

The demographic consequences of mutualism: ants increase host-plant fruit production but not population growth

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Abstract The impact of mutualists on a partner's demography depends on how they affect the partner's multiple vital rates and how those vital rates, in turn, affect population growth. However, mutualism studies rarely measure effects on multiple vital rates or integrate them to assess the ultimate impact on population growth. We used vital rate data, population models and simulations of long-term population dynamics to quantify the demographic impact of a guild of ant species on the plant *Ferocactus wislizeni*. The ants feed at the plant's extrafloral nectaries and attack herbivores attempting to consume reproductive organs. Ant-guarded plants produced significantly more fruit, but ants had no significant effect on individual growth or survival. After integrating ant effects across these vital rates, we found that projected population growth was not significantly different between unguarded and ant-guarded plants because population growth was only weakly influenced by differences in fruit production (though strongly influenced

by differences in individual growth and survival). However, simulations showed that ants could positively affect long-term plant population dynamics through services provided during rare but important events (herbivore outbreaks that reduce survival or years of high seedling recruitment associated with abundant precipitation). Thus, in this seemingly clear example of mutualism, the interaction may actually yield no clear benefit to plant population growth, or if it does, may only do so through the actions of the ants during rare events. These insights demonstrate the value of taking a demographic approach to studying the consequences of mutualism.

Keywords Ant plant · Cactus demography · Integral projection model · Protection mutualism · Sonoran Desert

Introduction

Mutualisms can strongly influence the distribution and abundance of species and shape biological communities (Stachowicz 2001), but the mechanisms by which mutualists influence the demography of their partners are complex and poorly understood. Ecologists typically consider an interaction to be mutualistic if one species positively affects certain vital rates (i.e., survival, individual growth, fecundity or recruitment) of another species, and vice versa. This designation can be problematic when assessing mutualist impacts on partner population dynamics because positive effects on one or more of the partner's vital rates may not be strong enough to result in a biologically meaningful positive effect on the partner's overall population growth rate due to neutral or negative effects on other vital rates (Bronstein 2001). However, mutualism studies rarely measure effects on multiple vital rates or integrate them to assess ultimate

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impacts on population growth, as required to test whether mutualists actually benefit partner population dynamics.

To assess the impact of mutualists on partner population growth, researchers must take a demographic approach that considers the effects of the interaction on a partner's multiple vital rates, as well as the influence of those vital rates on population dynamics. Population growth rates are typically more strongly influenced by changes in some vital rates than others (Caswell 2001), and these differences can play a key role in determining the demographic importance of the effects of mutualists (or other interactors) on different vital rates (Ehrlén 2002; Miller et al. 2009; Palmer et al. 2010). For example, in populations with long-lived individuals that have high adult survival but low probability of advancement to adulthood, population growth tends to be more strongly influenced by changes in adult survival than by changes in fecundity (Silvertown and Franco 1993). In these populations, positive effects of mutualists on fecundity may fail to translate into biologically meaningful positive effects on population growth because of the weak influence of fecundity on population growth.

In addition, the costs and benefits of any interaction can vary with environmental conditions, leading to variability in the effects of mutualists on a partner's vital rates and population growth rate (Chamberlain et al. 2014; Mayer et al. 2014). If the positive demographic effects of mutualists are rarely experienced (e.g., only manifested during periods of exceptional stress or opportunity), but large when they do occur, then the long-term net effect of mutualists on partner population growth can be positive even if the interaction typically has a neutral or negative impact. Coupling empirical data with simulations of long-term population dynamics provides a way for ecologists to explore and evaluate the possible effects of infrequent but influential events that may only rarely be observed in field studies.

We examined how mutualists can affect a partner's population dynamics by studying the demography of the long-lived cactus *Ferocactus wislizeni* in the context of its interaction with a guild of ant species. The ants feed at the plant's extrafloral nectaries and attack herbivores attempting to consume reproductive buds, flowers and fruits. Previous research found that guarding by ants can increase plant fruit production (Ness et al. 2006). However, ant effects on other vital rates or overall population dynamics had not been studied.

To assess the effects of ants on plant vital rates and population growth, we combined a demographic study of marked *F. wislizeni* individuals with surveys for ants guarding those individuals to address the following questions:

1. What is the effect (positive, neutral or negative) of ants on plant vital rates (fruit production, individual growth and survival)?

2. What is the net effect of ants on plant population dynamics?

We assessed the effects of the ant guild as a whole, as well as ant-species-specific effects. We then used stochastic population models parameterized with the empirical data to simulate long-term plant population dynamics under a range of environmental conditions. We used these simulations to ask:

3. How might rare but potentially influential events that are either detrimental ("catastrophes") or beneficial ("bonanzas") alter the long-term impact of ants on plant populations?

Specifically, we assessed how the actions of ants during insect herbivore outbreaks (catastrophes) and years of high seedling recruitment associated with abundant precipitation (bonanzas) might alter the net effect of ants on long-term plant population dynamics.

Materials and methods

Study system

Ferocactus wislizeni (Cactaceae), the fishhook barrel cactus, is a long-lived plant abundant in the Sonoran and Chihuahuan Deserts of the southwestern US and northern Mexico. The plants are cylindrical and unbranched, and the top of the plant is ringed by extrafloral nectaries—small modified spines that exude nectar throughout the year (Morris et al. 2005). The extrafloral nectaries attract ants that feed on the nectar and are also likely to attack herbivorous insects (including hemipterans, particularly *Narnia pallidicornis*, orthopterans and pyralid caterpillars) attempting to consume nearby reproductive buds, flowers or fruits (Ness et al. 2006). Only one ant species guards an individual plant at a time, with only rare exceptions (Morris et al. 2005; Lanan and Bronstein 2013).

The study took place in the Sonoran Desert at the Desert Laboratory on Tumamoc Hill (32.22°N, 111.08°W) in Tucson, Arizona. The Desert Laboratory has been protected as an ecological preserve since 1907. At that time, a barbed-wire perimeter fence was installed to protect the area from livestock (Shreve 1929). The site supports resident populations of native wildlife that commonly disperse *F. wislizeni* fruit, including mule deer (*Odocoileus hemionus*), javelina (*Pecari tajacu*), coyote (*Canis latrans*) and gray fox (*Urocyon cinereoargenteus*).

Data collection

To model plant demographic processes, we marked and censused all *F. wislizeni* individuals in two plots (total area of 6.5 ha) in the Desert Laboratory every October from

2006 up to and including 2009, tracking a total of 393 plants. During each census, we determined which individuals were alive, measured their height (from ground surface to apical meristem) and counted the number of fruits on each plant [in October, fruits are mature but not yet dispersed (unpublished data)]. These data allowed us to model fruit production, individual growth and survival as functions of plant size (height). We observed that seedlings frequently established at the base of larger *F. wislizeni* individuals. Therefore, during each census we intensively searched for seedlings within 1 m of each marked plant and incorporated any new seedlings into subsequent censuses. We also searched randomly located quadrats (total area of 1219 m²) within our study plots to calculate seedling density away from marked plants. This density estimate along with the observed number of seedlings near marked plants would allow us to estimate the total number of newly recruited seedlings in the study plots each year. However, no seedlings were found in the randomly located quadrats, suggesting that recruitment away from established plants was extremely rare during the study. Thus, we simply used the counts of seedlings near marked individuals to estimate recruitment rate. Specifically, we estimated recruitment rate (number of seedlings surviving through their first year per fruit) as the total number of new seedlings in the current year divided by the total number of fruits produced by all plants in the previous year (so called anonymous recruitment), following Merow et al. (2014).

To determine which ant species (if any) was guarding each plant in each year, we surveyed marked plants for ants several times per year [5.1 ± 2.3 (mean $\pm$ SD) surveys per year]. In each survey, we assigned each plant to a “guarding state”—either “unguarded” if there were no ants around the extrafloral nectaries or “ant guarded” if there were. Within the ant-guarded group, plants were also assigned to ant-species-specific guarding states, with separate states for the three most common species (*Crematogaster opuntiae*,

Solenopsis xyloni and *Solenopsis aurea*) and a fourth state (“other ants”) for all other less common ant taxa, which included *Forelius* spp., *Camponotus* spp., *Dorymyrmex* spp. and *Myrmecocystus* spp. We defined the annual guarding state of a plant as the state most commonly observed in the 12 months preceding the demographic census. Multiple surveys per year were required because guarding states can change from season to season, though changes within a season are rare (Morris et al. 2005). Plants were in their annually assigned guarding states for 77 % of surveys on average (see Online Appendix 1 for more details on how we determined ant-guarding state).

Data analysis

To measure the effects of ants on plant vital rates, we fit non-linear models of fruit production, individual growth and survival, with plant size (height) and ant-guarding state as explanatory variables (Table 1). We also included study plot as a covariate in each model to control for spatial differences in the environment (e.g., soil characteristics), which could impact plant vital rates, and included year to control for temporal differences in the environment (e.g., weather). We fit the models using maximum likelihood and used Akaike’s information criterion with a correction for finite sample sizes (AIC_c) to select the best-fit functional form of each size-vital rate relationship (Burnham and Anderson 2002). We fit separate models for the overall effect of the ant guild on plant vital rates (guarding states were unguarded or ant guarded) and for ant-species-specific effects. Thus, assessing the effects of different ant species on plant vital rates did not detract from the statistical power of our analyses of the effects of the ant guild as a whole (see Online Appendix 2 for more details on the vital rate models).

To assess the effects of ants on plant population dynamics, we built size-structured integral projection models

Table 1 Functional form of the best-fit model for each vital rate

Vital rate model	Function	Error distribution
Fruiting probability (f_p)	$\text{logit}(f_p) = \iota + \alpha \left(1 - e^{-\frac{\rho}{\alpha}x}\right)$	Zero-inflated negative binomial
Fruit number given fruiting (f_n)	$\log(f_n) = \iota + \alpha \left(1 - e^{-\frac{\rho}{\alpha}x}\right)$	
Fruit number (f)	$f = f_p f_n$	
Mean annual growth (g)	$g = \alpha \left(1 - e^{-\frac{\rho}{\alpha}x}\right)$	Gaussian
SD of growth (g_{SD})	$g_{SD} = \rho x e^{-\frac{\rho}{\alpha}x}$	
Survival (s)	$\text{logit}(s) = \iota + \alpha \left(1 - e^{-\frac{\rho}{\alpha}x}\right) - x^\delta$	Binomial

For all functions, x is plant size (height), while *Greek letters* represent model parameters. The parameter ι controls the intercept, α controls the maximum value, ρ controls the initial rate of increase with size, and ψ and δ control the rate of decline at large sizes (not all parameters are found in each function, and the precise mathematical meaning of the parameters differs amongst functions). Parameters are themselves functions of ant-guarding state, plot and year

(IPMs) (Easterling et al. 2000; Merow et al. 2014) that used the vital rate models described above (averaging over the effects of plot and year), as well as estimates of the recruitment rate and size distribution of new seedlings, to estimate plant population growth rates for different guarding states (see Online Appendix 3 for more details on the IPMs). Because seedling recruitment is not directly associated with the mutualism (seeds and seedlings do not have extrafloral nectaries, so after dispersal they are not adjacent to extrafloral nectaries that attract ants), we did not model recruitment rate or seedling size as functions of guarding state. We used the IPMs to calculate the asymptotic population growth rate of plants in each guarding state as an integrated measure of ant effects on population growth. Because recruitment was the only vital rate we did not exhaustively measure (i.e., we did not search the entire 6.5-ha study area for seedlings), we tested how sensitive our conclusions about the effects of ant guarding on population growth were to uncertainty in recruitment rate estimation by varying recruitment rate in the IPMs and recalculating the effects of ant guarding on population growth.

To assess the significance of ant effects on the predicted mean value of each vital rate and on population growth rate, we performed two-sample, non-parametric bootstrap hypothesis tests comparing plants in the unguarded state to plants in each of the ant-guarded states (both the ant guild as a whole and each species-specific state). For the tests of ant-species-specific effects, we applied the Bonferroni correction for multiple comparisons.

To better understand the effects of ants on plant population growth rates, we performed a series of life table response experiments (LTREs) (Caswell 2001) modified for use with IPMs (Ellner and Rees 2006). The LTREs quantified how much of the difference in projected population growth rates between unguarded and ant-guarded plant populations (populations of plants guarded by any ant species, as well as the populations of plants guarded by specific ant species) was attributable to differences in each of the underlying vital rates. The LTREs combine information on how much each vital rate differed amongst plant populations and the relative influence of each vital rate on population growth.

Simulation experiments

We conducted computer simulation experiments to explore the influence of ant guarding on long-term plant population dynamics over a range of conditions beyond the scope of the empirical study. With these simulations, we assessed the possible effects of ants on plant populations during rare but potentially important events not observed in this study that could either be detrimental (catastrophes) or beneficial (bonanzas) for plant populations: herbivore outbreaks and

years with exceptionally high seedling recruitment associated with abundant precipitation, respectively. Despite their rarity, these types of events can have substantial impacts on long-term population dynamics (Morris and Doak 2002). The frequency and effects of these events are highly uncertain for *F. wislizeni*, so we covered a wide range of potential catastrophe/bonanza probabilities and impacts in the simulations to highlight which types, frequencies and magnitudes of events are likely to be important for population dynamics.

In all of these experiments, we simulated stochastic population dynamics for unguarded and ant-guarded (any species) plant populations using the IPMs fit with the empirical data. We did not consider ant-species-specific differences in these simulations because the empirical analyses did not suggest any species-specific effects (see “Results”). In each simulation, we began with two equal-sized populations of plants, one unguarded and one ant guarded. Each population started with 321 individuals, the total number of plants in the study plots at the beginning of the study. We then simulated population change each year for 50 years using stochastic versions of the IPMs. In each year of the simulations, a year from the empirical study (2007, 2008 or 2009) was randomly drawn with equal probability. The IPMs for unguarded and ant-guarded populations from the selected year were used to project each population 1 year forward in the simulation. In each year of the simulations, there was also a probability of an herbivore outbreak (in the catastrophe simulations) or enhanced seedling recruitment (in the bonanza simulations). Three years is a short period for characterizing stochastic population growth, so we only use the output of these hypothetical simulations to assess the potential effects of rare events on population dynamics, not to provide projections of population growth in a typical series of years.

Catastrophe simulations: effects of ants during herbivore outbreaks

In these simulations, we explored how episodic and potentially catastrophic herbivore outbreaks might modify the long-term effect of ants on *F. wislizeni* population dynamics. It is possible that ant guarding does not have a significant positive effect on plant population dynamics in non-outbreak years, but that benefits provided by ants in rare years with high levels of herbivory lead to a positive long-term effect (Stanton and Palmer 2011). Herbivores were not especially abundant during this study, but monitoring at this site over a longer time period showed that the percentage of *F. wislizeni* individuals with herbivores can vary substantially year to year, ranging from 0.2 to 15.6 % over 6 years (J. H. Ness, unpublished data). We simulated outbreaks of two types of herbivores: one that reduces fruit

production by consuming reproductive organs [e.g., the bug *Narnia pallidicornis* or grasshoppers in the genus *Melanoplus* (Mann 1969; Fitzpatrick et al. 2013)] and a second that reduces survival by damaging vegetative tissues [e.g., larvae of the beetle *Moneilema gigas* (Mann 1969)].

To examine the influence of these outbreaks on the long-term effect of ants on plant population growth, we simulated stochastic population dynamics for unguarded and ant-guarded plants using the IPMs we had developed, with the possibility of an outbreak occurring each year. We ran separate sets of simulations for outbreaks of herbivores that reduce fruit production and herbivores that reduce survival. When outbreaks stochastically occurred in the simulation, the fruit production or survival of unguarded plants was reduced by a prescribed proportion (we refer to this reduction as the outbreak “severity”), but the vital rates of ant-guarded plants were unaltered. We ran simulations for all combinations of outbreak probability and severity values (both ranged from 0 to 1 in increments of 0.02), and ran 1000 replicates for each combination. At the end of each replicate simulation, we calculated the difference in the number of individuals in the unguarded and ant-guarded populations, and took the median difference to represent the effect of ants on plant populations for the outbreak probability-severity combination.

Bonanza simulations: effects of ants during exceptionally high seedling recruitment years

In the second simulation experiment, we explored how years of exceptionally high seedling recruitment (bonanza years) may alter the long-term effect of ants on *F. wislizeni* population dynamics. Recruitment is often episodic, particularly in desert environments where significant seedling recruitment may only occur during rare years of abundant precipitation and low drought stress, which are commonly associated with El Niño events in the Sonoran Desert (Jordan and Nobel 1981, 1982; Bowers 1997; Drezner and Balling 2002; Drezner 2004; Pierson et al. 2013). In studies of other cactus species in this region, high seedling recruitment occurred in 5–20 % of years, with high variability across locations (Jordan and Nobel 1982; Turner 1990; Bowers 1997; Drezner and Balling 2002). There was also evidence that episodic high recruitment events associated with high precipitation might play an important role in the population dynamics of *F. wislizeni* at our study site (Online Appendix 4). In years when seedling recruitment (number of successfully established seedlings per fruit) is high, population growth will be more strongly influenced by the increases in fruit production associated with ant guarding because more seedlings recruit into the population per fruit than in a typical year. Thus, the positive effect of ants on fruit production in rare high-precipitation years

has the potential to produce positive long-term effects on plant population dynamics, even if ants have no effect on plant population growth in most years.

To examine how seedling recruitment bonanzas might alter long-term effects of ants on plant population growth, we again simulated stochastic population dynamics for unguarded and ant-guarded plant populations using the IPMs fit with empirical data. In each year of the simulations, there was a probability of a bonanza in which the recruitment rate observed in the empirical study was multiplied by a value between 1 and 1000 (we refer to this increase in recruitment as the “magnitude” of the bonanza). The increased recruitment applied equally to the unguarded and ant-guarded plant populations. We ran these simulations for all combinations of bonanza probability and magnitude values (probabilities of 0–1 in increments of 0.02, and magnitudes from 1 to 1000 in increments of 20), and ran 1000 replicates for each combination. At the end of each replicate simulation, we calculated the difference in the number of individuals in the unguarded and ant-guarded populations, and took the median difference to represent the effect of ants on plant populations for the bonanza probability-magnitude combination.

All analyses and simulations were done in R version 3.1.1 (R Core Team 2014).

Results

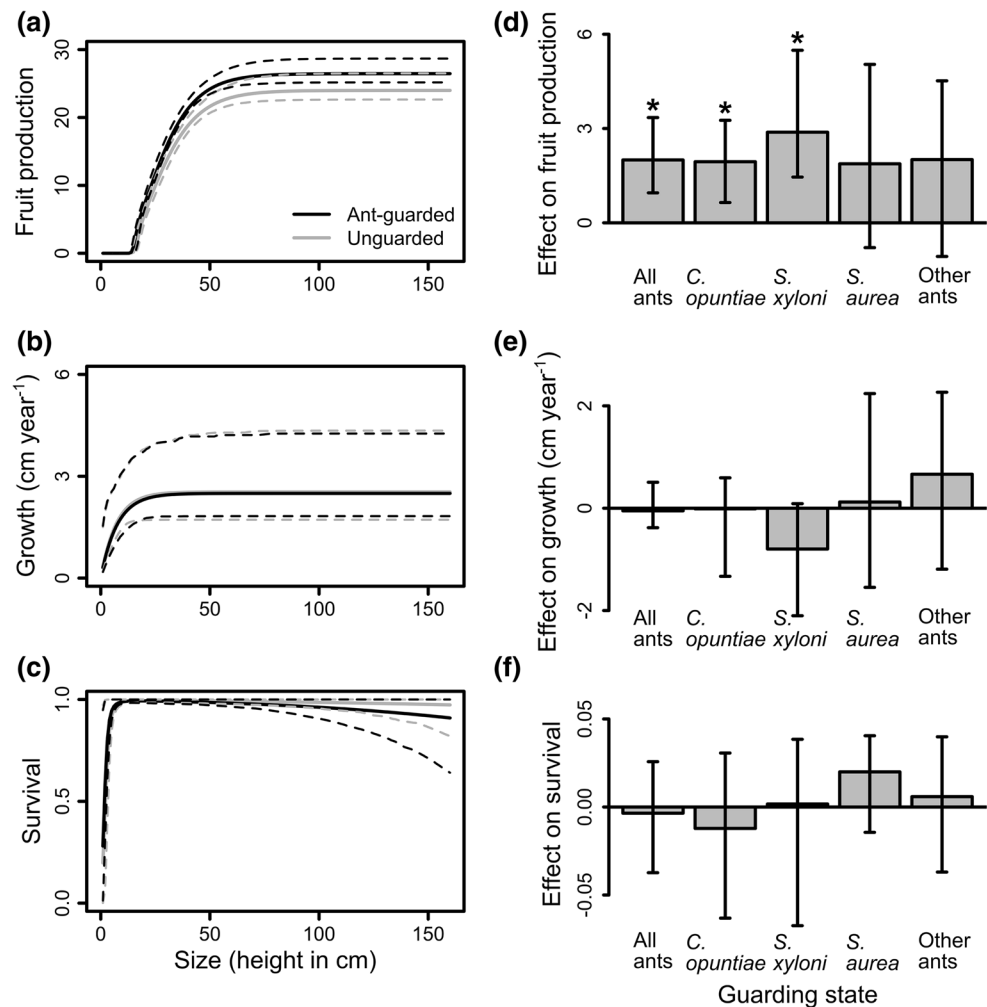
Frequency of different ant-guarding states

A roughly equal number of plants belonged to the unguarded and ant-guarded states over the 3 years of the surveys (44 and 56 % of the plants, respectively). Of the ant-guarded plants, most were guarded by *Crematogaster opuntiae* (68 %), followed by *Solenopsis xyloni* (18 %) and *Solenopsis aurea* (5 %), with the other ant species collectively making up 8 %.

Plant vital rates

Size was a strong predictor of fruit production, individual growth and survival. The differences in AIC_c values between the best-fit models describing these size-vital rate relationships and the corresponding null models without size (i.e., the delta AIC_c values for the null models) were 886, 207 and 61, respectively. These large delta AIC_c values indicate that including size in the models improves fit substantially (Burnham and Anderson 2002) and supports our use of size (plant height) as a covariate in the vital rate models and as the state variable structuring the IPM. Furthermore, the bootstrap confidence intervals for vital rate values as a function of size were generally narrow

Fig. 1 Vital rates for *Ferocactus wislizeni*. **a–c** Expected vital rate values for ant-guarded and unguarded plants as a function of size. *Dashed lines* show the 95 % bootstrap confidence intervals. **d–f** Effects of ant-guarding states on mean vital rate values compared to the unguarded state, with 95 % bootstrap confidence intervals. *Asterisks* indicate a significant effect ($p < 0.05$)



(Fig. 1a–c), suggesting that the models' characterization of these relationships was fairly accurate for the population during this study. The confidence intervals were narrower for fruit production and survival than individual growth.

Ants had differing effects on the different plant vital rates. The ant guild as a whole had a significantly positive effect on fruit production, increasing mean fruit production by 13 % compared to unguarded plants ($p < 0.001$) (Fig. 1d). All the ant species had positive effects on fruit production as well, with the effects of *C. opuntiae* (13 % increase) and *S. xyloni* (19 % increase) being statistically significant ($p = 0.004$, 0.008, respectively; Fig. 1d). However, neither the ant guild nor any of the individual ant species had a significant effect on individual growth or survival ($p > 0.05$ for both the raw and Bonferroni-adjusted p -values; Fig. 1e, f).

Population dynamics

We did not find a significant effect of ant guarding on projected plant population growth rate, either for the ant guild as a whole or for any individual species ($p > 0.05$

for both the raw and Bonferroni-adjusted p -values; Fig. 2). Unguarded and ant-guarded plants had projected population growth rates of -0.2 % (-2.4 to 3.3 %) and -1.0 % (-3.1 to 3.5 %), respectively (best estimate with 95 % bootstrap confidence intervals). Plant population growth was much more strongly influenced by differences in individual growth and survival than by differences in fruit production, as evidenced by the elasticity values of 0.987 for growth and survival (taken together) and 0.013 for fruit production and recruitment (taken together). Similarly, the LTREs showed that differences in survival between the unguarded state and each of the ant-guarded states had much bigger effects on differences in projected population growth than did differences in fruit production, with differences in individual growth having even smaller effects (Fig. 3).

Catastrophe simulations: effects of ants during herbivore outbreaks

The simulations of herbivore outbreaks suggested that episodic and catastrophic events can modify the

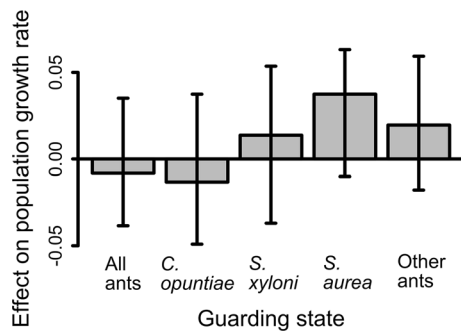


Fig. 2 Population growth for *F. wislizeni*. Effect of the ant-guarding states on projected population growth rate compared to the unguarded state, with 95 % bootstrap confidence intervals

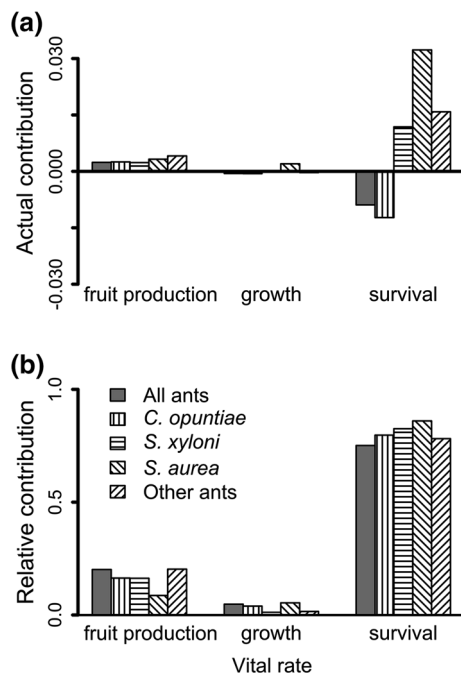


Fig. 3 Life table response experiments. **a** Contributions of differences in a vital rate to differences in projected population growth rate between the unguarded and ant-guarded plants. **b** Relative magnitude of those contributions

long-term effect of ants on plant population dynamics, and that outbreaks could have far more influence when the herbivores reduce survival as opposed to fruit production. In the simulated outbreaks of herbivores that reduce fruit production, the effect of ants on plant population growth became less negative with increasing outbreak probability and severity, but the effect of ants remained negative for all combinations of outbreak probability and severity (Fig. 4a). In the simulated outbreaks of herbivores that reduce survival, the effect of ants on plant population growth similarly became increasingly favorable as the probability and

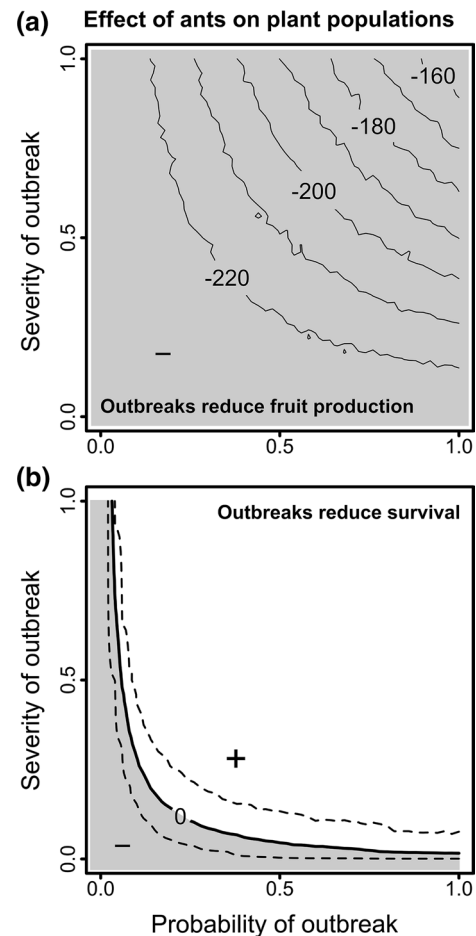


Fig. 4 Catastrophe simulations—influence of herbivore outbreaks on the effect of ants on plant populations. *Solid lines* are contours showing the median difference between the number of individuals in unguarded and ant-guarded populations at the end of the simulations as a function of annual outbreak probability and severity. *Gray shading* indicates ants had a negative effect on plant populations. **a** Outbreaks of herbivores that reduce fruit production. Ants had a negative effect on plant populations in all simulations. **b** Outbreaks of herbivores that reduce survival. In the region with the *plus sign* above the *upper dashed line*, ants had a positive effect on plant populations in 97.5 % of the simulations or more. In the region with the *minus sign* below the *lower dashed line*, ants had a positive effect on plant population size in 2.5 % of the simulations or less. The unevenness of the lines reflects the stochasticity in the simulations of population dynamics

severity of outbreaks increased, but the effect of ants also switched from negative to positive at moderately high values of outbreak probability and/or severity (Fig. 4b). For instance, when outbreaks occurred with an annual probability of 0.1, survival of unguarded plants needed to be reduced by 0.27 for ants to have a positive effect on population growth, and when outbreaks occurred with a probability of 0.2, survival of unguarded plants needed to be reduced by 0.13 for ants to have a positive effect.

Bonanza simulations: effects of ants during exceptionally high seedling recruitment years

The simulations of seedling recruitment bonanzas suggested that these episodic increases in recruitment can alter the long-term effect of ants on plant population dynamics and result in ants having a positive impact on plant populations via increased fruit production. In the simulated bonanzas, the effects of ants on population growth became more positive with increasing bonanza probability and magnitude, and the effect of ants switched from negative to positive at moderately high values of bonanza probability and/or magnitude (Fig. 5). For example, when bonanzas occurred with a probability of 0.1, recruitment needed to increase 450-fold for ants to have a positive effect on population growth, which corresponds to increasing the probability of a seed successfully establishing from the 0.00026 % observed in the study to 0.12 %. When bonanzas occurred with a probability of 0.2, recruitment needed to increase 130-fold for ants to have a positive effect, which corresponds to the probability of a seed successfully establishing increasing to 0.034 %.

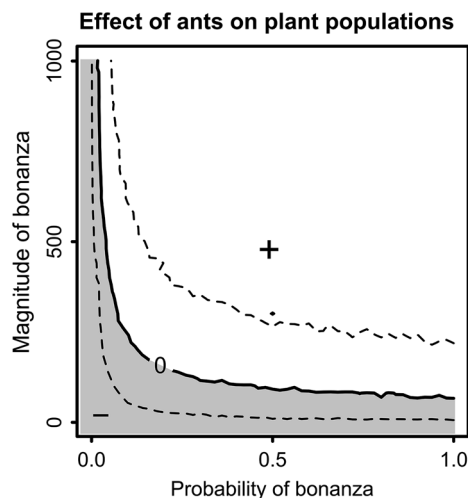


Fig. 5 Bonanza simulations—influence of episodic high seedling recruitment years on the effect of ants on plant populations. Axes show values of simulated annual seedling bonanza probability and magnitude. *Solid line* shows where unguarded and ant-guarded plant populations have the same number of individuals (i.e., median ant effect of 0). *Gray shading* indicates ants had a negative effect on plant populations. In the region with the *plus sign* above the *upper dashed line*, ants had a positive effect on plant populations in 97.5 % of the simulations or more. In the region with the *minus sign* below the *lower dashed line*, ants had a positive effect on plant population size in 2.5 % of the simulations or less. The unevenness of the lines reflects the stochasticity in the simulations of population dynamics

Discussion

The results of this study show how ants that visit the extrafloral nectaries of *Ferocactus wislizeni* may affect the plant's demography. In our empirical study, ant presence was associated with significantly higher fruit production (Fig. 1d), as would be expected because ants guard plant reproductive organs while feeding at extrafloral nectaries. However, ant presence was not associated with higher population growth rates (Fig. 2) because population growth was only weakly influenced by differences in fruit production. Even though ants did not have significant effects on individual growth or survival (Fig. 1e, f), variability in those vital rates overwhelmed the positive effect of ants on fruit production (Fig. 3) because plant population growth was strongly influenced by differences in those vital rates (regardless of whether ants caused those differences). In addition, the ant species all had similar effects (or lack of an effect) on plant population growth (Fig. 2), in contrast to other systems in which mutualist species had substantially different impacts on partner population dynamics (e.g., Bruna et al. 2014). Thus, ants did not appear to be important drivers of population dynamics during this study. However, ants may still have long-term positive effects on plant populations through their services during rare but important events, as suggested by our simulation experiments (Figs. 4, 5). Thus, in this example of a seemingly clear and canonical class of mutualism (ant-plant protection), the relationship may actually have a negligible effect on plant population dynamics, or may only benefit population dynamics through the action of ants during rare events. We discuss these two possibilities below.

Ants have a negligible effect on plant population dynamics

The most likely reason that *F. wislizeni* population growth during our empirical study was so weakly influenced by the increases in fruit production associated with ant guarding, and so strongly influenced by any variability in individual growth or survival, is the plant's demographic context—the values of the population's different vital rates. Populations with high adult survival and low probability of advancement to adulthood, such as the *F. wislizeni* population in our study, tend to be more strongly influenced by differences in survival (particularly adult survival) than by differences in fecundity (Silvertown and Franco 1993). In these populations, mutualisms primarily affecting aspects of fecundity (e.g., fruit production) will only have a biologically

meaningful positive influence on population growth when the effects on fecundity are very large.

Our conclusions about the effects of ants on plant population growth were not sensitive to uncertainty in our estimation of plant recruitment rates during the study (Online Appendix 5). However, there may be processes related to recruitment not accounted for by our estimates. For example, if susceptibility to seed predation increases with fruit and seed production, any positive influence of ant guarding on plant population growth via enhanced fruit production may be reduced. In addition, ants may deter pollinators as well as herbivores, which might lead to reduced seed number and mass per fruit (Ness 2006), counteracting the positive effect of ants on fruit production to some degree.

The partner's demographic context also played an important role in modulating the effect of mutualists on population growth in other studies. For example, Brodie et al. (2009), Feldman and Morris (2011), Geib and Galen (2012), and Rodriguez-Perez and Traveset (2012) found that the effects of fecundity-related mutualisms on the populations of plants with high adult survival and low probability of advancement to adulthood that they studied were fairly small, likely because of the weak influence of fecundity on population growth. Conversely, studies of populations with high rates of advancement to adulthood, in which population growth is more strongly influenced by differences in fecundity, have found that the increases in fecundity associated with mutualists did lead to increased population growth, even if those mutualists had negative effects on survival (Parker 1997; Rudgers et al. 2012). However, mutualists can substantially impact partner population dynamics via vital rates that have little influence on population growth if the effects of the mutualists are sufficiently large. For example, Godinez-Alvarez et al. (2002) found that variation in seed disperser quality can lead to marked differences in the population growth of a plant with high adult survival and low advancement to adulthood due to substantial differences in recruitment of the dispersed seeds, even though recruitment generally has only a weak influence on the growth of such populations.

The results of this demographic study and others demonstrate that understanding the impact of mutualists on partner population dynamics often requires quantitative assessments of how the mutualists affect multiple vital rates and how those vital rates combine to influence population growth. However, most mutualism studies measure effects on only a subset of partner vital rates. For example, there have been three recent meta-analyses of the effects of ants on plants, and while they address a number of crucial questions, they only considered the effects of ants on some of the focal plants' vital rates (Chamberlain and Holland 2009; Rosumek et al. 2009; Trager et al. 2010). Meta-analyses of other mutualisms have similarly focused on only a

subset of vital rates (Morris et al. 2007; Karst et al. 2008; Hoeksema et al. 2010; Saikkonen et al. 2010; Aslan et al. 2012; Zhang et al. 2012). Given the potential for the effects of mutualists on partner population growth to differ from the effects on the vital rate that appears most relevant, more primary studies that measure mutualist effects on partner population growth rates are needed to better determine how often mutualists actually benefit partner population dynamics.

The absence of a detectable positive effect of ants on plant population growth in our study raises the question of why the plants produce extrafloral nectar. One possible answer is that the cost of nectar is low, so even a weak positive effect of ants on fruit production favors nectar production. Alternatively, the extrafloral nectaries might be a vestigial trait that once benefited the plant during a time when ants provided useful protection, but no longer provide a biologically meaningful benefit. In fact, several studies have found that visitors to extrafloral nectaries fail to even produce a measurable reduction in herbivory, let alone a reduction large enough to affect the plant's population dynamics (Marazzi et al. 2013; Alma et al. 2015). Extrafloral nectaries are evolutionarily labile traits that have repeatedly been gained and lost within clades (Weber and Keeler 2013), so evolution in *F. wislizeni* may lead to the loss of extrafloral nectaries and an end to the interaction with ants. Such reversions of mutualists to autonomy are thought to have occurred frequently in a wide range of taxa (Sachs and Simms 2006). In addition, the costs and benefits of ant guarding may vary with environmental context (Rudgers and Strauss 2004) and the importance of ants for plant population dynamics may only be manifested during rare events, a possibility we discuss below.

Ants may benefit long-term plant population dynamics through services during rare events

Our simulations of long-term plant population growth in light of catastrophes and bonanzas (herbivore outbreaks and high recruitment years, respectively) suggest that ants may provide valuable services during these rare but important events that lead to positive long-term effects on plant population dynamics. Such *in silico* experiments can be helpful tools to extend knowledge of a species' demography and generate new hypotheses (Coulson 2012). First, the long-term effect of ants on *F. wislizeni* might depend on the occurrence of rare outbreaks of herbivores (potential catastrophes), particularly those that reduce survival. Given the weak effects of ants on plant population dynamics via fruit production and the strong influence of survival on population growth in our empirical study, as well as findings that ants can increase host-plant population growth substantially via enhanced survival in other studies (e.g.,

Bruna et al. 2014), we speculated that ants might benefit plants by improving survival during outbreaks of plant-killing insects. Our simulation results suggest that ants can increase plant population growth by maintaining high plant survival during these outbreaks, if these outbreaks are relatively frequent and/or severe (Fig. 4b). Thus, protection during intermittent periods of intense herbivory could be the most important benefit ants confer to host plants (Stanton and Palmer 2011). However, more observations are needed to determine the temporally varying effects of herbivores on *F. wislizeni* survival and how much ant guarding deters those herbivores. Our simulations also suggested that outbreaks of herbivores that reduce fruit production are unlikely to strongly modify the effects of ants on plant populations (Fig. 4a).

Second, the long-term effect of ants on *F. wislizeni* populations could depend on rare years of high seedling recruitment (bonanzas) that are often associated with high precipitation in desert environments. When recruitment is high, the sensitivity of population growth to differences in fruit production increases because more individuals are being added to the population per fruit. Thus, the increased fruit production associated with ant guarding becomes more valuable to population growth when recruitment rates are high. The more frequently these years of high recruitment occur and the greater the increases in recruitment during these events, the more likely ants are to benefit plant population dynamics (Fig. 5). Thus, the positive effects of ants on plant population growth may be conditional on adequate precipitation that allows ant-induced increases in fruit production to translate into greater population growth rates (Holland and Molina-Freaner 2013).

Similar to other studies at this location (Bowers 2000; Bowers and Pierson 2001), we observed low *F. wislizeni* recruitment, particularly away from sheltering adult plants. However, this study and the others occurred during medium to low precipitation years with presumably low recruitment rates relative to exceptionally wet years. The relatively low recruitment rates may explain why we did not observe a positive effect of ants on plant population dynamics at our study site, which might be strongly affected by episodic high recruitment events during rare, high precipitation years (Online Appendix 4).

The apparent importance of high precipitation years for recruitment suggests that climate change may alter recruitment, and thus the effects of ants on plant populations. Likely increases in temperature and possible reductions in precipitation in this region (Cayan et al. 2013) may reduce the frequency of years with low drought stress, which could lead to fewer seedling bonanzas, disrupting recruitment and the positive effects of ants on population growth.

These simulation results illustrate why caution must be used when interpreting structured population analyses.

Vital rates that appear unimportant (i.e., have low elasticity) in some or even most years, such as fruit production and recruitment in this study, and the processes associated with those vital rates, such as ant protection, can still be important for long-term population dynamics because: (1) some vital rates have the potential for large increases (e.g., recruitment), leading to large changes in population growth despite low current elasticity; and (2) the elasticity of vital rates can increase substantially with changes in vital rate values (Bruna 2003). Long-term studies of recruitment rates that cover a wide range of annual precipitation values would help elucidate the potential for episodically wet years to modify the effects of ants on *F. wislizeni* population growth.

Our results demonstrate the kind of understanding that can be gained from moving beyond measuring the effects of mutualists on individual vital rates to measuring the interaction's ultimate impact on population dynamics. In addition, coupling empirical and simulation approaches can lead to a better understanding of potential long-term effects of these interactions and highlight areas of new empirical research that would yield important insight into the demographic consequences of mutualism.

Author contribution statement K. R. F. analyzed the data and wrote the manuscript. J. H. N., J. L. B. and W. F. M. conceived and designed the study, and provided advice throughout.

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