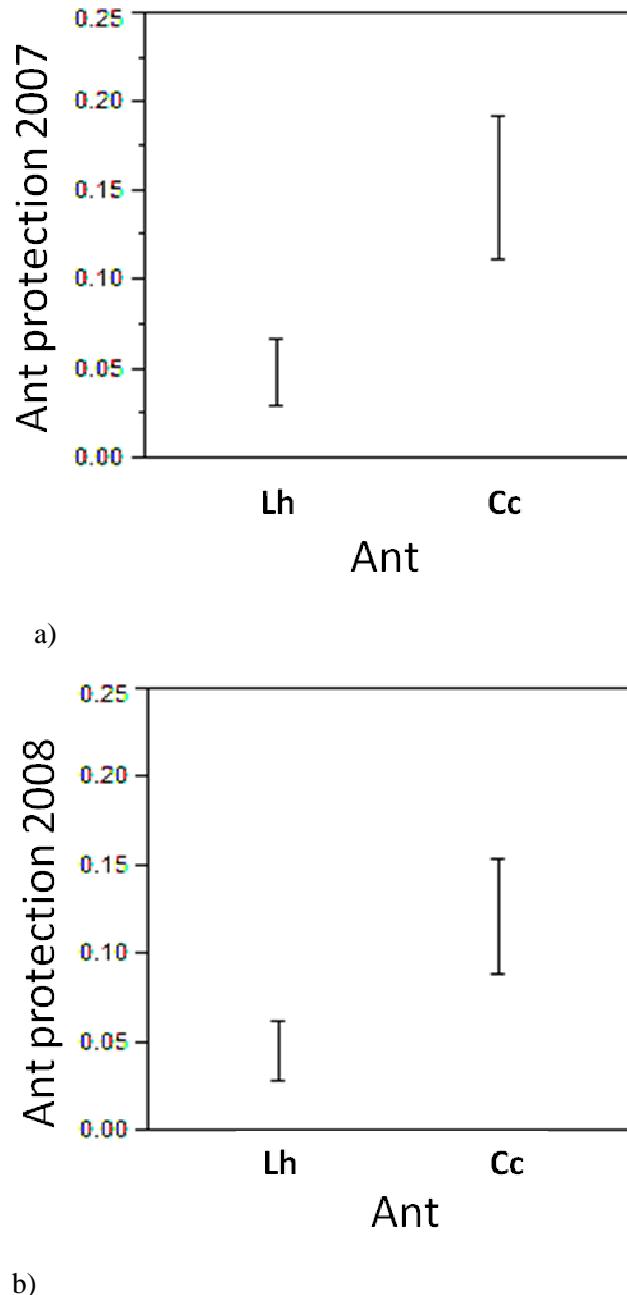


Figure 1.13 Average ranges of ant protection estimated by fitting the Michaelis-Menten equation to ant frequency data across seasons using the upper and lower 95% confidence intervals of estimated b values derived from *Manduca sexta* introductions. Protection differed between *L. humile* (Lh) and *C. californica* (Cc) in a) 2007 and b) 2008 (Protection averaged across seasons for 2007: $t=7.55$, $df = 110$, $p < 0.0001$, and 2008: $t=6.18$, $df = 128$, <0.0001).

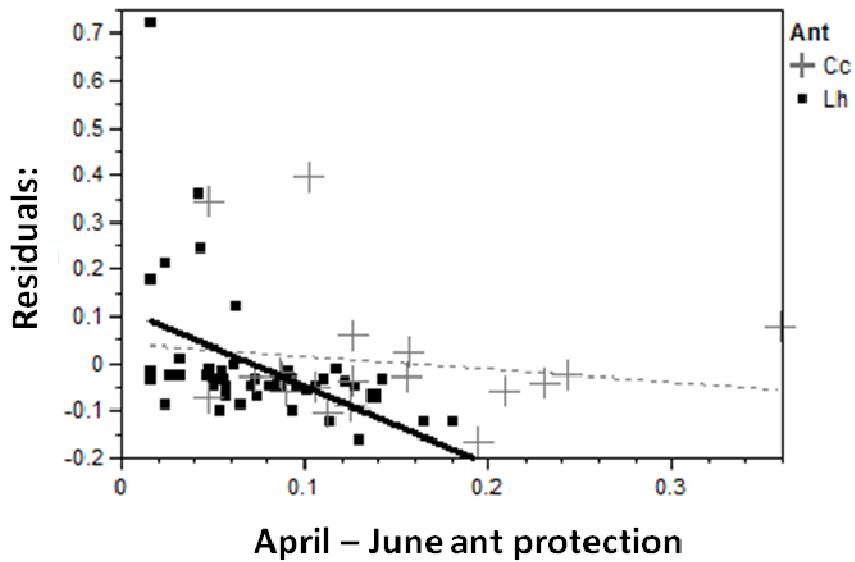


Figure 1.14 The effect of ant protection on leaf-footed bugs. In 2007 removal of leaf-footed bugs by *L. humile* (Lh) decreased with increasing levels of protection (2007 bud phase partial regression leaf-footed bugs (controlling for cactus volume) $F_{3,64} = 3.99$, $p = 0.0115$, estimate *protection* = -0.955, $p = 0.0038$, interaction *protection*ant tending cactus* = -0.69, $p = 0.0332$). No effect was observed for cacti in uninvaded areas occupied by *C. californica* (Cc). Each datum is an individual cactus.

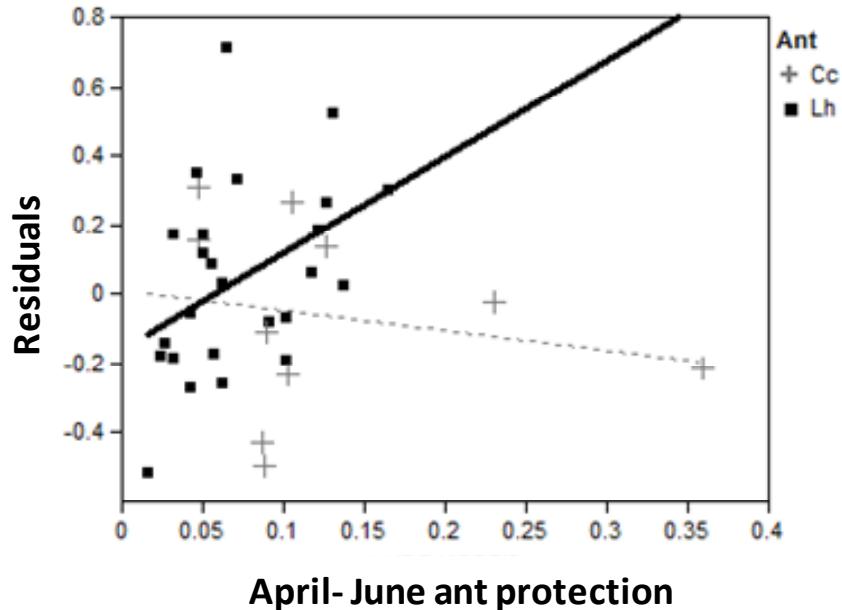


Figure 1.15 The effect of ant protection on seed weight. Residuals of individual seed mass on seed number per fruit (to control for size versus number trade-off). Argentine ant protection resulted in higher values of mass per seed (Bud phase 2007 Model *cactus tended by L. humile or C. californica* $F_{3,34} = 2.01$, $p = 0.1317$, interaction term $L. humile * protection = 1.68$, $p = 0.0448$). Each datum is an individual cactus.

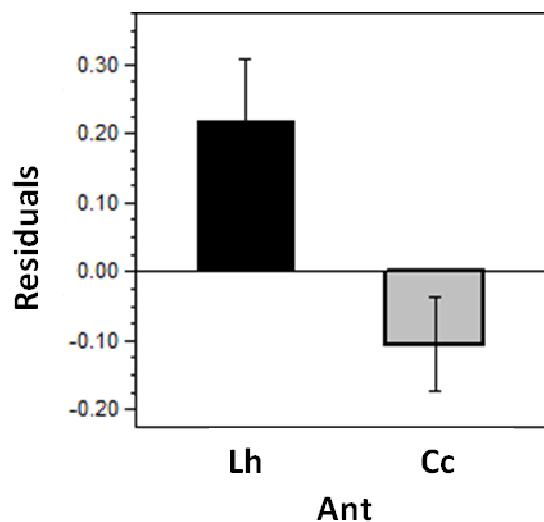


Figure 1.16 Ant presence in flowers: residuals of the number of ants observed within flowers (controlling for flower number) for cacti tended by *L. humile* (Lh) or *C. californica* (Cc). Argentine ants were more often observed foraging within flowers compared to *C. californica* (Bud phase given ant present: $t = 2.33$, $df = 616$, $p = 0.0198$).

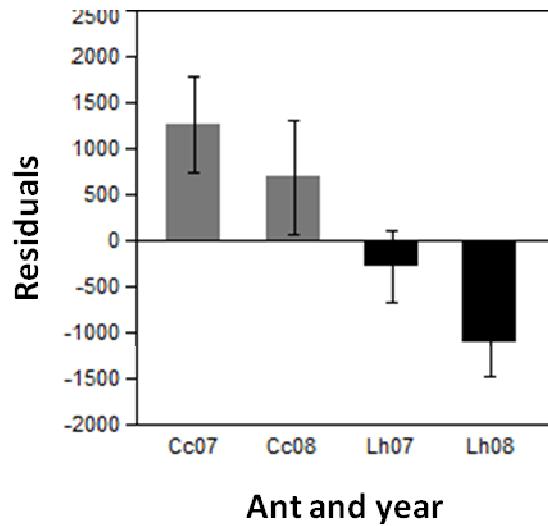


Figure 1.17 Pollinator harassment leads to reduced seed set: residual values of seed set (controlling for fruit set) for cacti tended by *L. humile* (Lh) or *C. californica* (Cc) during the spring of 2007 and 2008. Cacti tended by Argentine ants consistently produced fewer seeds compared to those tended by *C. californica*.

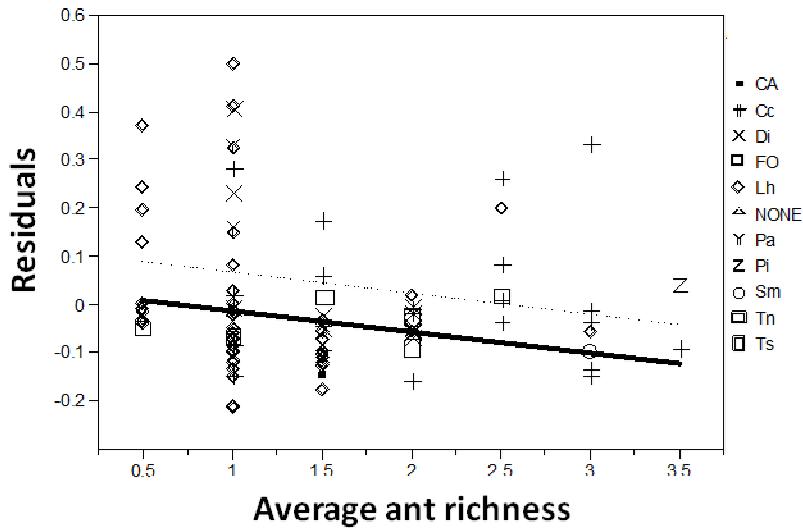


Figure 1.18 The effect of ant richness on leaf-footed bugs. Increasing ant richness reduced the presence of leaf-footed bugs on *F. viridescens*. Residual values of the proportion of cacti occupied by leaf-footed bugs (controlling for cactus volume) on average ant richness during 2007 and 2008 (2007 and 2008 average annual values ANCOVA: $F_{2,112} = 3.50$, $p = 0.0338$; richness effect $F_{1,112} = 4.07$, $p = 0.0463$; invaded versus unininvaded: $F_{1,112} = 5.84$, $p = 0.0176$). The solid line indicates invaded areas, the dashed line unininvaded areas. See figure 1.6 for ant abbreviations.

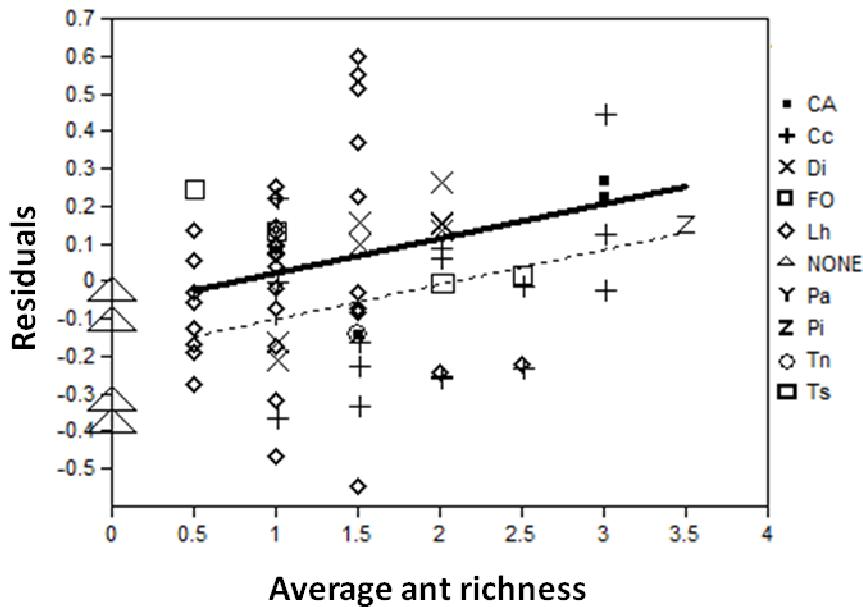


Figure 1.19 The effect of ant richness on seed weight. Increased levels of ant richness were associated with heavier *F. viridescens* seeds. Residual values of mass per seed (controlling for seed number per fruit) on average ant richness during 2007 and 2008 (average annual values fruit subsets ANCOVA: $F_{2,67} = 3.38$, $p = 0.0399$; richness effect: $F_{1,67} = 5.26$, $p = 0.0250$). Invaded areas had significantly heavier seeds with increased ant richness (invaded versus uninvaded effect: $F_{1,67} = 4.19$, $p = 0.0446$). *Camponotus* ($n = 3$) and *Formica* ($n = 2$) species were pooled due because ants in these genera were difficulties to identify to species during surveys. The solid line indicates invaded areas, the dashed line uninvaded areas. See figure 1.6 for ant abbreviations.

Table 1.1 The average fraction of cacti that were occupied by ants during 50 surveys in 2007 and 2008 for invaded areas (n = 52 cacti, n = 76 cacti) and uninvaded areas (n = 28, n = 36). Standard errors are in parentheses. Difficult species to identify were pooled at the genus level and include *Camponotus* (3) and *Formica* (2).

	Invaded	Uninvaded
<i>Linepithema humile</i>	0.18 (0.24)	0
<i>Crematogaster californica</i>	0.03 (0.0034)	0.20 (0.016)
<i>Dorymyrmex insanus</i>	0.03 (0.004)	0.029 (0.0055)
<i>Prenolepis imparis</i>	0	0.020 (0.006)
<i>Camponotus</i>	0	0.018 (0.005)
<i>Tapinoma sessile</i>	0	0.033 (0.009)
<i>Formica</i>	0	0.024 (0.005)
<i>Pseudomyrmex apache</i>	0	0.010 (0.003)
<i>Solenopsis xyloni</i>	0	0.0087 (0.0025)
<i>Solenopsis molesta</i>	0	0.004 (0.0016)
<i>Temnothorax nevadensis</i>	0	0.01 (0.0018)
<i>Temnothorax andrei</i>	0	<0.01
<i>Pheidole pilifera</i>	0	<0.01
<i>Pheidole vistana</i>	0	<0.01
<i>Pogonomyrmex subnitidus</i>	0	<0.01
<i>Myrmecocystus mimicus</i>	0	<0.01
<i>Brachymyrmex</i>	0	<0.01
Native ants pooled	0.07 (0.0066)	0.33 (0.028)
Leaf-footed bugs	0.095 (0.0068)	0.13 (0.011)
Adult Leaf-footed bugs	0.068 (0.0061)	0.097 (0.0092)
Juvenile Leaf-footed bugs	0.037 (0.0055)	0.052 (0.0095)

Table 1.2 Reproductive variables for *Ferocactus viridescens*. Plants associated with *L. humile* or *C. californica* were averaged when possible across 2007 and 2008.

<i>F. viridescens</i> fitness variable	<i>L. humile</i>	<i>C. californica</i>
Observed : expected reproductive units	(39) 1.13 ± 0.06	(15) 1.01 ± 0.12
Surviving units : units produced	(39) 0.87 ± 0.07	(15) 0.77 ± 0.10
Fruitset	(39) 7 ± 0.73	(15) 6 ± 1.00
Fruit dry weight (mg)	(36) 832 ± 36	(14) 762 ± 85
Seed mass per fruit (mg)	(36) 364 ± 26	(14) 305 ± 51
Mass per seed (mg)	(39) 0.82 ± 0.04	(15) 0.75 ± 0.06
Seed number per fruit (mg)	(36) 453 ± 27	(14) 431 ± 68
Seed set	(36) 4017 ± 554	(14) 3292 ± 843
Plant total seed biomass (mg)	(36) 3291 ± 491	(14) 2456 ± 692

APPENDIX

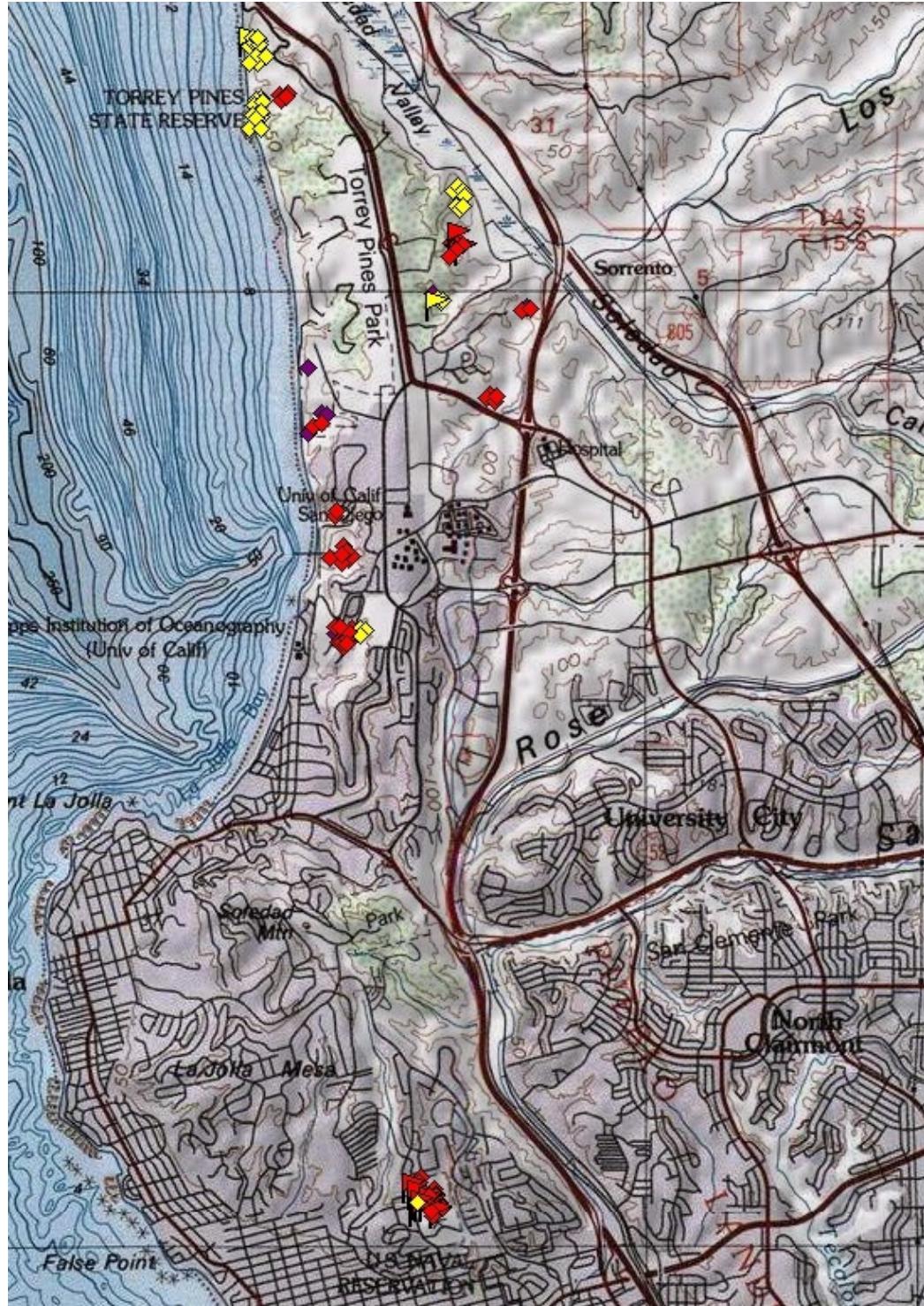


Figure A.1 Map of study area showing cacti either occupied by native ants (yellow diamonds), Argentine ants (red diamonds), or mixed indicating seasonal turnover (purple diamonds). Yellow and red flags indicate no ant presence for surveys conducted in 2007 or 2008. See figures A.2-A.4 for more detail.

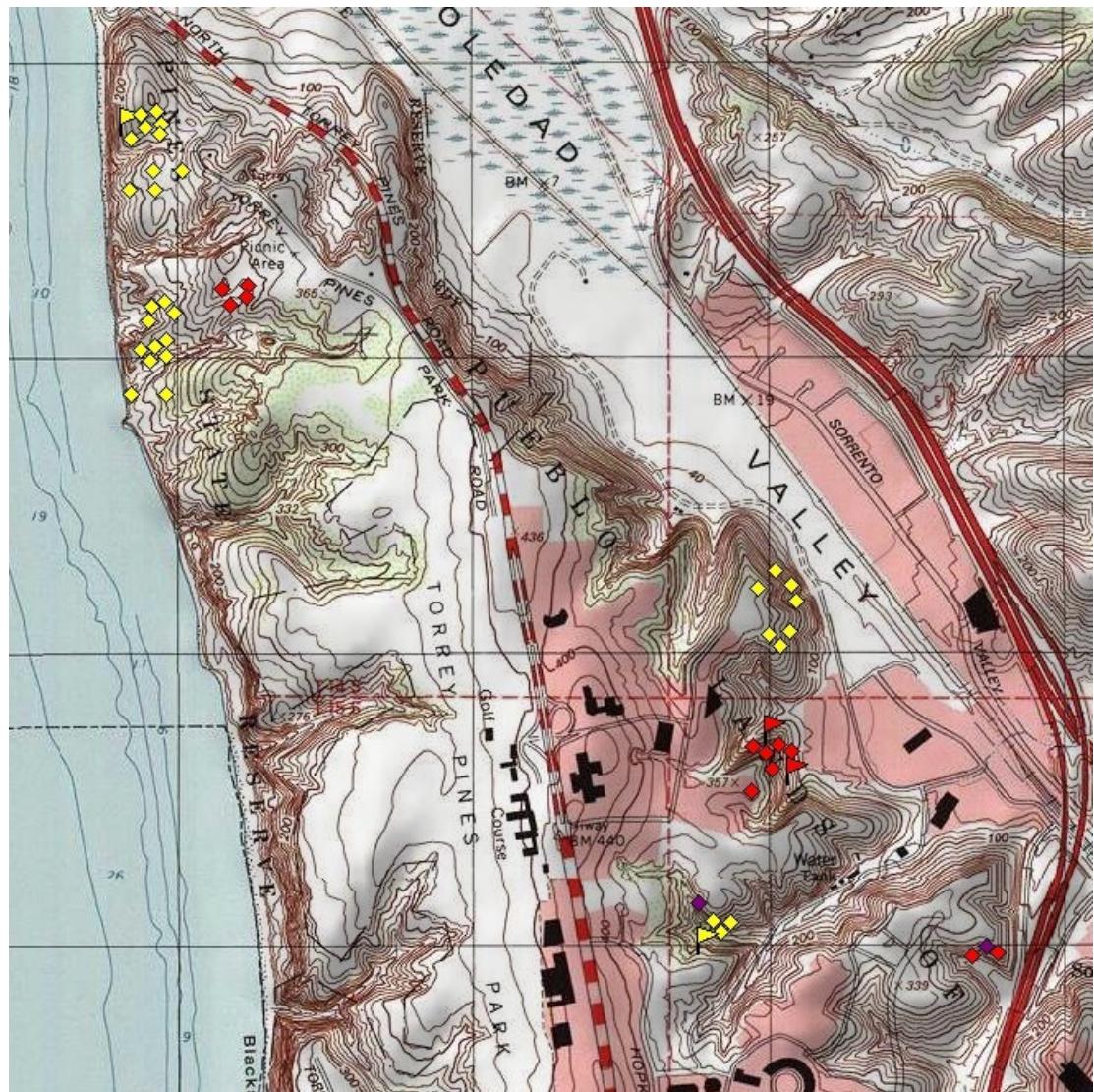


Figure A.2 Detailed map of the northernmost section of the study area showing cacti either occupied by native ants (yellow diamonds), Argentine ants (red diamonds), or mixed indicating seasonal turnover (purple diamonds). Yellow and red flags indicate no ant presence for surveys conducted in 2007 or 2008.

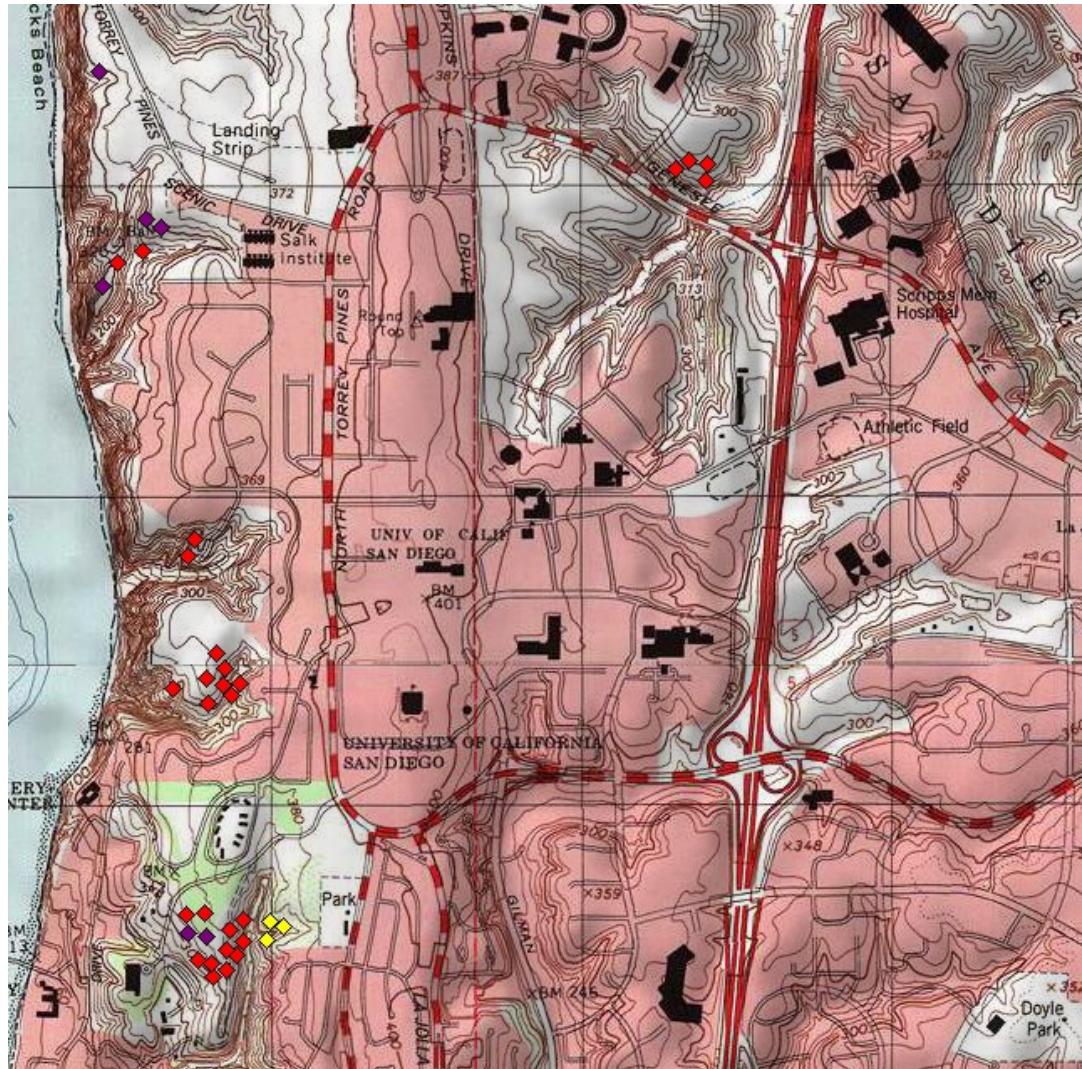


Figure A.3 Detailed map of study area around UCSD showing cacti either occupied by native ants (yellow diamonds), Argentine ants (red diamonds), or mixed indicating seasonal turnover (purple diamonds).

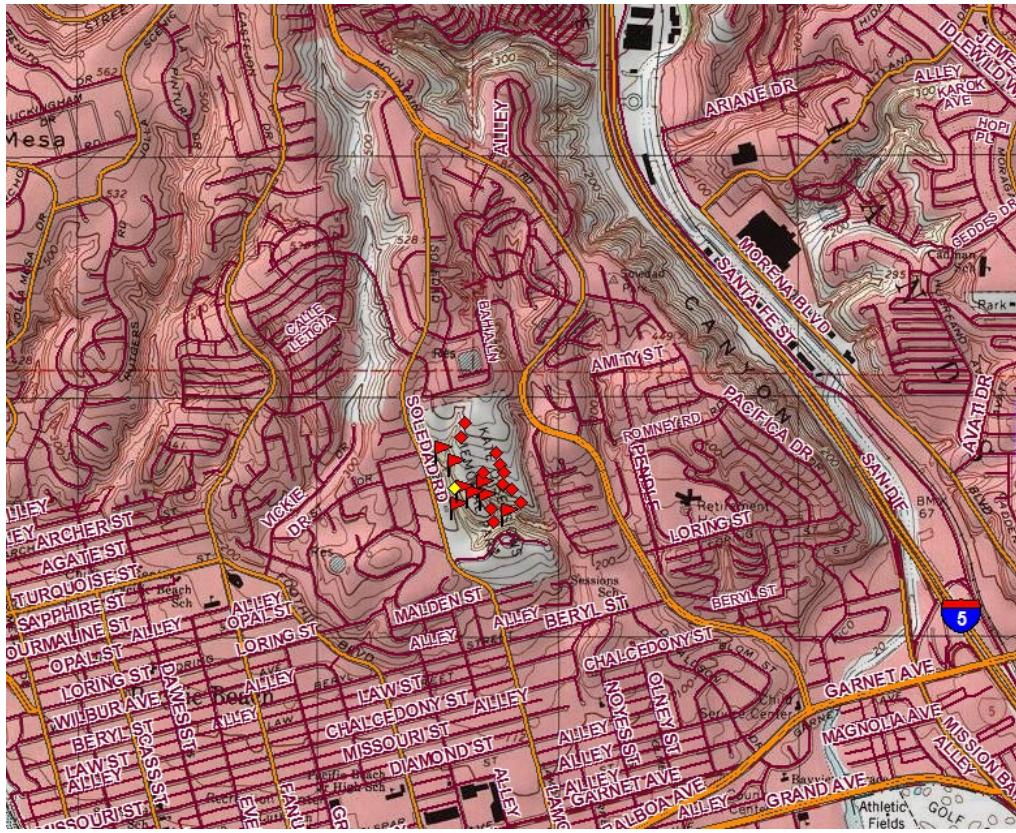


Figure A.4 Detailed map of southernmost study area (Kate Sessions Park). Cacti were added to the observational survey in 2008. Cacti from this site were either occupied by native ants (yellow diamonds) or Argentine ants (red diamonds). The red flags indicate no Argentine ant presence for surveys conducted in 2007 or 2008.

Figure A.5 Fraction of cacti occupied by leaf-footed bugs in invaded and uninvaded areas in 2007 and 2008.

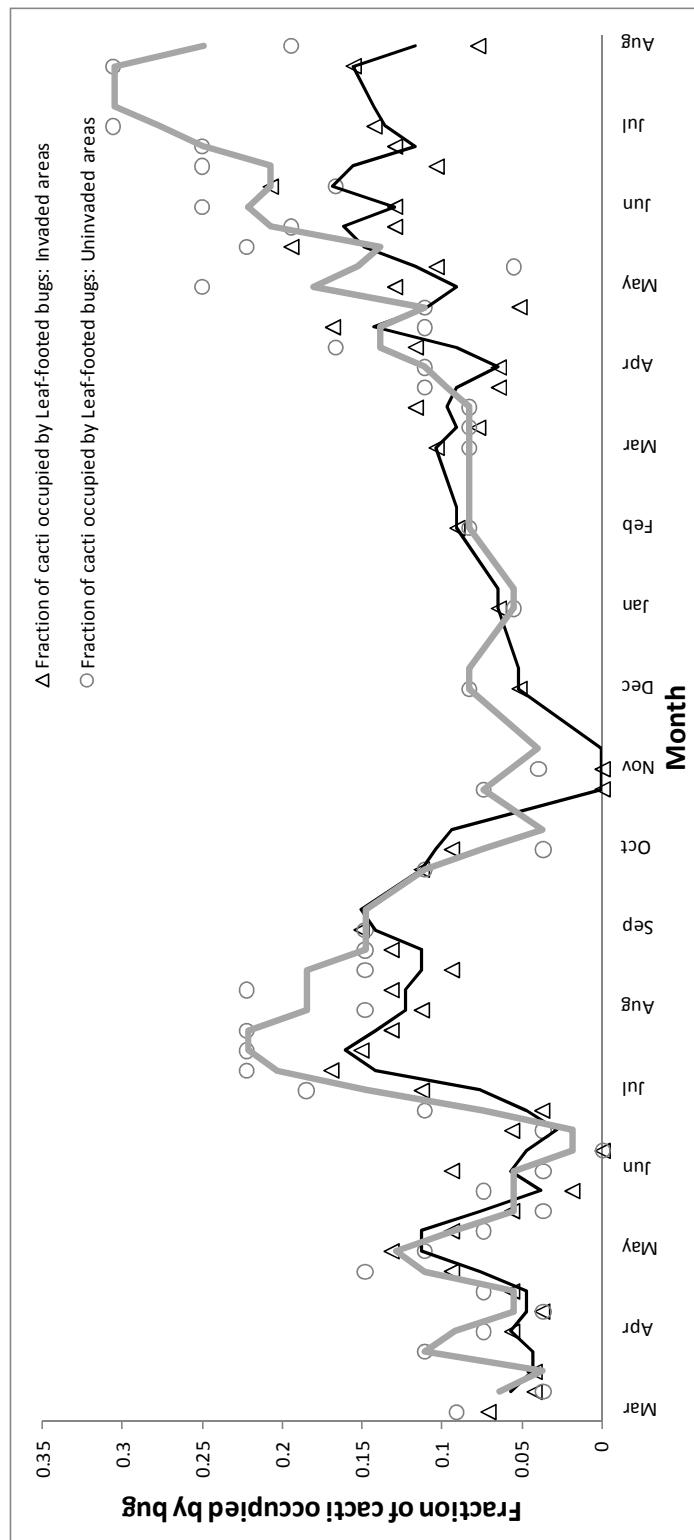


Figure A.6 The fraction of cacti occupied by ants and leaf-footed bugs in invaded areas during 2007 and 2008.

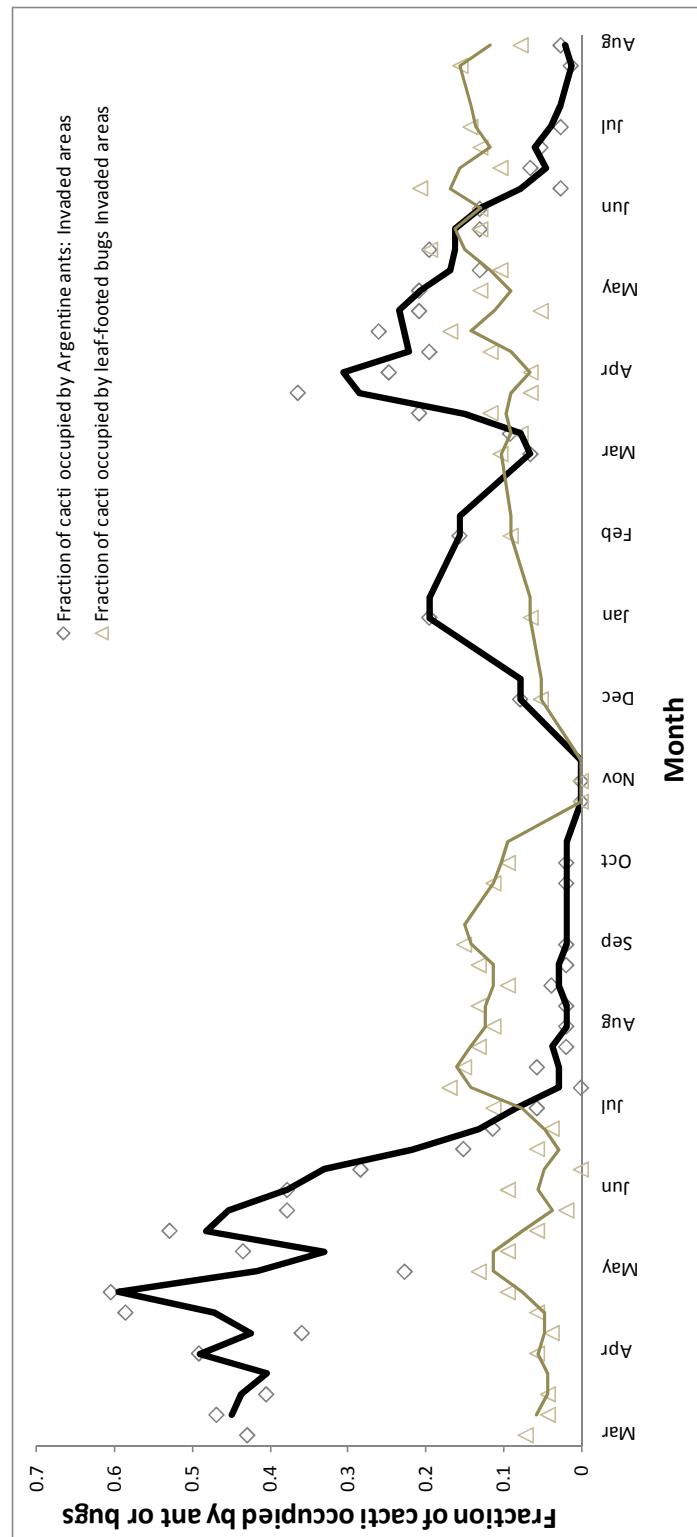
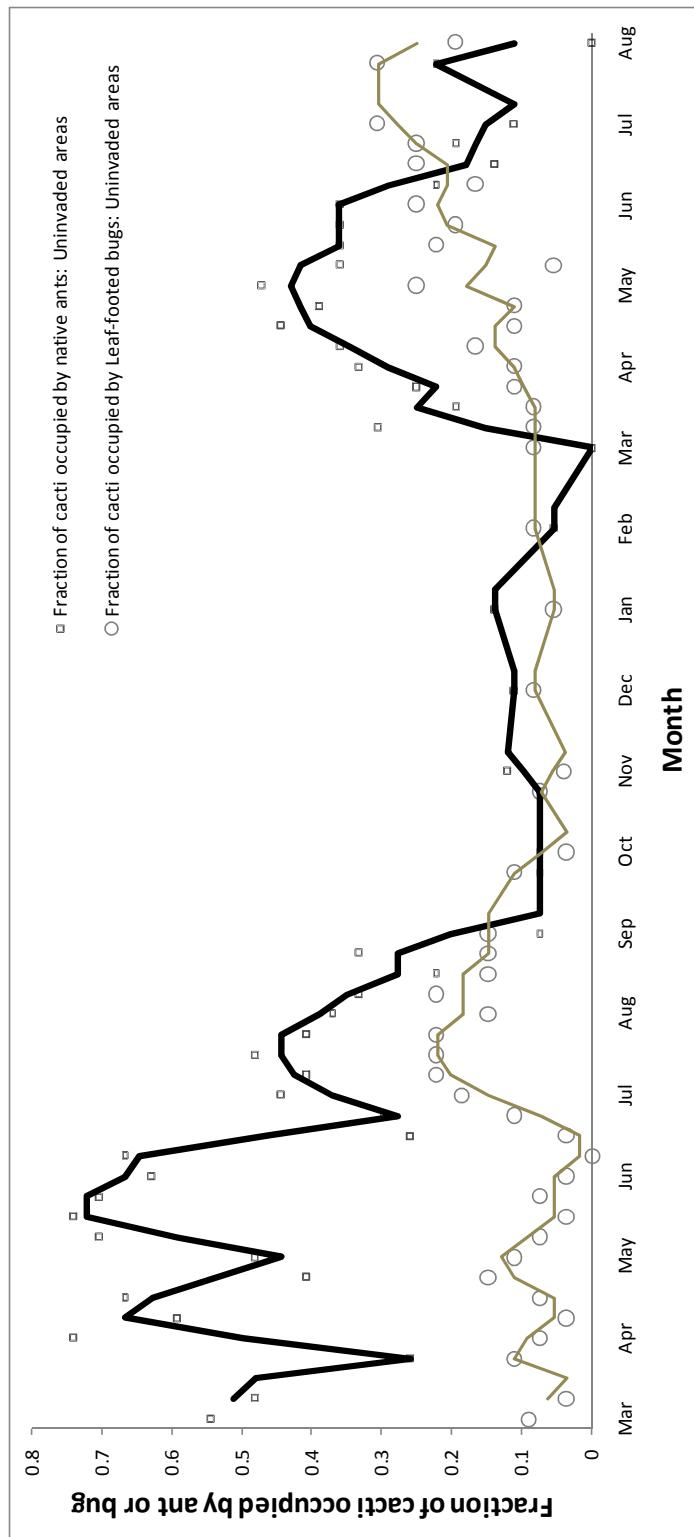


Figure A.7 The fraction of cacti occupied by native ants and leaf-footed bugs in uninvaded areas during 2007 and 2008.



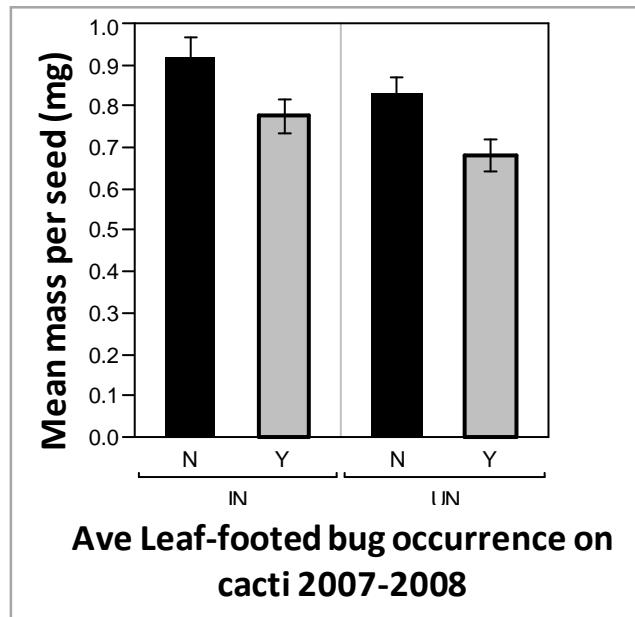
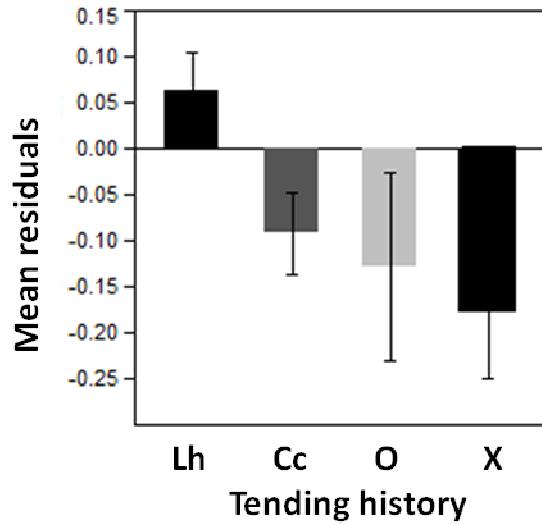
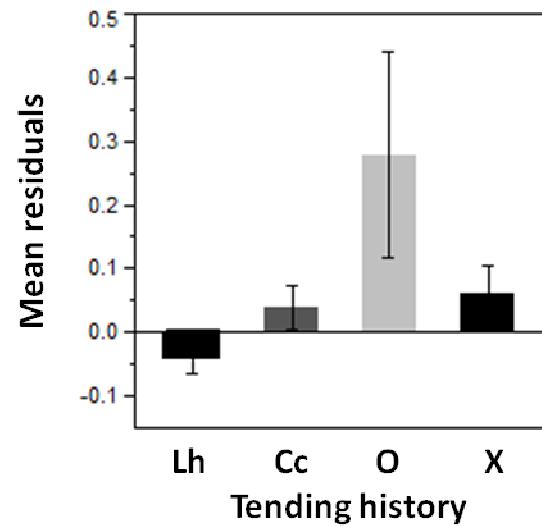


Figure A.8 Mass per seed did not differ between invaded and uninvaded areas for cacti that either did not have (N) or did have (Y) leaf-footed bugs. The similarity in mass per seed values for sites with or without leaf-footed bugs suggests similar growing conditions in invaded and uninvaded sites. (2007- 2008: leaf-footed bugs = N: $t = -1.15$ df =49 $p = 0.2533$; 2007-2008 leaf-footed bugs = Y: $t = -1.69$, df =57, $p = 0.0963$).



a)



b)

Figure A.9 The effect of tending history on mean seed weights and leaf-footed bug occupation. Based on patterns of ant visitation, cacti were categorized as follows: *L. humile* (Lh), *C. californica* (Cc), unintended in invaded areas, (X), or unintended in uninvaded areas (O). a) Mean mass per seed (controlling for seed number per fruit) versus ant tending history for all observations in 2007 and 2008: $F_{3,77} = 3.72$, $p = 0.0149$. b) Proportion of cacti occupied by leaf-footed bugs (controlling for cactus volume) versus tending history ($F_{3,83} = 4.37$, $p = 0.0067$). Despite higher observations of leaf-footed bugs, uninvaded areas did not sustain as much damage from herbivory as did invaded areas.

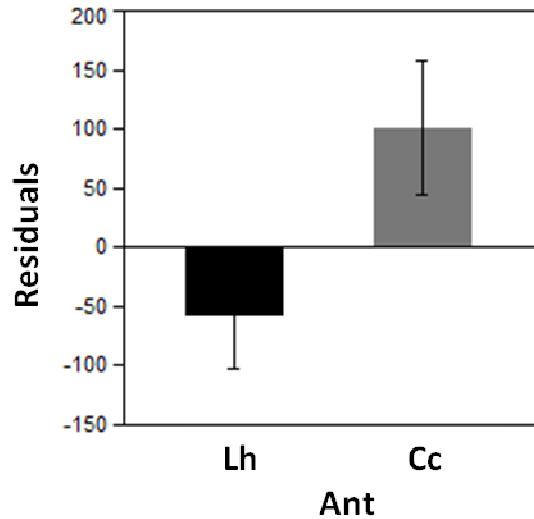


Figure A.10 Further evidence of potential pollinator harassment by *L. humile*. Residual values of seed number per fruit (controlling for fruit dry weight) compared across cacti tended by *L. humile* (Lh) or by *C. californica* (Cc). The presence of *L. humile* (Lh) on cacti in the spring was associated with reduced seed number per fruit (2007 $t = 2.05$, $df = 33$, $p = 0.0477$, but not 2008).

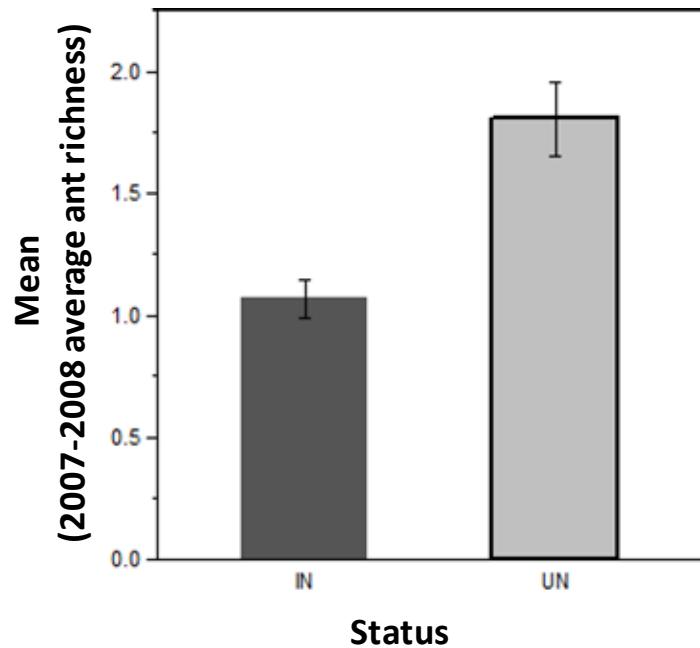


Figure A.11 Average ant richness as a function of invasion status: IN = invaded, UN = uninvaded. Richness here is a measure of the different kinds of ant species that visited a cactus during 2007 and 2008. Some ant species were pooled as they were indistinguishable in the field during the survey period.

Table A.1 GPS coordinates of cacti used in the study throughout 2007 and 2008. Cacti marked with an * were added in 2008.

Cactus code	N	W	Elevation (m)	STATUS
BLK1-1	32 52 41.64	117 14 54.54	78	Invaded
BLK1-2	32 52 41.58	117 14 54.6	78	Invaded
GP1-1	32 53 31.68	117 15 6.42	84	Invaded
GRD1-1	32 55 16.56	117 15 18.84	97	Invaded
*KATE10-1	32 48 47.46	117 14 21.06	95	Invaded
*KATE10-2	32 48 47.4	117 14 20.88	94	Invaded
*KATE1-1	32 48 48.66	117 14 11.94	99	Invaded
*KATE2-1	32 48 47.58	117 14 11.52	98	Invaded
*KATE2-2	32 48 47.64	117 14 11.34	89	Invaded
*KATE2-3	32 48 47.52	117 14 11.34	92	Invaded
*KATE2-4	32 48 47.22	117 14 11.1	93	Invaded
*KATE2-5	32 48 47.16	117 14 11.1	93	Invaded
*KATE3-1	32 48 46.5	117 14 10.5	90	Invaded
*KATE4-1	32 48 45.72	117 14 11.46	84	Invaded
*KATE4-2	32 48 45.72	117 14 11.16	87	Invaded
*KATE4-3	32 48 45.72	117 14 11.58	84	Invaded
*KATE4-4	32 48 45.72	117 14 11.64	79	Invaded
*KATE5-1	32 48 46.02	117 14 12	84	Invaded
*KATE5-2	32 48 46.44	117 14 12.06	85	Invaded
*KATE6-1	32 48 48.84	117 14 16.32	85	Invaded
*KATE7-1	32 48 48.18	117 14 17.1	82	Invaded
*KATE7-2	32 48 48.18	117 14 17.22	84	Invaded
*KATE7-3	32 48 48.42	117 14 17.52	83	Invaded
*KATE8-1	32 48 45.6	117 14 20.16	87	Invaded
*KATE8-2	32 48 45.66	117 14 20.52	86	Invaded
*KATE8-3	32 48 45.96	117 14 20.4	87	Invaded
*KATE9-1	32 48 56.46	117 14 20.34	121	Invaded
*KATE9-2	32 48 56.58	117 14 20.76	119	Invaded

Table A.1 Cont.

Cactus code	N	W	Elevation (m)	STATUS
KN1-1	32 52 30.3	117 14 50.82	108	Invaded
KN1-3	32 52 30.24	117 14 50.88	108	Invaded
KN2-1	32 52 27.72	117 14 52.32	101	Invaded
KN2-2	32 52 27.66	117 14 52.32	101	Invaded
KN2-3	32 52 27.6	117 14 52.32	101	Invaded
KN2-4	32 52 27.54	117 14 52.26	101	Invaded
KN3-1	32 52 27.48	117 14 53.88	128	Invaded
KN4-1	32 52 27.48	117 14 56.82	92	Invaded
PH1-1	32 53 21.84	117 13 52.74	97	Invaded
PH1-2	32 53 21.84	117 13 52.68	97	Invaded
PH1-3	32 53 21.78	117 13 52.68	97	Invaded
PH1-4	32 53 21.78	117 13 52.62	97	Invaded
PHII1-1	32 53 52.8	117 13 38.46	81	Invaded
PHII1-2	32 53 52.8	117 13 38.4	81	Invaded
PHII1-3	32 53 52.86	117 13 38.46	81	Invaded
SALK1-1	32 53 14.52	117 15 0.12	81	Invaded
SALK1-2	32 53 14.46	117 15 0.12	81	Invaded
SALK1-3	32 53 14.58	117 15 0.12	81	Invaded
SALK1-4	32 53 14.58	117 15 0.06	81	Invaded
SALK2-1	32 53 8.46	117 15 5.46	94	Invaded
SK1-1	32 51 58.92	117 14 51.84	96	Invaded
SK1-2	32 51 58.8	117 14 52.08	93	Invaded
SK1-3	32 51 58.74	117 14 52.2	106	Invaded
SK2-1	32 52 0.42	117 14 50.22	112	Invaded
SK2-2	32 52 0.36	117 14 50.22	100	Invaded
SK2-3	32 52 0.48	117 14 50.22	102	Invaded
SK2-4	32 52 0.84	117 14 49.74	135	Invaded
SK3-1	32 51 59.4	117 14 50.58	101	Invaded

Table A.1 Cont.

Cactus code	N	W	Elevation (m)	STATUS
SK4-1	32 52 4.14	117 14 44.04	105	Invaded
SK4-2	32 52 3.9	117 14 44.22	104	Invaded
SK4-3	32 52 3.96	117 14 44.28	102	Invaded
SK5-1	32 52 0.24	117 14 52.62	85	Invaded
SK5-2	32 52 0	117 14 52.74	95	Invaded
SK5-3	32 52 0.12	117 14 52.38	95	Invaded
SK5-4	32 52 1.86	117 14 54.48	99	Invaded
SK5-5	32 52 1.74	117 14 53.82	96	Invaded
SK5-6	32 52 1.74	117 14 54.18	97	Invaded
SKIM1-1	32 54 12.9	117 14 8.76	104	Invaded
SKIM1-2	32 54 12.9	117 14 8.7	104	Invaded
SKIM1-3	32 54 12.9	117 14 8.64	104	Invaded
SKIM1-4	32 54 12.96	117 14 8.58	104	Invaded
SKIM1-5	32 54 13.02	117 14 8.76	104	Invaded
SKIM1-6	32 54 12.9	117 14 8.82	104	Invaded
SKIM1-7	32 54 12.84	117 14 8.76	104	Invaded
TPII1-1	32 55 3.66	117 15 19.92	76	Invaded
TPII1-2	32 55 3.72	117 15 19.86	76	Invaded
TPII1-3	32 55 3.78	117 15 19.8	76	Invaded
TPII1-4	32 55 3.84	117 15 19.74	76	Invaded
TSRI1-1	32 53 56.04	117 14 14.04	93	Invaded
CO1-1	32 54 30.3	117 14 7.92	103	Uninvaded
CO1-2	32 54 30.3	117 14 7.86	103	Uninvaded
CO1-3	32 54 30.24	117 14 7.86	103	Uninvaded
CO2-1	32 54 32.1	117 14 6.96	85	Uninvaded
CO2-2	32 54 32.16	117 14 6.96	85	Uninvaded
CO3-1	32 54 26.64	117 14 7.86	93	Uninvaded
CO3-2	32 54 26.7	117 14 7.86	93	Uninvaded

Table A.1 Cont.

Cactus code	N	W	Elevation (m)	STATUS
CO3-3	32 54 26.64	117 14 7.8	93	Uninvaded
*GUY1-1	32 55 22.38	117 15 30.18	66	Uninvaded
*GUY1-2	32 55 22.56	117 15 30.66	59	Uninvaded
*GUY2-1	32 55 23.7	117 15 30.42	65	Uninvaded
*GUY2-2	32 55 23.28	117 15 30.18	65	Uninvaded
*GUY2-3	32 55 23.34	117 15 29.28	71	Uninvaded
*GUY3-1	32 55 22.2	117 15 27.36	61	Uninvaded
*GUY3-2	32 55 22.56	117 15 27.24	59	Uninvaded
*GUY3-3	32 55 22.98	117 15 27.66	65	Uninvaded
*GUY3-4	32 55 22.98	117 15 27.78	65	Uninvaded
PG1-1	32 55 17.4	117 15 25.62	69	Uninvaded
PG2-1	32 55 16.14	117 15 28.08	64	Uninvaded
PG2-2	32 55 16.02	117 15 28.08	64	Uninvaded
PG2-3	32 55 16.08	117 15 28.14	64	Uninvaded
RZ1-1	32 55 2.58	117 15 25.56	51	Uninvaded
RZ1-2	32 55 2.64	117 15 25.62	51	Uninvaded
RZ1-3	32 55 2.58	117 15 25.74	51	Uninvaded
RZ1-5	32 55 2.58	117 15 25.44	51	Uninvaded
TP1-1	32 54 53.46	117 15 27.78	34	Uninvaded
TP1-2	32 54 54	117 15 30	34	Uninvaded
TSRI1-2	32 53 55.98	117 14 13.98	93	Uninvaded
TSRI1-3	32 53 55.92	117 14 13.92	93	Uninvaded
TSRI1-4	32 53 55.86	117 14 13.86	93	Uninvaded
TSRI1-5	32 53 55.8	117 14 13.8	93	Uninvaded
YP1-1	32 54 58.92	117 15 26.94	43	Uninvaded
YP1-2	32 54 58.98	117 15 26.94	43	Uninvaded
YP1-3	32 54 59.04	117 15 27	43	Uninvaded
YP1-4	32 54 58.92	117 15 27.12	43	Uninvaded
YP1-5	32 54 58.92	117 15 27.18	43	Uninvaded

Table A.2 The range of estimated ant protection according to year and season (Bud phase = April - June, Fruit phase = July-October). Mean protection is listed with standard errors in parenthesis. Included are the upper and lower 95% confidence intervals for each ant species. Cacti were assigned as either dominated by *L. humile* or by *C. californica* if they made up at least half of the ant occupation observations. Argentine ants provided less protection than did *C. californica* during the April-June bud versus flowering stage of *F. viridescens* development in 2007 ($t = 4.38$, $df = 63$, $p < 0.0001$) and 2008 ($t = 5.46$, $df = 63$, $p < 0.0001$). Argentine ants also provided less protection during the production of fruits in 2007 ($t = 5.38$, $df = 69$, $p < 0.0001$) and 2008 ($t = 6.03$, $df = 69$, $p < 0.0001$).

Linepithema humile

	2007		2008	
	Bud phase	Fruit phase	Bud phase	Fruit phase
Lower 95%	0.11 (0.009)	0.03 (0.008)	0.11 (0.011)	0.02 (0.006)
Mean protection	0.07 (0.006)	0.02 (0.006)	0.07 (0.008)	0.01 (0.004)
Upper 95%	0.05 (0.004)	0.01 (0.004)	0.05 (0.005)	0.01 (0.003)

Crematogaster californica

	2007		2008	
	Bud phase	Fruit phase	Bud phase	Fruit phase
Lower 95%	0.20 (0.027)	0.18 (0.036)	0.19 (0.018)	0.12 (0.025)
Mean protection	0.16 (0.022)	0.14 (0.029)	0.14 (0.015)	0.09 (0.020)
Upper 95%	0.12 (0.018)	0.11 (0.023)	0.11 (0.012)	0.07 (0.015)

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