

# An Integral Projection Modeling Approach to Understanding Demographic Effects of Multispecies Mutualisms

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## Abstract

<sup>1</sup> Mutualisms are widespread species interactions with diverse and dynamic consequences. They are considered more context dependent than other species interactions, meaning there are many different factors which change the outcomes of interactions between mutualists, including partner diversity. Partner diversity has become a central focus in the field of mutualisms, expanding previous work from primarily pairwise to multispecies mutualisms. It has been shown that pairwise studies are poor predictors of the effects of multispecies mutualistic interactions. The diversity of partners in a multi-species mutualism causes varied demographic effects on the population of the focal mutualist which can be explained by several mechanisms: portfolio effect, complementarity, and sampling effect.

I use the plant-ant multi-species mutualism in which, the cactus *Cylindropuntia imbricata* (tree cholla) produce extrafloral nectar and the ants, *Crematogaster opuntiae*, *Liometopum apiculatum*, *Forelius pruinosus*, and rarer species, provide defense from various herbivores and seed predators. I used 18 years of data collected from plant demographic censuses, which includes data such as size, survival, reproductive status, flowers produced, and ant partner for all plants in 8 30×30 m plots at the Sevilleta National Wildlife Refuge in central New Mexico. With this data I parameterize a series of Bayesian hierarchical generalized linear vital rate models to determine the impacts of different partners on the focal mutualists. I found that different ant partners had different impacts on the vital rates of the tree cholla. Specifically, *C. opuntiae* tended plants had advantages in both growth and survival when small, and large *L. apiculatum* tended plants had floral viability advantages. With these models I constructed an Integral Projection Model in which I could vary the presence of each partner, creating different “diversity scenarios”, to determine under which diversity scenario the focal mutualist experienced the highest plant fitness, and which mechanism(s) may explain the effects of partner diversity. I found that the all scenar-

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<sup>1</sup>I think this is too long for Am Nat requirements. Also, use “we”. I think you just pasted in an abstract that you used elsewhere, so I will work on this once you write a real abstract for the Am Nat paper.

ios which included the partner *L. apiculatum* resulted in the highest possible fitness for the tree cholla. Results further suggest that diversity benefits in this system are driven by sampling effect  
27 , meaning *L. apiculatum* ants are the "best" partner. I also found that partner diversity benefits the focal mutualist in this system in the form of portfolio effect by buffering the tree cholla from the effects of inter-annual variation. This study highlights how partner diversity can increase  
30 the overall benefits a focal mutualist receives. It also highlights the importance of a mechanistic understanding to explain the benefits of this diversity across systems.

## Introduction

Mutualisms are species interactions where all participants receive net benefits, leading to higher individual fitness and increased population growth rates. They are widespread species interactions (Axelrod and Hamilton, 1981; Bronstein, 1994; Chamberlain et al., 2014; Frederickson, 2013; Leigh, 2010) but can deteriorate into commensalism or parasitism under conditions that elevate costs or dampen benefits (Bahia et al., 2022; Mandyam and Jumpponen, 2014; Rodriguez-Rodriguez et al., 2017; Song et al., 2020; Thrall et al., 2007). Mutualisms are considered more context dependent than other species interactions (Chamberlain et al., 2014; Frederickson, 2013), meaning the magnitude and sign of interaction strength are often determined by environmental conditions and species' identities (Leigh, 2010; Noe and Hammerstein, 1994).

Mutualism is defined at the level of a species pair (+/+ ) but these interactions are embedded within multi-species communities, and growing evidence suggests that pairwise interactions are poor predictors of the net effects of multi-species mutualism (Afkhami, 2014; Bascompte, 2009; Dattilo et al., 2014; Palmer et al., 2010). A focal mutualist may interact with multiple guilds of partner types (e.g., plants that interact with pollinators, seed dispersers, soil microbes, and ant defenders) or with multiple partner species within the same guild (e.g., plants visited by multiple pollinator species). Within a mutualist guild, partner species often differ in the amount or type of goods or services they provide, making partner identity an important source of context-dependence in mutualism (Stanton, 2013). Whether and how partner diversity modifies the demographic effects of mutualistic interactions remain open questions within relevance in applied settings (Rogers et al., 2014).

There are multiple mechanisms by which partner diversity can influence the net benefits accrued by a focal mutualist, mirroring the mechanisms by which, at a larger scale of organization, biodiversity can influence ecosystem function Barrett et al. (2015); Ushio (2020); Yeung et al. (2006). First, when there is a hierarchy of fitness effects (a consistent ranking of best to worst mutualists), a more diverse sample of the partner community may be more likely to include the

best partner Frederickson (2013). This can lead to an apparent benefit of diversity driven by a sampling effect Batstone (2018). However, if partner associations are mutually exclusive (a focal mutualist may engage with only one partner at a time), then partner diversity may impose opportunity costs, leading to negative effects of a diverse mutualist assemblage relative to exclusive association with the single best partner (Miller, 2007). Second, even within a single mutualist guild, the benefits conferred by alternative partner species can vary in type and not just degree Bronstein et al. (2006); Stachowicz and Whitlatch (2005); Stanton (2013). This can lead to a positive effect of partner diversity through complementarity of alternative functions Batstone (2018). Interference or synergies between partners can make their combined effect different than the expected from the sum of complementary functions Afkhami (2014). Third, partner species can have species-specific responses to environmental variation, either spatially (Ollerton et al., 2006) or temporally (Alarcón et al., 2008). Multiple partners can therefore act as a 'portfolio' that stabilizes fitness benefits and protection across spatial or temporal heterogeneity, leading to positive effects of partner diversity through the portfolio effect Batstone (2018); Horvitz and Schemske (1990); Lázaro et al. (2022).

Partner diversity can have different effects depending on whether partners are present all at once or sequentially (partner turnover) (Barrett et al., 2015; Bruna et al., 2014; Dattilo et al., 2014; Djiéto-Lordon et al., 2005; Ness et al., 2006; Ushio, 2020). Sequential associations are likely when alternative partners engage in interference competition for access to a shared mutualist Batstone (2018); Kiers et al. (2003); Trøjelsgaard et al. (2015); Wulff (2008). Turnover can happen at different timescales, from minutes to years (Horvitz and Schemske, 1986; Oliveira et al., 1999). The frequency of partner turnover can impact the level of benefits received by the focal mutualist, particularly if the benefits continue to accumulate with successive turnover (e.g., when sequential partners provide complementary functions) or if they saturate over time (Fiala et al., 1994; Sachs et al., 2004). Directionality of turnover can also influence effects of partner diversity if partner identity changes consistently across ontogeny of a focal mutualist (Dejean et al., 2008; Fonseca et al., 2003; Noe and Hammerstein, 1994). For example, plant susceptibility to enemies can

change across life stages (Barton and Koricheva, 2010; Boege and Marquis, 2005), so the benefits of defensive mutualism with ants are greatest when more defensive partner species align with more vulnerable life stages (Dejean et al., 2008; Djiéto-Lordon et al., 2005).

Defensive ant-plant mutualisms – where plants provide food and/or housing to ants that in turn defend them from enemies – are widespread interactions that offer valuable model systems for the ecology and evolution of mutualism (Bronstein, 1998; Bronstein et al., 2006). Extrafloral nectar (EFN) bearing plants can serve as dietary resources that promote ant abundance and colony size (Byk and Del-Claro, 2011; Donald and Miller, 2022; Ness et al., 2006, 2009). Presence of defensive ant partners is often linked to reductions in herbivory (Rudgers, 2004; Trager et al., 2010) and demographic advantages for the plant partner (Báez et al., 2016). Defensive ant-plant mutualisms are commonly multi-species, where a guild of ant partner species share, and often compete for, a plant mutualist (Agrawal and Rutter, 1998; Beattie, 1985; Bronstein, 1998; Trager et al., 2010). Ant partners can vary in their ability to deter herbivores (Bruna et al., 2014), and visitation by low quality ant partners can prevent visitation by higher quality partners, consequently causing a reduction in fitness through missed opportunity costs (Fraser et al., 2001; Frederickson, 2005). Susceptibility to herbivory can also vary significantly throughout the life stages of the plant (Boege and Marquis, 2005), suggesting that the order and timing of successive partners is important to the fitness impacts of the combined partner guild (Barton and Koricheva, 2010; Boege and Marquis, 2005; Fonseca et al., 2003). Herbivore identity and pressure can vary inter-annually Wetzal et al. (2023), much like mutualist identity and presence, meaning the threat plants face can vary just as much as the protection they receive due to temporal stochasticity. Recent studies have begun to investigate how ant partner diversity affects plant fitness (Afkhami, 2014; Dattilo et al., 2014; Fiala et al., 1994; Gaume et al., 1998; Ludka et al., 2015; Palmer et al., 2010) However, little is known about the combined effects of partner identity, directional partner turnover, and temporal stochasticity, particularly because the necessary long-term data are rarely available.

This study examined the consequences of partner diversity in a food-for-protection mutu-

alism between the tree cholla cactus (*Cylindriopuntia imbricata*), a long-lived EFN-bearing plant, and multiple species of ant partners. Previous studies have shown that herbivory by specialized insect herbivores negatively affects plant fitness Miller et al. (2009), and ant defense reduces herbivore damage Miller (2007). Tree cholla are tended by two common ant species (*Liometopum apiculatum* and *Crematogaster opuntiae*) and several infrequent species, all of which are ground-nesting. These ant species locally co-occur but individual plants are typically tended by only one species that patrols the plant around-the-clock and maintains control of the plant's nectar resources for an entire growing season (Donald and Miller, 2022; Ohm and Miller, 2014). Switches between partner species, or between vacancy and ant occupancy, commonly occur from one growing season to the next (Miller, 2007). Prior experiments suggested a hierarchy of mutualist quality, with *Liometopum apiculatum* providing strong fitness benefits through anti-herbivore defense and *Crematogaster opuntiae* having net negative fitness effects because herbivore deterrence is outweighed by deterrence of pollinators (Miller, 2007; Ohm and Miller, 2014). However, those studies did not integrate the demographic effects of ant defense across the plant life cycle, nor did they account for inter-annual fluctuations in the herbivore populations (data on herbivory is included in supplementary documents).

We used a unique long-term data set that allows us to explore mutualistic associations with multiple partner species, longitudinal turnover in partner identity at the individual level, and how the demographic effects of alternative partner species varied across plant size structure and nearly 20 years of inter-annual fluctuations. We used this observational data set, contextualized by previous experiments, to ask whether and through which mechanism(s) partner diversity affects the fitness benefits of ant visitation for the focal plant partner. Specifically, we asked:

1. What are the demographic effects of association with alternative partners and how do these effects fluctuate across years?
2. What are the frequency and direction of partner turnover across the plant life cycle?
3. What is the net effect of partner diversity on plant fitness, and what mechanism(s) explain(s)

138 this effect?

We used a hierarchical Bayesian statistical approach to estimate demographic vital rates for hosts in different states of ant occupancy and to quantify state-dependent partner turnover from the long-term data. We then used a stochastic, multi-state integral projection model (IPM) that combines diverse effects on vital rates and pathways of partner turnover to quantify effects of partner diversity on plant fitness.

## 144 Methods

### *Study System*

This study was conducted in the Los Piños mountains, a small mountain chain located on the Sevilleta National Wildlife Refuge, a Long-term Ecological Research site (SEV-LTER) in central New Mexico, USA. This is an area characterized by steep, rocky slopes, and perennial vegetation including grasses (*Bouteloua eriopoda* and *B. gracilis*), yuccas, cacti, and junipers. Tree cholla cacti are common in high Chihuahuan desert habitats, with their native range spanning the southwestern USA (Benson, 1982). These arborescent plants produce cylindrical segments with large spines. In the growing season (May to August in New Mexico), the plants initiate new vegetative segments and flower buds at the ends of existing segments. While most plants produce new segments every season, only those which are reproductively mature produce flower buds. Like other EFN-bearing cacti, tree cholla secrete nectar from specialized glands on young vegetative segments and flower buds (Ness et al., 2006; Oliveira et al., 1999). Flower buds produce more and higher-quality EFN than vegetative segments, making reproductive cholla valuable mutualist partners. Smaller cholla produce little to no EFN, so larger cholla, especially flowering individuals, are generally more highly tended (Miller, 2014).

Tree cholla EFN is harvested by various ant species. At SEV-LTER, cholla are visited primarily by two species of ground-nesting ants, *Crematogaster opuntiae* and *Liometopum apiculatum*, as well as other rarer species, including *Forelius pruinosus* and unidentified species of *Aphaenogaster* and



*Camponotus*. *L. apiculatum* are the most frequent visitors with 25% – 60% of tree cholla tended by these ants, followed by *C. opuntiae* visiting between 5% – 20% of cacti depending on the year (Donald and Miller, 2022). Between 30%–80% of cacti remain vacant in any given year. These ants rarely co-occur on a plant, likely due to interspecific competition (Miller, 2007): staged introductions of *C. opuntiae* to *L. apiculatum*-tended plants, and vice versa, provoke aggressive responses by resident ants (A. Campbell, *personal observation*). Each cholla is visited by a single ant species for the duration of a season, and the species of the visitors can change from one season to the next. In late August, the tree cholla stop producing EFN and the ants vacate until the next growing season.

There are a variety of insect herbivores and seed predators which specialize on tree cholla (Mann, 1969). A weevil of the genus *Gerstaeckeria* feeds on vegetative and reproductive structures and implants their larvae within the plant tissue for the winter. A cactus bug, *Narnia pallidicornis*, (Hemiptera: Coreidae) feeds on all cholla parts with a preference for the reproductive structures (Miller et al., 2006). A seed predator, *Cahela ponderosella*, (Lepidoptera: Pyralidae) attacks developing fruits pre-dispersal and oviposits in open flowers mid-growing season where larvae burrow into the ripening ovary. These predators can have significant negative impacts on plant fitness of and depress population growth (Miller et al., 2009). There is experimental evidence that tree cholla tended by *L. apiculatum* and *C. opuntiae* experience less herbivory than plants from which ants were excluded (Miller, 2007).

## *Data Collection*

This study is based a long-term demographic data set spanning 2004 to 2023 at SEV-LTER. From 2004 to 2008, we censused 134 plants distributed across three spatial blocks. This initial census group was discontinued in 2009, when we established six 30 × 30-meter plots and tagged all tree cholla within those plots. Two additional 30 × 30-meter plots were added in 2011, and this group of eight plots has since been censused annually through 2023 (with the exception of 2020 due to the covid shutdown). For all plants, in May or early June of each year we recorded plant survival

189 since the last survey and, for survivors, we recorded the height (cm), maximum crown width  
(cm), and crown width perpendicular to the maximum (cm). Size measurements were used to  
calculate plant volume ( $cm^3$ ) based on the volume of an elliptical cone. We recorded reproductive  
192 effort as counts of viable and aborted flowerbuds. We recorded the ant species present (or  
vacancy if no ants present). Occurrences of more than one ant species on one plant were rare  
(less than 5% of observed ant species), and for the purpose of this analysis we classified the  
195 plant as being occupied by the more abundant species. Plots were searched for new recruits each  
year, and these were added to the census. In total, the data set included 1141 unique individuals  
and 19 plant-year observations. These data were used to fit vital rate models (survival, growth,  
198 reproduction) as functions of plant size and ant occupancy state.

We used additional, smaller data sets from previously published studies to estimate seed and  
seed bank parameters. Ohm et al. (Ohm and Miller, 2014) provide data on the number of seeds  
201 per fruit for plants tended by *L. apiculatum*, *C. opuntiae*, or no ants (experimental exclusion). Miller  
et al. (Miller et al., 2009) provide data on seed entry to the seed bank and seedling germination  
and survival rates.

### 204 *Multi-state Integral Projection Model*

Integral Projection Models describe population dynamics in discrete time, with functions that  
relate vital rates to continuous state variables. While IPMs are a natural choice for populations  
207 with continuous size structure, they can also be modified to accommodate a combination of  
continuous and discrete state variables, as we do here. We constructed a multi-state IPM that  
stitches together population structure associated with plant size and ant state, allowing us to  
210 determine the individual fitness effects of each ant species and the composite effects of multiple  
partners, with their transition dynamics modeled explicitly.

Given the low frequency of ant species other than *L. apiculatum* and *C. opuntiae* (7.78% of  
213 observed ants) we combined observations of all other ants into an “other” category, such that  
our models included four possible ant states: vacant, *L. apiculatum*, *C. opuntiae*, and “other”. The

“other” category was made of unidentified ant species (2.8% of observed ants), unknown species  
 216 belonging to the geni *Aphenogaster* (0.4%), *Camponotus* (0.9%), *Tetramorium* (0.02%), *Brachymyrmex*  
 (0.02%), a honeypot ant (0.08%), and *Forelius pruinosus* (3.5%). Ant state is included as a predictor  
 variable in sub-models where there are biologically realistic pathways through which ants could  
 219 impact the outcome of that process. For example, ant partners defend cacti from herbivores, and  
 prior experimental work indicates that ant tending can reduce vegetative tissue loss and floral  
 abortion. Therefore, ant state was included in sub-models for survival, growth, and flowerbud  
 222 viability. In contrast, we have no reason to expect that ant tending can directly influence the  
 probability of flowering and flowerbud production, independently of its influence on plant size.  
 Therefore, these sub-models included plant size but not ant state as predictor variables.

225 Following previous studies, we modeled the tree cholla life cycle using continuously size-  
 structured plants where  $n(x, a)_t$  gives the number of plants of size  $x$  and ant state  $a$  in year  $t$ ,  
 plus two discrete seed banks ( $B_t^1$  and  $B_t^2$ ) corresponding to 1 and 2-year old seeds. Seed bank  
 228 dynamics are given by:

$$B_{t+1}^1 = \delta \sum_{a=1}^A \int_L^U \kappa(a') P(x; \boldsymbol{\tau}^P) F(x; \boldsymbol{\tau}^F) V(a; \boldsymbol{\tau}_a^V) n(x, a)_t dx$$

$$B_{t+1}^2 = (1 - \gamma_1) B_t^1$$

231 In these equations  $x$  and  $x'$  indicate the size of a plant in years  $t$  and  $t + 1$  respectively,  $a$  and  $a'$   
 indicate the ant partner of a plant in years  $t$  and  $t + 1$ . Functions  $P(x; \boldsymbol{\tau}^P)$  and  $F(x; \boldsymbol{\tau}^F)$  give the  
 probability of flowering in year  $t$  and the number of flowerbuds produced in year  $t$ , respectively,  
 234 by plants of size  $x$ . The proportion of flowerbuds that remain viable through fruit set ( $V(a; \boldsymbol{\tau}_a^V)$ )  
 and the number of seeds per fruit ( $\kappa(a)$ ) are dependent on ant state  $a$  but not size. The vector  $\boldsymbol{\tau}$   
 gives year-specific deviates (with mean zero) and appears in functions for which we can estimate  
 237 temporal stochasticity from the long-term data; superscripts indicate the corresponding vital  
 rate and subscripts indicate that deviates are specific to plants in ant state  $a$  and year. Seed  
 production is integrated over the size distribution, from the lower  $L$  to upper  $U$  size limits, and  
 240 summed over all possible ant states ( $A = 4$ ) giving total seed production. Seeds are multiplied

by the probability of seed dispersal and survival ( $\delta$ ) to give the number of seeds that enter the one-year old seed bank. Plants can recruit out of the year-one seed bank with probability  $\gamma_1$  or  
 243 transition to the two-year seed bank with a probability of  $1 - \gamma_1$ . Seeds in the two-year seed bank are assumed to either germinate with probability  $\gamma_2$  or die.

For the above-ground part of the life cycle, the number of plants of size  $x'$  and ant state  $a'$  in  
 246 year  $t + 1$  ( $n(x', a')_{t+1}$ ) is given by survival/growth transitions from size  $x$  and ant state  $a$  in year  $t$ , plus germination out of the seed banks:

$$n(x', a')_{t+1} = (\gamma_1 B_t^1 + \gamma_2 B_t^2) \eta(x') \omega \rho_0(a') +$$

$$\sum_{a=1}^A \int_L^U S(x, a; \tau_a^S) G(x', x, a; \tau_a^G) \rho(x, a, a'; \tau^e) n(x, a)_t dx$$

The first term estimates the number of individuals recruiting from a one or two-year seed bank to  
 252 a plant of size  $x'$  and ant state  $a'$  based on the recruit size distribution  $\eta(x')$  and the probability of seedling survival ( $\omega$ ) from germination (late summer) to the census (May). This term is multiplied by  $\rho_0(a')$ , which gives the probability that a new recruit has ant state  $a'$  at its first  
 255 appearance in our census ( $\sum_{a'} \rho_0(a') = 1$ ). The second term represents all possible transitions from size  $x$  and ant  $a$  to size  $x'$  and ant  $a'$ , conditioned on survival. Survival from initial size  $x$  ( $S(x, a; \tau_a^S)$ ) and growth from size  $x$  to  $x'$  ( $G(x', x, a; \tau_a^G)$ ) are both dependent on initial size and  
 258 ant state. As above, these functions include inter-annual variability through year-specific deviates that can vary by ant state ( $\tau_a$ ). Ant transition function  $\rho(a', a, x; \tau^p)$  gives the probability that an individual transitions from ant state  $a$  to  $a'$  in the next census, conditional on initial size  $x$ . This  
 261 function includes inter-annual variability through year-specific intercepts which are consistent across ant states ( $\tau^p$ ).

### *Statistical modeling and parameter estimation*

264 We parameterized the IPM using a series of generalized linear mixed models (GLMMs) in a hierarchical Bayesian framework to serve as vital rate sub-models. Vital rate models included spatial and temporal random effects associated with plot and year variation, respectively, and

267 included plant size ( $\log(\text{cm}^3)$ ;  $x, x'$ ), ant partner state ( $a, a'$ ), or both as fixed-effect predictor variables. In addition to vital rate models describing plant demographic performance, we also fit a sub-model to predict transition between ant states conditional on plant size and previous  
 270 ant state. All models were fit using R version 4.2.2 and Rstan package (R Core Team (2023); Stan Development Team (2023)). Unless otherwise mentioned, all used vague priors.

The vital rate models take the form of the function:

$$f(\mu) = \beta_0 + \beta_1 x + \dots + u + w$$

where  $u \sim N(0, \sigma_{yr}^2)$  is the year random effect with year specific deviates of  $\sigma_{yr}$  (which parame-  
 273 terizes the  $\tau$  vector), and  $w \sim N(0, \sigma_{plot}^2)$  is the plot random effect with plot specific variance of  $\sigma_{plot}$ . Some models deviate from this general model, which will be specified below.

*Growth.* The growth sub-model ( $G(x', x, a; \tau_a^G)$ ) gives the probability of future size given the fixed effects of previous size  $x$  and previous ant partner  $a$  and random effects of plot  $w$  and year  $u$  which interacts with ant state  $a$ . We fit this model to the size in year  $t + 1$  ( $y^G$ ) using the location-scale parameterization of the student  $t$  distribution and the identity link function, because in preliminary analyses we found that size transition data were more fat-tailed than a Gaussian distribution could accommodate.

$$y^G \sim \text{StudentT}(\hat{v}, \hat{G}, \hat{\sigma})$$

Student  $t$  distributions are dependent on three parameters,  $\hat{v}$ ,  $\hat{G}$ , and  $\hat{\sigma}$ .  $\hat{G}$  is the mean of the distribution, and in our case is expressed as a second-order polynomial with ant-size interactions because preliminary analysis found this was a better fit to slightly concave data.  $\hat{v}$  is the shape parameter which determines how thin the tails of the distribution are.  $\hat{\sigma}$  is the scale parameter which determines how wide the distribution is. Both  $\hat{v}$  and  $\hat{\sigma}$  are size dependent because preliminary analyses revealed that there was size dependence in both variance and kurtosis.

$$\hat{\sigma} = \beta_0^\sigma + \beta_1^\sigma x$$

$$\hat{v} = \beta_0^v + \beta_1^v x$$

276 *Survival.* The survival model ( $S(a, x; \tau_a^S)$ ) estimates the probability of survival from year  $t$  to year  $t + 1$ , with fixed effects of the previous size of the cholla  $x$  and ant partner  $a$  in year  $t$  and random effects of plot  $w$  and year  $u$  which interacts with ant state  $a$ . We fit this model to the survival data  $y^S$  using a Bernoulli distribution and the logit link function  $y^S \sim \text{Bern}(\hat{S})$ .

*Reproduction.* The reproduction model ( $P(x'; \tau^P)$ ) estimates the probability of reproducing in year  $t + 1$ , with fixed effects for the size  $x'$  in year  $t + 1$  and random effects of plot  $w$  and year  $u$ . We fit this model to the reproductive data  $y^R$  using a Bernoulli distribution and a logit link function:

$$y^P \sim \text{Bern}(\hat{P})$$

*No. Flowers.* The total flowers model ( $F(x'; \tau^F)$ ) estimates the total flowers produced by a plant in year  $t + 1$ , with fixed effects of size  $x'$  in year  $t + 1$  and random effects of plot  $w$  and year  $u$ . We fit this model to flowerbud count data  $y^F$  using a zero-truncated negative binomial distribution with a log transformation:

$$y^F \sim \text{0TruncatedNegativeBinom}(\hat{F}, \hat{\phi})$$

$$\log(\hat{\phi}) = \beta_0^\phi$$

*Flowerbud viability.* The viability model ( $V(a; \tau_a^V)$ ) estimates the proportion of flowers produced by a plant which are viable (not aborted) in year  $t + 1$ , with fixed effects of ant partner  $a$  in year  $t$  and random effects of plot  $w$  and year  $u$  which interacts with ant state  $a$ . We fit this model to floral abortion data  $y^V$  using a Binomial distribution and a logit link function:

$$y^V \sim \text{Binom}(\hat{V})$$

*Seeds Per Fruit.* With data Miller et al. (2006), we fit a model for the number of seeds produced by every fruit on a cholla ( $\kappa(a')$ ) in year  $t + 1$  based on the ant partner  $a'$  in year  $t + 1$ . We fit this model to seed data  $y^\kappa$  using a Negative Binomial distribution and the log link function:

$$y^\kappa \sim \text{NegativeBinomial}(\hat{\kappa}, \hat{\phi})$$

$$\hat{\phi} = \beta_0^\phi$$

279 The data used for this model did not include data on ants in the “other” category, so we used the data from vacant plants to parameterize seeds per flower for plants with “other” ants in the IPM.

*Ant Transitions.* The ant transition model ( $\epsilon(x, a, a'; \boldsymbol{\tau}^\epsilon)$ ) estimates the probability of a cactus being visited by an ant partner  $a'$ , with fixed effects of the previous size  $x$  and the previous ant partner  $a$  in year  $t$  and random effects of plot  $w$  and year  $u$ . We fit this model to ant partner data from year  $t + 1$   $a'$  using a multinomial distribution with a logit link function:

$$y^\epsilon \sim \text{Multinomial}(\hat{\epsilon})$$

*Recruit Size Distribution.* We fit this model to recruit size data  $y''$  using a Normal distribution with the identity link function:

$$y'' \sim N(\hat{\eta}, \hat{\sigma})$$

282 where  $\hat{\sigma}$  is estimated with a non-informative prior.

*Germination.* With germination data Miller (2007), we fit two models for the probability of germinating from the first year seedbank ( $\gamma_1$ ) or the second year seedbank ( $\gamma_2$ ) in year  $t + 1$ , with no fixed or random effects. These models were fit to germination data  $y^{\gamma_1}, y^{\gamma_2}$  using the binomial distribution with logit link functions:

$$y^{\gamma_1} \sim \text{Binomial}(\hat{\gamma}_1)$$

$$y^{\gamma_2} \sim \text{Binomial}(\hat{\gamma}_2)$$

*Pre-Census Survival.* With recruit census data Miller et al. (2006), we fit a model for the probability of a seedling (which germinates in early Fall) surviving to when we census in May ( $\delta$ ) of year  $t + 1$  (accounting for missed mortality events), with fixed effects of the previous size  $x$

and random effects of the transect  $m$ . We fit this model to pre-census survival data  $y^\delta$  using a Bernoulli distribution with a logit link function:

$$y^\delta \sim \text{Bern}(\hat{\delta})$$

where  $m \sim N(0, \sigma_{\text{transect}}^2)$  is the random effect of transect where the recruited individual was analyzed for survival.

285 *Parameter estimation.* To obtain posterior estimates of the demographic parameters, we fit models using Markov chain Monte Carlo (MCMC) simulations via STAN run through version 4.0.2 of R R Core Team (2023); Stan Development Team (2023). For each model, we obtained three chains  
288 of 10,000 iterations, each with randomly chosen initial conditions. The first 1,500 iterations were discarded. We did not thin the chains, thus all samples were retained following burn-in. We assessed parameter convergence between and within chains (Figures 1 – 7 b). To assess the  
291 overall model fit we carried out posterior predictive checks to examine how well the fitted model can generate simulated data similar to the real data (Figures 1 – 7 a). All estimated parameters are available in Table 1.

## 294 *IPM Analysis*

We constructed two stochastic IPMs in order to simulate ant combinations that don't exist in real life with two different versions of environmental variation. The first is referred to as the  
297 stochastic IPM, in which we include random annual variation in the model and allow each ant partner to respond distinctly to annual variation. The second is referred to as the stochastic null IPM, in which we include random annual variation in the model, but force each ant partner to  
300 respond in the same way to annual variation. By analyzing the stochastic model we can estimate the fitness of the cholla under these simulated combinations. By comparing the stochastic model to the stochastic null model we can identify what mechanisms may explain differences in cholla  
303 fitness with different ant partners. In this section I first explain how a simple deterministic IPM



is developed before diving into how we created our more complex stochastic and stochastic null models.

306 Analyzing an IPM requires discretizing the continuous IPM kernel into an approximating matrix. Size variable  $x$  is discretized into  $b$  bins, resulting in a  $b \times b$  matrix. In our model there is additional complexity in the form of transitions between ant partners, leading to a matrix size  
309 of  $Ab \times Ab$  where  $A$  is the number of unique combinations of  $a$  and  $a'$  (how many possible ant transitions there are). Our model also has two additional discrete states (year one and year two seed banks) leading to a final matrix size of  $A(b + 2) \times A(b + 2)$ . We used  $b = 200$  bins after  
312 stability analysis to determine how many bins were needed to consistently estimate the same lambda. We extend the integration limits  $L$  and  $U$  (the lowest and highest size values observed) to avoid unintentional eviction Williams et al. (2012).

315 Traditionally, in a bayesian IPM, rather than having one set of parameters to populate an approximating matrix and estimate population fitness ( $\lambda$ ), we use 1,000 draws from the posterior distributions of our bayesian statistical models to populate 1,000 approximating matrix and  
318 estimate a 1,000 element distribution for  $\lambda$ . After preliminary stability analysis we found that 1,000 random posterior draws leads to the same estimate of  $\lambda$  as any greater number of posterior draws. In a stochastic bayesian IPM, the estimation of each individual  $\lambda$  in the distribution comes  
321 from a geometric mean of many values. Rather than a single approximating matrix for each value of  $\lambda$ , we take the geometric mean of 500 approximating matrices with year-ant-specific effects, resulting in a stochastic version of populationfitness ( $\lambda_S$ ). These year-ant-specific effects are cal-  
324 culated as random effects for each unique combination of year and ant species included in our data. While we do not have data on how the ant species actually fluctuate annually, we are able to measure how the effects of the ant species on plants fluctuate annually. Each of these 500 ap-  
327 proximating matrices have the same draw from the posterior distribution, but are assigned the year-ant-specific effects of a random year of our data (year-ant-specific effects are sampled randomly with replacement). We chose to use 500 year-specific values, because our  $\lambda_S$  calculations  
330 stabilized after 500 year-specific values. To calculate a single  $\lambda_S$  for these 500 year-ant-specific

estimates, we take the geometric mean of the 500 dominant eigenvalues<sup>2</sup> for a single stochastic  $\lambda_S$ . This process is repeated for each of the 1,000 random posterior draws, leading to a distribution of 1,000 stochastic  $\lambda_S$  values. To calculate the stochastic null bayesian IPM we use the exact same process, but the year-specific values used to calculate the stochastic null  $\lambda_{SN}$  are not ant specific, forcing all ant species to have the same effects on their cactus partners in response to environmental variation.

In the both versions of our IPM, this process is repeated separately for every combination of ant partners: complete vacancy; *C. opuntiae* and vacancy; other and vacancy; *L. apiculatum*, *C. opuntiae*, and vacancy, *L. apiculatum*, other, and vacancy; *C. opuntiae*, other, and vacancy; and all ant partners and vacancy. Each partner scenario includes vacancy in addition to the combination of partners being analyzed for added realism because we have never observed a population of cacti in which all are occupied.

We can compare the distributions of  $\lambda_S$  in many ways, but have chosen two moments in particular: the means and the proportion of each distribution that is greater than another. To calculate this second moment, we can subtract each  $\lambda_S$  distribution from the others (e.g.<sup>3</sup>  $\lambda_{S,Vacant} - \lambda_{S,C.opuntiae\&Vacant}$ ) to determine which partner scenario leads to a higher fitness for the cactus population. The proportion of the resulting vector that is greater than zero allows us to give a probabilistic estimate of which combination results in the greatest fitness. The magnitude of this proportion is how we determine the magnitude of difference between the resulting population fitnesses.

Using only the  $\lambda_S$  distributions from the stochastic IPM we can determine which scenario leads to the highest fitness, which will tell us if there are benefits to diversity in this system, any other finding indicates that there is quantitative evidence that diversity benefits this system. If the partner scenario which leads to the highest possible population fitness is vacancy, this indicates that there are no benefits to partner diversity. If all of the highest scenarios include a

<sup>2</sup>OK, I am not positive this is correct, but I have forgotten how to correctly describe it. Can we talk through this sentence?

<sup>3</sup>This notation may need to be revised somewhat

common ant partner, this indicates that there is a single best partner. This quantitative finding  
357 that one particular partner leads to all highest possible population fitnesses is evidence that  
sampling effect explains the benefits of partner diversity. If the highest scenario includes all  
possible ant partners, this indicates there is a synergy which occurs when all partners interact.  
360 This quantitative finding indicates that complementarity is the mechanism which explains the  
benefits of partner diversity in this system.

Using the  $\lambda_S$  distribution and the  $\lambda_{SN}$  distribution, from both the stochastic IPM and the  
363 stochastic null IPM, we can determine if having multiple partners can buffer the cactus popula-  
tion from environmental variation. The difference in the full partner scenario and vacancy ( $\lambda_{S,All}$   
-  $\lambda_{S,Vacant}$ ) can be interpreted as the effect of having all partners when each ant species has unique  
366 effects on the cacti in response to annual variation. The difference in the full partner scenario  
and vacancy ( $\lambda_{SN,All}$  -  $\lambda_{SN,Vacant}$ ) can be interpreted as the effect of having all partners when  
each ant species has the same effects on the cacti in response to annual variation. The proportion  
369 of the resulting vectors that are greater than 0 allows us to give probabilistic estimates of the  
effects of partner diversity on the fitness of the cacti in a varying environment under two ant  
scenarios. These two distributions can again be subtracted ( $\lambda_S - \lambda_{SN}$ ), allowing us to determine  
372 the difference in effects of partner diversity in two annually varying scenarios. The proportion of  
the resulting vector that is greater than 0 gives us a probabilistic estimate of how strongly partner  
diversity buffers the population from environmental variation when the effects of each partner  
375 fluctuate uniquely. This quantitative finding that the effects of partner diversity in the stochastic  
IPM are greater than those in the stochastic null IPM indicate that portfolio effect can explain  
some benefits of partner diversity in this system.

378 4

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<sup>4</sup>*I focused on several things throughout this rewrite of the methods: I tried to go straight into talking about the stochastic IPM, I focused on explaining rationale for specific numbers better, I tried to update notation to be clearer, and I tried to explain more clearly... not sure if I've accomplished these, let me know*

## Results

*What are the demographic effects of association with alternative parnters and  
how do these effects fluctuate across years?*

### *The demographic effects of alternative ant partners*

*Growth Model.* We found evidence that ant visitation enhances cactus growth and that partner identity can influence the growth trajectory of cholla (Figure 1). Tree cholla experience positive mean growth rates across all partners at small to medium sizes with the highest chances of shrinking occurring at the largest sizes (Figure 1e). Plants with *C. opuntiae* ant partners experience the highest mean growth rates across all but the largest sizes, where they experience comprable growth to the other tended plants (Figure 1a). Plants with *L. apiculatum* ants experience the lowest mean growth rates at the smallest sizes and the second lowest at all other sizes (Figure 1b). Plants with other ants experience the second highest mean growth rates across all but the largest sizes, where they experience the highest growth rates (Figure 1c.) Plants with no partners experience the second lowest growth rates at small sizes, after which they experience the lowest growth rates (Figure 1d).

Using the method of subtracting one size distribution from another we were able to determine how confident we are that the size of cholla visited by one combination of ant partners is greater than another.  $G_{Crematogaster} - G_{Vacant}$  returns a vector which is 89% positive, meaning we are 89% confident that when *C. opuntiae* ants are partners the size of the cholla is greater than the size of the cholla with no ant partners. Given the evidence that plants visited by *C. opuntiae* experience the highest mean growth rates we have reported our confidence that this partner is associated with the highest growth rates below. We are 88% and 70% confident that plants tended by *C. opuntiae* ants experience higher mean growth rates across sizes than plants tended by *L. spiculatum* ants or other ants respectively. We are 89%, 65%, and 94% confident that plants with no partners experience lower mean growth rates across all sizes than plants tended by *C.*

*opuntiae*, *L. apiculatum*, or other ants respectively.

405 *Survival Model.* We found evidence that ant visitation enhances the survival of medium to large plants, and that partner identity has a significant impact on survival for smaller plants (Figure 2). Tree cholla experience between 7.7% and 99.9% survival rates depending on their size and ant partner (Figure 2e). Smaller cacti all have lower survival rates, while larger cacti have higher survival rates, all nearing 100% when they reach their largest observed sizes. Plants with *C. opuntiae* ants experience the highest mean survival rates across all sizes (Figure 2a). Plants with 411 *L. apiculatum* ants experience the lowest mean survival rates when small and the second highest mean survival rates across all other sizes (Figure 2b). Plants with other ants experience the second lowest mean survival rates across all sizes (Figure 2c). Plants with no partners experience 414 the second highest survival rates at small sizes, after which they experience the lowest survival rates (Figure 2d).

Using the method of subtracting one survival distribution from another we were able to 417 determine how confident we are that the survival of cholla visited by one combination of ant partners is more likely than another.  $S_{Crematogaster} - S_{Vacant}$  returns a vector which is 82% positive, meaning we are 82% confident that when *C. opuntiae* ants are partners the survival of the cholla 420 is more likely than the survival of the cholla with no ant partners. Given the evidence that plants visited by *C. opuntiae* experience the highest mean survival rates we have reported our confidence that this partner is associated with the highest survival rates below. We are 63% 423 and 100% confident that plants tended by *C. opuntiae* ants experience higher mean survival rates across all sizes than plants tended by *L. spiculatum* ants or other ants respectively. We are 82%, 68%, and 64% confident that plants with no partners experience lower mean survival rates across 426 all sizes than plants tended by

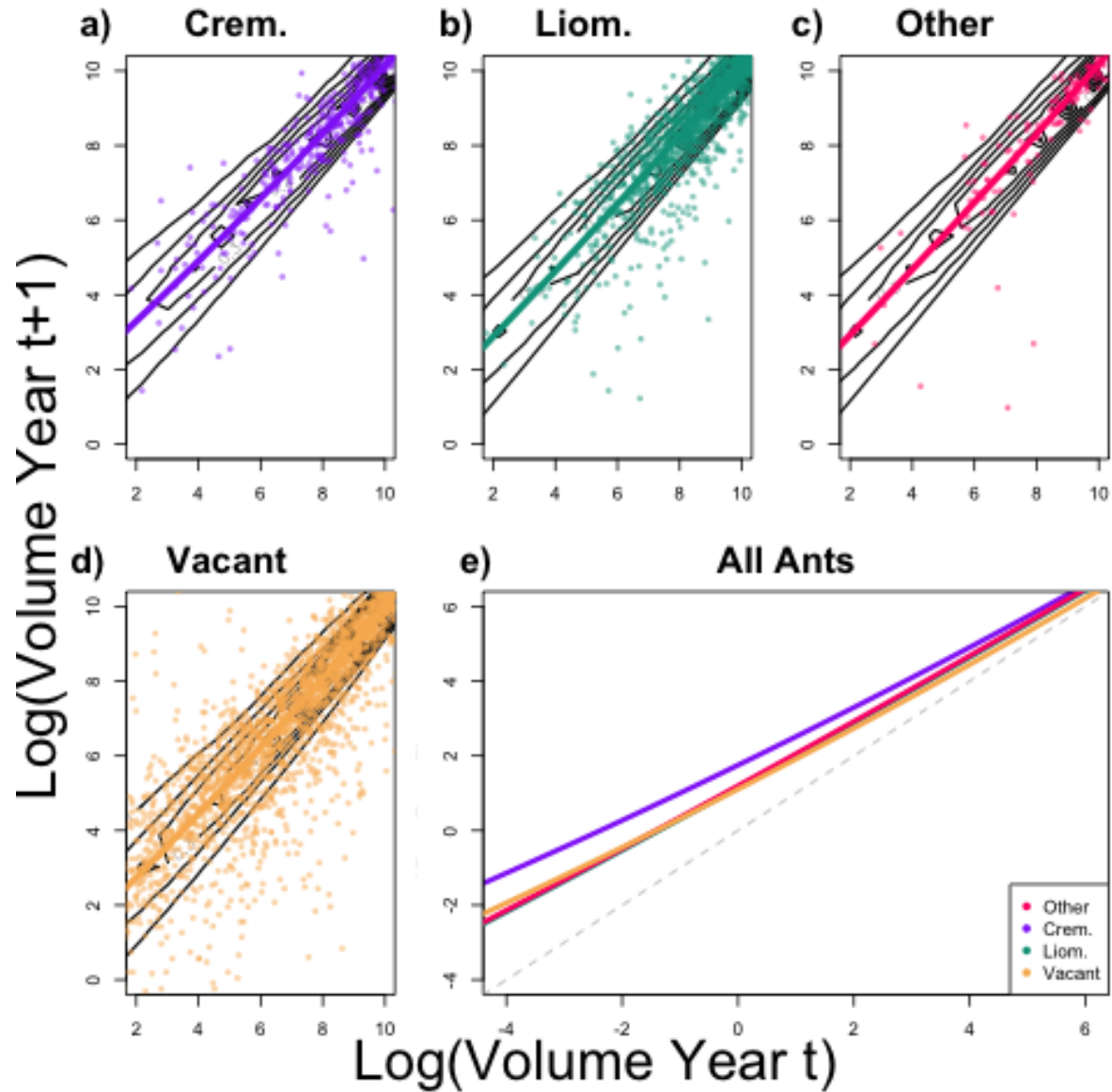


Figure 1: This figure shows the next predicted size of cholla based on previous size with each individual ant partner. The solid colored lines (seen in all panels) are the next mean predicted size of cholla. The points (seen in panels a-d) are the observed data which informs these estimates. The black countour lines (seen in a-d) appear at 5% increments showing where 5%, 10%, etc. of the data is expected to fall. The grey dashed line (in panel e only) shows the line where the next predicted size is the same as the previous (aka there is no growth on this line and below this line is shrinkage).

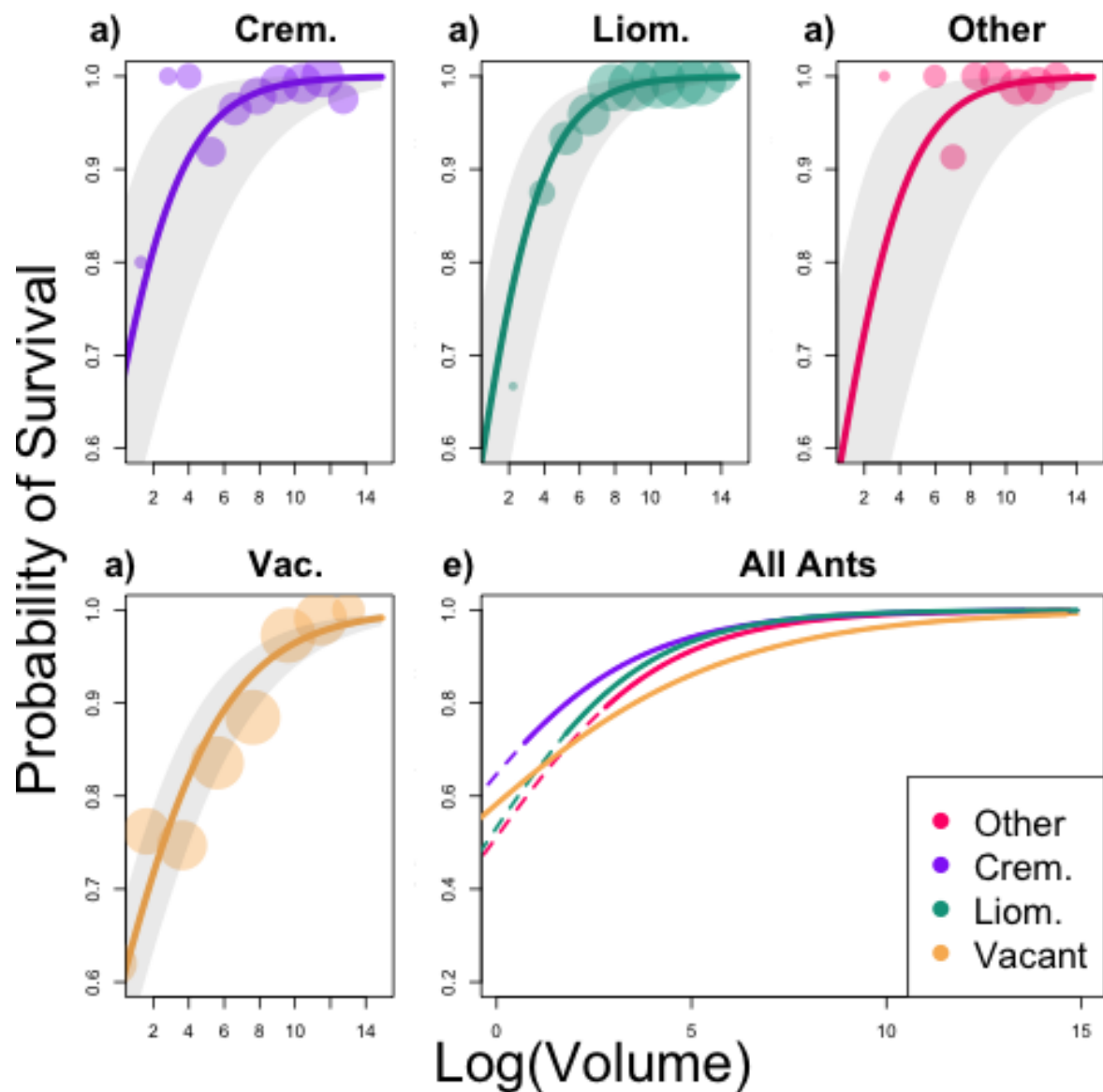


Figure 2: This figure shows the estimated survival rates based on the size of the cactus with each individual ant partner. The solid colored lines (shown on all panels) indicate the mean estimated survival rates. The dashed lines (shown in panel e) indicate extrapolations beyond existing data (where we estimated survival for plants tended by ants where we had never seen a tended cactus of that size). The grey area around the solid lines (shown in panels a-d) show the 90% confidence interval for the estimates. The colored dots are the real data binned by size to show how our estimates align with real survival observations. A larger circle means we had more data on survival of plants of this size with this partner.

*Viability Model.* We found evidence that ant visitation leads to increased floral viability rates and that ant identity can influence the strength of viability. Tree cholla that are reproducing in year  $t$  experience between 39% and 96% viability rates of flowers (Figure ??). The ant partners make a difference in the mean viability rate of flowers, with *L. apiculatum* tended plants experiencing the highest mean viability rate (at 86%, Figure 3b), followed by other tended plants (at 75%, Figure 3c), *C. opuntiae* tended plants (at 74%, Figure 3a) and vacant plants (at 71%, Figure 3d).

Using the method of subtracting one viability distribution from another we were able to determine how confident we are that the floral viability of cholla visited by one combination of ant partners is greater than another.  $V_{Liomatopum} - V_{Vacant}$  returns a vector which is 99% positive, meaning we are 99% confident that when *L. apiculatum* ants are partners the floral viability of the cholla is greater than the cholla with no ant partners. Given the evidence that plants visited by *L. apiculatum* experience the highest viability rates we have reported our confidence that this partner is associated with the highest viability rates below. We are 98% and 97% confident that *L. apiculatum* tended plants experience higher viability rates than plants tended by *C. opuntiae* or other ants respectively. We are 95% and 69% confident that vacant plants experience lower viability rates than plants tended by *C. opuntiae* ants or other ants respectively.



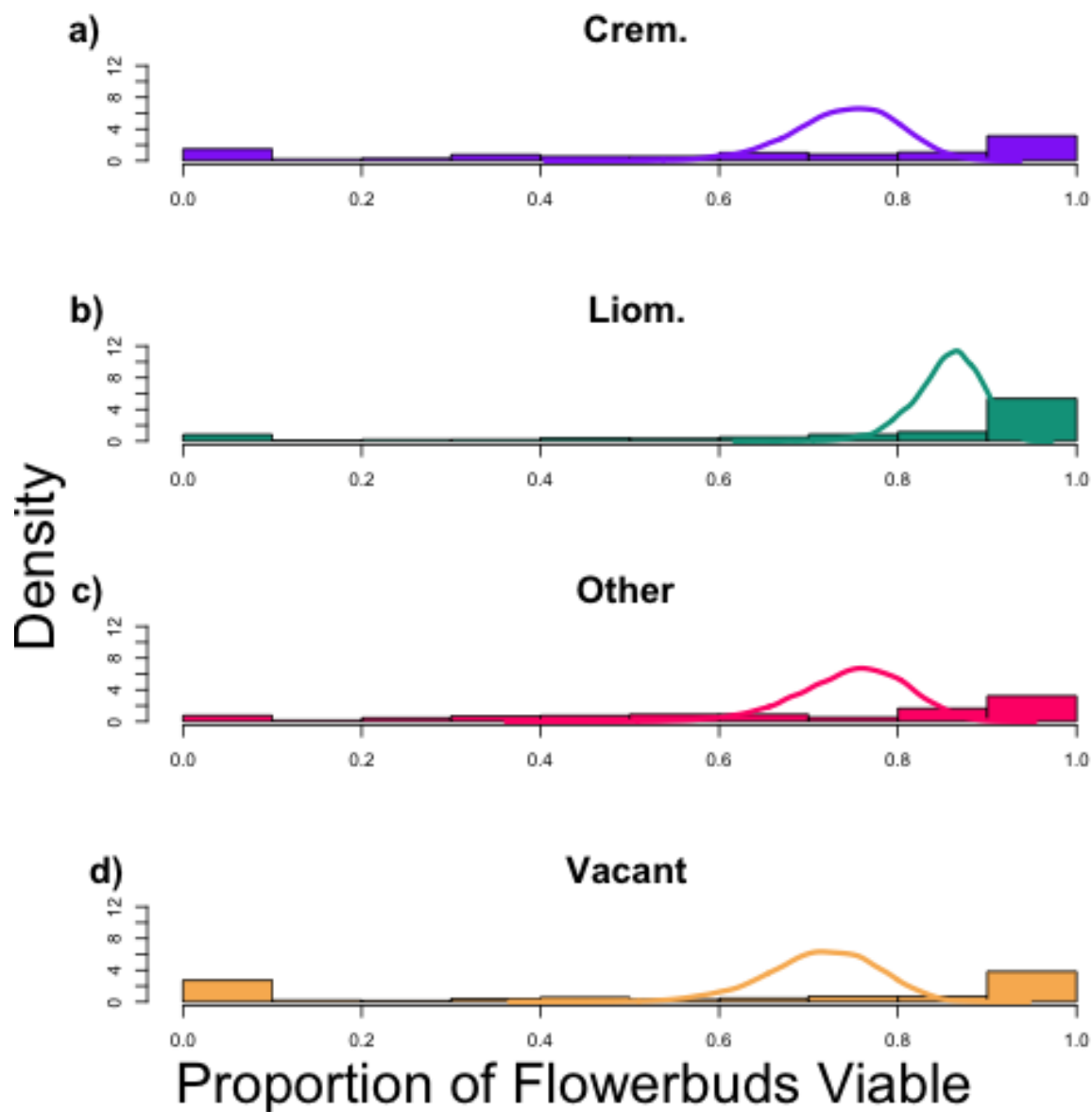


Figure 3: This figure shows the estimated distributions of floral viability rates compared to observed distributions of floral viability rates of cholla based on ant partner identity. The solid lines indicate the estimated viability distribution. The colored histograms represent the observed viability rates of plants with that partner.

444 *The role of annual fluctuations in demographic effects of ant partners*

We found evidence that annual variation impacts the effect of ant partner on various demographic traits (Figure 4). The effects of each partner on demographic measure vary uniquely  
447 across temporal fluctuations, making partner identity important to track in conjunction with annual variation. Specifically, where some ants offered greater than average benefits in one year, other species offered reduced benefits in the same year, indicating that each ant partner reacts  
450 differently to the fluctuating environment.

Each demographic trait was not affected equally by the intersection of ant partner and annual fluctuations. We looked at the mean effect of each ant partner on growth (figure 4a), survival  
453 (Figure 4b), and viability (Figure 4c) rates across all the years included in our study. Where the mean effect is exactly 0 there is missing ant data due to variation in censusing focus. This is an indirect way to analyze how temporal fluctuation impacts our system without attributing  
456 the effects to a specific climate variables. Where the mean effect is positive, ant presence increases the respective estimated growth, survival, or viability rates in response to environmental fluctuations, and where the mean effect is negative, the opposite occurs. We found the general  
459 magnitude of variation was the smallest for the growth rate, meaning annual variation affected the growth of plants the least, followed by survival then viability.

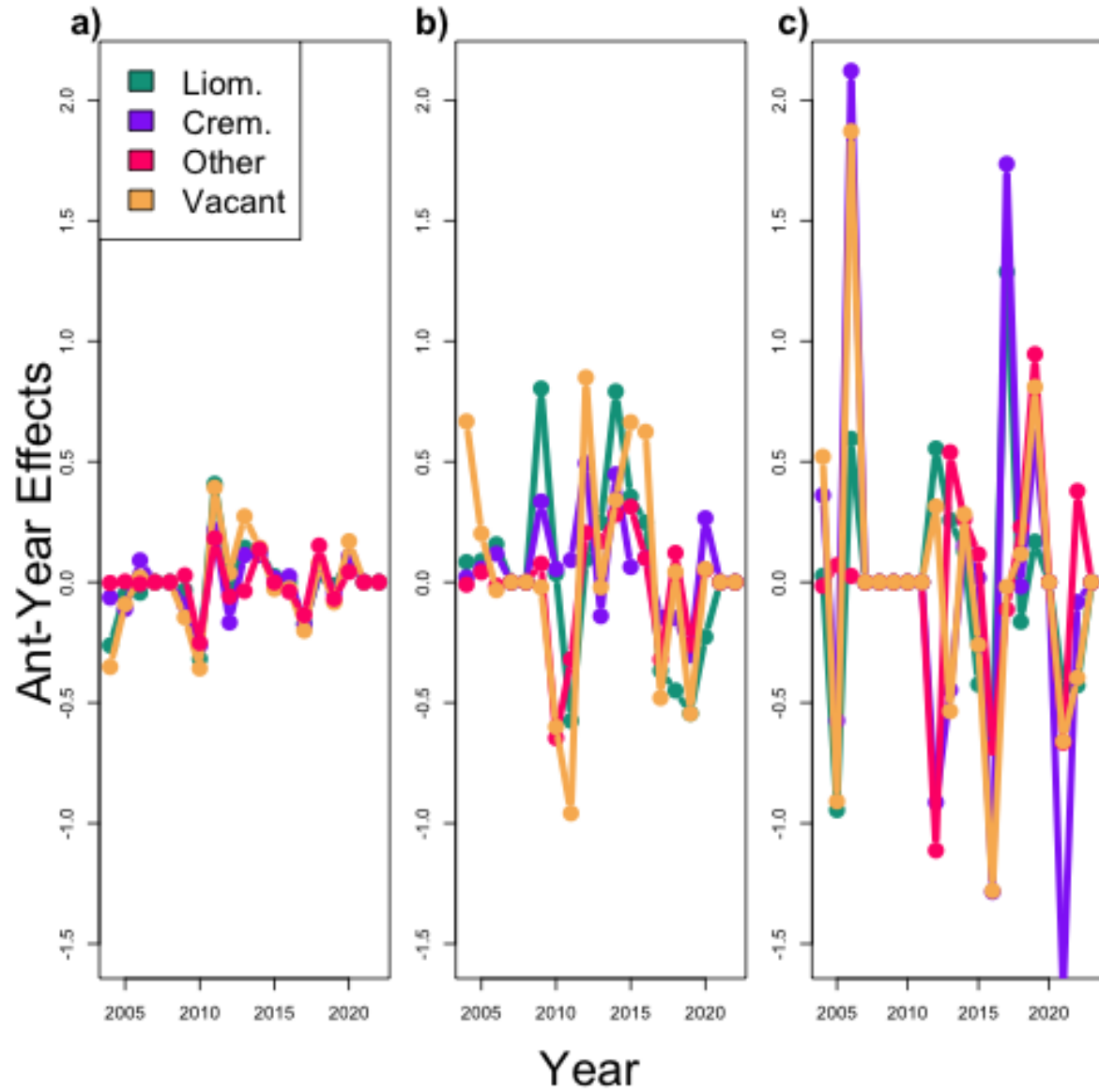


Figure 4: This figure shows the mean affect of each ant partner on a) the estimated next size, b) the estimated survival, and c) the floral viability of cacti across every year of our study. These values are estimated from the fitted random effects of ant and year in our models. Each point represents the mean of the random effect of the identified model, ant, and year (e.g. the lowest dot in panel b) represents the mean effect of vacancy on survival rates in year 2011).

*What are the frequency and direction of partner turnover across the plant life cycle?*

We found that there is a high frequency of partner turnover observed in this system with very distinct directional patterns. Small plants are almost always vacant (Figure 5b-d), if they were previously tended by a partner, they are likely to become vacant again (Figure 5a). As the size of the plants increases, the probability of becoming tended increases as well, though it is not equally likely to be tended by all partners.

*L. apiculatum* ants become the most likely next partner in the case of most large plants, with the exception of a large plant which was previously tended by *C. opuntiae*. Plants which were previously tended by *C. opuntiae* ants are most likely to remain tended by *C. opuntiae* ants. This indicates that these species may follow the well documented retention-discovery trade off exhibited by many ants, with *L. apiculatum* ants excelling at discovery and colonization of new plants and *C. opuntiae* ants excelling at plant retention season after season. The overall frequency of these partners, however is a potential alternative explanation to this discovery-retention trade off. *L. apiculatum* ants are by far the most frequent ant partners, accounting for 75% of the occupied cacti, while *C. opuntiae* and other ants account for 17% and 8% of occupied cacti respectively. This high frequency of *L. apiculatum* ants may lead to the inflation of turnover to *L. apiculatum* from other ants.

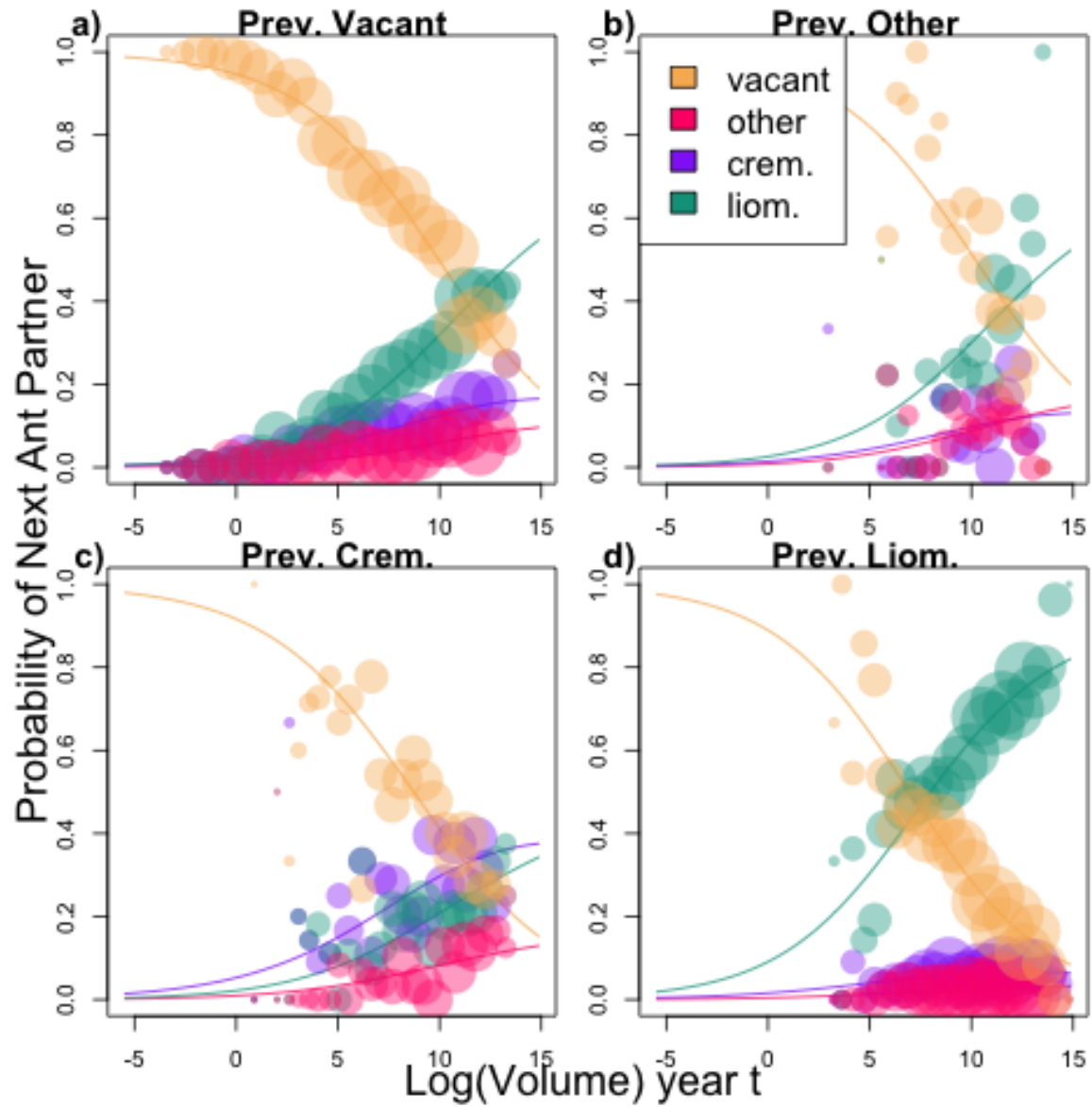


Figure 5: This figure shows the probability of being tended by each ant partner or vacant based on the size of the plant. Each panel shows these probabilities for a different previous ant state. The solid lines represent the mean probability of being tended by a specific partner. The colored points are the real data binned by size to show how our estimates align with real visitation observations. A larger circle means we had more data on visitation of plants of this size with this previous partner.

*What is the net effect of partner diversity on plant fitness, and what  
mechanism(s) explain(s) this effect?*

We found that partner diversity was beneficial in this system. The lowest mean fitness was  $\lambda_{S,Vacant}$ , the fitness of the cholla with no partners (Figure 6b). By subtracting the distributions  $\lambda_{S,any} - \lambda_{S,Vacant}$ , we found that we are between 82% and 100% confident that having any partner leads to a higher population fitness than having no partner. If you consider just the number of partners (ignoring the identity), what you find is actually that the more partners are present, the higher the fitness of the cacti (Figure 6b), though this increase is primarily driven by the presence of *L. apiculatum*.

Despite this apparent synergy, when partner identity was considered, we found the benefits of partner diversity could be explained by Sampling Effect. We believe the benefits of partner diversity are heavily driven by the presence of a single best partner rather than overall synergy. All simulated combinations of ant partners which included *L. apiculatum* were nearly equal and the highest possible fitness estimated for the cholla. This indicates that *L. apiculatum* are the single best partner for the cholla under existing conditions. Based on the definitions of Sampling Effect and Complementarity we use in this study (Batstone, 2018), it is clear that Sampling Effect can explain the benefits of partner diversity in the cholla system.

It is possible that this, like the frequency of partner turnover to *L. apiculatum*, is driven by the extreme frequency of *L. apiculatum* ants in comparison to others. With this in mind, we simulated the population fitness with equal probability for transitioning to any ant state. We found ..... from the simulations with different transition probabilities.<sup>6</sup>

We found evidence of portfolio effect, meaning the presence of multiple partners did not buffer against the potentially negative effects of annual fluctuations. The effect of all ant partners can be measured as  $\lambda_{All} - \lambda_{Vacant}$  (Figure 7). We are 94% confident that when all ants are present the cholla experience higher fitness than when no ants are present according to both the

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<sup>6</sup>*This feels like the most natural progression to me.*

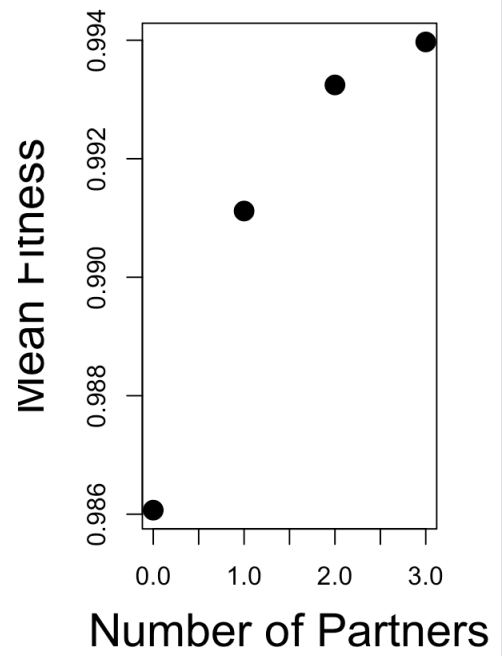
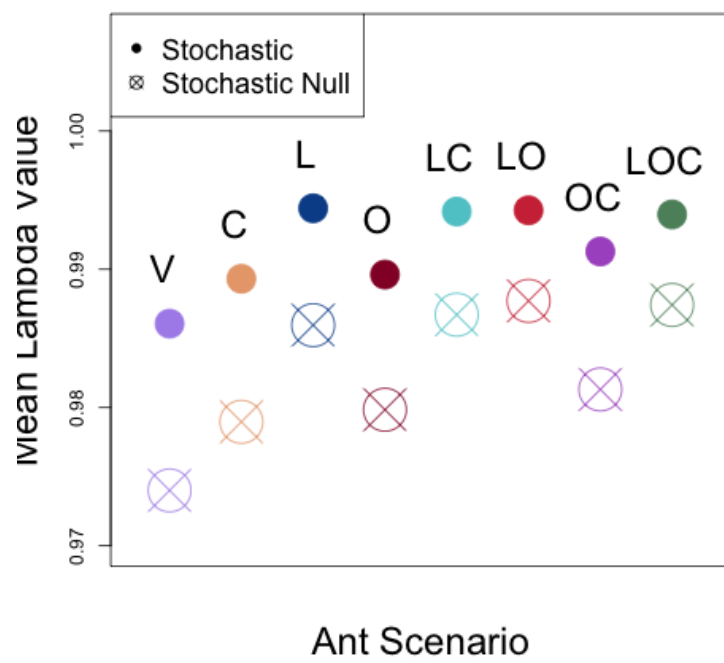


Figure 6: Panel a) shows the mean values of the estimated  $\lambda_S$  (filled in circles) and  $\lambda_{SN}$  (empty circles with an X) for each simulated combination of ant partners. The letters above the points correspond to what ant partners are present (V = Vacant, C = *C. opuntiae*, L = *L. apiculatum*, O = other). Panel b) shows the mean values of the estimated  $\lambda_S$  for

stochastic and stochastic null model. When subtracting these two resulting vectors from each other  $((\lambda_{S,All} - \lambda_{S,Vacant}) - (\lambda_{SN,All} - \lambda_{SN,Vacant}))$ , we found that we are only 52% confident that partners offer higher benefits when able to respond uniquely to a fluctuating environment. There is no real difference between the two scenarios, meaning we have no evidence of portfolio effect.<sup>7</sup>

## Discussion

<sup>8</sup> The large, long-lived tree cholla produce EFN which tempts several species of ant partners to protect them from herbivores and seed predators. Many studies have looked at multispecies mutualisms and the how having a variety of partners leads to variation in demographic effects Bascompte (2019); Báez et al. (2016); Ford et al. (2015); Palmer et al. (2010); Stachowicz and Whitlatch (2005). Because these tree cholla interact with only one ant partner at a time, it is a unique system in which to parse out the individual effects of each ant partners, both in isolated settings or in combinations we cannot test in the real world. <sup>9</sup>

We asked what effects the partners which interact with tree cholla (*C. opuntiae*, *L. apiculatum*, and more<sup>10</sup>) have on the vital rates of tree cholla. Using a system of heirarchical bayesian models we found that there were discernable differences in the effects that each partner had on vital processes of the focal mutualist. The different vital rates vary in importance across tree cholla ontogeny. Several of them are negatively impacted by the presence and pressure of herbivores and seed predators Miller et al. (2009, 2006) and positively impacted by the presence of ant partners Miller (2007). The predators and herbivores target new growth and flowers, leading

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<sup>7</sup>I am not sure if I have explained enough here honestly.

<sup>8</sup>I have not commented too heavily here because I would like to talk through what we want this section to achieve. Currently, most of this section is actually describing results, whereas the pupose is to interpret and contextualize results, and connect them to the broader literature. Some of your content here is actually better at describing results than you had in the Results section, because it includes that element of “how is this connected to the question” that was missing from the Results section.

<sup>9</sup>This is a good start. In general, I suggest opening the Discussion section with a brief summary of what you were trying to learn in this study, what you found, and its broader significance. This paragraph does a little of that, but I think it can be stronger.

<sup>10</sup>I would not say this.



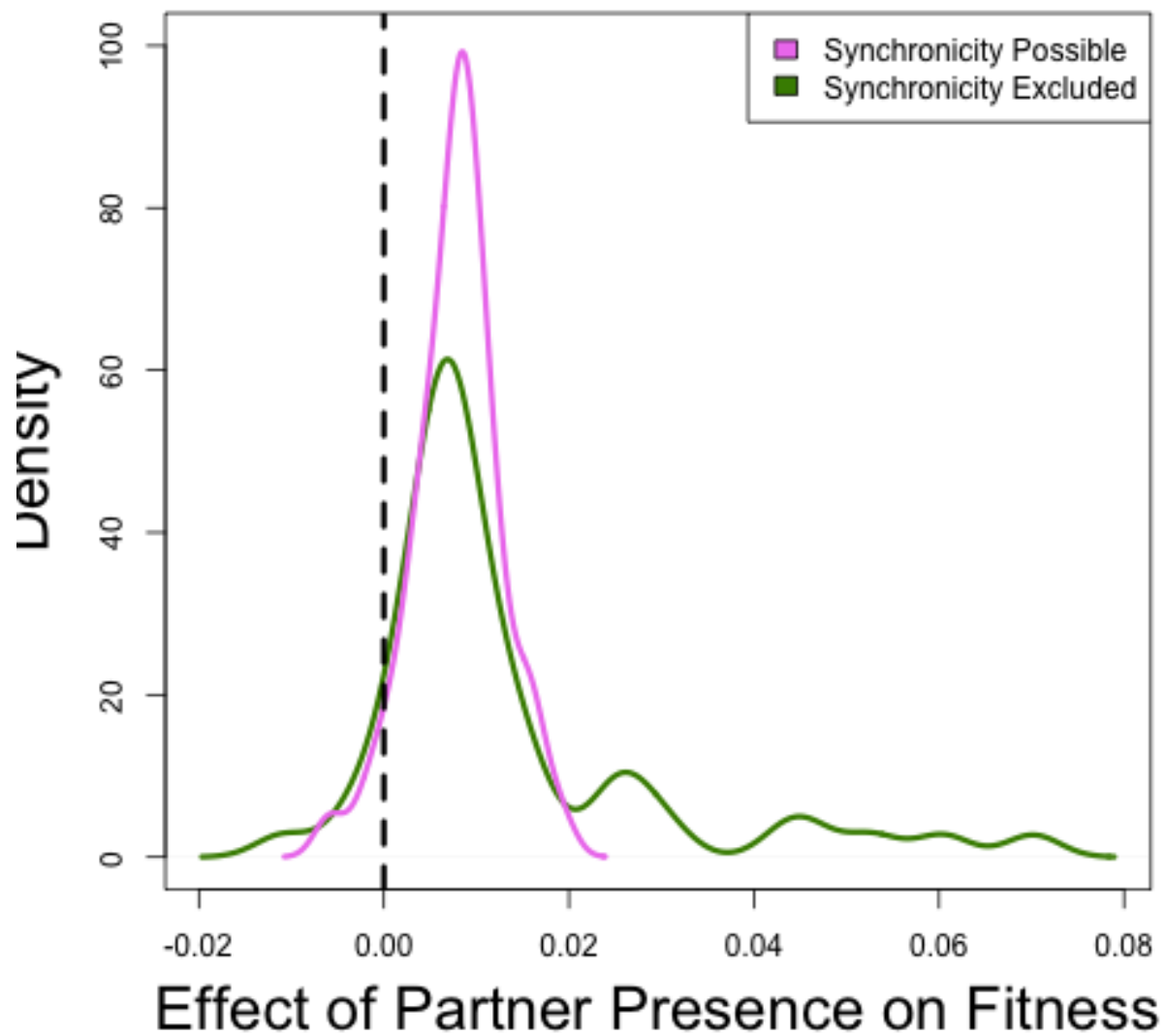


Figure 7: This figure shows the distribution of  $\lambda_{S,All} - \lambda_{S,Vacant}$  in pink and  $\lambda_{SN,All} - \lambda_{SN,Vacant}$  in green. The vertical dashed line shows where the effect of partners on the fitness of the cholla is 0 (to the left the partners have a negative effect, to the right the partners are beneficial).

to negative impacts on the growth rates, survival rates, and floral viability rates of tree cholla  
Agrawal (2004); Louda and Potvin (1995). The presence of the ant partners can reduce those  
525 negative effects.

It has been previously hypothesized that there is a hierarchy of partners due to the ability for  
*L. apiculatum* ants to defend the cacti from seed predators and herbivores Miller (2007). These  
528 prior results would suggest that all vital rates that are affected by ant partners would be boosted  
the most by the presence of *L. apiculatum* ants, this is not what we found. Our results suggest  
that different partners differ significantly in their effects on vital rates.

Prior to reproduction, the tree cholla experience only growth and survival. *C. opuntiae* tended  
ants are associated with the highest growth rates and survival rates of plants. This indicates that  
*C. opuntiae* ants may be good ants for pre-reproductive tree cholla plants. Reproducing plants  
534 experience a probability of reproducing, flower production, and floral abortion. **Floral abortion is  
heavily affected by seed predators Miller et al. (2008)<sup>11</sup>**, which the ants defend the cacti, leading  
to increased floral viability. We specifically found that tree cholla experienced the highest floral  
537 viability rates when tended by *L. apiculatum* ants. This indicates that *L. apiculatum* ants may be  
good partners for reproducing plants.

These results together would suggest that complementarity may be the underlying mecha-  
540 nism that explains why partner diversity is beneficial in this system.

We have shown that the identity of partners is important to the processes that define tree  
cholla fitness. Now we need to analyze the dynamics of partner turnover which dictate the  
543 identity of tree cholla partners and therefore the effects of vital rates on the tree cholla. With our  
models we were able to identify both the direction, frequency, and distinct patterns of partner  
turnover.

In the literature, it is clear that the frequency of partner turnover can have big effects on  
the fitness of the focal mutualist Fiala et al. (1994); Horvitz and Schemske (1986); Oliveira et al.  
(1999); Sachs et al. (2004). In some systems high frequency of turnover is necessary to resiliency

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<sup>11</sup>*Seed predators do not influence floral abortion.*

and leads to higher fitness benefits Trøjelsgaard et al. (2015), while in other systems loyalty is the most beneficial Batstone (2018). While the purpose of this paper is not to establish which would be most beneficial in this system, we were able to identify the pattern. Small plants are almost entirely vacant in this system until they grow large enough to begin producing significant amounts of EFN. Our model shows that once they do produce EFN, plants experience a relatively significant amount of turnover. Mid-sized and large plants which were either vacant or tended by other ants are most likely to become tended by *L. apiculatum* ants in the next year, thereby experiencing partner turnover. Plants which were tended by *L. apiculatum* or *C. opuntiae* ants are most likely to remain tended by the same partners multiple years in a row. This indicates that *C. opuntiae* ants and *L. apiculatum* ants are loyal partners which retain the same plants year after year with regularity.

As established in previous studies, the direction of partner turnover is important when the identity of partners impacts the quality of benefits recieved Alonso (1998); Dejean et al. (2008); Fonseca et al. (2003); Noe and Hammerstein (1994). In our study we found that there are distinct patterns to the direction of partner turnover. Specifically, most plants are tended by *L. apiculatum* ants at some point, because vacant plants, other tended plants, and *L. apiculatum* tended plants are all most likely to be tended by *L. apiculatum* ants. This indicates that while *L. apiculatum* ants are loyal to their own plants and return multiple years in a row to the same ones, they are also strong colonizers.

The combination of partner identity, partner turnover, and temporal stochasticity gives us the unique power to consider both the fitness of the tree cholla under different partner scenarios (as some have done before Palmer et al. (2010)<sup>12</sup>) and a unique set of mechanisms (Batstone (2018)) which explain how the multi-partner interactions lead to fitness differences. We found that the combination of accurate partner transitions with partner identity<sup>13</sup> affected the fitness of the tree cholla in interesting and dynamic ways. Namely, a best partner emerged in this analysis,

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<sup>12</sup>There is more than just the Palmer pape. Be sure that you are comprehensive in your use of the literaure, include non-ant-plant studies,

<sup>13</sup>Not sure what this means.

which was surprising given the nature of our vital rate findings. The variation in best partner for each vital rate suggested the potential that the different ant partners had some level of unique specialty in what they offered, which would support complementarity as the mechanism which explained the effects of partner diversity Stachowicz and Whitlatch (2005); Stanton (2013). The results of our IPM however differ from this prediction.

Using the stochastic IPM we developed, we found evidence of sampling effect rather than complementarity. We found that *L. apiculatum* was the single best partner, and that all diversity scenarios where *L. apiculatum* was present resulted in the highest possible fitness of tree cholla. This indicates that despite the fact that *L. apiculatum* partnership does not result in the highest growth and survival rates, it is still the overall best partner.

Using the stochastic null IPM and the stochastic IPM we compared the fitness boost received by all ant partners when ants effects varied separately across years and when they did not. When all ants responded to inter-annual variability the same way (shown in the stochastic null IPM) we found that the fitness boost received from partners was larger than the fitness boost received when ants responded to inter-annual variability differently. This indicates that having multiple possible partners benefits the tree cholla by buffering the potentially negative effects of inter-annual variation.

<sup>14</sup> This paper shows the importance of long-term datasets in investigating species interactions and calls for further use of long-term data. Previously studies have analyzed how partner identity and partner turnover impact focal mutualist fitness Barrett et al. (2015); Bruna et al. (2014); Dejean et al. (2008); Fonseca et al. (2003); Noe and Hammerstein (1994); Trøjelsgaard et al. (2015). Separate studies have analyzed how inter-annual variability impacts focal mutualists Alarcón et al. (2008); Alonso (1998); Horvitz and Schemske (1990); Lázaro et al. (2022); Ollerton et al. (2006). The long term dataset we used gave us the unique ability to consider the combined effects of partner identity, partner turnover, and temporal stochasticity.<sup>15</sup>

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<sup>14</sup>What this all means more broadly?? I'm currently not sure what to do with this. Tom: that's the entire Discussion!

<sup>15</sup>This is really good. More of this!

This paper has limitations, specifically surrounding the driving forces behind the ant-plant interactions. We revealed the dynamics of partner turnover and showed that different ant partners are correlated with different fitness benefits. As of now, the driving mechanisms behind how ant species come to interact with individual plants is still unknown and could be subject to future work.<sup>16</sup>

## Acknowledgments

This should be drafted.

## Data and Code Availability

This should be drafted.

## Appendix A: Additional Methods and Parameters

This is not referenced in the paper, to my knowledge, and I think you need to think more deeply about what content should go into appendices and why.

## Literature Cited

Afkhami, M. (2014). Multiple mutualist effects: conflict and synergy in multispecies mutualisms. *Ecology*, 95(4):833–844.

Agrawal, A. A. (2004). the american naturalist.

Agrawal, A. A. and Rutter, M. T. (1998). Dynamic anti-herbivore defense in ant-plants: The role of induced responses.

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<sup>16</sup>*This feels a little weak and incomplete.*

Alarcón, R., Waser, N. M., and Ollerton, J. (2008). Year-to-year variation in the topology of a  
618 plant-pollinator interaction network. *Oikos*, 117(12):1796–1807.

Alonso, L. E. (1998). Spatial and temporal variation in the ant occupants of a facultative ant-plant.  
*Biotropica*, 30:201–213.

621 Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 122:1390–1396.

Bahia, R., Lambertucci, S. A., Plaza, P. I., and Speziale, K. L. (2022). Antagonistic-mutualistic  
interaction between parrots and plants in the context of global change: Biological introductions  
624 and novel ecosystems. *Biological Conservation*, 265(November 2021):109399.

Barrett, L. G., Bever, J. D., Bissett, A., and Thrall, P. H. (2015). Partner diversity and identity  
impacts on plant productivity in acacia-rhizobial interactions. *Journal of Ecology*, 103:130–142.

627 Barton, K. E. and Koricheva, J. (2010). The ontogeny of plant defense and herbivory: Character-  
izing general patterns using meta-analysis. *The American Naturalist*, 175(4):481–493.

Bascompte, J. (2009). Disentangling the web of life. *Science*, 325:414–416.

630 Bascompte, J. (2019). Mutualism and biodiversity. *Current Biology*, 29(11):R467–R470.

Batstone, R. T. (2018). Using niche breadth theory to explain generalization in mutualisms.  
*Ecology*, 99(5):1039–1050.

633 Beattie, A. (1985). *The Evolutionary Ecology of Ant-Plant Mutualisms*.

Benson, L. (1982). Cacti of the united states and canada.

Boege, K. and Marquis, R. J. (2005). Facing herbivory as you grow up: The ontogeny of resistance  
636 in plants. *Trends in Ecology and Evolution*, 20:441–448.

Bronstein, J. L. (1994). Conditional outcomes in mutualistic interactions. *TREE*, 9(6):214–217.

Bronstein, J. L. (1998). The contribution of ant-plant protection studies to our understanding of  
639 mutualism. *bioTropica*, 30(2):150–161.

Bronstein, J. L., Bronstein, J. L., Alarcón, R., and Geber, M. (2006). The evolution of plant – insect mutualisms. *New Phytologist*, pages 412–428.

642 Bruna, E. M., Izzo, T., Inouye, B., and Vasconcelos, H. (2014). Effect of mutualist partner identity on plant demography. *Ecology*, 95(12):3237–3243.

Byk, J. and Del-Claro, K. (2011). Ant-plant interaction in the neotropical savanna: Direct beneficial  
645 effects of extrafloral nectar on ant colony fitness. *Population Ecology*, 53:327–332.

Báez, S., Donoso, D. A., Queenborough, S. A., Jaramillo, L., Valencia, R., and Dangles, O. (2016).  
Ant mutualism increases long-term growth and survival of a common amazonian tree. *Ameri-  
648 can Naturalist*, 188(5).

Chamberlain, S. A., Bronstein, J. L., and Rudgers, J. A. (2014). How context dependent are species interactions? *Ecology Letters*, 17(7):881–890.

651 Dattilo, W., Marquitti, F. M. D., Guimaraes, P. R., and Izzo, T. J. (2014). The structure of ant-plant ecological networks: Is abundance enough? *Ecology*, 95:475–485.

Dejean, A., Djieto-Lordon, C., Cereghino, R., and Leponce, M. (2008). Ontogenetic succession  
654 and the ant mosaic: An empirical approach using pioneer trees. *Basic and Applied Ecology*, 9.

Djiéto-Lordon, C., Dejean, A., Ring, R. A., Nkongmeneck, B. A., Lauga, J., and McKey, D. (2005).  
Ecology of an improbable association: The pseudomyrmecine plant-ant tetraponera tessmanni  
657 and the myrmecophytic liana vitex thyrsoflora (lamiaceae) in cameroon. *Biotropica*, 37(3):421–430.

Donald, M. L. and Miller, T. E. (2022). Does ant–plant mutualism have spillover effects on the  
660 non-partner ant community? *Ecology and Evolution*, 12(1):e8524.

Fiala, B., Grunsky, H., Maschwitz, Ulrich K Linsenmair, E., Linsenmair, K., and Maschwitz, H.  
U. G. (1994). Diversity of ant-plant interactions: protective efficacy in macaranga species with  
663 different degrees of ant association. *Oecologia*, 97.

Fonseca, C. R., Benson, W. W., and Zoologia, D. D. (2003). Ontogenetic succession in amazonian ant trees. *Oikos*, 102(2):407–412.

666 Ford, K. R., Ness, J. H., Bronstein, J. L., and Morris, W. F. (2015). The demographic consequences of mutualism: ants increase host-plant fruit production but not population growth. *Oecologia*, 179:435–446.

669 Fraser, A. M., Axen, A. H., and Pierce, N. E. (2001). Assessing the quality of different ant species as partners of a myrmecophilous butterfly. *Oecologia*, 129:452–460.

Frederickson, M. E. (2005). Ant species confer different partner benefits on two neotropical myrmecophytes. *Oecologia*, 143:387–395.

Frederickson, M. E. (2013). Rethinking mutualism stability: Cheaters and the evolution of sanctions. *Quarterly Review of Biology*, 88(4):269–295.

675 Gaume, L., Mckey, D., and Terrin, S. (1998). Ant-plant-homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. *Ecological Entymology*.

678 Horvitz, C. and Schemske, D. (1986). Seed dispersal of a neotropical myrmecochore : Variation in removal rates and dispersal distance. *bioTropica*, 18(4):319–323.

Horvitz, C. and Schemske, D. (1990). Spatiotemporal variation in insect mutualists of a neotropical herb. *Ecology*, 71.

Kiers, E. T., Rousseau, R. A., West, S. A., and Denison, R. F. (2003). Host sanctions and the legume-rhizobium mutualism. *Nature*, 425(6953):78–81.

684 Lázaro, A., Gómez-Martínez, C., González-Estévez, M. A., and Hidalgo, M. (2022). Portfolio effect and asynchrony as drivers of stability in plant–pollinator communities along a gradient of landscape heterogeneity. *Ecography*, 2022(3):1–14.



- 687 Leigh, E. G. (2010). The evolution of mutualism. *Journal of Evolutionary Biology*, 23:2507–2528.
- Louda, S. M. and Potvin, M. A. (1995). Effect of inflorescence-feeding insects on the demography and lifetime of a native plant. *Ecology*, 76:229–245.
- 690 Ludka, J., Levan, K. E., and Holway, D. A. (2015). Infiltration of a facultative ant-plant mutualism by the introduced argentine ant: effects on mutualist diversity and mutualism benefits. *Ecological Entomology*, 40.
- 693 Mandyam, K. G. and Jumpponen, A. (2014). Mutualism-parasitism paradigm synthesized from results of root-endophyte models. *Frontiers in Microbiology*, 5(DEC):1–13.
- Mann, J. (1969). Cactus-feeding insects and mites. *Smithsonian Inst.*
- 696 Miller, T. E. (2007). Does having multiple partners weaken the benefits of facultative mutualism? a test with cacti and cactus-tending ants. *Oikos*, 116(3):500–512.
- Miller, T. E. (2014). Plant size and reproductive state affect the quantity and quality of rewards to animal mutualists. *Journal of Ecology*, 102(2):496–507.
- 699 Miller, T. E., Louda, S. M., Rose, K. A., and Eckberg, J. O. (2009). Impacts of insect herbivory on cactus population dynamics: Experimental demography across an environmental gradient. *Ecological Monographs*, 79(1):155–172.
- 702 Miller, T. E., Tenhumberg, B., and Louda, S. M. (2008). Herbivore-mediated ecological costs of reproduction shape the life history of an iteroparous plant. *American Naturalist*, 171:141–149.
- 705 Miller, T. E., Tyre, A. J., and Louda, S. M. (2006). Plant reproductive allocation predicts herbivore dynamics across spatial and temporal scales. *American Naturalist*, 168(5):608–616.
- Ness, J. H., Morris, W., and Bronstein, J. L. (2006). Integrating quality and quantity of mutualistic service to contrast ant species protecting *ferocactus wislizeni*. *Ecology*, 87(4):912–921.
- 708

Ness, J. H., Morris, W. F., and Bronstein, J. L. (2009). For ant-protected plants, the best defense is a hungry offense. *Ecology*, 90:2823–2831.

711 Noe, R. and Hammerstein, P. (1994). Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating no (1 ). *Behav Ecol Sociobiol*, 35:1–11.

Ohm, J. R. and Miller, T. E. (2014). Balancing anti-herbivore benefits and anti-pollinator costs of defensive mutualists. *Ecology*, 95(10):2924–2935.

Oliveira, P. S., Rico-Gray, V., Díaz-Castelazo, C., and Castillo-Guevara, C. (1999). Interaction between ants, extrafloral nectaries and insect herbivores in neotropical coastal sand dunes: Herbivore deterrence by visiting ants increases fruit set in *opuntia stricta* (cactaceae). *Functional Ecology*, 13(5):623–631.

Ollerton, J., Johnson, S. D., and Hingston, B. A. (2006). Geographical variation in diversity and specificity of pollination systems. In *Plant–pollinator interactions: from specialization to generalization.*, number January 2006, pages 282–308. Academia.edu.

Palmer, T. M., Doak, D. F., Stanton, M. L., Bronstein, J. L., Kiers, T. E., Young, T. P., Goheen, J. R., and Pringle, R. M. (2010). Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *PNAS*, 107(40):17234–17239.

R Core Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rodriguez-Rodriguez, M. C., Pedro, J., and Valido, A. (2017). Functional consequences of plant-animal interactions along the mutualism-antagonism gradient. *Ecology*, 98(5):1266–1276.

729 Rogers, S. R., Tarpy, D. R., and Burrack, H. J. (2014). Bee species diversity enhances productivity and stability in a perennial crop. *PloS one*, 9(5):e97307.

Rudgers, J. A. (2004). Enemies of herbivores can shape plant traits: Selection in a facultative ant-plant mutualism. *Ecology*, 85:192–205.

Sachs, J. L., Mueller, U. G., Wilcox, T. P., and Bull, J. J. (2004). The evolution of cooperation. *Quarterly Review of Biology*, 79(2):135–160.

735 Song, C., Ahn, S. V., Rohr, R. P., and Saavedra, S. (2020). Towards probabilistic understanding about the context-dependency of species interactions. *Trends in Ecology and Evolution*, 35(5):384–396.

738 Stachowicz, J. J. and Whitlatch, R. B. (2005). Multiple mutualists provide complementary benefits to their seaweed host. *Ecology*, 86(9):2418–2427.

Stan Development Team (2023). RStan: the R interface to Stan. R package version 2.32.3.

741 Stanton, M. L. (2013). Interacting guilds: Moving beyond the pairwise perspective on mutualisms. *The American Naturalist*, 162:510–523.

Thrall, P. H., Hochberg, M. E., Burdon, J. J., and Bever, J. D. (2007). Coevolution of symbiotic  
744 mutualists and parasites in a community context. *Trends in Ecology and Evolution*, 22(3):120–126.

Trager, M. D., Bhotika, S., Hostetler, J. A., Andrade, G. V., Rodriguez-Cabal, M. A., Mckeeon,  
747 C. S., Osenberg, C. W., and Bolker, B. M. (2010). Benefits for plants in ant-plant protective mutualisms: A meta-analysis.

Trøjelsgaard, K., Jordano, P., Carstensen, D. W., and Olesen, J. M. (2015). Geographical variation  
750 in mutualistic networks: Similarity, turnover and partner fidelity. *Proceedings of the Royal Society B: Biological Sciences*, 282(1802).

Trøjelsgaard, K., Jordano, P., Carstensen, D. W., and Olesen, J. M. (2015). Geographical variation  
753 in mutualistic networks: Similarity, turnover and partner fidelity. *Proceedings of the Royal Society B: Biological Sciences*, 282.

Ushio, M. (2020). Interaction capacity underpins community diversity. *BioRxiv*.

- 756 Wetzel, W. C., Inouye, B. D., Hahn, P. G., Whitehead, S. R., and Underwood, N. (2023). Annual  
review of ecology, evolution, and systematics variability in plant-herbivore interactions. *Annu.  
Rev. Ecol. Evol. Syst.* 2023, 54:2023.
- 759 Williams, J. L., Miller, T. E. X., and Ellner, S. P. (2012). Avoiding unintentional eviction from  
integral projection models. *Ecology*, 93:2008–2014.
- Wulff, J. L. (2008). Life-history differences among coral reef sponges promote mutualism or  
762 exploitation of mutualism by influencing partner fidelity feedback. *The American Naturalist*,  
171.
- Yeung, T., Terebiznik, M., Yu, L., Silviu, J., Abidi, W. M., Philips, M., Levine, T., Kapus, A.,  
765 and Grinstein, S. (2006). Receptor activation alters inner surface potential during phagocytosis.  
*Science*, 313:347–351.

## Tables

## Figure legends

## Supplementary Materials

### *Herbivory Data*

### *Model Checks*

For each model fitted, we conducted two tests to determine if the fit was acceptable to use in our IPM. First, we checked the convergence of each parameter. Below we show the convergence of all  $\beta$  terms listed in the Statistical Modeling subsection of Methods. Second, we checked the posterior fit, comparing the estimated values of each model to the  $y$  values of the actual data. We show these posterior checks below, split by ant partner where relevant.

### *Statistical Models – Results*

Below are the results reported of all statistical models not described in the main body of the text.

*Reproduction Model.* The probability of a plant reproducing in a given year is highly size dependent. The mean probability of reproducing remains at about 0% until the plant reaches a medium size, after which the mean probability of reproducing increases steadily before reaching about 100% at large sizes.

*Seeds Per Flower Model.* Each viable flower on a plant produces between 97 and 257 seeds. This number is affected by the ant partner present. *C. opuntiae* tended plants produce a mean of 148 seeds per flower. *L. apiculatum* tended plants produce a mean of 149 seeds per flower.<sup>17</sup> Vacant

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<sup>17</sup>These results are not consistent with Ohm and Miller, where *Crem* had lower seeds than *Liom*. I would check this. This section should also reference that paper because these are not new results.

Parameter	Median (95% CI)	Prior Distribution
growth xi intercept vacant $\beta_{01}^g$	-5.210899(-5.686865, -5.491787)	sDE
growth xi intercept other $\beta_{02}^g$	-5.8288(-5.956217, 1.766021)	asdf
growth xi intercept <i>C. opuntiae</i> $\beta_{03}^g$	-4.529523(-6.0770390, 0.1222112)	asdf
growth xi intercept <i>L. apiculatum</i> $\beta_{04}^g$	-5.106802(-5.4499944, 0.5453901)	asdf
growth xi size dependent vacant $\beta_{11}^g$	asdf	asdf
growth xi size dependent other $\beta_{12}^g$	asdf	asdf
growth xi size dependent <i>C. opuntiae</i> $\beta_{13}^g$	asdf	asdf
growth xi size dependent <i>L. apiculatum</i> $\beta_{14}^g$	sadf	asdf
growth omega intercept $\omega_0^g$		
growth omega size dependent $\omega_1^g$		
growth alpha intercept $\alpha_0^g$		
growth alpha size dependent $\alpha_1^g$		
1-year germination intercept $\alpha^{\gamma_1}$		
2-year germination intercept $\alpha^{\gamma_2}$		
survival intercept vacant $\beta_{01}^s$		
survival intercept other $\beta_{02}^s$		
survival intercept <i>C. opuntiae</i> $\beta_{03}^s$		
survival intercept <i>L. apiculatum</i> $\beta_{04}^s$		
survival size dependent vacant $\beta_{11}^s$		
survival size dependent other $\beta_{12}^s$		
survival size dependent <i>C. opuntiae</i> $\beta_{13}^s$		
survival size dependent <i>L. apiculatum</i> $\beta_{14}^s$		
flowering intercept $\beta_0^f$		
flowering size dependent $\beta_1^f$		
viability intercept vacant $\beta_{01}^v$		
viability intercept other $\beta_{02}^v$		
viability intercept <i>C. opuntiae</i> $\beta_{03}^v$		
viability intercept <i>L. apiculatum</i> $\beta_{04}^v$	46	

Table 1: This table includes the median estimates, the 95% confidence intervals, and the prior distribution for each parameter in each model.

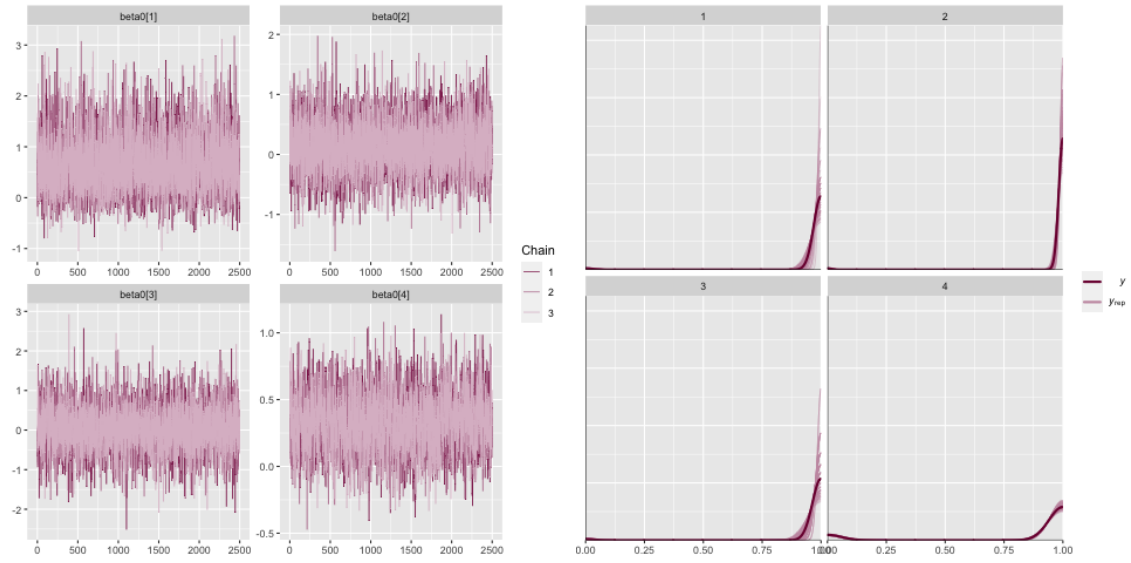


Figure 1: The a) posterior convergence of the parameters estimated by the survival model and the b) posterior distribution of survival estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean survival distribution (black line) of the real data.

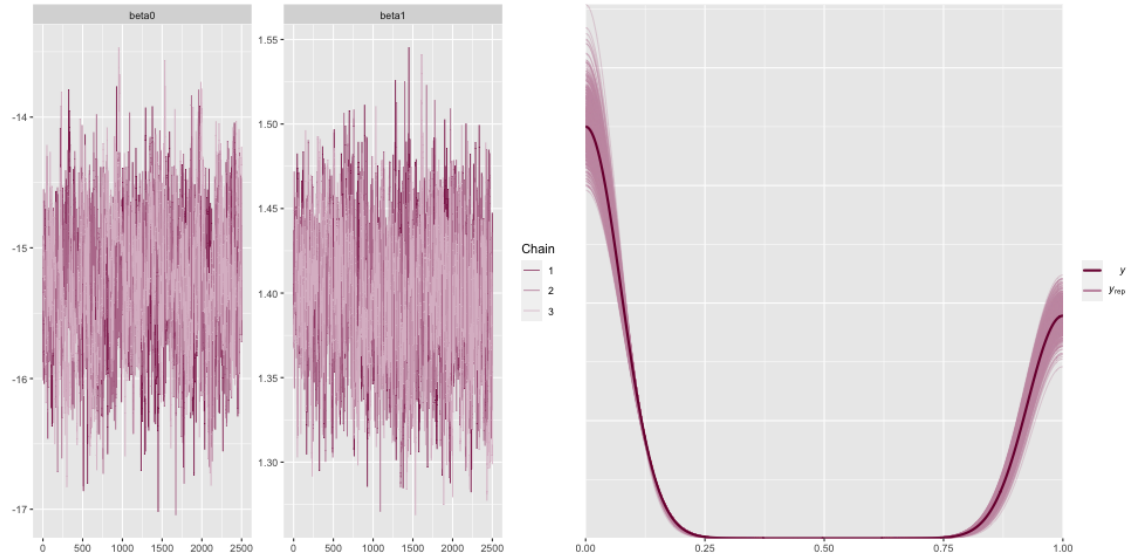


Figure 2: The a) posterior convergence of the parameters estimated by the reproduction model and the b) posterior distribution of reproductive status estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean reproductive status distribution (black line) of the real data.

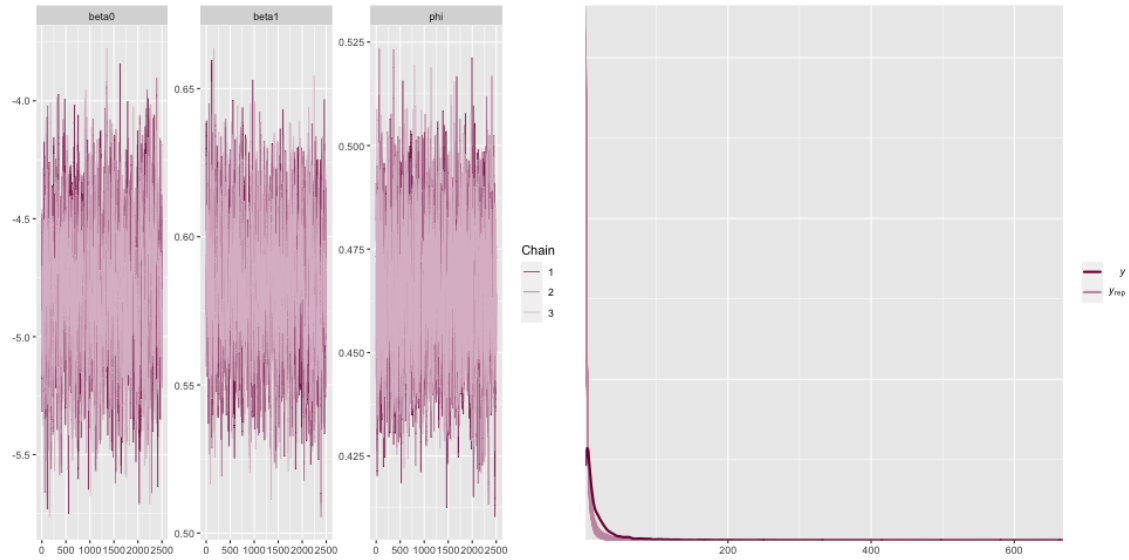


Figure 3: The a) posterior convergence of the parameters estimated by the number of flowers model and the b) posterior distribution of the number of flowers estimated (pink lines) compared to the mean distribution of observed flowers (black line).



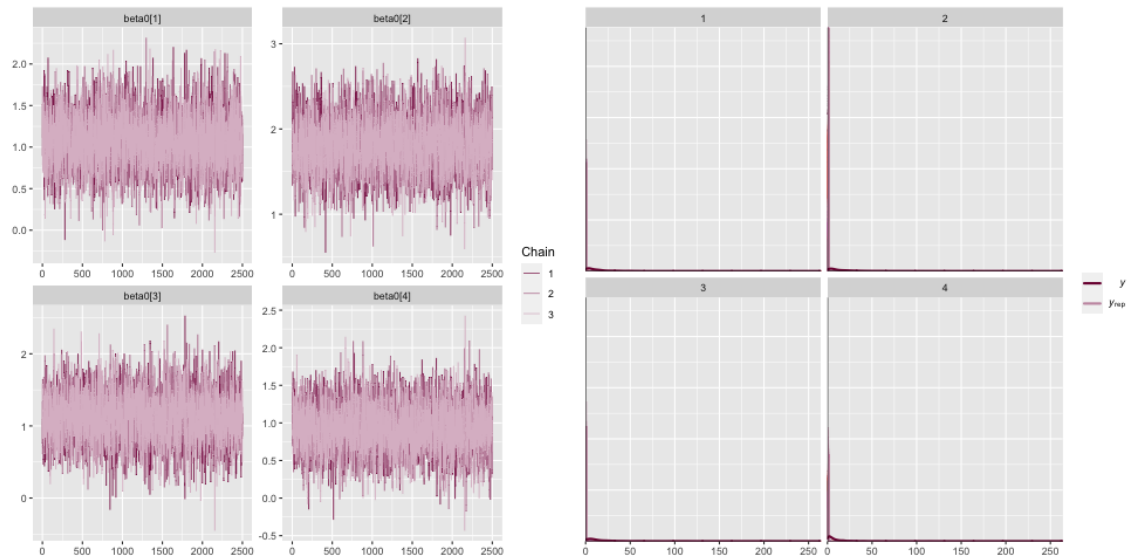


Figure 4: The a) posterior convergence of the parameters estimated by the viability model and the b) posterior distributions of floral viability estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean floral viability distribution (black line) of the real data.

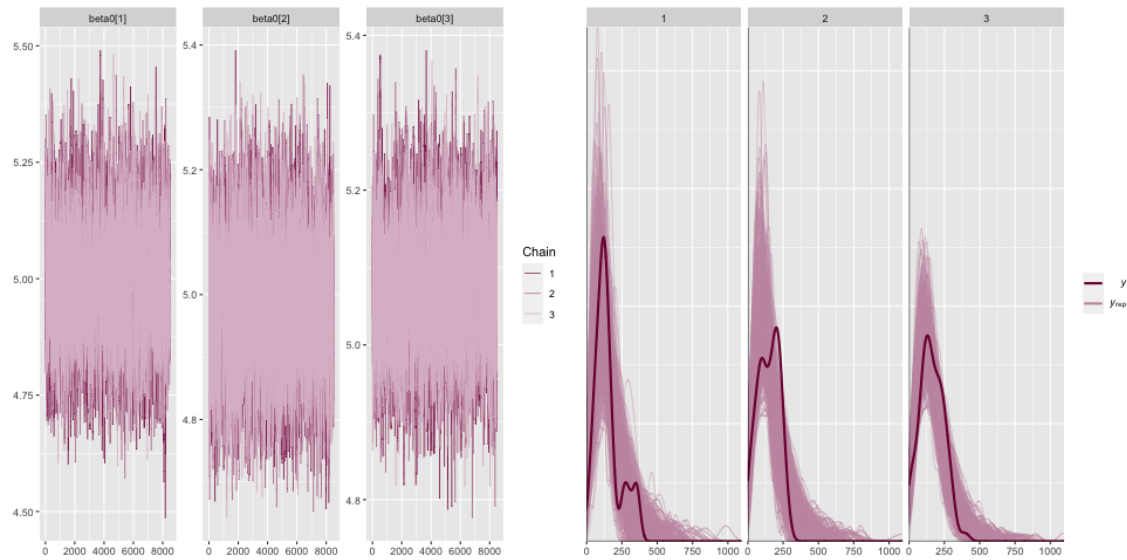


Figure 5: The a) posterior convergence of the parameters estimated by the seeds per fruit model and the b) posterior distributions of seeds per fruit estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = vacant) compared to the mean seeds per fruit distribution (black line) of the real data.

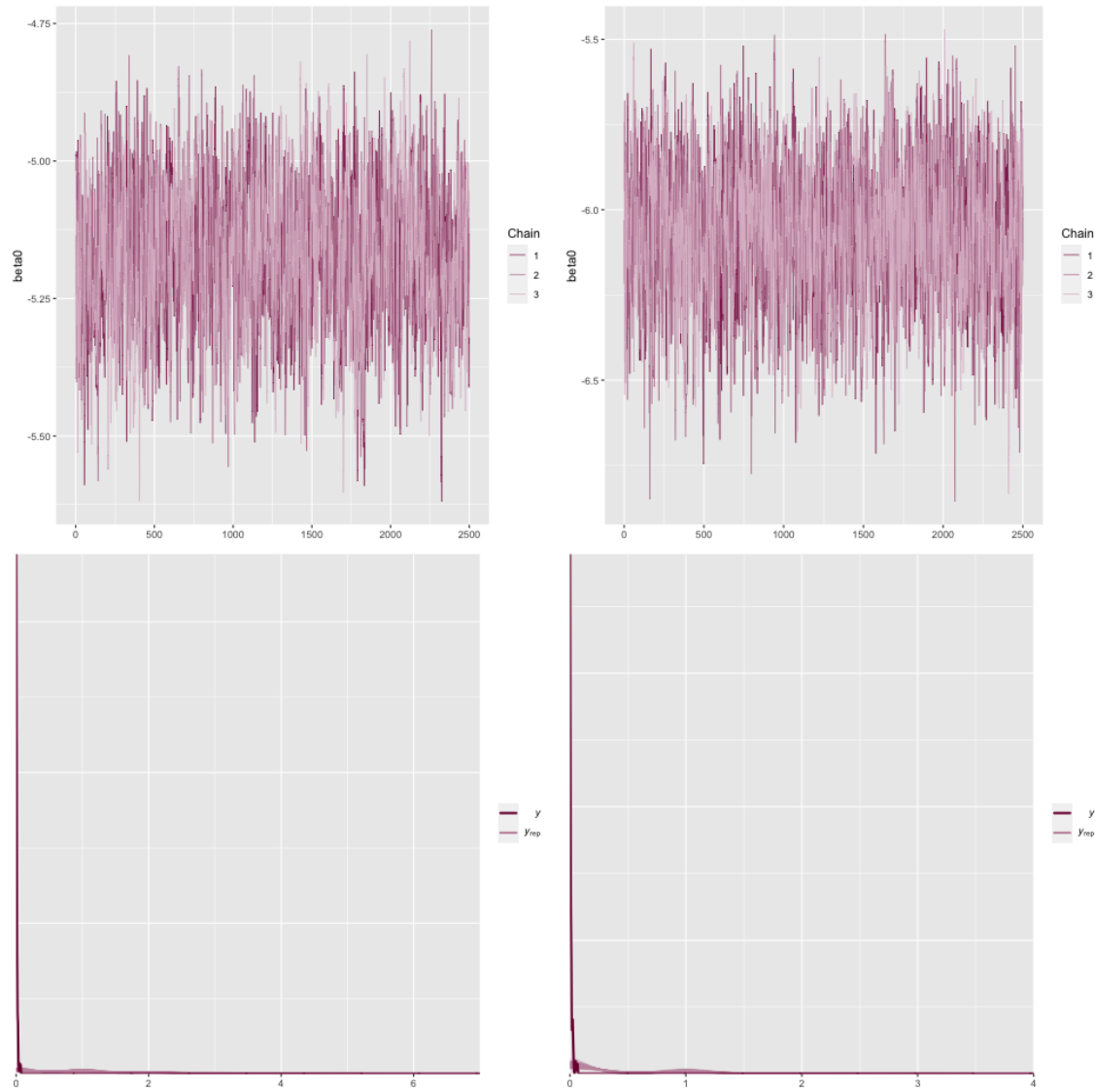


Figure 6: The a-b) posterior convergence of the parameters estimated by the germination from year one seedbank and germination from year two seedbank models respectively. The c-d) posterior distributions of floral viability estimates (pink lines) compared to the mean germination distribution (black line) of the real data for first year germinants and second year germinants respectively.

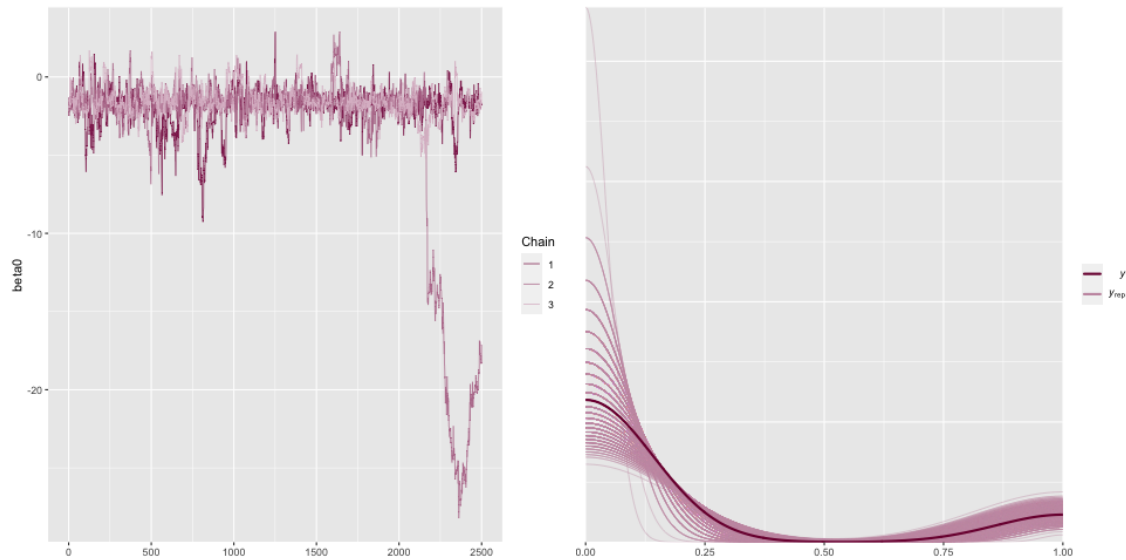


Figure 7: The a) posterior convergence of the parameters estimated by the pre-census survival model and the b) posterior distribution of the pre-census survival estimated (pink lines) compared to the mean distribution of observed pre-census survival (black line).

plants produce a mean of 160 seeds per flower. We are 73% and 78% confident that vacant plants produce more seeds per flower on average than plants tended by *C. opuntiae* and *L. apiculatum* ants respectively.

*Precensus Survival Model.* Pre-census seed survival rates fall between 0% and 95% with the mean pre-census seed survival at 18%.

*Germination Model.* Seeds have a significantly higher probability of germinating in year one than in year two. Seeds in year one experience germination rates between 50% and 100% with a mean of 62% germination. Seeds in year two experience germination rates between 50% and 98% with a mean of 58% germination.

New recruits are expected to be between the sizes of  $0.11 \text{ cm}^3$  and  $0.38 \text{ cm}^3$  with a mean size of  $0.20 \text{ cm}^3$ .<sup>18</sup>

<sup>18</sup>Move to an appendix. These results are not relevant for the questions at hand.

Videos If you have videos, journal style for them is generally similar to that for figures.