

Infiltration of a facultative ant–plant mutualism by the introduced Argentine ant: effects on mutualist diversity and mutualism benefits

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Abstract. 1. Ant–plant mutualisms have been the focus of considerable empirical research, but few studies have investigated how introduced ants affect these interactions. Using 2 years of survey data, this study examines how the introduced Argentine ant [*Linepithema humile* (Mayr)] differs from native ants with respect to its ability to protect the extrafloral nectary-bearing coast barrel cactus (*Ferocactus viridescens*) in Southern California.

2. Eighteen native ant species visited cacti in uninvaded areas, but cacti in invaded areas were primarily visited by the Argentine ant. The main herbivore of the coast barrel cactus present at the study sites is a leaf-footed bug (*Narnia wilsoni*).

3. Herbivore presence (the fraction of surveys in which leaf-footed bugs were present on individual cacti) was negatively related to ant presence (the fraction of surveys in which ants were present on individual cacti). Compared with cacti in uninvaded areas, those in invaded areas were less likely to have herbivores and when they did had them less often.

4. Seed mass was negatively related to herbivore presence, and this relationship did not differ for cacti in invaded areas versus those in uninvaded areas.

5. Although the Argentine ant might provide superior protection from herbivores, invasion-induced reductions in ant mutualist diversity could potentially compromise plant reproduction. The cumulative number of ant species on individual cacti over time was lower in invaded areas and was associated with a shortened seasonal duration of ant protection and reduced seed mass. These results support the hypothesis that multiple partners may enhance mutualism benefits.

Key words. Ant–plant interaction, cactus, extrafloral nectaries, facultative mutualism, herbivory, invasion, mutualist.

Introduction

Facultative mutualisms commonly involve multiple species of mutualists. The maintenance of such mutualisms remains puzzling given that partners may often differ in the quality of services they provide. Variation in partner traits can turn reciprocally beneficial relationships into commensal or even parasitic interactions (Stanton *et al.*, 1999) and has stimulated investigation into the basis of partner quality (Ness *et al.*, 2006) and the consequences of having multiple partners (Stachowicz & Whitlatch, 2005; Miller, 2007; Rosumek *et al.*, 2009; Palmer

et al., 2010). Shifts in partner identity may reduce mutualism benefits when species that provide inferior services exclude species offering superior services (Bronstein, 2001). In contrast, in cases where mutualist partners offer comparable services, mutualist diversity can act as insurance against local declines in any one species (Winfree *et al.*, 2007).

Interactions involving ants and plants include facultative mutualisms in which plants produce extrafloral nectaries (EFNs) that attract ants, which either prey upon or drive off herbivores (Rico-Gray & Oliveira, 2007). Recent meta-analyses on ant–plant interactions confirm that ant protection benefits plants (Chamberlain & Holland, 2009; Rosumek *et al.*, 2009; Trager *et al.*, 2010), but surprisingly little is known about how introduced ants affect the outcome of facultative ant–plant

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interactions (Lach, 2003; Ness & Bronstein, 2004). Compared with native ant species, introduced ants might provide superior protective services, given that they can attain high densities, behave aggressively towards a variety of arthropods, and show strong preferences for carbohydrates (Holway *et al.*, 2002a; Lach, 2003). Alternatively, reductions in native ant diversity resulting from ant invasions might lead to declines in native ant species that offer superior or more consistent plant protection relative to that provided by the invader (Lach, 2003; see also Mikassa *et al.*, 2013).

Existing studies on the role of introduced ants in facultative ant–plant mutualisms report inconsistent results (Ness & Bronstein, 2004; Lach *et al.*, 2010; Lach & Hoffmann, 2011; Savage & Rudgers, 2013). In a review of this topic, Ness and Bronstein (2004) found that just over half (9/15) of studies published at the time found evidence for plants benefiting from protection by introduced ants. Most of the studies listed by Ness and Bronstein (2004), however, did not determine whether introduced ants differed from native ants with respect to the magnitude of the benefits that plants receive. Lach and Hoffmann (2011) reported that only three published studies (including their own) perform this type of comparison, and these studies also report mixed results. On the EFN-producing *Acacia lamprocarpa*, for example, Lach and Hoffmann (2011) found that the introduced ant *Anoplolepis gracilipes* F. Smith more quickly discovered surrogate herbivores and recruited to them in greater numbers compared with how the native ant *Oecophylla smaragdina* Fabricius responded. These differences, however, did not translate into superior plant protection; leaf herbivory on *Acacia lamprocarpa* was higher on trees with *A. gracilipes* compared with that on trees with *O. smaragdina* (Lach & Hoffmann, 2011).

Here we examine an apparent facultative mutualism involving ants and the coast barrel cactus (*Ferocactus viridescens*) in Southern California. Our system provides a unique opportunity to examine how ant invasions affect mutualism benefits through reductions in mutualist diversity. First, the coast barrel cactus produces EFNs attractive to a variety of ant species, including the introduced Argentine ant [*Linepithema humile* (Mayr)]. Although individual cacti are usually occupied by one ant species at a time, ants replace one another such that cacti vary in the number of ant species present over the course of the growing season and across years. Second, few native ants persist in areas invaded by the Argentine ant in Southern California (Suarez *et al.*, 1998; Holway, 2005; Glenn & Holway, 2008). Cacti growing in invaded areas thus have a reduced pool of potential mutualists available to provide protection. To investigate the potential consequences of this reduction in mutualist diversity, we use 2 years of observational survey data for cacti in both invaded and uninvaded areas to examine three hypotheses: (i) increasing ant presence decreases herbivore presence, (ii) increasing herbivore presence negatively affects plant reproduction, and (iii) mutualism benefits increase with mutualist diversity. To our knowledge, this study is the first study of a facultative ant–plant protection mutualism to test how plant reproduction differs in response to native ant presence versus introduced ant presence. This system also offers insights into

the potential for introduced species to compromise mutualism benefits by reducing the diversity of native mutualists.

Materials and methods

Ferocactus viridescens is a succulent plant restricted to coastal sage scrub habitat on well-drained slopes in coastal San Diego County, California, U.S. and northwestern Baja California, Mexico (Ingram, 2008). The coast barrel cactus bears modified spines on its crown that produce extrafloral nectar during the winter, spring, and summer. Cacti bloom from April to June and produce fruit from July into early fall. Focal cacti in this study were patchily distributed along a 15-km stretch of coastline in San Diego Co. from Kate O. Sessions Memorial Park (32.814°N, 117.238°W) in the south to Torrey Pines State Reserve in the north (32.923°N, 117.258°W). Scrub habitat in this area is presently a mosaic of sites occupied by native ants and sites invaded by the Argentine ant (Glenn & Holway, 2008; LeVan *et al.*, 2014). Based on the distribution of the Argentine ant during the time of the study (2007–2008), we designated cacti as either invaded or uninvaded and (prior to any analyses) selected individuals that were spatially interspersed across multiple invaded and uninvaded areas [see LeVan *et al.* (2014) for a map of the study region that shows the location of cacti in invaded and uninvaded areas]. Cacti from invaded and uninvaded areas did not differ in size, blooming period, number of floral buds, or number of flowers (LeVan *et al.*, 2014). Although fruit production is not strictly a function of environmental variation, we further observed that cacti from invaded and uninvaded sites did not differ with respect to the number of fruits produced (LeVan *et al.*, 2014). Lastly, the major categories of pollinators did not differ in their visitation frequency on cacti from the two different kinds of sites (LeVan *et al.*, 2014).

From March 2007 to August 2008, we conducted weekly, diurnal surveys of 80 cacti (2007) and 113 cacti (2008 – 80 cacti from 2007 plus 33 new plants). These cacti were unevenly distributed among invaded sites ($n = 76$) and uninvaded sites ($n = 37$); fewer cacti were available to study in uninvaded areas because of the ongoing invasion of the Argentine ant in this region (Suarez *et al.*, 1998; Holway, 2005; Glenn & Holway, 2008). During every survey, we determined the number and identity of ants and herbivores on each cactus and also recorded the numbers of floral buds, flowers, and fruits. Surveys took place when the temperature in cactus crowns was approximately 30 (± 4.4) °C; these are conditions under which the common ant species in this system remain active. To measure temperature, we used an infrared thermometer (Radio Shack® #220-0325, spot size = 1.6 mm).

During the 2-year survey period, we detected 18 native ant species visiting coast barrel cacti in uninvaded areas, but cacti in invaded areas were primarily visited by the Argentine ant (Table 1). An additional three native ant species (*Monomorium ergatogyna* Wheeler, *Myrmecocystus testaceus* Emery, and *Camponotus hyatti* Emery) were observed on non-focal *F. viridescens* individuals within uninvaded portions of the study area. Native ants that visit the coast barrel cactus include a mixture of xerophilic species (e.g. *Dorymyrmex insanus* Buckley and *Solenopsis xyloni* McCook), cold-tolerant species

Table 1. Ant and bug presence on coast barrel cacti.

Species	Invaded (<i>n</i> = 76 cacti)	Uninvaded (<i>n</i> = 36 cacti)
<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> spp.	0	0.018 (0.005)
<i>Tapinoma sessile</i>	0	0.033 (0.009)
<i>Formica</i> spp.	0	0.024 (0.005)
<i>Pseudomyrmex apache</i>	<0.01	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 depilis</i>	0	<0.01
Leaf-footed bugs	0.095 (0.0068)	0.13 (0.011)

*Includes *Camponotus dumetorum* and *C. fragilis*.

†Includes *Formica moki* and *F. francoueri*.

Table entries are mean (\pm SE) proportions of ant and bug visitation (number of surveys in which a species was observed on a cactus/total number of surveys for that cactus) averaged across cacti in invaded and uninvaded areas.

[e.g. *Prenolepis imparis* (Say) and *Tapinoma sessile* (Say)], and species restricted to California floristic province (e.g. *Crematogaster californica* Wheeler and *Camponotus dumetorum* Wheeler).

We estimated herbivore presence as the fraction of surveys in which leaf-footed bugs [*Narnia wilsoni* Van Duzee (Hemiptera: Coreidae)] were present on individual cacti. This bug is the most common and conspicuous herbivore on *F. viridescens* at our study sites and feeds on floral buds and developing fruits with its beak-like proboscis (Fig. 1). We used individual seed mass to estimate costs of herbivory because *N. wilsoni* directly feeds on floral buds and developing fruits and because seed mass is important in determining seedling survival in plants generally (Baker, 1972; Bowers & Pierson, 2001; Moles & Westoby, 2004). To estimate seed mass for individual cacti, we haphazardly selected 1–3 fruits from each cactus in the summers of 2007 and 2008. We collected all fruit within a several week window to ensure that, for an individual plant, an approximately equal amount of time had elapsed between flowering and fruit harvest. Fruits were harvested when they no longer appeared to have a physiological connection to the parent plant (and were thus easily removed). We weighed a mixed sub-sample of seeds ($n = 100$) from the fruit from each plant, and then estimated the mass of an individual seed by dividing the weight of the sub-sample by 100. In this data set, there was no significant relationship between seed mass and seed number per fruit.

We used analysis of covariance (ANCOVA) to test three main hypotheses involving the following response variables: herbivore presence (the fraction of surveys in which leaf-footed bugs were observed on individual cacti), ant presence (the fraction of

**Fig. 1.** An adult *Narnia wilsoni* feeds on a floral bud of the coast barrel cactus.

surveys in which ants were observed on individual cacti), and herbivore damage (seed mass). For cacti sampled in 2007 and 2008, we used mean values for each variable in each ANCOVA. All ANCOVAs were conducted in R (R Core Team, 2012). The first hypothesis tested was that herbivore presence (response variable) decreases with increasing ant presence (covariate). To test this hypothesis, we used the residuals of herbivore presence after correcting for cactus size (estimated as the volume of a sphere in cm^3), because of the positive relationship between cactus size and herbivore presence (simple linear regression: $F_{1,111} = 40.24$, $P < 0.001$, $R^2 = 0.22$; mean values used for cacti sampled in both years). The second hypothesis tested was that seed mass (response variable) decreases with increasing herbivore presence (covariate). To test this hypothesis, we used the residuals of seed mass after correcting for cactus size as the response variable, because of the positive relationship between cactus size and seed mass (simple linear regression: $F_{1,111} = 26.78$, $P < 0.001$, $R^2 = 0.14$; mean values used for cacti sampled in both years). The third hypothesis tested was that seed mass increases with mutualist richness (i.e. the cumulative number of ant species present on individual cacti over time). For each focal cactus, we determined the number of ant species present during the 2 years of the study and then determined whether mutualist richness (covariate) explained a significant amount of variation in seed mass (i.e. residuals of seed mass after correcting for cactus size).

In our tests of each of the three hypotheses outlined in the previous paragraph, we included independent variable terms for the invasion status of individual cacti (i.e. invaded versus uninvaded) as well as the interaction between invasion status and the covariate in the model (i.e. ant presence, herbivore presence, or mutualist richness). For all three ANCOVAs, the interaction term was non-significant ($P > 0.05$), and we reran the model without this term. We also ran comparable analyses using mean herbivore abundance and mean ant abundance (time averaged over weekly surveys for individual cacti) and obtained qualitatively similar results to those in which we used ant and herbivore presence as variables. For this reason, we report results only for models run with ant and herbivore presence. Ancillary analyses in this study were also conducted in R and included two-sample *t*-tests, simple linear regressions, and chi-square tests. Summary statistics are mean \pm 1 SE, unless otherwise noted.

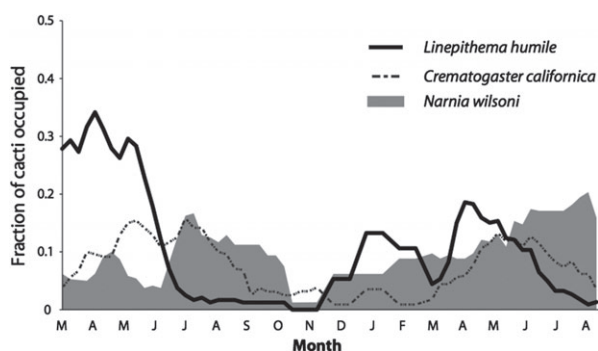


Fig. 2. The proportion of coast barrel cacti that were occupied by *Linepithema humile* (solid line) in invaded areas, *Crematogaster californica* (dashed line) in uninvaded areas, and leaf-footed bugs (shaded) on all cacti during weekly field surveys conducted from March 2007 to August 2008.

Results

Ant and herbivore presence on cacti

Ants and herbivores on the coast barrel cactus exhibited strongly seasonal patterns of activity. In both years of the study, ants visited cacti most often in spring and summer and became infrequent visitors by fall (Fig. 2). Visitation by *C. californica*, which was the most common native ant present on cacti in uninvaded areas (Table 1; Fig. 2), peaked 1–2 months after the peak of *L. humile* visitation (Fig. 2). Across the 2-year survey period, ant presence on cacti in invaded areas was lower compared to that in uninvaded areas [two-sample *t*-test: $t = 2.40$, d.f. = 111, $P = 0.01$; 0.23 ± 0.021 (invaded) versus 0.32 ± 0.035 (uninvaded); mean values used for cacti sampled in both years]. Leaf-footed bugs were primarily present on cacti in spring and summer (Fig. 2), which corresponds to when cacti bloom (April–June) and produce fruit (June–July).

Ant protection and the costs of herbivory

Our data support the hypothesis that ants protect cacti from herbivores. Herbivore presence (corrected for cactus size) decreased with increasing ant presence (Fig. 3a; Table 2). This model also revealed that cacti in invaded areas, on average, had reduced herbivore presence compared with those in uninvaded areas (Fig. 3a; Table 2). Moreover, 52.6% of cacti in invaded areas lacked bugs throughout the 2-year survey period compared with only 24.3% of cacti in uninvaded areas (chi-square test: $\chi^2 = 8.12$, d.f. = 1, $P = 0.004$).

Our data also support the hypothesis that herbivory negatively affects seed mass. Seed mass (corrected for cactus size) declined with increasing herbivore presence, and this relationship did not differ for cacti in invaded and uninvaded sites (Fig. 3b; Table 2). Seed mass also did not differ between cacti in invaded and uninvaded areas: mass per seed [two-sample *t*-test: $t = 0.14$, d.f. = 111, $P = 0.89$; 0.64 ± 0.047 mg (invaded) versus 0.68 ± 0.049 mg (uninvaded); mean values used for cacti sampled in both years].

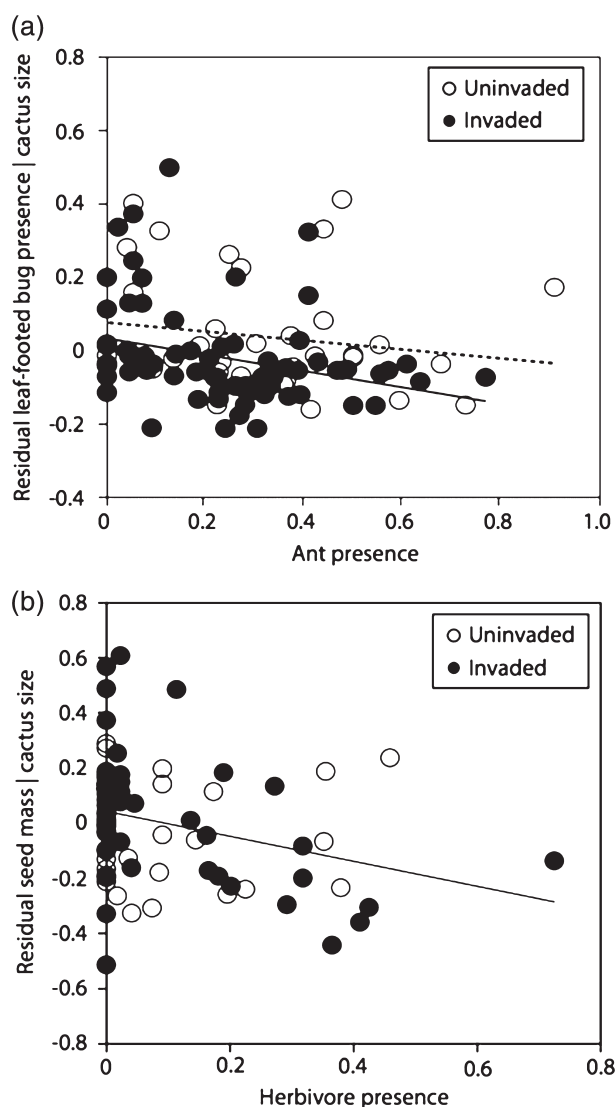


Fig. 3. (a) Residual herbivore presence (controlling for cactus size) versus ant presence, and (b) residual seed mass (controlling for cactus size) versus herbivore presence. For both (a) and (b), herbivore and ant presence equals the fraction of surveys during which herbivores or ants, respectively, were observed on individual cacti. Each data point represents an individual cactus; mean values were used for cacti surveyed in both years. In (a) lines depict linear regressions for cacti in invaded (solid) or uninvaded (dashed) sites; for (b) solid line shows linear regression for all data pooled.

Mutualist diversity and the quality of protection

The displacement of native ants by the Argentine ant reduced the number of ant species available to tend individual cacti (Table 1). Over the 2 years of the study individual cacti in invaded areas averaged 1.3 ± 0.11 (mean \pm 1 SE) visiting ant species, whereas individual cacti in uninvaded areas averaged 2.4 ± 0.22 visiting ant species (two-sample *t*-test: $t = 4.94$, d.f. = 111, $P < 0.001$; mean values used for cacti sampled in both years). Although the cumulative number of ant species present

Table 2. Analysis of covariance (ANCOVA) results for the relationships depicted in Figs 3 and 4.

Response variable	Independent variables	Coefficient \pm SE	<i>T</i>	<i>P</i>
Herbivore presence	Ant presence (covariate)	-0.29 ± 0.093	-3.12	0.003
	Invasion status	0.12 ± 0.041	2.84	0.006
	Model fit: $F_{2,81} = 6.77$, $P = 0.0019$, $R^2 = 0.14$			
Seed mass	Herbivore presence (covariate)	-0.54 ± 0.14	-3.95	0.0002
	Invasion status	-0.05 ± 0.06	-0.086	0.39
	Model fit: $F_{2,81} = 8.91$, $P = 0.0032$, $R^2 = 0.18$			
Seed mass	Mutualist richness (covariate)	0.085 ± 0.036	2.33	0.022
	Invasion status	-0.11 ± 0.06	-1.72	0.090
	Model fit: $F_{2,76} = 3.72$, $P = 0.028$, $R^2 = 0.084$			

None of the interaction terms were significant when the full models were run; results from reduced models shown in this table.

on individual cacti was related to whether the Argentine ant was present, it was independent of both cactus volume (simple linear regression: $F_{1,111} = 0.061$, $P = 0.81$, $R^2 = 0.003$; mean values used for cacti sampled in both years) and fruit production (simple linear regression: $F_{1,111} = 1.04$, $P = 0.31$, $R^2 = 0.012$; mean values used for cacti sampled in both years). Although individual cacti were nearly always visited by only one ant species at a time (94.3% of surveys of cacti with ants had only one species present at the time of each survey), changes in the ant species present were not uncommon, especially on cacti in uninvaded areas. Cacti in invaded areas that experienced changes in the identity of the tending ant species were those visited early in the season by *L. humile* and then later by *C. californica*, *D. insanus*, or both. One cactus in an invaded area was visited by *C. californica* and *D. insanus* on multiple occasions, and on one survey visit by one *Pseudomyrmex apache* Creighton worker.

The higher number of tending ant species at uninvaded sites was associated with increased ant presence and increased seed mass. The fraction of surveys in which ants were observed on cacti (i.e. ant presence) increased with the number of ant species present on individual cacti over time (simple linear regression: $F_{1,111} = 43.73$, $P < 0.001$, $R^2 = 0.43$; mean values used for cacti sampled in both years). Seed mass (corrected for cactus size) increased with increasing ant richness in the model that excluded the non-significant interaction term between invasion status and ant richness (Fig. 4; Table 2).

Discussion

This study considers how reductions in ant diversity that result from invasion by the Argentine ant affect benefits received by a shared mutualist partner, the coast barrel cactus. Across all cacti, herbivore presence was negatively related to ant presence, and seed mass was negatively related to herbivore presence. These results support the notion that EFN-bearing cacti benefit from ant protection (Oliveira *et al.*, 1999; Ness *et al.*, 2006; Miller, 2007). These analyses also revealed that the Argentine ant might provide superior protection compared with that offered by native ants. Compared with cacti in uninvaded areas and after correcting for cactus size, cacti in invaded areas were less likely to have herbivores and when they did had them less often. Benefits received by cacti in invaded areas, however, may be muted by reductions in mutualist diversity that result from

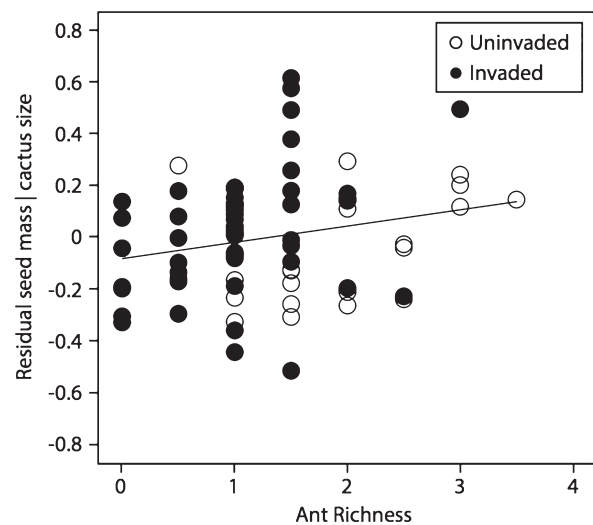


Fig. 4. Residual seed mass (controlling for cactus size) versus ant richness on individual cacti. Each data point represents an individual cactus; mean values were used for cacti surveyed in both years. Non-integer values of ant richness result from averaging across the 2 years of the study. Line depicts linear regression for all data pooled.

invasion by the Argentine ant. Both the seasonal duration of ant protection and seed mass, for example, increased with increasing mutualist diversity, which averaged lower in invaded areas than it did in uninvaded areas.

In the context of ant–plant interactions, surprisingly few studies have directly compared native and introduced ants with respect to their ability to protect host plants from herbivores (Ness, 2003; Lach & Hoffmann, 2011). Although we did not directly measure how ants interacted with herbivores, in invaded areas herbivores were more likely to be absent and when they were present, their presence was reduced (Fig. 3a) compared with patterns of herbivore presence in uninvaded areas. The ability of the Argentine ant to recruit rapidly (Holway, 1999) and to form large colonies may contribute to its ability to ward off herbivores. Unlike surrogate herbivores, which are often relatively immobile (Ness *et al.*, 2006) or purposefully restrained (Lach & Hoffmann, 2011), the adult leaf-footed bugs prominent in this system (Fig. 1) are heavily sclerotised and readily fly. Ants in this system thus likely serve more

as deterrents than as predators with respect to the protective services they provide.

Increasing herbivore presence was associated with decreased seed mass. Cacti in invaded and uninvaded areas, however, did not differ from one another in terms of seed mass as a function of herbivore presence (Fig. 3b; Table 2). This latter result suggests that differences in herbivore presence on cacti in invaded and uninvaded areas (Fig. 3a) may be too small to affect seed production. Although the Argentine ant may provide superior protection from herbivores (compared to native ants as a whole), it also reduces ant mutualist diversity (Table 1), which was positively related to seed mass (Fig. 4). These positive and negative aspects of Argentine ant presence appear to balance each other out as estimates of seed mass for cacti in invaded areas, and uninvaded areas did not differ. That said, additional information about how seed production interacts with environmental variation to influence germination and ultimately recruitment is needed to determine how ant tending by different ant species affects cactus reproductive success. Nonetheless, the net effect of Argentine ant presence in the coast barrel cactus system seems likely to be negative because of the ability of this invader to disrupt pollination services provided by bees (see also Ness, 2006). Compared with *C. californica*, for example, the Argentine ant more often visits cactus flowers and when it does occurs in higher numbers in flowers (LeVan *et al.*, 2014). Perhaps for this reason, cactus bees (*Diadasia* spp.), which are the most common pollinator in this system, spend less time visiting flowers on cacti tended by the Argentine ant compared with cacti tended by *C. californica*. Reduced visit duration by *Diadasia* probably underlies reductions in seed number experienced by cacti in invaded areas (LeVan *et al.*, 2014).

The positive relationship between seed mass and ant mutualist diversity observed in this study supports the notion that multiple partners can enhance mutualism benefits (Palmer *et al.*, 2010). In the present system, multiple ant mutualists appeared to provide protection under a wider range of physical conditions than would be possible if only a single ant species was present. The full complement of native ants present at uninvaded sites (Table 1), for example, included species primarily active early in the season (March–April), when conditions are relatively cool and moist, and species mostly present later in the season (May–August), when conditions are relatively warm and dry. At invaded sites, in contrast, ant mutualist diversity is reduced (Table 1), and *L. humile* stopped tending cacti by mid-summer (Fig. 2) when conditions probably became unsuitable for this species, which is relatively intolerant of hot, dry conditions and exhibits higher rates of water loss compared with common native ants (e.g. *C. californica* and *D. insanus*) (Holway *et al.*, 2002b; Schilman *et al.*, 2005). This function of mutualist diversity might be especially important in ant–plant interactions in which ant mutualists exhibit distinct environmental tolerances but perform broadly overlapping functional roles within the mutualism.

The continued introduction of ants into new environments as well as increases in the ranges of introduced species already established will no doubt lead to an increasing number of ant–plant interactions in which introduced ants become key participants (Lach, 2003; Lach *et al.*, 2010). Compared with native ants, introduced ants could provide superior protection

from herbivores, but they can also reduce the diversity and availability of native ant mutualists (Lach, 2003). Given that variation in the identity of tending ant species is a common feature of facultative ant–plant mutualisms (Horvitz & Schemske, 1990; Oliveira *et al.*, 1999; Morris *et al.*, 2005), a better understanding of how invasion-induced changes in mutualist diversity affect the outcome of these interactions seems warranted.

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