

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

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Abstract

¹ 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 scenarios which included the partner *L. apiculatum* resulted in the highest possible fitness for the tree

¹I think this is too long for Am Nat requirements. Also, use “we”.

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 among the most 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 and herbivores² 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

²notice that "herbivores" does not fit here, at least not yet. you have not said anything about ants and plants, you are talking very generally. put yourself in the mind of a reader as you write, this will help ensure that ideas appear in an order that can be digested.

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
84 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
87 more vulnerable life stages (Dejean et al., 2008; Djitéto-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
90 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
93 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
96 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
102 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
105 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.,
108 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 mutualism 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 populations³.

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?

³I would be careful here – unless you are using the herbivore counts I don't think you have data on this.

135 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) this effect?

138 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
141 combines diverse effects on vital rates and pathways of partner turnover to quantify effects of partner diversity on plant fitness.

Methods

Study System

144 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
147 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 south-
150 western 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
153 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
156 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).

159 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
162 *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
165 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
168 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.

171 There are a variety of insect herbivores and seed predators which specialize on tree cholla
(Mann, 1969). A weevil of the genus *Gerstaekeria* feeds on vegetative and reproductive structures
and implants their larvae within the plant tissue for the winter. A cactus bug, *Narnia pallidicornis*,
174 (Hemiptera: Coreidae) feeds on all cholla parts with a preference for the reproductive struc-
tures (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
177 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
180 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
183 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
186 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 since the last survey and, for survivors, we recorded the height (cm), maximum crown
189 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 effort as counts of viable and aborted flowerbuds. We recorded the ant species
192 present (or vacancy if no ants present). Occurrences of more than one ant species on one plant
were rare (⁴), and for the purpose of this analysis we classified the plant as being occupied by the
more abundant species. Plots were searched for new recruits each year, and these were added
195 to the census. In total, the data set included # unique individuals and # plant-year observations.

⁵ These data were used to fit vital rate models (survival, growth, reproduction) as functions of
plant size and ant occupancy state.

198 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
per fruit for plants tended by *L. apiculatum*, *C. opuntiae*, or no ants (experimental exclusion). Miller
201 et al. (Miller et al., 2009) provide data on seed entry to the seed bank and seedling germination
and survival rates.

Multi-state Integral Projection Model

204 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
with continuous size structure, they can also be modified to accommodate a combination of
207 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

⁴quantify

⁵update numbers

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* ⁽⁶⁾ 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 and ant species which occurred at relatively low frequencies compared to *C. opuntiae* and *L. apiculatum* (such as unknown species belonging to the genus *Aphenogaster* and unknown species belonging to the genus *Camponotus*).⁷ Ant state is included as a predictor variable in sub-models where there are biologically realistic pathways through which ants could 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 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.

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 dynamics are given by:

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

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

Functions $P(x'; \boldsymbol{\tau}^P)$ and $F(x'; \boldsymbol{\tau}^F)$ ⁸ give the probability of flowering and the number of flowerbuds

⁶Quantify this.

⁷I think you can do better than this because we actually have the designated species in the data. I would report here the actual breakdown (percentages) of species in the “other” group. I expect *Forelius* will be a big chunk of it.

⁸These should be x not x' because we modeled flowering and fertility in year t based on size in year t .

produced, respectively, by plants of size x' in year t . The proportion of flowerbuds that remain viable through fruit set ($V(a; \tau_a^V)$) and the number of seeds per fruit ($\kappa(a')$ ⁹) are dependent on ant state a but not size. The vector τ gives year-specific deviates (with mean zero) and appears in functions for which we can estimate 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 ¹⁰. Seed production is integrated over the size distribution, from the lower L to upper U size limits, and summed over all possible ant states (A) giving total seed production. Seeds are multiplied by the probability of seed dispersal and survival (δ) 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 γ_1 or 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 γ_2 or die.

For the above-ground part of the life cycle, the number of plants of size x' and ant state a' in 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 a plant of size x' and ant state a' based on the recruit size distribution $\eta(x')$ and the probability of seedling survival (ω) 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 appearance in our census ($\sum_{a'}^A \rho_0(a') = 1$). 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 ant state. As above, these functions include inter-annual variability through year-specific deviates

⁹Why is this a' ? I think it should be a . More generally, I think you need to explain your use of primes and how readers should interpret them at the start of model exposition.

¹⁰Why does the tau vector for viability have the a subscript but the others do not?

that can vary by ant state (τ_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 function includes inter-annual variability through year-specific intercepts which are consistent across ant states (τ^p).

Statistical modeling and parameter estimation

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 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 ant state. All models were fit using Stan and Rstan⁽¹¹⁾. Unless otherwise mentioned, all models use vague priors.

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 . We fit this model to size data at the end of the transition year y^G using the location-scale parameterization of the student t distribution, because in preliminary analyses we found that size transition data were more fat-tailed than a Gaussian distribution could accommodate. Specifically, the model was:

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

$$\hat{G} = \beta_0^G + \beta_1^G \times x + \beta_2^G \times a + \beta_3^G \times x \times a + \beta_4^G \times x^2 + \beta_5^G \times a \times x^2 + u + w$$

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

$$\hat{\nu} = \beta_0^\nu + \beta_1^\nu \times x$$

¹¹*Cite Stan and RStan.*

270 where $u \sim N(0, \sigma_{yr \times a}^2)$ is the year random effect with year specific variance of σ_{yr} with ant a in
year t , and $w \sim N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot} . Ants are
included as predictors here because ant partners defend cholla from herbivores, preventing the
273 loss of limbs and therefore shrinking.

Survival. The survival model ($S(a, x; \tau_a^S)$) estimates the probability of survival y^S 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 , using a Bernoulli distribution:

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

$$\text{logit}(\hat{S} = \beta_0^S) + \beta_1^S \times x + \beta_2^S \times a + \beta_3^S \times x \times a + u + w$$

where $u \sim N(0, \sigma_{yr \times a}^2)$ is the year random effect with year specific variance of σ_{yr} and ant state
 a in year t , and $w \sim N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot} . A
276 Bernoulli distribution was chosen here because the only two possible outcomes are survival or
death. Ants are included as predictors here because ant partners defend cholla from herbivores
and predators, decreasing the likelihood of mortality due to either of these.

Reproduction. The reproduction model ($P(x'; \tau^P)$) estimates the probability of reproducing y^P in
year $t + 1$, with fixed effects for the size x' in year $t + 1$ and random effects of plot w and year u ,
using a Bernoulli distribution:

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

$$\text{logit}(\hat{P}) = \beta_0^P + \beta_1^P \times x' + u + w$$

279 where $u \sim N(0, \sigma_{yr}^2)$ is the year random effect with year specific variance of σ_{yr} , and $w \sim$
 $N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot} .

Flowers. The total flowers model ($F(x'; \tau^F)$) estimates the total flowers produced by a plant y^F
in year $t + 1$, with fixed effects of size x' in year $t + 1$ and random effects of plot w and year u ,

using a Negative Binomial distribution:

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

$$\log(\hat{F}) = \beta_0^F + \beta_1^F \times x' + u + w$$

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

where $u \sim N(0, \sigma_{yr}^2)$ is the year random effect with year specific variance of σ_{yr} , and $w \sim$
 282 $N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot} .

Viability. The viability model ($V(a; \tau_a^V)$) estimates the proportion of flowers produced by a plant which are viable (not aborted) y^V in year $t + 1$, with fixed effects of the ant partner of the cactus a in year t and random effects of plot w and year u , using a Binomial distribution:

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

$$\text{logit}(\hat{V}) = \beta_0^V \times a + u + w$$

where $u \sim N(0, \sigma_{yr \times a}^2)$ is the year random effect with year specific variance of σ_{yr} and ant state a in year t , and $w \sim N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot} . Ants
 285 are included as predictors here because they defend the cacti from seed predation which can lead to floral abortion.

Ant Transitions. The ant transition rates model ($\epsilon(x, a, a'; \tau^\epsilon)$) estimates the probability of a cactus being visited by an ant partner a' y^ϵ , with fixed effects of the previous size of the cholla x and the previous ant partner a in year t and random effects of plot w and year u , using a Multinomial distribution:

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

$$\text{logit}(\epsilon) = \beta_0^\epsilon + \beta_1^\epsilon \times x + \beta_2^\epsilon \times a + u$$

where $u \sim N(0, \sigma_{yr}^2)$ is the year random effect with year specific variance of σ_{yr} . Ant partners are
 288 included as predictors here because partners may choose to return to the same cholla repeatedly or choose new ones, therefore the previous partner may be a good indicator of the next partner.

Recruit Size Distribution. The recruit size model ($n(x, a')$) estimates the size distribution of all recruits y^{η} from a given year $t + 1$, with no fixed or random effects, using a Normal distribution:

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

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

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

Germination. With germination data from [Miller et al., 2007](#)¹², we fit two Bayesian generalized linear models for the probability of germinating from a seed in the first year (γ_1) or the second year (γ_2) in year $t + 1$, with no fixed or random effects, using a Binomial distribution:

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

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

$$\text{logit}(\hat{\gamma}_1) = \beta_0^{\gamma_1}$$

$$\text{logit}(\hat{\gamma}_2) = \beta_0^{\gamma_2}$$

Pre-Census Survival. With data collected in a [2005-2006](#)^{13*****} recruit census, we fit a Bayesian generalized linear model for the probability of a seedling surviving to May (δ) of year $t + 1$ (accounting for missed mortality events), with fixed effects of the previous size x and random effects of the transect m , using a Bernoulli distribution:

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

$$\text{logit}(\hat{\delta}) = \beta_0^{\delta} + m$$

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

¹²[CITE](#)

¹³[FIX](#)

Seeds Per Flower. With data from [Miller 2007](#)^{14*****}, we fit a Bayesian generalized linear model for the number of seeds produced by every flower on a cholla ($\kappa(a')$) in year $t + 1$ based on the ant partner a' in year $t + 1$, using a Negative Binomial distribution:

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

$$\hat{\kappa} = \beta_0^\kappa \times a'$$

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

Ant partners are included as predictors here because they reduce floral abortion rates and therefore may lead to higher numbers of seeds.¹⁵

MCMC Simulations. 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 3 chains of 10,000 iterations, each with randomly chosen initial conditions. The first 1,500 iterations were discarded as burn-in to eliminate transience associated with initial conditions. We did not thin the chains, thus all samples were retained. To assess the convergence of our models we assessed between and within chain convergence, the resulting figures are included in supplemental documents. To assess the 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. Large differences in the two indicate a poor model fit and can be assessed visually (figures included in supplemental documents). All estimated parameters are available in the data. Data and code for all vital rate models is included in the supplemental information.

IPM Analysis

Analyzing an IPM requires discretizing the composite IPM into a matrix to calculate the dominant eigenvalue. In a traditional IPM x is discretized into b bins, replacing the continuous kernel

¹⁴[CITE](#)

¹⁵*This paragraph needs to address how we assigned seed number to the "other" category.*

into a $b \times b$ matrix, in this case there is additional complexity in the form of transitions between ant partners. Each combination of previous ant state a and next ant state a' represents a unique set of plants in the population and therefore must be discretized individually, leading to a matrix size of $mb \times mb$ where m is the number of unique combinations of a and a' (how many possible ant transitions there are). In this model we have two additional discrete states (year one and year two seed banks) leading to a final matrix size of $m(b + 2) \times m(b + 2)$. We used $b = 200$ bins. We extend the integration limits L and U to avoid unintentional eviction Williams et al. (2012). Traditionally, in a deterministic IPM the asymptotic population growth rate λ is estimated as the dominant eigenvalue of the discrete kernel. In a deterministic bayesian IPM, we create 1,000 discrete kernels with a unique set of parameters from our bayesian statistical models to estimate 1,000 λ values as a distribution. In a deterministic version 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. In order to calculate stochastic λ distributions for each ant scenario, every one of the 1,000 parameter-iteration associated λ s actually comes from the mean of 5,000 year-specific estimations each associated with a year random effect which was randomly selected from the 18 years of data.

We compare the distributions of λ across each combination of ant partners to whether sampling effect or complementarity is at play in the system. To compare the distributions of two hypothetical populations, A and B, we subtract the vector of 1,000 λ_A estimations of one population from the 1,000 λ_B estimations of the other ($\lambda_A - \lambda_B$). If the average of these differences is positive, population A has a higher λ than B, if the average is 0, they are equal, and if the average is negative, population B has a higher λ than A.

To determine if sampling effect is at play in a system, we must first determine if there is a "best" partner, by determining which single ant association is correlated with the highest λ estimation. We can do this by comparing the distributions of each λ and finding the one which is larger than all others. Then we must show that the λ of a population with all possible partners

is equal to that of λ of a population with only the "best" partner, by comparing the distributions as described earlier. If it is significantly larger then complementarity is potentially at play (more on this in the next paragraph). If it is significantly smaller, this indicates that rather than positive effects of partner diversity, there are actually important costs of partner diversity that dampen the population growth rate.

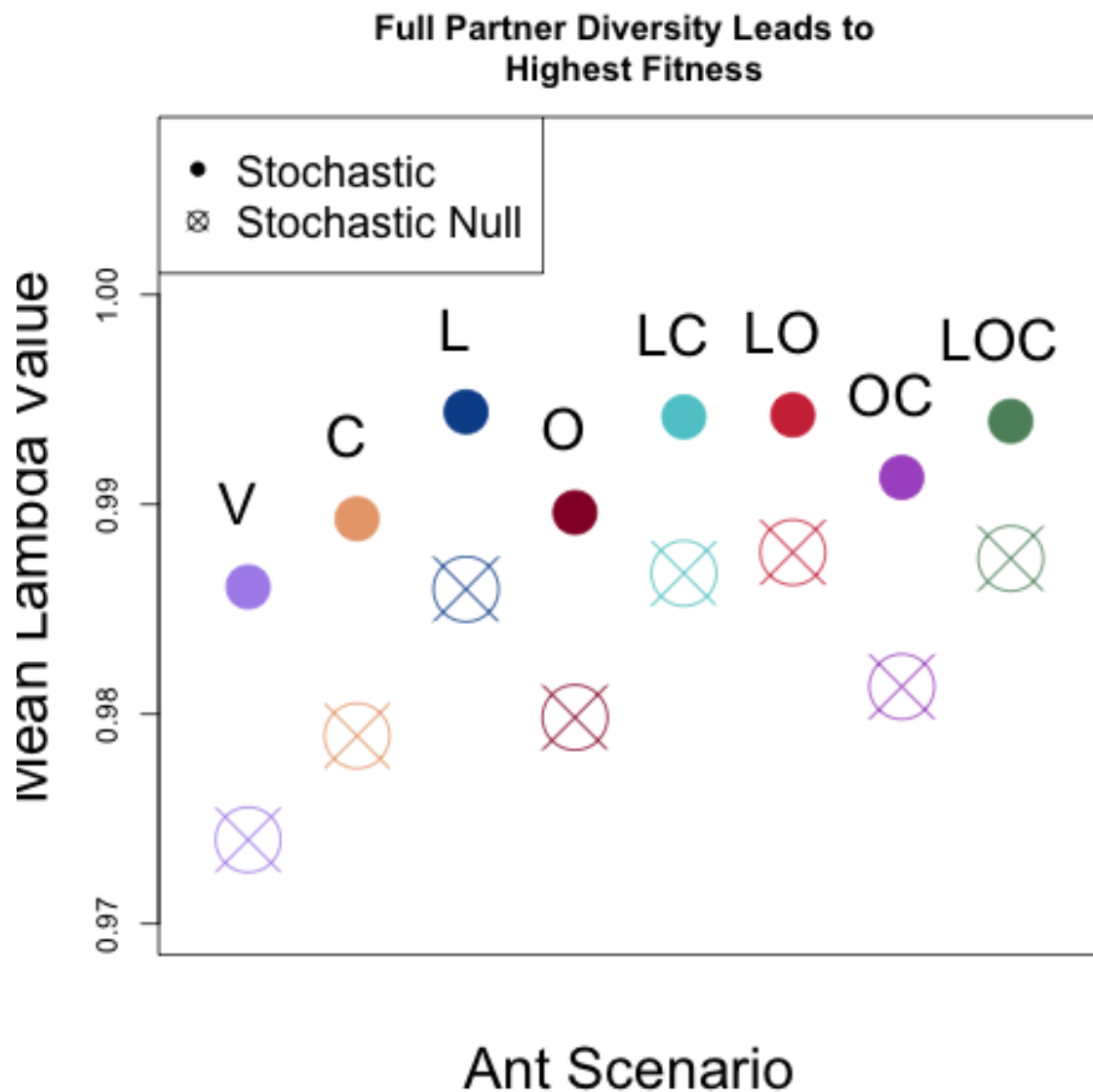
To determine if complementarity is at play in a system, we must determine if the partner scenario which leads to the highest λ is the most partner diverse scenario. We can do this by comparing the distribution of λ of a population with all possible partners to the distribution of λ of all other populations. If the λ of a population with all possible partners is the largest, it indicates that complementarity is at play. If neither the conditions for sampling effect or complementarity, it indicates that rather than positive effects of partner diversity, there are actually costs of diversity.

To determine if portfolio effect is at play we must show that partner diversity buffers the population from environmental variation. To do this we parameterized a new set of bayesian statistical models in which year random effects were not ant specific, meaning the effects of ant partners were not able to covary with year effects (the scenario in which all ant partners must respond to annual variation the same way and portfolio effect is not possible). The new estimations of year random effects are $u \sim N(0, \sigma_{yr}^2)$ with year specific variance of σ_{yr} . With this version of the IPM (now referred to as the stochastic null IPM) we followed the same approach to calculate distributions of stochastic λ s for each ant scenario. We can estimate the effects of partner diversity on the focal mutualist by calculating the difference in λ distributions between populations with no partners and populations with all partners present. Then we can compare the difference in the effects of partner diversity on the focal mutualist calculated from the stochastic and stochastic null IPMs respectively. If the stochastic difference is greater than the stochastic null difference, this indicates that partner diversity is more beneficial under varying environments and therefore portfolio effect is at play.

Results

IPM Analysis

Using the results of the stochastic IPM, we determined if complementarity or sampling effect was at play within this system. We found that populations of tree cholla which have no partners have a mean fitness of $\lambda = 0.9861$???. Populations with only one ant partner present (*L. apiculatum*, *C. opuntiae*, or other ants) have a mean fitness of $\lambda = 0.9944$, $\lambda = 0.9893$, and $\lambda = 0.9896$ respectively. Populations with two ant partners present (*L.apiculatum* and *C. opuntiae*, *L.apiculatum* and other, or *C. opuntiae* and other) have a mean fitness of $\lambda = 0.9942$, $\lambda = 0.9943$, and $\lambda = 0.9913$ respectively. Populations with all ant partners present have a mean fitness of $\lambda = 0.9940$. The only partner scenarios where $\lambda > 0.99$ are when *L. apiculatum* ants are present with any other ant partner. The means are not the only important result. We used bayesian modeling, so each of these λ estimations has a distribution rather than a single estimate. By subtracting one of these distributions from the other, the difference from 0 tells us how much larger or smaller the distributions are with a percent confidence. Any ant partner is shown to lead to an increase in fitness of the tree cholla in these results. We are between 82% to 100% confident that having any ant parnter leads to a higher λ than having no partners.



We are between 84% and 100% confident that any diversity scenario where *L. apiculatum* ants are included as partners leads to a higher λ for the tree cholla than any diversity scenario without these parnters. These results indicate that sampling effect, not complementarity, is at play in this system.

Using the stochastic null IPM results, we found that when ant partners responded the same way to inter-annual variation similar patterns were found, though the magnitude of the patterns were somewhat different. We used the results of the stochastic null IPM to determine if portfolio

effect is at play. We found that both the stochastic model and stochastic null model resulted in
387 higher fitness when all ants are present compared to no partners 94% of the time. These results
differed in the magnitude of fitness boost recieved from partners. In the stochastic IPM, tree
cholla with all ants present resulted in a λ that was 0.008 greater than tree cholla with no ants
390 present; in the stochsatic null IPM, tree cholla with all ants rpresent resulted in a λ that was 0.013
greater than tree cholla with no ants present. We are 52% confidence that the difference is greater
when inter-annual effects were not ant dependent (in the stochastic null model). This indicates
393 that portfolio effect is at play, if only weakly evident.

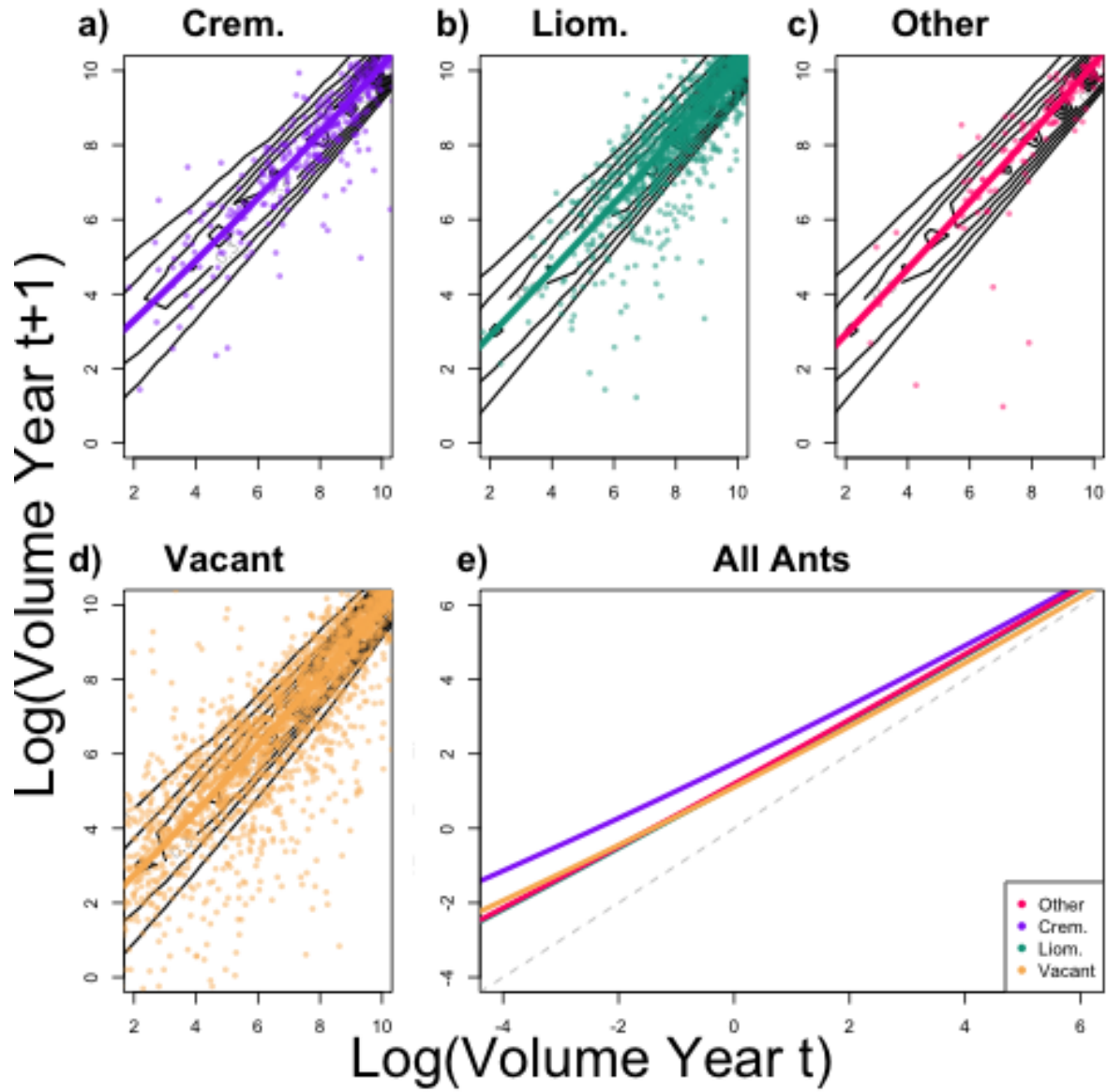


Figure 1: asdasdf

Growth Model. 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 1e. The mean growth rate expected for plants that are 10 cm^3 or smaller in year t is $10.01 \text{ cm}^3/\text{yr}$, 4.65

cm^3/yr , $7.44\text{ }cm^3/yr$, and $5.14\text{ }cm^3/yr$ when tended by *C. opuntiae*, *L. apiculatum*, other ants, or
 399 no ants respectively. The mean growth rate expected for plants that are between $10\text{ }cm^3$ and
 $150\text{ }cm^3$ in year t is $2.81\text{ }cm^3/yr$, $2.11\text{ }cm^3/yr$, $2.49\text{ }cm^3/yr$, and $1.75\text{ }cm^3/yr$ when tended by *C.*
opuntiae, *L. apiculatum*, other ants, or no ants respectively. The mean growth rate expected for
 402 plants that are larger than $150\text{ }cm^3$ in year t is $1.28\text{ }cm^3/yr$, $1.21\text{ }cm^3/yr$, $1.29\text{ }cm^3/yr$, and 1.10
 cm^3/yr when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. Plants with
C. opuntiae ant partners experience the highest mean growth rates across all but the largest sizes,
 405 where they experience comparable growth to the other tended plants 1a. Plants with *L. apiculatum*
 ants experience the lowest mean growth rates at the smallest sizes and the second lowest at all
 other sizes 1b. Plants with other ants experience the second highest mean growth rates across all
 408 but the largest sizes, where they experience the highest growth rates 1c. Plants with no partners
 experience the second lowest growth rates at small sizes, after which they experience the lowest
 growth rates 1d.

411 We are 89%, 88%, and 70% confident that plants tended by *C. opuntiae* ants experience higher
 mean growth rates across sizes than plants tended by no partners, *L. apiculatum* ants, or other
 ants respectively. We are 89%, 65%, and 94% confident that plants with no partners experience
 414 lower mean growth rates across all sizes than plants tended by *C. opuntiae*, *L. apiculatum*, or other
 ants respectively.

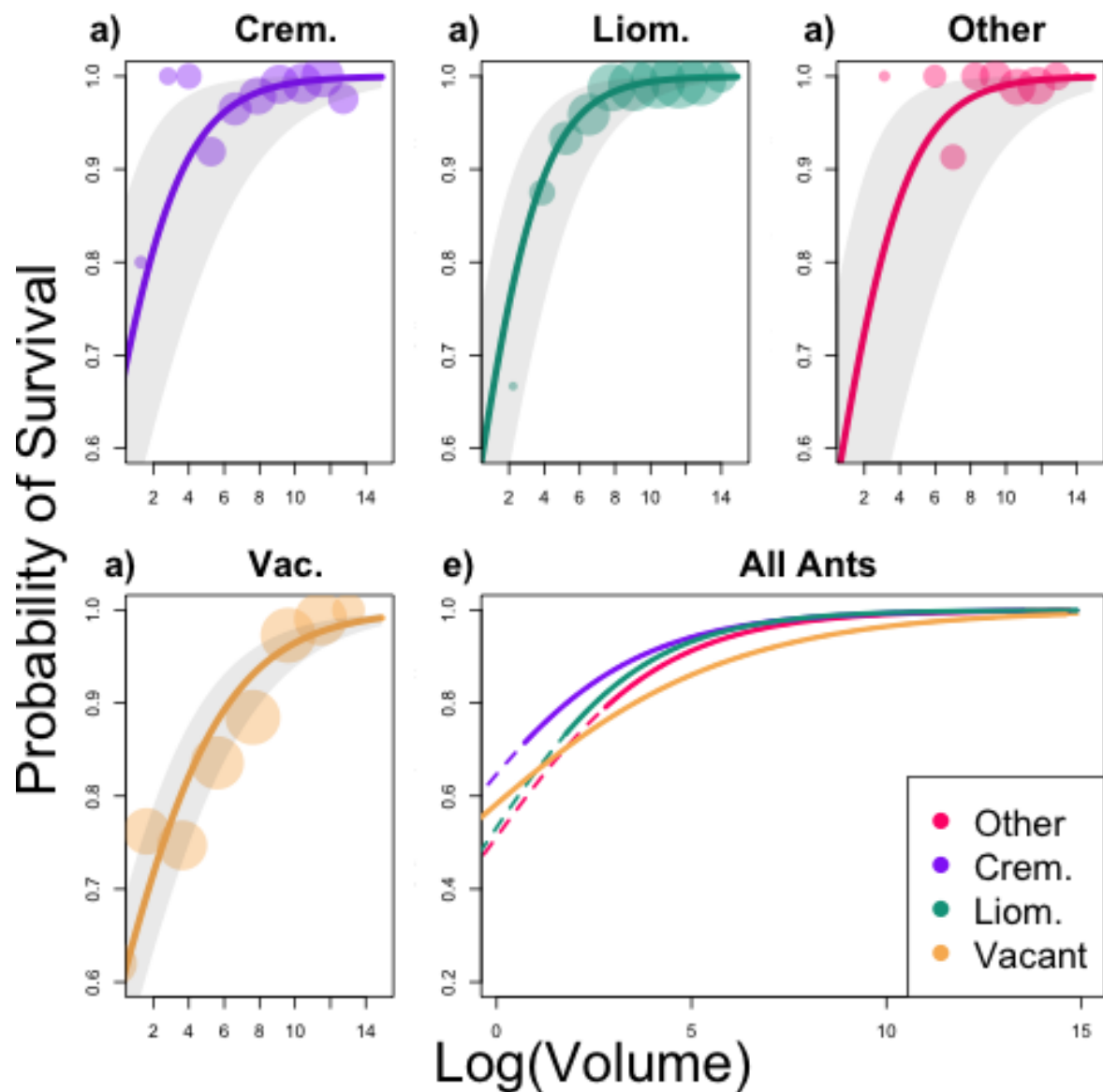


Figure 2: asdasdf

Survival Model. Tree cholla experience between 7.7% and 99.9% survival rate depending on their size and ant partner 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. The mean survival rate expected for plants that are 10 cm^3 or smaller in year t is 48%, 37%, 37%, and 47% when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. The mean survival rate

expected for plants that are between 10 cm^3 and 150 cm^3 in year t is 90%, 87%, 84%, and 80% when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. The mean survival rate expected for plants that are larger than 150 cm^3 in year t is 99%, 99%, 98%, and 95% when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. Plants with *C. opuntiae* ants experience the highest mean survival rates across all sizes 2a. Plants with *L. apiculatum* ants experience the lowest mean survival rates when small and the second highest mean survival rates across all other sizes 1b. Plants with other ants experience the second lowest mean survival rates across all sizes 1c. Plants with no partners experience the second highest survival rates at small sizes, after which they experience the lowest survival rates 1d.

We are 82%, 63%, and 100% confident that plants tended by *C. opuntiae* ants experience higher mean survival rates across all sizes than plants tended by no partners, *L. apiculatum* ants, or other ants respectively. We are 82%, 68%, and 64% confident that plants with no partners experience lower mean survival rates across all sizes than plants tended by *C. opuntiae*, *L. apiculatum*, or other ants respectively.

Flowering Model. There is a clear size effect on the number of flowers produced. The mean number of flowers produced by a plant remains at 0 until the plant reaches medium sizes after which the mean number of flower produced increases exponentially to about 40 flowers per plant per year at large sizes. The mean number of flowers produced for a plant that is 150 cm^3 or smaller in year t is ;1 flower per plant. The mean number of flowers produced for a plant that is larger than 150 cm^3 in year t is 8.7 flowers per plant.

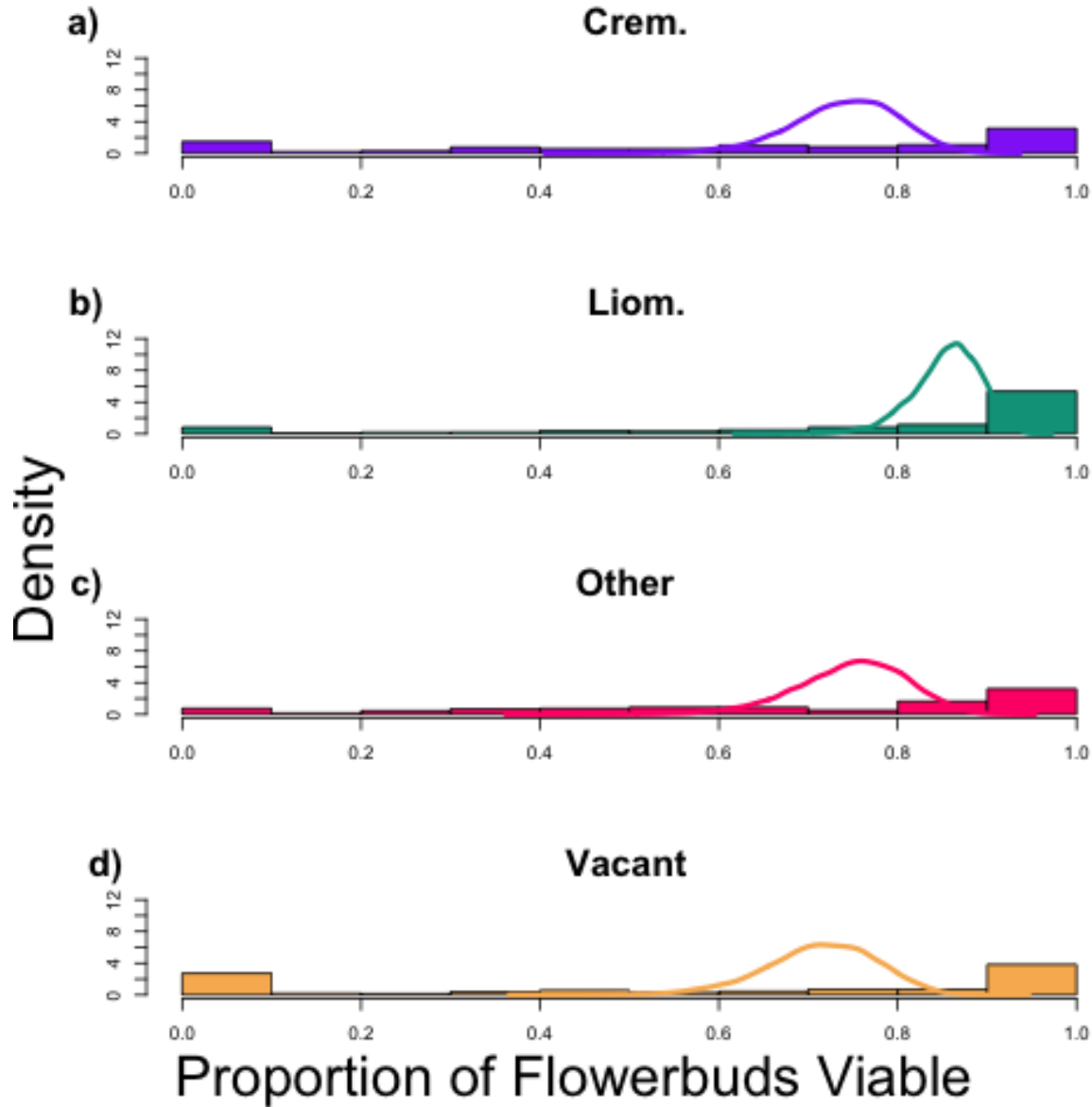


Figure 3: asdasdf

441 *Viability Model.* Tree cholla that are reproducing in year t experience between 39% and 96% viability rates of flowers 3. 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%),
 444 followed by other tended plants (at 75%), *C. opuntiae* tended plants (at 74%) and vacant plants (at 71%). We are 99%, 98%, and 97% confident that *L. apiculatum* tended plants experience higher

viability rates than plants tended by no partners, *C. opuntiae*, or other ants respectively. We are
447 95% and 69% confident that vacant plants experience lower viability rates than plants tended by
C. opuntiae ants or other ants respectively.

Reproduction Model. The probability of a plant reproducing in a given year is highly size de-
450 pendent. 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.

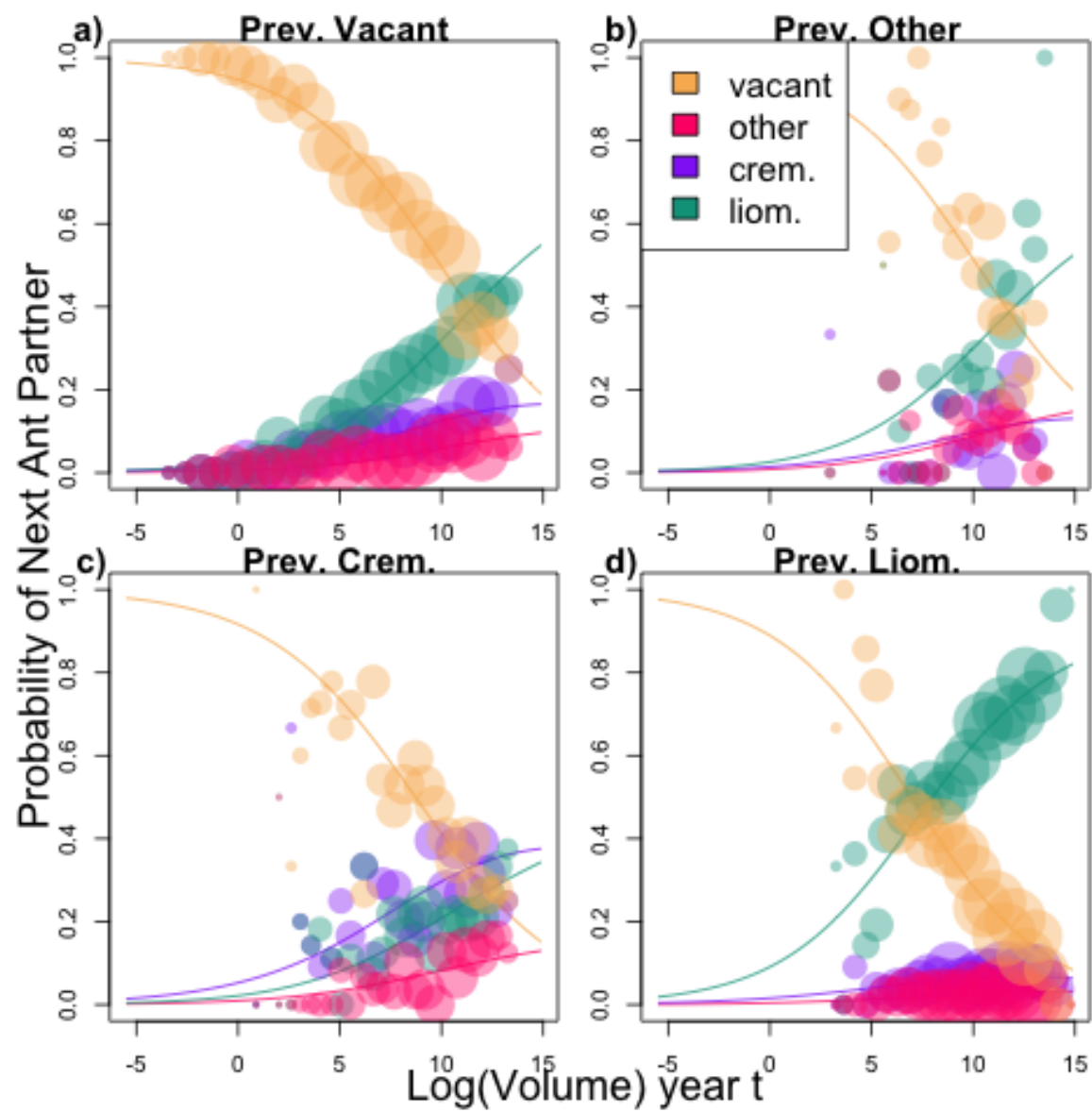
453 *Seeds Per Flower Model.* Each viable flower on a plant produces between 97 and 257 seeds. This
number is affected by the ant partner present. *C. opuntiae* tended plants produce a mean of 148
seeds per flower. *L. apiculatum* tended plants produce a mean of 149 seeds per flower. Vacant
456 plants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

459 *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
462 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.

465 New recruits are expected to be between the sizes of 0.11 cm^3 and 0.38 cm^3 with a mean size
of 0.20 cm^3 .

Ant Transition Model. All small plants are most likely to be vacant, while large plants are much
468 more likely to be occupied by one ant or another. *L. apiculatum* ants are the most likely tender
in year $t + 1$ for all large plants that were not previously tended by *C. opuntiae* ants in year t ,



while *C. opuntiae* ants tended plants in year t are most likely to remain tended by *C. opuntiae* ants
in year $t + 1$. We are 93%, 89%, 86%, and 93% confident that plants that are smaller than 150
 cm^3 in year t will be vacant in year $t + 1$ when they were tended by no partners, *C. opuntiae*, *L.*
apiculatum, or other ants respectively in year t .

We are 75%, 100%, and 100% confident that plants which were previously tended by *L. apic-*
ulatum and larger than 150 cm^3 in year t are more likely to be tended by *L. apiculatum* ants in
year $t + 1$ than be vacant, tended by *C. opuntiae*, or other ants in year $t + 1$. We are 35%, 100%,
and 100% confident that plants which were previously vacant and larger than 150 cm^3 in year
 t are more likely to be tended by *L. apiculatum* ants in year $t + 1$ than be vacant, tended by *C.*
opuntiae, or other ants in year $t + 1$. We are 32%, 100%, and 100% confident that plants which
were previously tended by other ants and larger than 150 cm^3 in year t are more likely to be
tended by *L. apiculatum* ants in year $t + 1$ than be vacant, tended by *C. opuntiae*, or other ants in
year $t + 1$.

We are 37%, 100%, and 100% confident that plants which were previously tended by *C.*
opuntiae and larger than 150 cm^3 in year t are more likely to be tended by *C. opuntiae* ants in year
 $t + 1$ than be vacant, tended by *L. apiculatum*, or other ants in year $t + 1$.

¹⁶ Plants which were previously vacant will most likely remain vacant until large. We expect
that between 81% and 98% of tree cholla which are smaller than 150 cm^3 with no partners in year
 t are going to be vacant in year $t + 1$. We expect that between 11% and 55% of tree cholla which
are larger than 150 cm^3 with no partners in year t are going to be tended by *L. apiculatum* ants
in year $t + 1$. We expect that between 6% and 17% of tree cholla which are larger than 150 cm^3
with no partners in year t are going to be tended by *C. opuntiae* ants in year $t + 1$. We expect that
between 2% and 10% of tree cholla which are larger than 150 cm^3 with no partners in year t are
going to be tended by other ants in year $t + 1$.

Plants which were previously tended by *C. opuntiae* will most likely be vacant or tended by
C. opuntiae ants in the next year depending on size. We expect that between 74% and 97% of tree

¹⁶Or I can do this section like this:

cholla which are smaller than 150 cm^3 and tended by *C. opuntiae* in year t are going to be vacant in year $t + 1$. We expect that between 8% and 34% of tree cholla which are larger than 150 cm^3 and tended by *C. opuntiae* in year t are going to be tended by *L. apiculatum* ants in year $t + 1$. We expect that between 15% and 38% of tree cholla which are larger than 150 cm^3 and tended by *C. opuntiae* in year t are going to be tended by *C. opuntiae* ants in year $t + 1$. We expect that between 3% and 13% of tree cholla which are larger than 150 cm^3 and tended by *C. opuntiae* in year t are going to be tended by other ants in year $t + 1$.

Plants which were previously tended by *L. apiculatum* will most likely be vacant or tended by *L. apiculatum* in the next year depending on size. We expect that between 64% and 97% of tree cholla which are smaller than 150 cm^3 and tended by *L. apiculatum* in year t are going to be vacant in year $t + 1$. We expect that between 30% and 82% of tree cholla which are larger than 150 cm^3 and tended by *L. apiculatum* in year t are going to be tended by *L. apiculatum* ants in year $t + 1$. We expect that between 4% and 7% of tree cholla which are larger than 150 cm^3 and tended by *L. apiculatum* in year t are going to be tended by *C. opuntiae* ants in year $t + 1$. We expect that between 1% and 3% of tree cholla which are larger than 150 cm^3 and tended by *L. apiculatum* in year t are going to be tended by other ants in year $t + 1$.

Plants which were previously tended by other ants will most likely be vacant or tended by other ants in the next year depending on size. We expect that between 82% and 99% of tree cholla which are smaller than 150 cm^3 and tended by other ants in year t are going to be vacant in year $t + 1$. We expect that between 10% and 53% of tree cholla which are larger than 150 cm^3 and tended by other ants in year t are going to be tended by *L. apiculatum* ants in year $t + 1$. We expect that between 4% and 13% of tree cholla which are larger than 150 cm^3 and tended by other ants in year t are going to be tended by *C. opuntiae* ants in year $t + 1$. We expect that between 3% and 15% of tree cholla which are larger than 150 cm^3 and tended by other ants in year t are going to be tended by other ants in year $t + 1$.

Discussion

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.

We asked what effects the partners which interact with tree cholla (*C. opuntiae*, *L. apiculatum*, and more) 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 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 negative effects.

It has been previously hypothesized that their is a heirarchy of partners due to the ability for *L. apiculatum* ants to defend the cacti from seed predators and herbivores Miller (2007). These 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

experience a probability of reproducing, flower production, and floral abortion. Floral abortion is heavily affected by seed predators Miller et al. (2008), which the ants defend the cacti, leading to increased floral viability. We specifically found that tree cholla experienced the highest floral 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 mechanism 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 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 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)) 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 affected the fitness of the tree cholla in interesting and dynamic ways. Namely, a best partner emerged in this analysis, 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 recieved 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 recieved 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.

¹⁷ 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.

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.

Acknowledgments

Data and Code Availability

Appendix A: Additional Methods and Parameters

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¹⁷ *What this all means more broadly?? I'm currently not sure what to do with this*

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Tables

Figure legends

777

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

Parameter	Median (95% CI)	Prior Distribution
growth xi intercept vacant β_{01}^g	-5.210899(-5.686865, -5.491787)	sDE
growth xi intercept other β_{02}^g	-5.8288(-5.956217, 1.766021)	asdf
growth xi intercept <i>C. opuntiae</i> β_{03}^g	-4.529523(-6.0770390, 0.1222112)	asdf
growth xi intercept <i>L. apiculatum</i> β_{04}^g	-5.106802(-5.4499944, 0.5453901)	asdf
growth xi size dependent vacant β_{11}^g	asdf	asdf
growth xi size dependent other β_{12}^g	asdf	asdf
growth xi size dependent <i>C. opuntiae</i> β_{13}^g	asdf	asdf
growth xi size dependent <i>L. apiculatum</i> β_{14}^g	sadf	asdf
growth omega intercept ω_0^g		
growth omega size dependent ω_1^g		
growth alpha intercept α_0^g		
growth alpha size dependent α_1^g		
1-year germination intercept α^{γ_1}		
2-year germination intercept α^{γ_2}		
survival intercept vacant β_{01}^s		
survival intercept other β_{02}^s		
survival intercept <i>C.opuntiae</i> β_{03}^s		
survival intercept <i>L. apiculatum</i> β_{04}^s		
survival size dependent vacant β_{11}^s		
survival size dependent other β_{12}^s		
survival size dependent <i>C. opuntiae</i> β_{13}^s		
survival size dependent <i>L. apiculatum</i> β_{14}^s		
flowering intercept β_0^f		
flowering size dependent β_1^f		
viability intercept vacant $\beta_0 1^v$		
viability intercept other $\beta_0 2^v$		
viability intercept <i>C. opuntiae</i> $\beta_0 3^v$		
viability intercept <i>L. apiculatum</i> $\beta_0 4^v$	44	