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 imbracata* (tree cholla) pro- duce 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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[1]*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 , 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 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 herbivores[2] 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

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[2]*notice that "herbiviores" 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 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 Wetzel 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 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 populations[3].

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?

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

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?

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.

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 south-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 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. Cambpell, *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 *Gerstaekeria* 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

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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 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 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 ([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 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.

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 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

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 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

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[4]*quantify*

[5]*update numbers*

determine the individual fitness effects of each ant species and the composite effects of multiple partners, with their transition dynamics modeled explictly.

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

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[6] *Quantify this.*

[7] *I 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 Forelious will be a big chunk of it.*

[8] *These 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 ($V(a; \boldsymbol{\tau_a^V})$) and the number of seeds per fruit ($\kappa(a')$[9]) 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 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 ($A = 4$) 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:

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

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

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 ($S(x, a; \boldsymbol{\tau_a^S})$) and growth from size x to x' ($G(x', x, a; \boldsymbol{\tau_a^G})$) are both dependent on initial size and ant state. As above, these functions include inter-annual variability through year-specific deviates

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[9] *Why 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.*

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

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that can vary by ant state (τ_a). Ant transition function $\rho(a', a, x; \tau^\rho)$ 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^ρ).

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 ($log(cm^3)$; 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 used 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. [12] 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[13], because in preliminary analyses we found that size transition data were more fat-tailed than a Gaussian distribution could accommodate.

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[11]*Cite Stan and RStan.*

[12]*You need to go a little farther than this, because the fixed effects are arranged as a second-order polynomial with size-ant interactions. That needs to be explained and the choice of polynomial should be justified. You also do not describe the size-dependence in variance and kurtosis. Also, I would subscript the u as u_a, then explain what that means. The u_a is important to describe in a biologically meaningful way because this is how the portfolio effect is tested. Finally, notice that the tau vector does not actually appear in the model. This is a problem. You can solve it by changing u to tau, or vice versa.*

[13]*Don't kill me but I think we should either figure out a skewed t or go back to the skew normal. But just to comment on the text as is, you need to describe the three parameters of the t (e.g., G-hat is the mean) in order for the equations to make sense.*

Specifically, the model was:

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

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

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

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

[14] 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[15], 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 vegetative tissue loss.[16]

Survival. The survival model ($S(a, x; \boldsymbol{\tau_a^S})$) estimates the probability of survival y^{S}[17] 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:

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

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

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}.[18]

Reproduction. The reproduction model ($P(x'; \boldsymbol{\tau^P})$) estimates the probability of reproducing y^{P}[19] in year $t + 1$, with fixed effects for the size x' in year $t + 1$ and random effects of plot w and year

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[14]*I think the equations will be more readable if you do not use the $\times$ symbol for multiplication.*

[15]*This description is not correct. The variance is not ant-specific, the deviates are.*

[16]*I think this is unnecessary since you provide the rationale for ant effects in the beginning of this section.*

[17]y^S *is not the probability of survival*

[18]*Much of this is redundant with the growth model, and likely redundant with models below. Think about efficient ways to economize text so that you are not re-explaining the same things across sub-models.*

[19]*Same comment:* y^P *is not the probability of reproducing.*

u, using a Bernoulli distribution:

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

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

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 ($F(x'; \boldsymbol{\tau^F})$) 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 zero-truncated 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 $w \sim N(0, \sigma_{plot}^2)$ is the plot random effect with plot specific variance of σ_{plot}.

Flowerbud viability. The viability model ($V(a; \boldsymbol{\tau_a^V})$) estimates the proportion of flowers produced by a plant which are viable (not aborted) y^V[20] in year $t+1$, with fixed effects of ant partner a in year t and random effects of plot w and year u, using a Binomial distribution:

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

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

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}.

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[20]y^V *is not the proportion of viable buds.*

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' y^ϵ[21], with fixed effects of the previous size of the cholla[22] x and the previous ant partner a in year t and random effects of plot w and year u, using a multinomial distribution:

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

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

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

Recruit Size Distribution. The recruit size model ($(n(x, a'))$)[23] estimates the size distribution of all recruits y^η[24] 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[25], we fit two Bayesian generalized linear models[26] for the probability of germinating from a seed in the first year (γ_1) or the second year (γ_2)[27] in year $t + 1$, with no fixed or random effects, using a binomial distribution:

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

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

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[21]*This is not the probability of being visited.*

[22]*I will not make this comment everywhere but notice that "of the cholla" does basically no work in this sentence. It is very clear to readers at this point that "size" refers to size of the cholla, so these words can be cut. More generally, edit your own writing to remove words (or sentences) like this that take up space but provide no new information.*

[23]*Not the correct notation.*

[24]*Think deeply about what the y's represent and how you can better describe them.*

[25]*CITE*

[26]*they are all Bayesian glms so no need to say this here.*

[27]*This can be described more accurately by referring to the 1 and 2 yo seed banks.*

16

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

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

Pre-Census Survival. With data collected in a 2005-2006[28]********** 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[29]), with fixed effects of the previous size x and random effects of the transect m, using a Bernoulli distribution:

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

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

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

Seeds Per Flower. With data from Miller 2007[30]********, we fit a Bayesian generalized linear model for the number of seeds produced by every flower[31] on a cholla ($\kappa(a')$) in year $t+1$ based on the ant partner a' in year $t+1$, using a Negative Binomial[32] distribution:

$$y^\kappa \sim 0TruncatedNegativeBinomial(\hat{\kappa}, \hat{\phi})$$

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

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

Ant partners are included as predictors here because they reduce floral abortion rates and therefore may lead to higher numbers of seeds. [33]

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[28]*FIX*

[29]*This could be explained more clearly, including the natural history that recruitment occurs months earlier than the census, so we need to account for mortality during that time.*

[30]*CITE*

[31]*This is not seeds per flower, it is seeds per fruit, since the viability model accounts for the probability that a flower becomes a fruit. I would actually move this earlier to follow that order of events.*

[32]*Not sure why this is written as zero-truncated.*

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

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 3[34] chains 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 (Fig.[35]). 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 (Fig.[36]). All estimated parameters are available in the data. [37] Data and code for all vital rate models is included in the supplemental information.[38]

IPM Analysis

[39] Analyzing an IPM requires discretizing the continuous IPM kernel into an approximating matrix to calculate the dominant eigenvalue[40]. 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 of $mb \times mb$ where m is the number of unique combinations of a and a' (how many possible ant transitions there are).[41] Our model also has 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.[42] We extend the integration limits L and U to avoid unintentional eviction Williams et al. (2012).[43]

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[34]*Spell out numbers less than ten.*

[35]*reference figure*

[36]*reference figure*

[37]*What does this mean?*

[38]*I do not know what this refers to. Am Nat (and most journals) requires a data accessibility statement that will need to include details of data and code availability.*

[39]*I think this section needs to start with an overview paragraph desciding in plain English what you are trying to do with the fitted model, before getting into any technical details.*

[40]*The dominant eigenvalue is but one of many, MANY forms of "analysis" of an IPM. I would cut this bit that I highlighted.*

[41]*I think what you call m here is actually just A, the total number of ant states.*

[42]*It is also useful to briefly acknowledge why 200.*

[43]*You have not said how you estimate L and U from the data.*

18

Traditionally, in a deterministic IPM the asympotic population growth rate λ is estimated as the dominant eigenvalue of the discrete kernel. In a deterministic bayesian IPM,[44] we create 1,000 discrete kernels with a unique set of parameters[45] from our bayesian statistical models to estimate 1,000 λ values as a distribution. In a deterministic version of our IPM[46], 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.[47] In order to calculate stochastic λ distributions for each ant scenario, every one of the 1,000 parameter-iteration associated λs comes from the mean of 5,000 year-specific estimations each associated with a year random effech which was randomly selected from the 18 years of data. [48]

We compare the distributions of λ across each combination of ant partners to whether sampling effect or complementarity is at play in the system.[49] To compare the distributions of two hypothetical populations, A and B[50], 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.[51]

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[44]*I thought you were only using the two types of stochastic models (and I have not read ahead).*

[45]*This should explicitly refer to samples from the posterior distribution of parameter values*

[46]*At this point, it is not clear to readers how many "versions" you have and why, which is why an overview paragraph providing a "roadmap" will be an important addition.*

[47]*Rationale for why single ant scenarios are coupled with vacancy should be better developed.*

[48]*Even having worked on this with you for a long time, I cannot follow what you are saying here. This will need careful editing so that the methods and rationale for those methods (just as important!) are crystal-clear.*

[49]*I do not think you have sufficiently developed the logic for how these comparisons inform hypotheses about different mechanisms. Also, and this is a matter of taste, I find the language "at play in the system" to be not very scientific and would prefer to phrase this more precisely.*

[50]*It is not clear what this toy example stands in for in the real model.*

[51]*I think this could be edited to more effectively communicate what is gained from these contrasts. The average will never be exactly zero. The important element, IMO, is that we gain a probabilistic estimate of which combinations have higher or lower fitness, given the data.*

To determine if sampling effect is at play in a system[52], we must first determine if there is a "best" partner, by determining which single ant association is correlated with the highest λ[53] estimation. We can do this by comparing the distributions of each λ and finding the one which is larger than all others.[54] Then we must show[55] 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 complimentarity, it indicates that rather than positive effects of partner diversity, there are actuallly 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 re-

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[52]*Ditto previous comment re: "at play". But it is also important to recognize, as I have emphasized before, that these are mechanisms that could explain positive diversity effects. Your writing here presumes a positive diversity effect.*

[53]*Here and elsewhere, it is important to use correct notation for fitness. λ is population mean fitness in a constant environment. λ_S is population mean fitness in a stochastic environment. If you are talking about stochastic environments, you should be using λ_S. I also think it would be helpful to notate either λ with ant partner, e.g. λ^C is fitness corresponding to exclusive association with Crematogsaster. I think that would help communicate methods.*

[54]*Distributions are not larger than one another. They have properties – moments – that can differ, like the mean or standard deviation. Be more precise here.*

[55]*I don't like "must show" – sounds like we are hunting for something.*

spond 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}.[56] With this verision of the IPM (now referred to as the stochastic null IPM) we followed the same approach to calculate distributions of stochastic λs for each ant scenario.[57] 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.

[58]

Results

[59]

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[56]*This needs to be explained earlier, in the statistical estimation sections, so that this section can focus on teasing out mechanisms from the model. I also think you need to better explain what the random year effects represent, biologically. We do not have any data on how the ants are actually fluctuating, but we do know something about how the effects of the ants on plants fluctuates. That is a critical nuance and it does not currently come through. I am also wondering whether it would be preferable to have the a coefficients temporally fluctuate rather than making the u ant-specific. Or are these effectively the same thing? (we could probably figure it out on a whiteboard)*

[57]*It is still not clear if what you described above was based on deterministic or stochastic λ.*

[58]*General comment: the methods for this analysis are a little complicated, which is an inevitable consequence of asking a complex question. In these cases, a writer needs to really step up to communicate something complicated in a way that is sufficiently simple that it can be easily understood and, ideally, replicated. I think with focused effort you can significantly improve this section. Again: put yourself in the shoes of the reader and think about what they need from you in order to "get it".*

[59]*I strongly suggest re-structuring the Results section such that each sub-section is titled with a question from the end of the Intro, and the content of the sub-section answers that question.*

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 $\lambda = 0.9940$.[60] 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[61], 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.[62]

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[60] *This is not an effective use of Results text. You are just reporting values – this is why we have figures!*

[61] *I recommend less emphasis on this. It is not the only way to get a distribution of lambda values, I don't think it is the most important thing to emphasize about the study, and you risk rankling reviewers who might think you are trying to sound impressive with "fancy statistics".*

[62] *Where can readers see this result? You say there are distributions lambdas and differences but you do not show them, and that will need to be remedied. ALso, in terms of fitness contrasts, I think it is more important to start with the Vacant – All Ant contrast. "all ants" is our best representation of what is happening in nature, so it is relevant to first ask if there is evidence that these interactions, collectively, are beneficial, and then use the hypothetical scenarios to unpack how those benefits arise.*
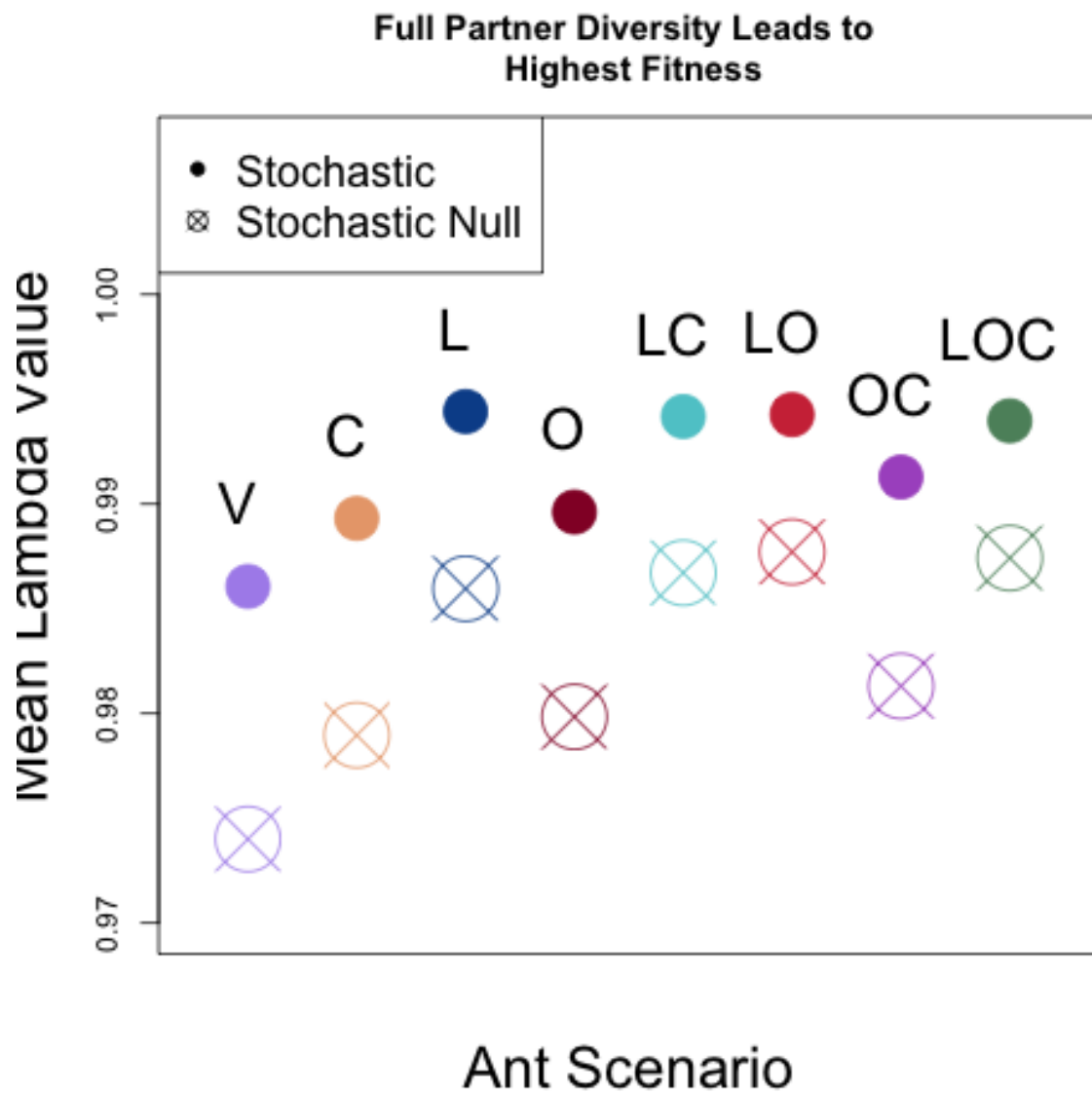
Figure 1: THIS FIGURE HAS NO LEGEND. Are you sure this is not deterministic and stochastic? I am surprised that both stochastic models would be this different.

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.[63]

[64] 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 higher fitness when all ants are present compared to no partners 94% of the time[65]. These results differed in the magnitude of fitness boost received 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 present; in the stochsatic null IPM, tree cholla with all ants rpesent resulted in a λ that was 0.013 greater than tree cholla with no ants present. We are 52% confident that the difference is greater when inter-annual effects were not ant dependent (in the stochastic null model).[66] This indicates that portfolio effect is at play, if only weakly evident. [67]

Statistical Modeling

[68]

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[63]*I suspect we may get some push-back on this interpretation, because the sampling effect is a mechanisms to explain benefits of diversity. Based on your results, there are no benefits of diversity, there is just a best partner. I am not suggesting to entirely discard the sampling effect idea, but it is important to recognize that when you discuss these mechanisms, they are mechanisms for positive diversity effects. So the absence of any diversity effect seems like an important result to contextualize how you interpret evidence for a sampling effect.*

[64]*Throughout this paragraph and much of the results section, you are not explicitly referencing figures, so it is not always clear what is the basis for some of your assertions. Also, the figures need legends.*

[65]*This is not a measure of time, it is a measure of confidence based on the posterior probability of the parameters given the data.*

[66]*If I understand this correctly (and I am not sure because you are not showing the results) then it is equally likely that fitness is either higher or lower when ant effects do or do not fluctuate synchronously – this tells me there is no evidence for a portfolio effect.*

[67]*This is not a very scientific statement.*

[68]*In my opinion it does not make sense to have the statistical modeling results follow the IPM results. But I also think the results would benefit from restructuring around the motivating questions (which would put vital rates first).*
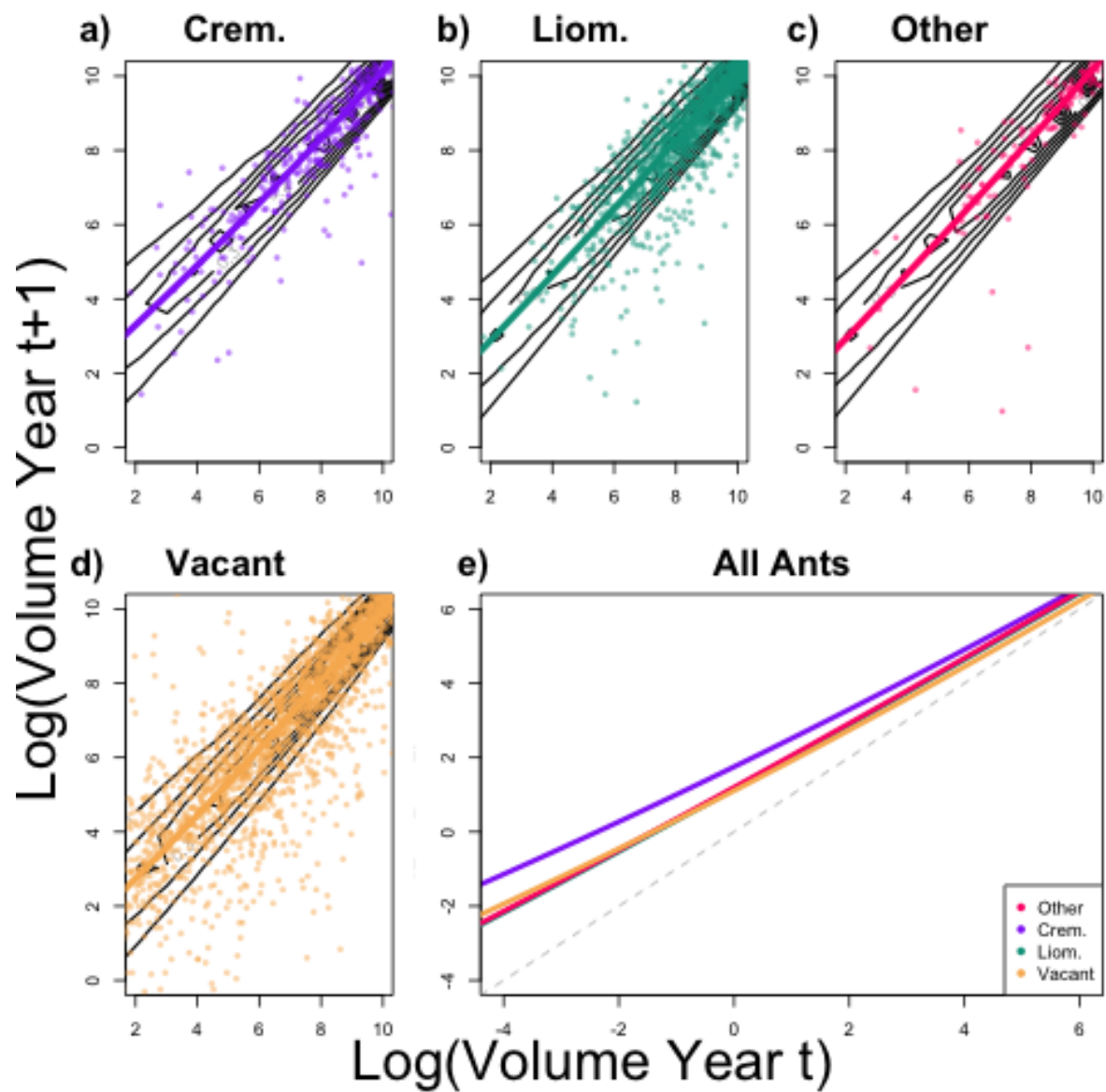
Figure 2: THIS FIGURE NEEDS A CAPTION

Growth Model. [69]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 2e[70]. The mean growth rate expected for plants that are 10 cm^3 or smaller in year t is 10.01 cm^3/yr, 4.65 cm^3/yr, 7.44 cm^3/yr, and 5.14 cm^3/yr when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. The mean growth rate expected for plants that are between 10 cm^3 and 150 cm^3 in year t is 2.81 cm^3/yr, 2.11 cm^3/yr, 2.49 cm^3/yr, and 1.75 cm^3/yr when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. The mean growth rate expected for plants that are larger than 150 cm^3 in year t is 1.28 cm^3/yr, 1.21 cm^3/yr, 1.29 cm^3/yr, and 1.10 cm^3/yr when tended by *C. opuntiae*, *L. apiculatum*, other ants, or no ants respectively. [71] 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 2a. Plants with *L. apiculatum* ants experience the lowest mean growth rates at the smallest sizes and the second lowest at all other sizes 2b. Plants with other ants experience the second highest mean growth rates across all but the largest sizes, were they experience the highest growth rates2c. Plants with no partners experience the second lowest growth rates at small sizes, after which they experience the lowest growth rates 2d.

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 parnters, *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.[72]

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[69]*Here and elsewhere, begin paragraphs with the main result that you want readers to see. In this case I think you want a topic sentence to emphasize that there is evidence that ant visitation enhances cactus growth, partner identity can influence the growth trajectory. That is a simple statement but it captures the essential reason why you did this analysis in the first place. That connection to your motivating questions is often lacking.*

[70]*When you reference figures like this the ref function only returns the number, so you need to type "Figure".*

[71]*Similar to my comment above, this type of recapitulation of the figure is not a very effective use of space.*

[72]*The empirical basis for these assertions is not clear. I am also a little confused because the text above makes it sounds like the ranks are dependent on size.*
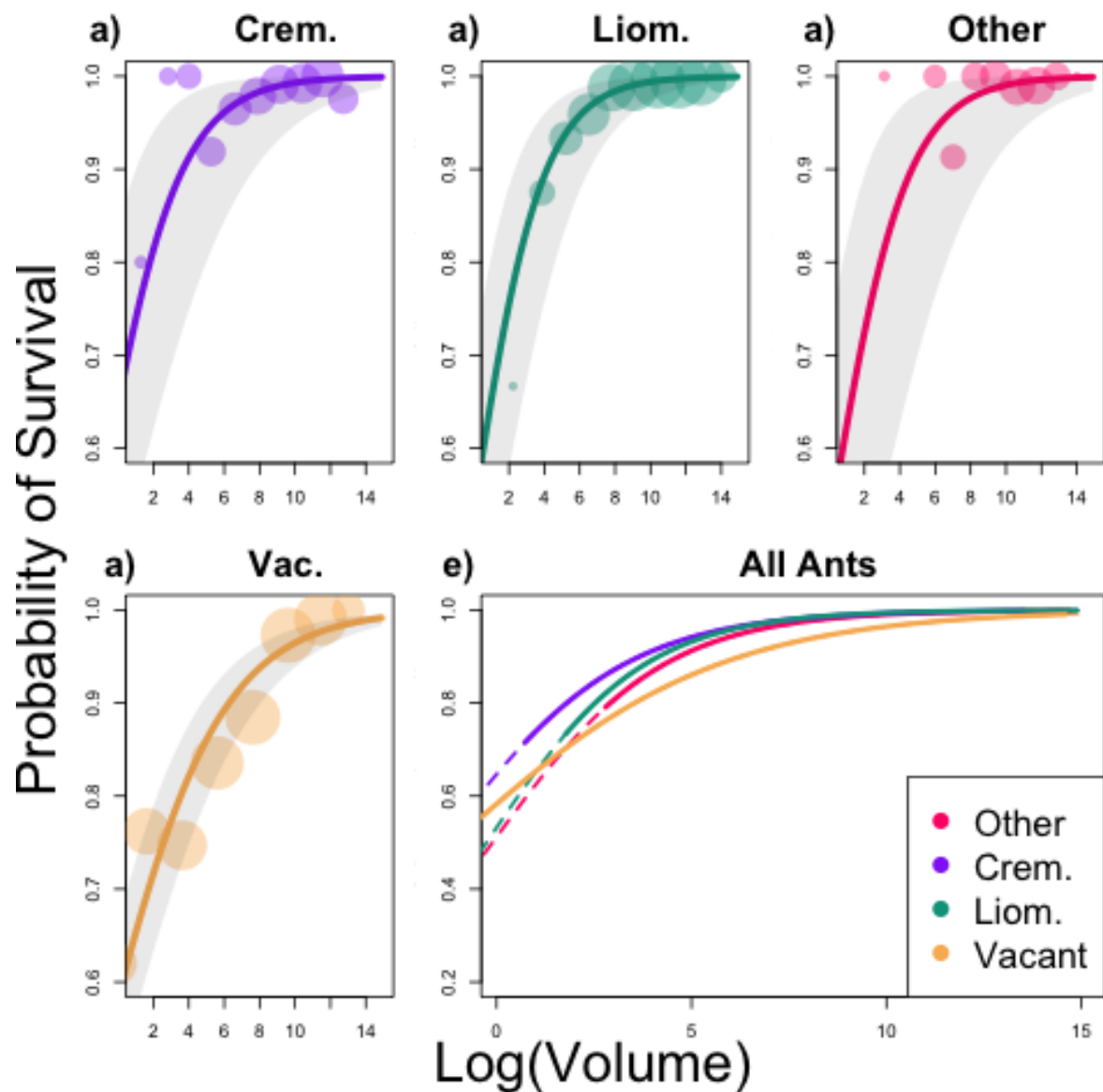
Figure 3: THIS FIGURE NEEDS A CAPTION, AND IT SHOULD EXPLAIN THE DASHED LINES AMONG OTHER THINGS.

Survival Model. Tree cholla experience between 7.7% and 99.9% survival rate depending on their size and ant partner 3e. 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 3a. Plants with *L. apiculatum* ants experience the lowest mean survival rates when small and the second highest mean survival rates across all other sizes 2b. Plants with other ants experience the second lowest mean survival rates across all sizes 2c. Plants with no partners experience the second highest survival rates at small sizes, after which they experience the lowest survival rates 2d.

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 parnters, *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 all sizes than plants tended by *C. opuntiae*, *L. apiculatum*, or other ants respectively.[73]

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 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.[74]

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[73]*Most of my comments from previous sections apply here, and it is uncear why you select specific contrasts to report statistical confidence but not others.*

[74]*If you are not showing these figures in the main text that you should provide them in an appendix, and reference them there. In fact, anywhere there is no role for ants I would move all those results to an appendix section. It is not clear to me whether you text here is referring to the prob flowering model, the number of flowerbuds model, or both.*
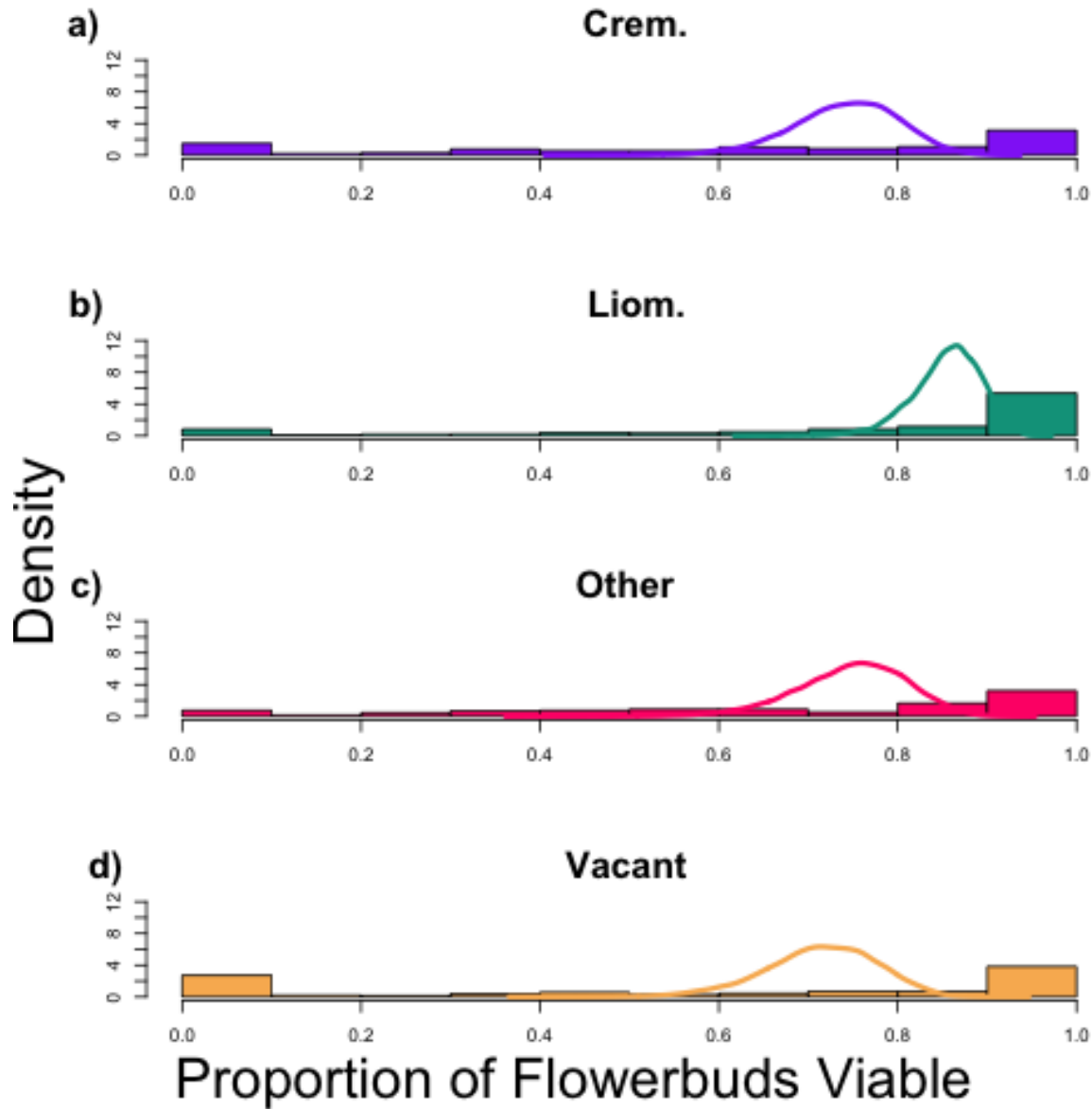
Figure 4: THIS FIGURE NEEDS A CAPTION.

Viability Model. Tree cholla that are reproducing in year t experience between 39% and 96% viability rates of flowers 4. 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%), 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 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 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. [75] Vacant 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 cm^3 and 0.38 cm^3 with a mean size of 0.20 cm^3.[76]

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[75]*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.*

[76]*Move to an appendix. These results are not relevant for the questions at hand.*

₄₅₉ *Ant Transition Model.* ⁷⁷ All small plants are most likely to be vacant, while large plants are much more likely to be occupied by one ant or another. *L. apiculatum* ants are the most likely tender[78] in year $t + 1$ for all large plants that were not previously tended by *C. opuntiae* ants

₄₆₂ 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.*

₄₆₅ *opuntiae, L. apiculatum*, or other ants respectively in year t.[79]

We are 75%, 100%, and 100% confident that plants which were previously tended by *L. apiculatum* and larger than 150 cm^3 in year t are more likely to be tended by *L. apiculatum* ants in

₄₆₈ 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.*

₄₇₁ *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

₄₇₄ 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

₄₇₇ $t + 1$ than be vacant, tended by *L. apiculatum*, or other ants in year $t + 1$.

⁸⁰ Plants which were previously vacant will most likely remain vacant until large. We expect

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[77]*This section is hard to read, and I think it needs to be restructured in a way that is guided by what you want readers to know as it relates to your questions. You provide lots and lots of statistics and contrasts without much context for why these matter and how they should be interpreted. I suggest you think about the patterns that emerge for you in the figure, and re-write this section with that in mind. I do not think this is much value in breaking it down into the four ant states. You should be able to describe transition dynamics in an engaging and succinct way in just a paragraph or two.*

[78]*Not sure I would use this as a noun.*

[79]*Statements like these do not feel strongly motivated, and I am not sure what you want me to know as it relates to the motivating questions.*
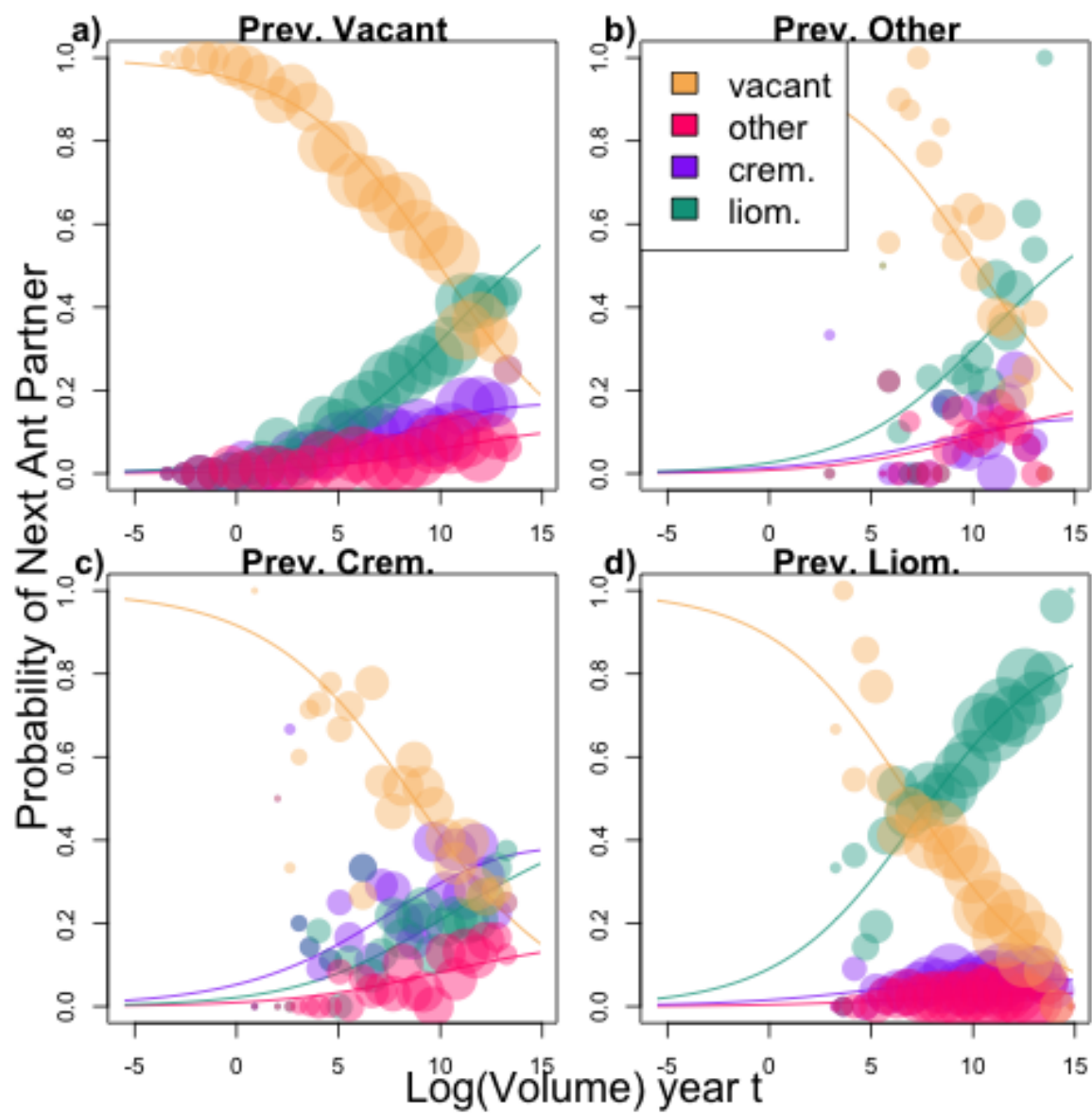
[80]*Or I can do this section like this:*

Figure 5: THIS FIGURE NEEDS A CAPTION.

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 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 byother 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

[81] 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. [82]

We asked what effects the partners which interact with tree cholla (*C. opuntiae*,*L. apiculatum*, and more[83]) 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

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[81]*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.*

[82]*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.*

[83]*I would not say this.*

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)[84], 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

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[84]*Seed predators do not influence floral abortion.*

552 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 freqency of turnover is necessary to resiliency and leads to higher fitness benefits Trøjelsgaard et al. (2015), while in other systems loyalty is

555 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

558 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

561 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

564 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);

567 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

570 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.

573 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)[85]) and a unique set of mechanisms (Batstone

576 (2018)) which explain how the multi-partner interactions lead to fitness differences. We found

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[85]*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,*

that the combination of accurate partner transitions with partner identity[86] 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 diveristy 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 recieved 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.

[87] 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.

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[86]*Not sure what this means.*

[87]*What this all means more broadly?? I'm currently not sure what to do with this. Tom: that's the entire Discussion!*

(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.[88]

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. [89]

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.

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[88]*This is really good. More of this!*
[89]*This feels a little weak and incomplete.*

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Tables

Figure legends

774 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 $C.\ opuntiae$ β_{03}^g	$-4.529523(-6.0770390, 0.1222112)$	asdf
growth xi intercept $L.\ apiculatum$ 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 $C.\ opuntiae$ β_{13}^g	asdf	asdf
growth xi size dependent $L.\ apiculatum$ 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 $C.opuntiae$ β_{03}^s		
survival intercept $L.\ apiculatum$ β_{04}^s		
survival size dependent vacant β_{11}^s		
survival size dependent other β_{12}^s		
survival size dependent $C.\ opuntiae$ β_{13}^s		
survival size dependent $L.\ apiculatum$ β_{14}^s		
flowering intercept β_0^f		
flowering size dependent β_1^f		
viability intercept vacant $\beta_0 1^v$		
viability intercept other $\beta 02^v$		
viability intercept $C.\ opuntiae$ $\beta_0 3^v$		
viability intercept $L.\ apiculatum$ $\beta_0 4^v$		