

Thank you, next: demographic consequences of partner diversity and turnover in a multi-species ant-plant mutualism

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Abstract

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. *Cylindropuntia imbricata* (tree cholla) produce extrafloral nectar and various ant partners provide defense from herbivores and seed predators. We used plant demographic censuses to parameterize a series of Bayesian hierarchical generalized linear vital rate models to determine the impacts of different partners on the focal mutualists. We constructed an Integral Projection Model in which we simulate different combinations of ant partners that don't occur in the wild. The hierarchical models revealed that different ant partners had different impacts on the cholla vital rates. Specifically, *C. opuntiae* tended plants had advantages in both growth and survival when small, and large *L. apiculatum* tended plants had floral viability advantages. The IPM results revealed that scenarios which included *L. apiculatum* resulted in the highest possible fitness for the tree cholla. This suggests that diversity benefits in this system are explained by sampling effect. This study highlights that partner diversity can increase the overall benefits a focal mutualist receives and the importance of a mechanistic understanding to explain the benefits of this diversity across systems.

Introduction

Mutualisms are species interactions where all participants receive net benefits, leading to higher individual fitness and increased population growth rates. They are widespread species interactions (9; 19; 25; 38; 45) but can deteriorate into commensalism or parasitism under conditions that elevate costs or dampen benefits (10; 48; 64; 68; 72). Mutualisms are considered more context dependent than other species interactions (25; 38), meaning the magnitude and sign of interaction strength are often determined by environmental conditions and species' identities (45; 58).

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 (4; 13; 27; 62). 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 contingency in mutualism (71). Whether and how partner diversity modifies the demographic effects of mutualistic interactions remain open questions within relevance in **applied settings**¹ (65).

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 (11; 77; 81). 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 (38). This can lead to an apparent benefit of diversity driven by a sampling effect (15) – but there is no benefit of diversity *per se*, only better and worse partners. If partner associations are mutually exclusive (a focal mutualist may engage with only one partner at a time), then partner diversity may impose op-

¹would be good if you could find another applied example to cite here

42 opportunity costs, leading to negative effects of a diverse mutualist assemblage relative to exclusive
association with the single best partner (51). Second, even within a single mutualist guild, the
benefits conferred by alternative partner species can vary in type and not just degree (21; 69; 71).
45 This can lead to a positive effect of partner diversity through complementarity of alternative
functions (15). Interference or synergies between partners can make their combined effect differ-
ent than the expected from the sum of complementary functions (4). Third, partner species can
48 have species-specific responses to environmental variation, either spatially (61) or temporally (7).
Multiple partners can therefore act as a 'portfolio' that stabilizes fitness benefits across spatial
or temporal heterogeneity, leading to positive effects of partner diversity through the portfolio
51 effect (15; 42; 44).

Partner diversity can have different effects depending on whether partners are present all at
once or sequentially (partner turnover) (11; 22; 27; 29; 56; 77). Sequential associations are likely
54 when alternative partners engage in interference competition for access to a shared mutualist
(15; 43; 75; 80). Turnover can happen at different timescales, from minutes to years (41; 60). The
frequency of partner turnover can impact the level of benefits received by the focal mutualist,
57 particularly if the benefits continue to accumulate with successive turnover (e.g., when sequential
partners provide complementary functions) or if they saturate over time (33; 67). Directionality
of turnover can also influence effects of partner diversity if partner identity changes consistently
60 across ontogeny of a focal mutualist (28; 34; 58). For example, plant susceptibility to enemies can
change across life stages (12; 18), so the benefits of defensive mutualism with ants are greatest
when more defensive partner species align with more vulnerable life stages (28; 29).

63 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 (20; 21). Extrafloral nectar (EFN) -bearing plants can
66 serve as dietary resources that promote ant abundance and colony size (23; 30; 56; 57). Presence
of defensive ant partners is often linked to reductions in herbivory (66; 74) and demographic
advantages for the plant partner (24). Defensive ant-plant mutualisms are commonly multi-

species, where a guild of ant partner species share, and often compete for, a plant mutualist (6; 16; 20; 74). Ant partners can vary in their ability to deter herbivores (22), and visitation by low quality ant partners can prevent visitation by higher quality partners, consequently causing a reduction in fitness through missed opportunity costs (36; 37). Susceptibility to herbivory can also vary significantly throughout the life stages of the plant (18), suggesting that the order and timing of successive partners is important to the fitness impacts of the combined partner guild (12; 18; 34). Herbivore identity and pressure can vary inter-annually (78), 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. Previous studies have investigated how ant partner diversity affects plant fitness (4; 27; 33; 39; 47; 62) 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 (53), and ant defense reduces herbivore damage (51). Tree cholla are tended by two common ant species (*Liometopum apiculatum* and *Crematogaster opuntiae*) and several additional rarer species, all of which collect EFN during foraging visits but their colonies are ground-nesting and not housed by the plants. 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 (30; 59). Switches between partner species, or between vacancy and ant occupancy, commonly occur from one growing season to the next (51). Prior experiments suggested a hierarchy of mutualist quality, with *Liometopum apiculatum* providing strong anti-herbivore defense and *Crematogaster opuntiae* having net negative effects because herbivore deterrence is outweighed by deterrence of pollinators (51; 59). However, previous studies in this system focused on single life stages (adult plants) or vital rates (seed production) and did not integrate the demographic

96 effects of ant defense across the life cycle, which may be essential for understanding net fitness
effects (e.g., 62). To our knowledge no previous study has incorporated inter-annual stochasticity
into models of ant-plant dynamics, which limits our understanding of diversity benefits that may
99 arise through the portfolio effect.

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
102 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 of ant-
plant associations, informed by previous ant exclusion experiments, to ask whether and through
105 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
108 effects fluctuate across years?
2. What are the frequency and direction of partner turnover across the plant life cycle?
3. What is the net effect of partner diversity on plant fitness, and what mechanism(s) explain(s)
111 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
114 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 (17). 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 (56; 60). Flower buds produce more and higher-quality EFN than vegetative
segments, making reproductive cholla valuable mutualist partners (52).

Tree cholla EFN is harvested by various ant species. At SEV-LTER, cholla are visited primar-
ily by two species of ground-nesting ants, *Crematogaster opuntiae* and *Liometopum apiculatum*, as
well as other rarer species, including *Forelius pruinosus* and unidentified species in the genera
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 de-
pending on the year (30). Between 30% – 80% of cacti remain vacant in any given year. Workers
of different species rarely co-occur on individual plants, likely due to interspecific competition
(51): staged introductions of *C. opuntiae* to *L. apiculatum*-tended plants, and vice versa, provoke
aggressive responses by residents (A. Campbell, *personal observation*). In Fall, tree cholla stop
producing EFN and the ants vacate until the next growing season.

Multiple insect herbivores and seed predators specialize on tree cholla (49). The Cerambycid

beetle *Moneilema appressum* and a weevil (Coleoptera: Curculionidae) of the genus *Gerstaekeria* feed on vegetative and reproductive structures as adults and their larvae feed internally. A cactus bug, *Narnia pallidicornis* (Hemiptera: Coreidae), feeds on all cholla parts with a preference for the reproductive structures (55). A seed predator, *Cahela ponderosella* (Lepidoptera: Pyralidae), oviposits in open flowers and larvae eat seeds in developing fruits. These predators can have significant negative impacts on plant fitness of and depress population growth (53). Prior experiments showed that ant-tended tree cholla experience less herbivory and seed predation than plants from which ants were excluded (51; 59).

Data Collection

This study is based on long-term demographic data spanning 2004 to 2023 at SEV-LTER. From 2004 to 2008, we censused 134 plants distributed across three spatial blocks. This initial census group was discontinued in 2009, when we established six 30 × 30-meter plots and tagged all tree cholla within those plots. Two additional 30 × 30-meter plots were added in 2011, and this group of eight plots has since been censused annually through 2023 (with the exception of 2020 due to the pandemic 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 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 measured reproduction as counts of viable and aborted flowerbuds. We recorded the ant species present (or vacancy if no ants present). Occurrences of more than one ant species on one plant were rare (less than 5% of observations), 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 1141 unique individuals and 19 year observations.

We used additional, smaller data sets from previously published studies to estimate seed and seed bank parameters. Ohm et al. 2014 provide data on the number of seeds per fruit for plants

tended by *L. apiculatum*, *C. opuntiae*, or no ants (experimental exclusion), accounting for their effects on pollinator visitation. Elder and Miller 2016 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 (32). 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 stochastic, multi-state IPM that stitches together population structure associated with plant size and ant state, allowing us to determine the individual fitness effects of each ant species and the composite effects of multiple partners, with ant transition dynamics and inter-annual variability modeled explicitly.

Given the low frequency of ant occupancy states other than *L. apiculatum* and *C. opuntiae* (<8% of observations) we combined all other ants into an “other” category, such that our multi-state IPM included four ant states: vacant, *L. apiculatum*, *C. opuntiae*, and Other. The “Other” category was made up of *Forelius pruinosus* (3.5% of observations), unidentified species belonging to the genera *Camponotus* (0.9%), *Aphaenogaster* (0.4%), *Myrmecocystus* (0.08%), *Tetramorium* (0.02%), *Brachymyrmex* (0.02%), and additional ants not identified to genus or species (2.8%).

Ant state is included as a predictor variable in IPM 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 or flowerbud production independently of its influence on plant size, so these sub-models do not include ant state as a predictor variable.

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:

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

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

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Functions $P(x; \boldsymbol{\tau}^P)$ and $F(x; \boldsymbol{\tau}^F)$ give the probability of flowering in year t and the number of flowerbuds produced in year t , respectively, by plants of size x . The proportion of flowerbuds that remain viable through fruit set ($V(a; \boldsymbol{\tau}_a^V)$) and the number of seeds per fruit ($\kappa(a')$) is dependent on ant state a . The vectors $\boldsymbol{\tau}$ give year-specific deviates (mean zero) and appear in functions for which we can estimate temporal stochasticity from the long-term data; superscripts indicate the corresponding vital rate and, when present, the a subscript indicates that deviates are specific to plants in ant state a . For example, temporal deviates $\boldsymbol{\tau}_a^V$ describe better- and worse-than-average years for flowerbud viability and plants in different ant states can fluctuate independently (good years for *L. apiculatum* -occupied plants may not be good years for *C. opuntiae*-occupied plants, for example). 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:

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

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

219

The first term in Eq. ² estimates the number of individuals recruiting from a one or two-year
 222 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
 225 first appearance in our census ($\sum \rho_0(a') = 1$). The second term represents all possible transitions
 from size x and ant a to size x' and ant a' , conditioned on survival. Survival ($S(x, a; \tau_a^S)$) 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,
 228 these functions include inter-annual variability through year-specific deviates that can vary by
 ant state (τ_a). Finally, 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
 231 includes inter-annual variability through year-specific intercepts which are consistent across ant
 states (τ^ρ).

Statistical modeling and parameter estimation

234 We parameterized the IPM using a series of generalized linear mixed models in a hierarchical
 Bayesian framework. Vital rate models included spatial and temporal random effects associated
 with plot and year variation, respectively (only year variation is used in the IPM), and included
 237 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 transitions between ant states conditional on plant size and previous ant state. As in
 240 the IPM, our statistical modeling assumed that demographic effects of ant occupancy are limited
 to survival, growth, and flowerbud viability.

²We should label equations. I am not sure why the equation label is not working here and I did not try to figure it out. It is
 probably something with the linenomath formatting.

Growth. We fit the growth sub-model ($G(x', x, a; \tau_a^G)$) to data on size in year $t + 1$ (y^G) using the skewed normal distribution to account left-skewed size transitions:

$$y_i^G \sim \text{SkewedNormal}(\hat{G}_i, \sigma_i, \alpha_i)$$

$$\hat{G}_i = \beta_{a[i]}^0 + \beta_{a[i]}^1 x_i + \beta_{a[i]}^2 x_i^2 + u_{\text{year}[i], a[i]} + w_{\text{plot}[i]}$$

The **mean**³ of the i th observation \hat{G}_i is a second-order polynomial with ant-size interactions because preliminary analysis found this was an improvement over a linear relationship. The year- and ant-specific random effect u (which parameterizes the τ_a^G vector) and plot-specific random effect w are normally distributed with variances σ_{year}^2 and σ_{plot}^2 , respectively. Parameters σ_i and α_i control residual variance and skewness, respectively, and were defined as linear functions of initial size x_i (σ_i is strictly positive and was modeled with a log link function). We assume growth variance and skewness were not dependent on ant occupancy state.

Survival. The survival sub-model ($S(a, x; \tau_a^S)$) estimates the probability of survival from year t to year $t + 1$, with fixed effects of size x and ant partner a in year t . We fit this model to the survival data (alive or dead) using a Bernoulli distribution and the logit link function, with a similar linear predictor as the growth model but without the second-order influence of size.

Reproduction. The flowering sub-model ($P(x; \tau^P)$) estimates the probability of reproducing in year t , with fixed effects for the size x and random effects of plot and year. We fit this model to the reproductive status data (vegetative or flowering) using a Bernoulli distribution and a logit link function, similar to the survival model above but with no ant effects. The flower bud function $F(x; \tau^F)$ estimates the total flowers produced by a reproducing plant in year t , with fixed effects of size x . We fit this model to flowerbud count data (sum of viable and aborted buds) using a zero-truncated negative binomial distribution with a log link and normally distributed year and plot random effects.

³I rewrote this for the skewed normal but I cannot remember if the location parameter is the mean, so you should double check this.

The flowerbud viability sub-model ($V(a; \tau_a^V)$) estimates the proportion of flowers produced by a plant that are viable (not aborted) in year t , with fixed effects of ant partner a in year t . We fit this model to floral viability data using a binomial distribution where trials and successes are given by the total number of flower buds and the number that are viable, respectively. This model used a logit link function and included random effects for plot and year following the same structure as the growth and survival models.

Additional reproductive parameters for the **number of seeds per fruit**⁴, probability of entry to the seed bank, germination rates, and recruit size were estimated following methods described in Appendix XX.

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

Parameter estimation. We fit models using Markov chain Monte Carlo (MCMC) simulations via STAN run through version 4.0.2 of R (63; 70). We used vague priors for all parameters. For each model, we obtained three chains of 10,000 iterations, discarding the first 1,500 iterations. We visually assessed parameter convergence between and within chains (Figures 1 – 7 b) and assessed overall model fit with posterior predictive checks to examine how well the fitted model can generate simulated data similar to the real data (Figures 1 – 7 a).

IPM Analysis

Analyzing an IPM requires discretizing the continuous IPM kernel into an approximating matrix. Size variable x is discretized into b bins, resulting in a $b \times b$ matrix. In our model there is additional complexity in the form of transitions between A ant partners and two additional discrete

⁴We need to briefly explain that this was any-specific, where those values come from, and how we deal with Other.

states (year one and year two seed banks), leading to a matrix size of $A(b + 2) \times A(b + 2)$. We
 285 used $b = 200$ bins (sufficient for numerically stable model outputs) and extended the integration
 limits beyond the minimum (L) and maximum (U) observed sizes to avoid unintentional eviction
 (79).

288 For stochastic analyses, we estimated the approximating matrix corresponding to each t to
 $t + 1$ transition year. To estimate population mean fitness in a stochastic environment (λ_S)
 we simulated population dynamics for 500 years by randomly sampling among the 19⁵ an-
 291 nual transition matrices, discarding the first 100 years of the simulation to minimize the in-
 fluence of initial conditions. Sampling observed transition matrices (rather than independently
 sampling regression coefficients) produces models that realistically capture inter-annual varia-
 294 tion by preserving correlations between vital rates (50). We tallied the total population size at
 each time step as $N_t = B_t^1 + B_t^2 + \sum_{a=1}^A \int n(x, a)_t dx$ and calculated the stochastic growth rate
 as $\log(\lambda_S) = E[\log(\frac{N_t}{N_{t+1}})]$ (?). We propagated uncertainty from the vital rate models using
 297 1000 draws from the joint posterior distribution of model parameters, resulting in a posterior
 distribution of λ_S and other derived quantities.

Partner diversity experiments

300 Using the fully parameterized multi-state IPM, we conducted simulation “experiments” to quan-
 tify how diversity and identity of ant partners influenced plant fitness (λ_S). From the fullest
 version of the model corresponding to the observed assemblage of partners, we created subsets
 303 corresponding to all eight possible scenarios of diversity and composition: no ant partners (com-
 plete vacancy); one ant partner (*C. opuntiae* only, *L. apiculatum* only, Other only); two partners
 (all pairwise combinations of *C. opuntiae*, *L. apiculatum*, and Other); and three partners (observed
 306 scenario of all ant states). These simulation experiments were made possible by extrapolating
 ant-specific demographic performance across the size distribution, even for combinations of size

⁵Is this right? The number of transition matrices should be one fewer than then number of years, but I don't remember what
 happens with 2020.

and ant occupancy that were rarely or never observed. For example, the no-partner scenario modeled a hypothetically ant-free cactus population, even though no such population exists to our knowledge, by applying the statistical knowledge gleaned from vacant plants (which were mostly small and non-reproductive) across the size distribution.

In all scenarios that included any ant partners, we preserved the observed pattern of size-dependent vacancy/occupancy (estimated through the ant transition sub-model) and manipulated partner identity conditional on occupancy. This means, for example, that the *C. opuntiae*-only scenario included two possible states, vacancy and occupied by *C. opuntiae*. Small, non-reproductive plants are typically vacant because they do not produce extrafloral nectar, and once plants begin producing nectar they are nearly always ant-tended (52). Our simulation experiments preserved this basic biology, avoiding tiny ant-occupied plants that do not and could not occur in nature.

Temporal stochasticity experiments

Under the portfolio effect hypothesis, partner diversity may confer a fitness advantage when the benefits of alternative partners are not perfectly synchronized across temporal environmental variation, yielding an advantage of a diverse “portfolio” of partners when the environment fluctuates. Our statistical estimation of ant-specific year random effects in the vital rates allows for this possibility. We constructed two versions of the stochastic, multi-state IPMs that allowed us to test this hypothesis by exploring two different scenarios of environmental variation. First, we evaluated the model using empirical estimates for the τ_a vectors that describe ant-specific year deviates. In this scenario, good years and bad years can differ between ant states, according to the empirical parameter estimates. We also quantified from the fitted random effects how tightly inter-annual variation was correlated between ant states.⁶ Second, we re-fit the ant-dependent vital rates (survival, growth, flowerbud viability) without ant-specific year random effects, thus assuming that plants in all ant states fluctuated synchronously in response to temporal environ-

⁶Worth doing!

mental variation. We evaluated a second, “synchronized” version of the model that effectively turns off any portfolio effect, holding all else equal. Both scenarios of temporal stochasticity, non-synchronized and synchronized, were run for all eight ant partner scenarios described above.

Statistical inference on fitness consequences of partner identity and diversity

The range of models we created generated many outputs; we focus our inference on the following specific contrasts. First, to determine whether ant occupancy and partner diversity are beneficial, we calculated a posterior distribution of λ_S for each of four partner richness levels (zero, one, two, three), averaging over composition scenarios within each level. Second, to determine whether each partner, in isolation, confers a fitness advantage and to rank alternative partners, we contrasted the fitness of each single partner scenario (*C. opuntiae* only, *L. apiculatum* only, Other only) against vacancy (zero partners). Third, to determine whether apparent benefits of diversity are due to the sampling effect or complementarity, we contrasted the fitness of multi-partner scenarios against the single best partner scenario. If the best multi-partner scenario exceeds the fitness associated with the best single partner, this would be interpreted as evidence of complementarity, a true benefit of diversity *per se*. Alternatively, the sampling effect hypothesis predicts that no multi-partner scenario yields higher plant fitness than the best single partner. It is also possible that multi-partner scenarios yield lower fitness than the single best partner, which would be consistent with opportunity costs of diversity. Fourth, to quantify any contribution of the portfolio effect, we contrasted λ_S of the full (three-partner) scenario for synchronized and non-synchronized responses to temporal stochasticity. If the portfolio effect confers a benefit of diversity, λ_S should be higher under non-synchronized temporal fluctuations.⁷

We base our statistical inferences on the posterior probability distributions of the contrasts described above. For example, the contrast of *C. opuntiae* with vacancy yields a posterior distribution of the difference in λ_S ($\Delta\lambda_{C-V}$). We can quantify from this distribution our certainty in

⁷*I am actually not sure whether we should look at this as stated, or whether we should compare the difference between all partners and vacancy for synchronous and non-synchronous (which is what I think you currently do.)*

the mutualistic effect of *C. opuntiae*, given the data, as $Pr(\Delta\lambda_{C-V} > 0)$. We apply similar logic to other contrasts described above.

Results

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

Over the 20-year data set, we found that ant partners influenced demographic performance of cactus hosts, and different ant partners had contrasting demoghraphic effects across host vital rates. Plants tended by *C. opuntiae* had a growth advantage, particularly for small plants, while plants in states of *L. apiculatum*, Other ants, and vacancy had indistinguishable growth trajectories (Figure 1).⁸ For all ant states, growth was left-skewed, with transitions to sizes below the mean were more common than sizes above the mean. Similarly, ant visitation enhances cactus survival, and ant partner identity has a significant impact on survival for smaller plants (Figure 2). Mean survival rates ranged from 7.7% to 99.9%, with the smallest plants the most vulnerable to mortality. *C. opuntiae*-occupied plants had a survival advantage over other ant states, particularly at smaller sizes, consistent with the positive effects on growth. At larger sizes, plants in any state of ant occupancy had a survival advantage over vacant plants.

⁸*Your draft had posterior probabilities associated with growth differences. I think it would be possble to keep the vital rate results very simple – like what I have here – and keep the posterior probability estimates for the IPM results. I am open to including posterior estimates for the vital rates but it is not clear to me how those values account for size, since we are comparing functions not single values. Let’s discuss.*

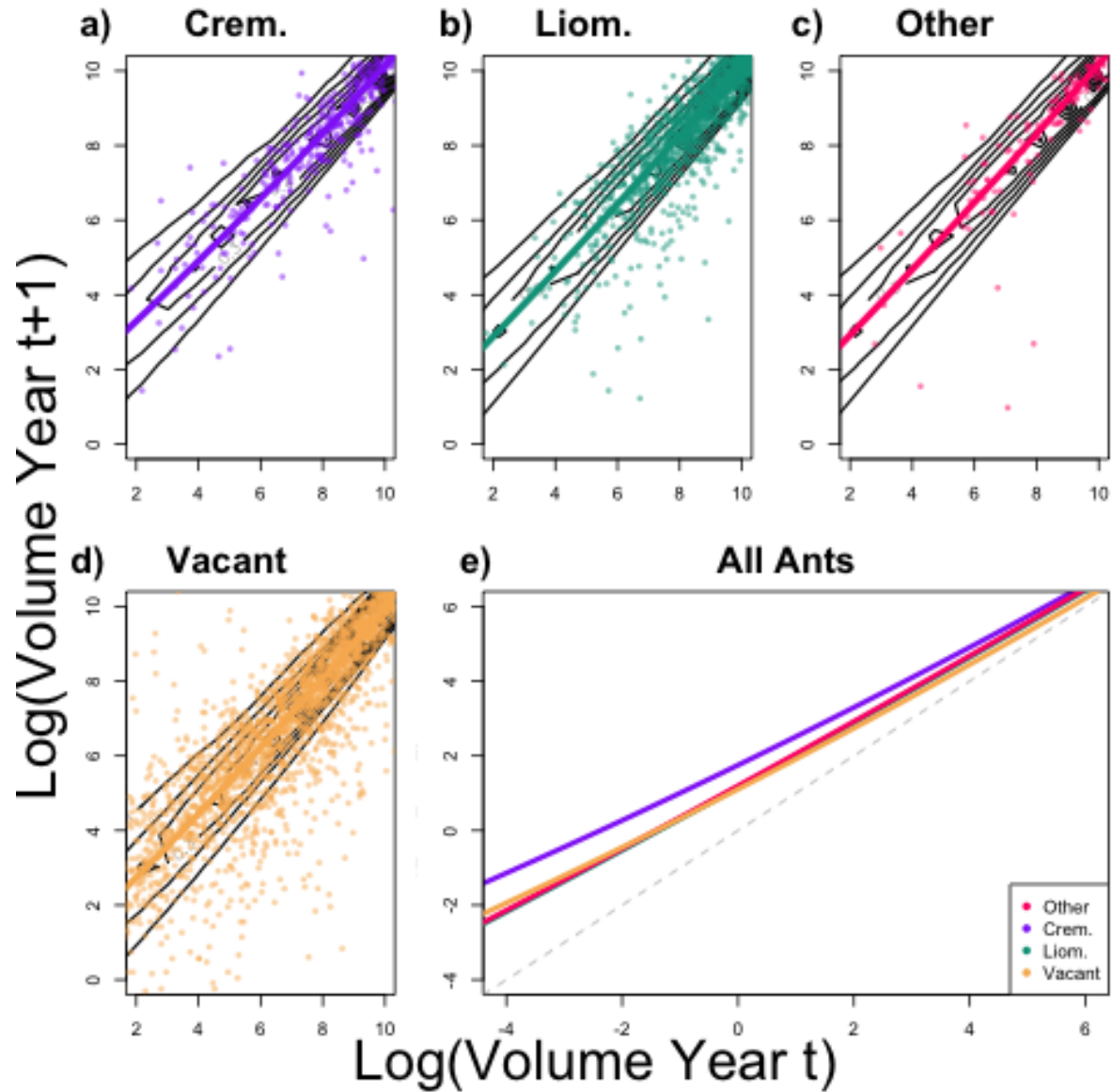


Figure 1: This figure shows the next predicted size of cholla based on previous size with each individual ant partner. The solid colored lines (seen in all panels) are the next mean predicted size of cholla. The points (seen in panels a-d) are the observed data which informs these estimates. The black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

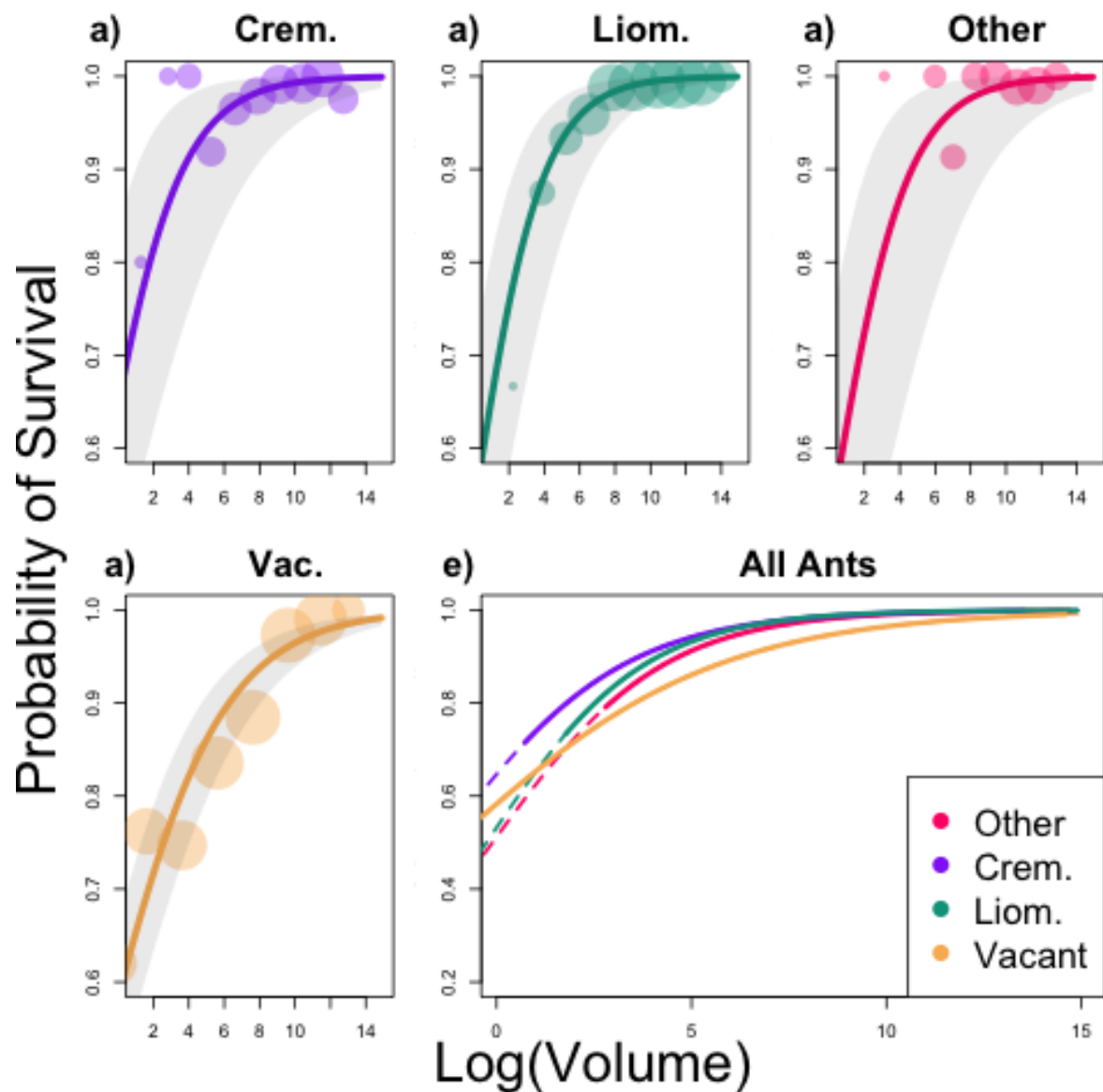


Figure 2: This figure shows the estimated survival rates based on the size of the cactus with each individual ant partner. The solid colored lines (shown on all panels) indicate the mean estimated survival rates. The dashed lines (shown in panel e) indicate extrapolations beyond existing data (where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

We found evidence that ant visitation leads to increased floral viability rates and that ant identity can influence the strength of viability benefits.⁹ Reproductive cacti experience between

375 39% and 96%¹⁰ viability rates of flowers (Figure ??). Ant partners influence the mean viability rate of flowers, with *L. apiculatum*-tended plants experiencing the highest mean viability rate (86%, Figure 3b), followed by *C. opuntiae* and Other tended plants (at 74-75%, Figure 3b,c), and
378 vacant plants had the lowest floral viability rate (71%, Figure 3d). Given the uncertainty of the parameter estimates, we are 98% and 97% confident that *L. apiculatum* tended plants experience higher viability rates than plants tended by *C. opuntiae* or other ants respectively. We are 95%
381 and 69% confident that vacant plants experience lower viability rates than plants tended by *C. opuntiae* ants or other ants respectively.

⁹Great example of an effective topic sentence for a Results paragraph. Sets the stage with the main result, and leaves the details for below.

¹⁰Unclear what this range indicates. The min to max would be 0 to 100%.

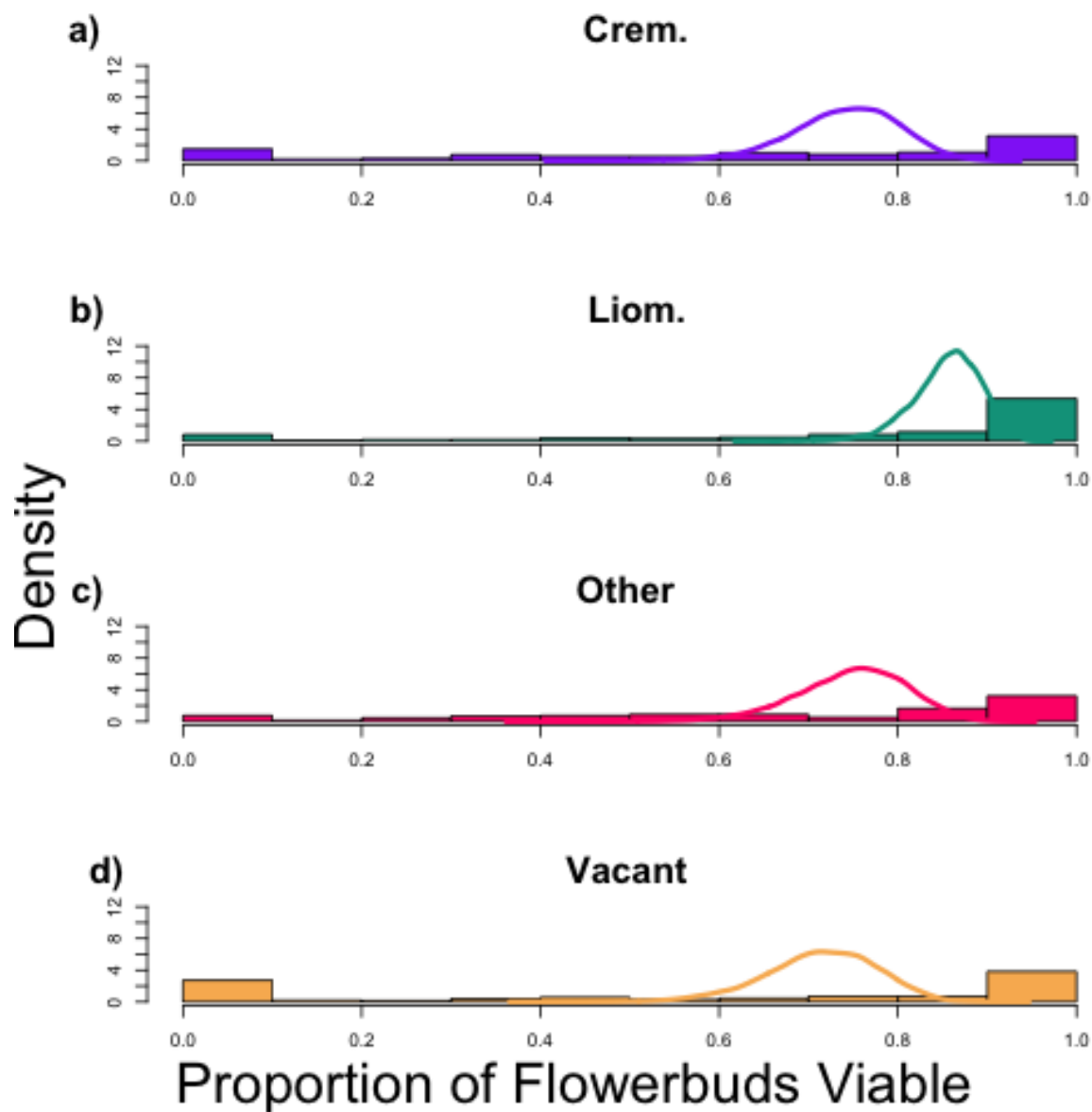


Figure 3: This figure shows the estimated distributions of floral viability rates compared to observed distributions of floral viability rates of cholla based on ant partner identity. The solid lines indicate the estimated viability distribution. The colored histograms represent the observed viability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

Inter-annual variation results¹³

¹¹*Should I include other model results here or just indicate that the rest are reported in an appendix/supplementary materials?*

¹²*I think you can include a short paragraph that briefly mentions that other vital rates are in the appendix.*

¹³*I think the text you had for this did not directly address the synchrony hypothesis, and it may be more informative to look at correlation coefficients rather than the time series, which are hard to make heads or tails of.*

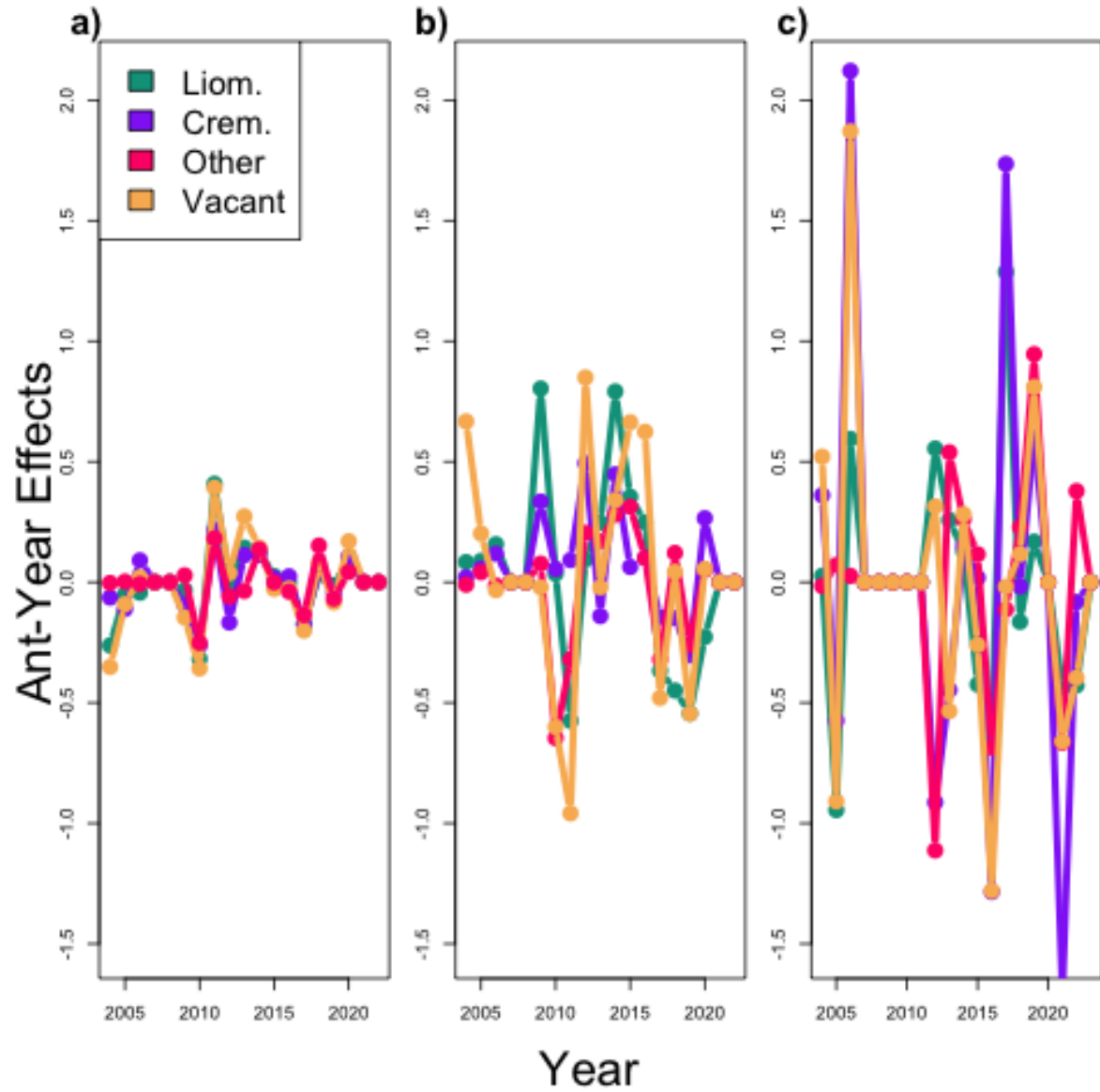


Figure 4: This figure shows the mean affect of each ant partner on a) the estimated next size, b) the estimated survival, and c) the floral viability of cacti across every year of our study. These values are estimated from the fitted random effects of ant and year in our models. Each point represents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

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

387 We found a **high frequency of partner turnover across transition years**¹⁴, with very distinct size-
dependence and directional patterns (Figure 5). Vacancy is the most likely ant state of small
plants ($\leq 10\log(\text{cm}^3)$). Even when small plants are ant-tended at the start of the transition year,
390 they are most likely to transition back to vacancy (Figure 5b-d). The probability of becoming
ant-tended increases with size, though it is not equally likely to be tended by all partners. For
large plants that are initially vacant or tended by *L. apiculatum* or Other ants, *L. apiculatum* is
393 the most likely next partner, suggesting that this partner species is able to colonize plants that
were previously vacant or occupied by Other ants, and effectively retain plants that it previously
occupied. *C. opuntiae* were also able to retain plants they previously occupied, but not as well
396 as *L. apiculatum*: for plants that begin the transition year with *C. opuntiae*, the probability that
those plants remain occupied by *C. opuntiae* at the end of the transition year is only slightly
greater than the probability of take-over by *L. apiculatum*, while take-over in the other direction is
399 extremely rare. It is also notable that transitions away from the initial state of *L. apiculatum* were
almost always transitions to vacancy (Figure 5d), while transitions away from the initial states of
C. opuntiae and Other were often transitions to other ants. This suggests a competitive hierarchy
402 whereby *L. apiculatum* may abandon low-value plants with little nectar production but is almost
never displaced from high-value plants.

¹⁴*could we estimate the global average turnover rate? Across all observed transitions, what fraction of plants switched ant states. I think that would be a good place to begin, then unpacking that into the effects of initial size and ants.*

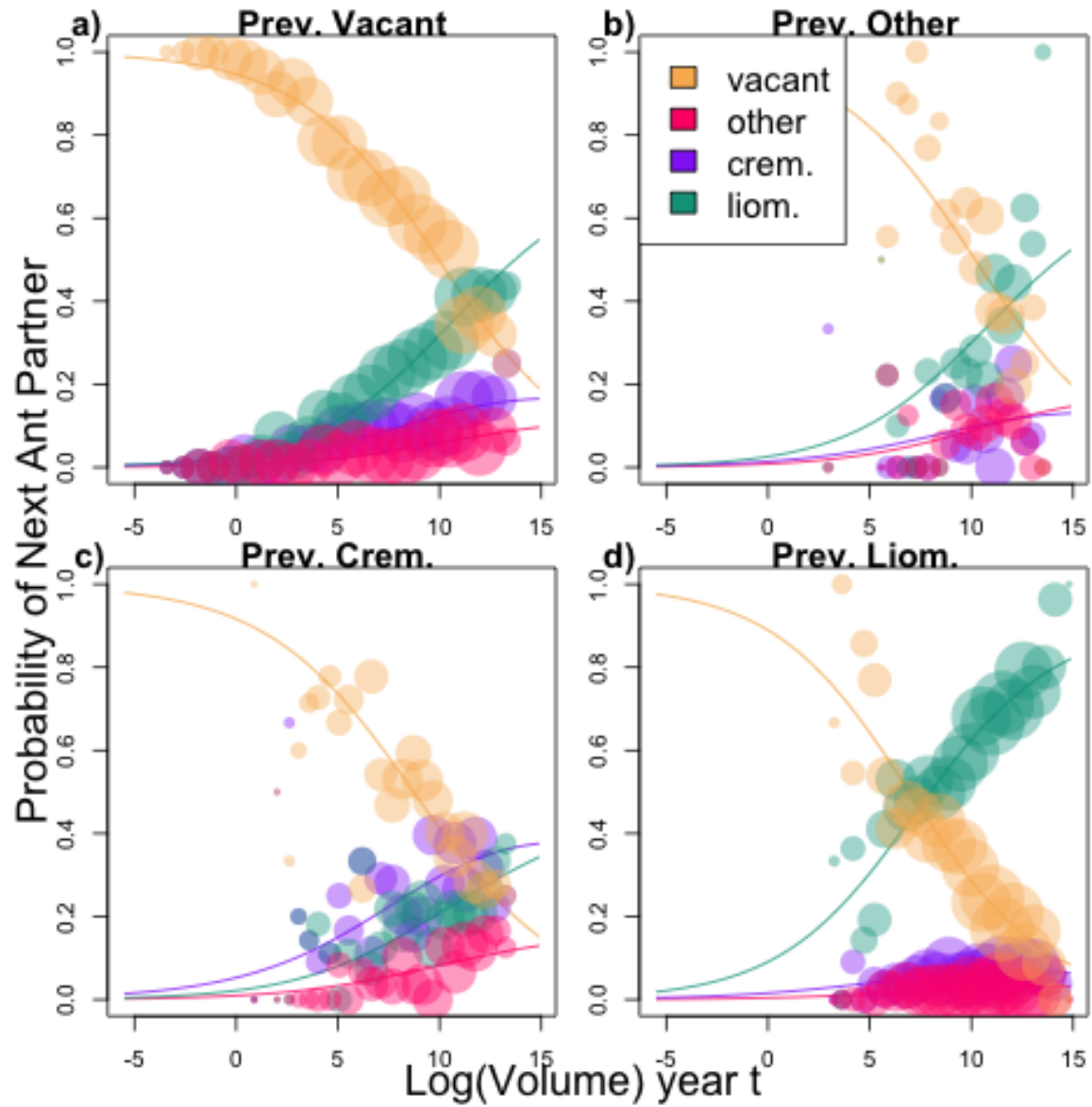


Figure 5: This figure shows the probability of being tended by each ant partner or vacant based on the size of the plant. Each panel shows these probabilities for a different previous ant state. The solid lines represent the mean probability of being tended by a specific partner. The colored points are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

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

By integrating vital rate results and ant transition dynamics into the multi-state IPM we can evaluate the fitness implications of different scenarios of partner diversity and identity. First, there was strong evidence that ant visitation had mutualistic fitness effects on plant partners. The lowest mean fitness was $\lambda_{S,Vacant}$, the fitness of the cholla with no partners (Figure 6b). Across all 1+ partner scenarios, we are 82–100% confident that any scenario of ant visitation elevates fitness. Furthermore, we find an apparent positive effect of partner diversity, with cactus fitness positive related to partner richness, averaging over partner identities (Figure 6b).

Despite this apparent synergy, when partner identity was considered, we found the benefits of partner diversity could be explained by Sampling Effect. We believe the benefits of partner diversity are heavily driven by the presence of a single best partner rather than overall synergy. All simulated combinations of ant partners which included *L. apiculatum* were nearly equal and the highest possible fitness estimated for the cholla. This indicates that *L. apiculatum* are the single best partner for the cholla under existing conditions. Based on the definitions of Sampling Effect and Complementarity we use in this study (15), it is clear that Sampling Effect can explain the benefits of partner diversity in the cholla system.

It is possible that this, like the frequency of partner turnover to *L. apiculatum*, is driven by the extreme frequency of *L. apiculatum* ants in comparison to others. With this in mind, we simulated the population fitness with equal probability for transitioning to any ant state. We found from the simulations with different transition probabilities.¹⁵

We found evidence¹⁶ of portfolio effect, meaning the presence of multiple partners did not buffer against the potentially negative effects of annual fluctuations. The effect of all ant partners can be measured as $\lambda_{All} - \lambda_{Vacant}$ (Figure 7). We are 94% confident that when all ants are

¹⁵This feels like the most natural progression to me.

¹⁶I think this should say “no evidence”??

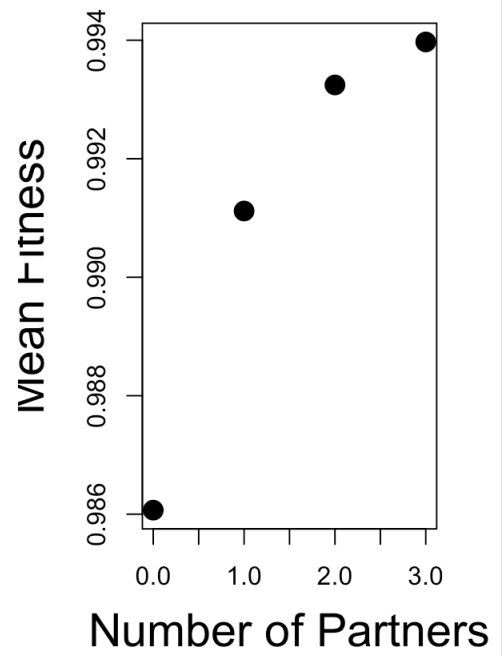
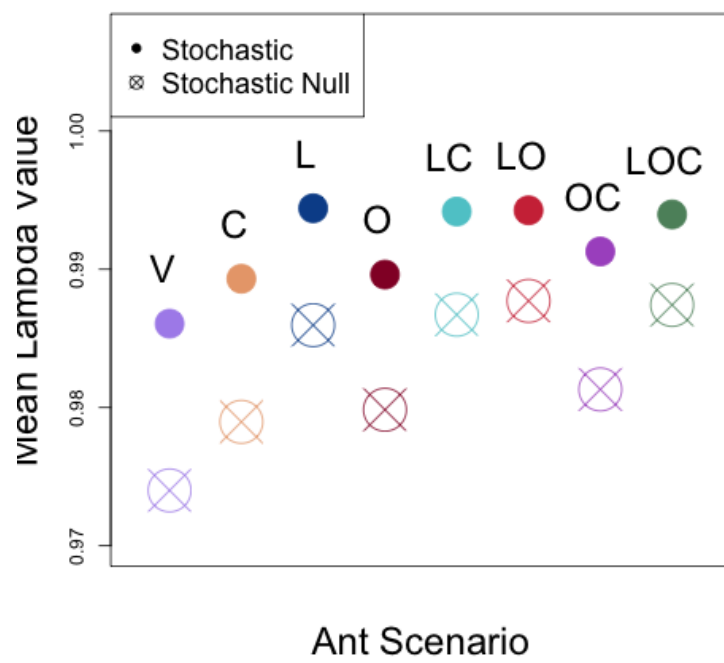


Figure 6: Panel a) shows the mean values of the estimated λ_S (filled in circles) and λ_{SN} (empty circles with an X) for each simulated combination of ant partners. The letters above the points correspond to what ant partners are present (V = Vacant, C = *C. opuntiae*, L = *L. apiculatum*, O = other).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

present the cholla experience higher fitness than when no ants are present according to both
 429 the synchronized and non-synchronized model scenarios. When subtracting these two resulting
 vectors from each other $((\lambda_{S,All} - \lambda_{S,Vacant}) - (\lambda_{SN,All} - \lambda_{SN,Vacant}))$, we found that we are only 52%
 confident that partners offer higher benefits when able to respond uniquely to a fluctuating en-
 432 vironment. **There is no real difference between the two scenarios, meaning we have no evidence
 of portfolio effect.**^{17 18}

Discussion – Real

435 Mutualisms commonly involve multiple partners but the ecological consequences of partner di-
 versity remain poorly understood. Here we show that partner identity can play an important role
 in determining both vital rates and population fitness. The results of our heirarchical models re-
 438 vealed that different ant partners had different effects on vital rates, with *C. opuntiae* tended plants
 experiencing advantages in growth and survival when small, and *L. apiculatum* tended plants ex-
 perienicing floral viability advantages. The results of our stochastic IPM revealed that all partner
 441 diversity scenarios which included *L. apiculatum* resulted in the highest possible fitness for tree
 cholla, suggesting that diversity benefits here are explained by sampling effect. The results of
 our stochastic null IPM revealed that there is no evidence of portfolio effect in our system. These
 444 results highlight that partner diversity can increase the overall benefits of a focal mutualism and
 the importance of a mechanistic understanding to explain the benefits of diversity across systems.

Similar studies have reported complementarity (1; 2; 3; 40; 62) while we found sampling effect
 447 explains the benefits of diversity in our system. This may have to do with the sheer number of *L.*
apiculatum in the system. None of these cited studies reported a single species with overwhelming
 frequency within their systems. In most cases of complementarity, there are relatively similar
 450 frequencies of each partner, which is not the case in our system. 75% of observed ants are *L.*

¹⁷I am not sure if I have explained enough here honestly.

¹⁸I agree with your interpretation, but let's come back to editing this after we talk through the best way to look at portfolio effect.

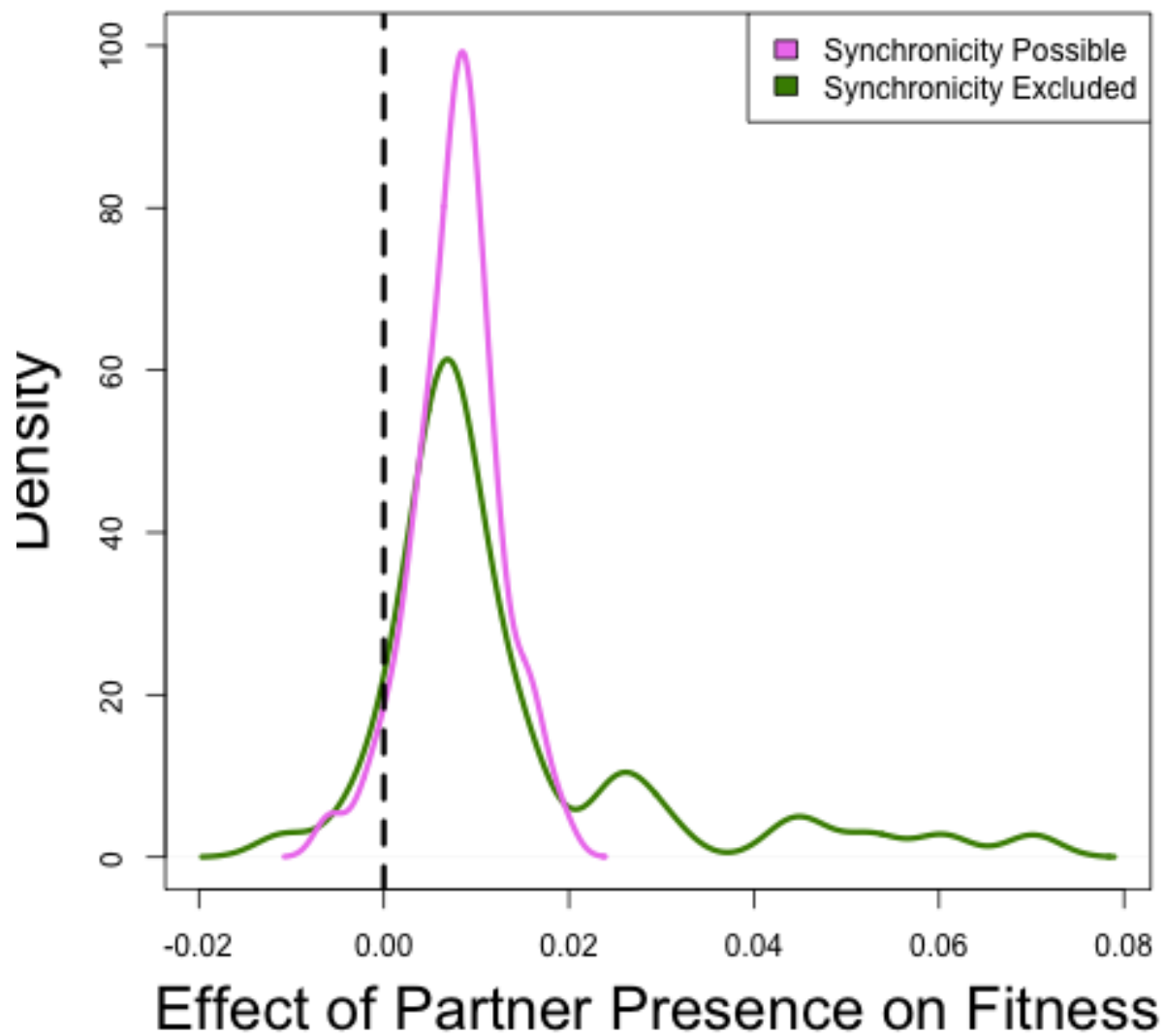


Figure 7: This figure shows the distribution of $\lambda_{S,All} - \lambda_{S,Vacant}$ in pink and $\lambda_{SN,All} - \lambda_{SN,Vacant}$ in green. The vertical dashed line shows where the effect of partners on the fitness of the cholla is 0 (to the left the partners have a negative effect, to the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

apiculatum in our system, while only 17% are *C. opuntiae*. Our vital rate results suggested we may find evidence of complementarity, with *C. opuntiae* appearing to boost growth and survival and *L. apiculatum* appearing to boost floral viability. We believe there may simply not be enough *C. opuntiae* in the system to have complementarity, leading instead to sampling effect driven by the overwhelming frequency of one ant.

In systems where there is one best partner, theory suggests that diversity should impose an opportunity cost of the form of interacting with "inferior" partners, meaning scenarios where more than just the best partner is available should result in decreased fitness¹⁹. We don't see this pattern emerge in our results, likely due to the nature of interactions.

Our work explicitly incorporated temporal environmental stochasticity, which raises the opportunity for portfolio effect as a mechanism of diversity benefits. Yet, we find no evidence of portfolio effect within our system. When partners exhibit different reactions to varying environments, interacting with multiple partners can lead to more consistent benefits across time (15). In our system, we do not directly measure the reactions of ant partners to temporal environmental stochasticity, rather we measure the effects of each partner on the cholla across time, allowing us to statistically quantify how the benefits received from each partner vary across time. We found that each ant partner had different effects on different vital rates across time, indicating they exhibit different reactions to varying environments, leading us to believe that portfolio effect could be possible in this system. We compared the fitness of cholla under simulations where the variation in benefits across time reflected what we found in nature to simulations where each ant was forced to react the same way to temporal variation (excluding the possibility of portfolio effect). We found the benefits were not stronger across time when the ants were allowed to vary naturally than when they were forced to react synchronously, indicating that portfolio effect does not explain the benefits of diversity in our system. Other portfolio effect studies (44; 73) found One study (Dallas and Kramer) found that while portfolio effect was easy to show in theoretical models, it is often very weak or nonexistent in empirical data across many systems. This indi-

¹⁹[get a citation here](#)

cates that it may be very difficult to detect, disguised by different mechanisms, or uncommon in real systems.

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 (11; 22; 28; 34; 58; 76). Separate studies have analyzed how inter-annual variability impacts focal mutualists (7; 8; 42; 44; 61). The long term dataset we used gave us the unique ability to consider the combined effects of partner identity, partner turnover, and temporal stochasticity.

First, we were able to look at many years of data to reveal the complex dynamics of partner turnover and identity, revealing that the frequency of *L. apiculatum* may be primarily responsible for the fitness of the cholla rather than any other ant partner observed. Fewer years of data would not have been able to show the distinct patterns of *L. apiculatum* taking over cacti that were previously tended by any other partners with as much clarity. Second, our long-term data set allowed us to test the portfolio effect. This data is required, because we must show that the partners react asynchronously to temporal environmental stochasticity for portfolio effect to even be possible. This is a great example of how long-term data may offer more power to test underlying mechanisms in similar systems. Finally, previous studies by (51) hypothesized that *C. opuntiae* may be a parasite based on the effects on the cholla cacti. Using more years of consecutive data in this system, we were able to show that *C. opuntiae*, while the worst individual partner in terms of the overall cholla fitness (Figure 6), increases the growth and survival rates of cacti prior to reproduction. The length of our data set has allowed us to dive into individual vital rates as well as overall fitness with more clarity.

Herbivory is an important driver of the fitness of cholla in this system, as herbivores directly impact the growth, survival, and reproductive efforts of the cacti. Despite this, we do not directly account for herbivory in our system.

In the future, further studies on the direct impacts of herbivory would bolster the results reported here and expand our knowledge within this system.

As with any study, there are limitations to consider when interpreting the results reported here. These results are based on observational data regarding ant effects on plant demography rather than experimental data, meaning we are able to determine correlations but not causation. We are able to report evidence that plants experience higher growth when associating with a particular partner, but we are not able to determine if the presence of the ant is the cause of the higher growth observed. It is possible, for example, that plants which attract *L. apiculatum* through nectar composition have a different pattern of resource allocation to growth and survival and this is what we are observing rather than a direct affect of *L. apiculatum* on the plant. This is a typical limitation of observational studies, but does not reduce the power or importance of our results, just the interpretation. However, we believe that the ants likely have direct impacts on the plant demography based on other studies which find *****²⁰. In the future, it would be interesting to verify the causation of our results through experimental manipulations. One further expansion could include nectar analysis of these cacti in conjunction with ant interactions to look not only at the ant partner impacts on the plant demography, but also at the ability of plants to attract specific partners through nectar composition shifts.

Another limitation of our study is that we are simulating populations through an IPM to estimate fitness, meaning we have to extrapolate beyond observed interaction. In our study, small plants are rarely seen with partners, yet we report on the expected effects of each ant on the growth and survival of plants from the size of new recruits to the largest plants. While we are confident in our model, there remains the small possibility of interactions which have never been observed occurring (such as a seedling tended by *L. apiculatum*). This means that our fitness estimations are based on extrapolations of our observed data, and while we have done what we can to be confident in our model, it is possible that our assumptions that observed patterns would continue beyond observed interactions could be incorrect. Another example of this includes our single partner simulations. We have no data on what the fitness of cholla would look like if the only ant partner possible was *C. opuntiae*, yet we offer an estimation based on the

²⁰[Find causal studies to show that ants really do things.](#)

effects of this partner in a diverse system. The many years of data and 10467 unique plant-year
531 observations included in our analysis allow us to have relatively high confidence in our outputs
despite extrapolations.

Discussion brainstorming:

534 1. Mini abstract paragraph - synthesis of question plus answers, and overall significance Topic
sentence:

2. COnnecting to broader patterns in the literature - address how complementarity or syner-
537 gies are commonly reported – why did we not see this, especially since the vital rates suggest
some complementarity - may involve the simulation experiments - some contrast with other sys-
tems where benefits of diversity have been found Topic sentence:

540 3. If there is one best partner then diversity should impose opportunity costs – why do we
not see this? - should address how some systems can host multiple partners at a time while
others (ours) can exclusive associations; for the latter diversity should only be costly if there is
543 one best partner?

4. Turnover - what's going on with turnover? what processes may drive the patters we see
- what is seen elsewhere in the lit (invertase papers may be an interesting reference? showing
546 plant “choice”) - patterns could be consistent with ant and or plant choice (currently a “black
box”) - this might address both frequency and direction (direction may lead to some discussion
of competition)

549 5. Portfolio effect - what is it, what does it predict, what did we find - what have other studies
found? Topic sentence:

6. Value of long-term data - includes turnover, portfolio effect - also address how the full de-
552 mographic data provides the correct insight into ant effects (eg We thought Crem was a parasite
based on less complete data)

7. Herbivory - this should underlie why these interactions are beneficial, so we need to
555 address this - this connects to portfolio effect, because fluctuations in herbivores (in conjunction
with ant-specific defenses against herbivores) would be why porfolio effect could occur

8. Limitations - confounds fundamental to observational data regarding ant effects on plant demography (correlation/causation problem) – maybe plants that attract Liom through nectar have a different pattern of allocation o growth and survival - cite experiments to support causal interpretation of observational patterns (ants really do stuff) - extrapolating effects of ants beyond the interactions that we can actually see (e.g., new recruits with Liom); and the counterfactual of a Liom-only population is another form of extrapolation

9. Future directions – maybe embed these into paragraphs above where we see opportunity to address limitations or extend the results – probably lots we can do with herbivory

Conclusion.

Appendices: 1. Herbivory 2. Additional methods and results 3. Posterior predictive checks and model convergence 4. Maybe ant transition simulations

Discussion

²¹ 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 (14; 24; 35; 62; 69). 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. ²²

We asked what effects the partners which interact with tree cholla (*C. opuntiae*, *L. apiculatum*, and more²³) have on the vital rates of tree cholla. Using a system of heirarchical bayesian models

²¹*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.*

²²*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.*

²³*I would not say this.*

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 (53; 55) and positively impacted by the presence of ant partners (51). 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 (5; 46). The presence of the ant partners can reduce those negative effects.

It has been previously hypothesized that there is a hierarchy of partners due to the ability for *L. apiculatum* ants to defend the cacti from seed predators and herbivores (51). 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 (54)²⁴**, 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

²⁴*Seed predators do not influence floral abortion.*

turnover.

In the literature, it is clear that the frequency of partner turnover can have big effects on the fitness of the focal mutualist (33; 41; 60; 67). In some systems high frequency of turnover is necessary to resiliency and leads to higher fitness benefits (76), while in other systems loyalty is the most beneficial (15). 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 received (8; 28; 34; 58). 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 (62)²⁵) and a unique set of mechanisms ((15)) which explain how the multi-partner interactions lead to fitness differences. We found that the combination of accurate

²⁵There is more than just the Palmer pape. Be sure that you are comprehensive in your use of the literaure, include non-ant-plant studies,

partner transitions with partner identity²⁶ 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 (69; 71). 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.

²⁷ 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 (11; 22; 28; 34; 58; 76). Separate studies have analyzed how inter-annual variability impacts focal mutualists (7; 8; 42; 44; 61). The long term dataset we used gave us the unique ability to consider the combined effects of partner identity, partner turnover, and temporal stochasticity.²⁸

This paper has limitations, specifically surrounding the driving forces behind the ant-plant

²⁶Not sure what this means.

²⁷What this all means more broadly?? I'm currently not sure what to do with this. Tom: that's the entire Discussion!

²⁸This is really good. More of this!

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.²⁹

Acknowledgments

This should be drafted.

Data and Code Availability

This should be drafted.

Appendix A: Additional Methods and Parameters

Seeds Per Fruit. With data(55), we fit a model for the number of seeds produced by every fruit on a cholla ($\kappa(a')$) in year $t + 1$ based on the ant partner a' in year $t + 1$. We fit this model to seed data y^κ using a Negative Binomial distribution and the log link function:

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

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

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

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

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

²⁹This feels a little weak and incomplete.

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

Germination. With germination data (51), we fit two models for the probability of germinating from the first year seedbank (γ_1) or the second year seedbank (γ_2) in year $t + 1$, with no fixed or random effects. These models were fit to germination data $y^{\gamma_1}, y^{\gamma_2}$ using the binomial distribution with logit link functions:

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

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

Pre-Census Survival. With recruit census data (55), we fit a model for the probability of a seedling (which germinates in early Fall) surviving to when we census in 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 . We fit this model to pre-census survival data y^δ using a Bernoulli distribution with a logit link function:

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

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

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

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Tables

Figure legends

Supplementary Materials

Herbivory Data

Model Checks

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

Statistical Models – Results

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

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

Seeds Per Flower Model. Each viable flower on a plant produces between 97 and 257 seeds. This number is affected by the ant partner present. *C. opuntiae* tended plants produce a mean of 148 seeds per flower. *L. apiculatum* tended plants produce a mean of 149 seeds per flower.³⁰ Vacant

³⁰These results are not consistent with Ohm and Miller, where *Crem* had lower seeds than *Liom*. I would check this. This section should also reference that paper because these are not new results.

Parameter	Median (95% CI)	Prior Distribution
growth xi intercept vacant 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 β_{01}^v		
viability intercept other β_{02}^v		
viability intercept <i>C. opuntiae</i> β_{03}^v		
viability intercept <i>L. apiculatum</i> β_{04}^v	49	

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

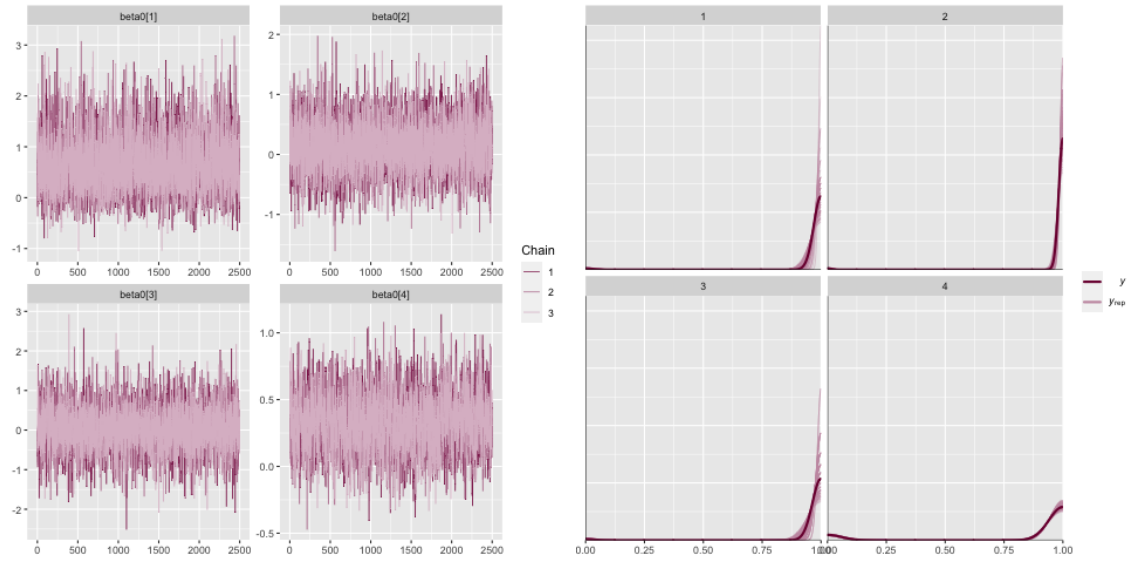


Figure 1: The a) posterior convergence of the parameters estimated by the survival model and the b) posterior distribution of survival estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean survival distribution (black line) of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

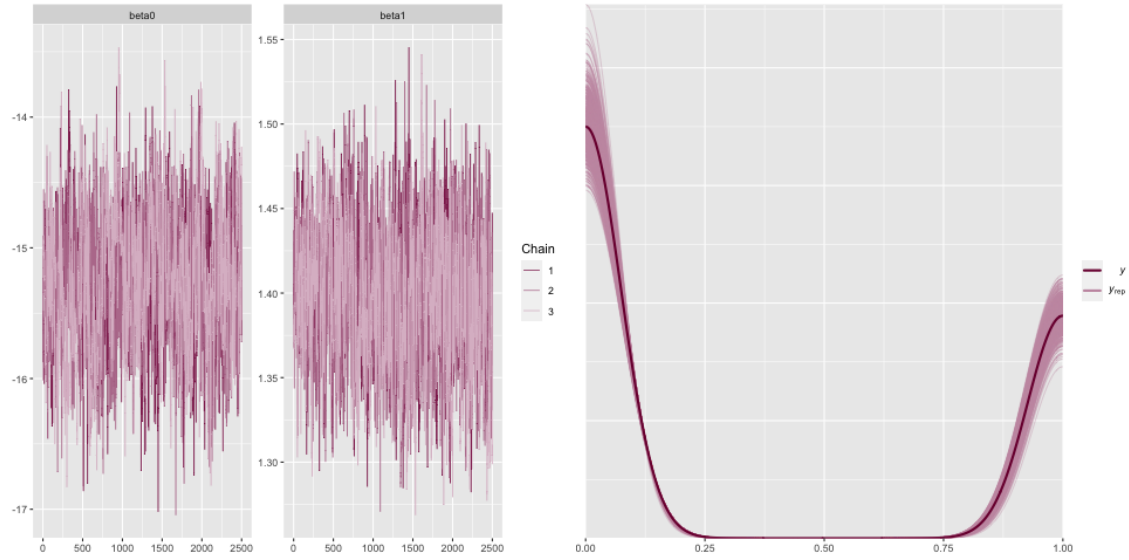


Figure 2: The a) posterior convergence of the parameters estimated by the reproduction model and the b) posterior distribution of reproductive status estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean reproductive status distribution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

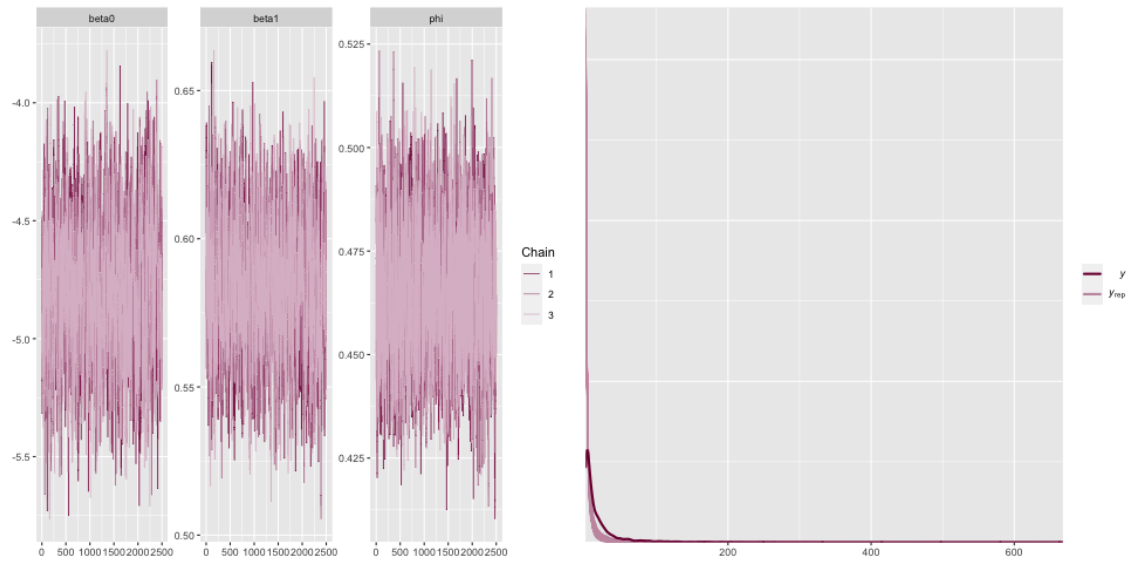


Figure 3: The a) posterior convergence of the parameters estimated by the number of flowers model and the b) posterior distribution of the number of flowers estimated (pink lines) compared to the mean distribution of observed flowers (black line).

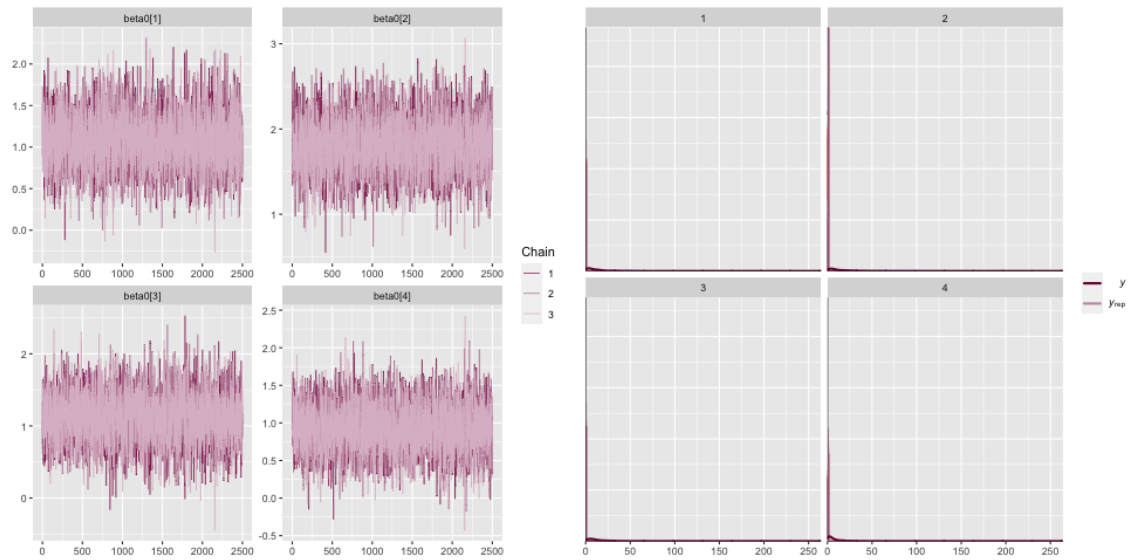


Figure 4: The a) posterior convergence of the parameters estimated by the viability model and the b) posterior distributions of floral viability estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = other, 4 = vacant) compared to the mean floral viability distribution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

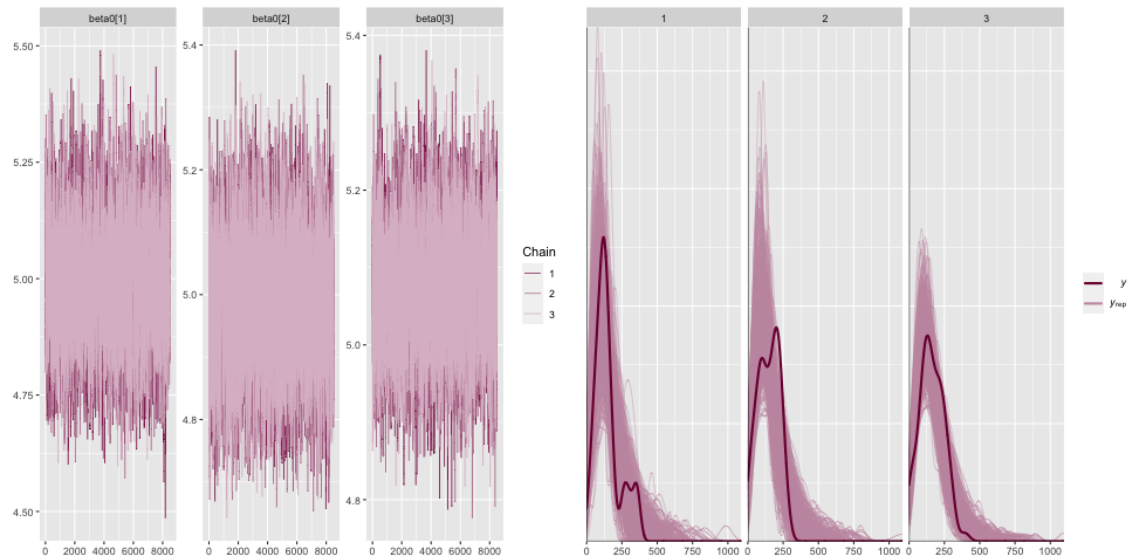


Figure 5: The a) posterior convergence of the parameters estimated by the seeds per fruit model and the b) posterior distributions of seeds per fruit estimates (pink lines) for each ant species (1 = *C. opuntiae*, 2 = *L. apiculatum*, 3 = vacant) compared to the mean seeds per fruit distribution (black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

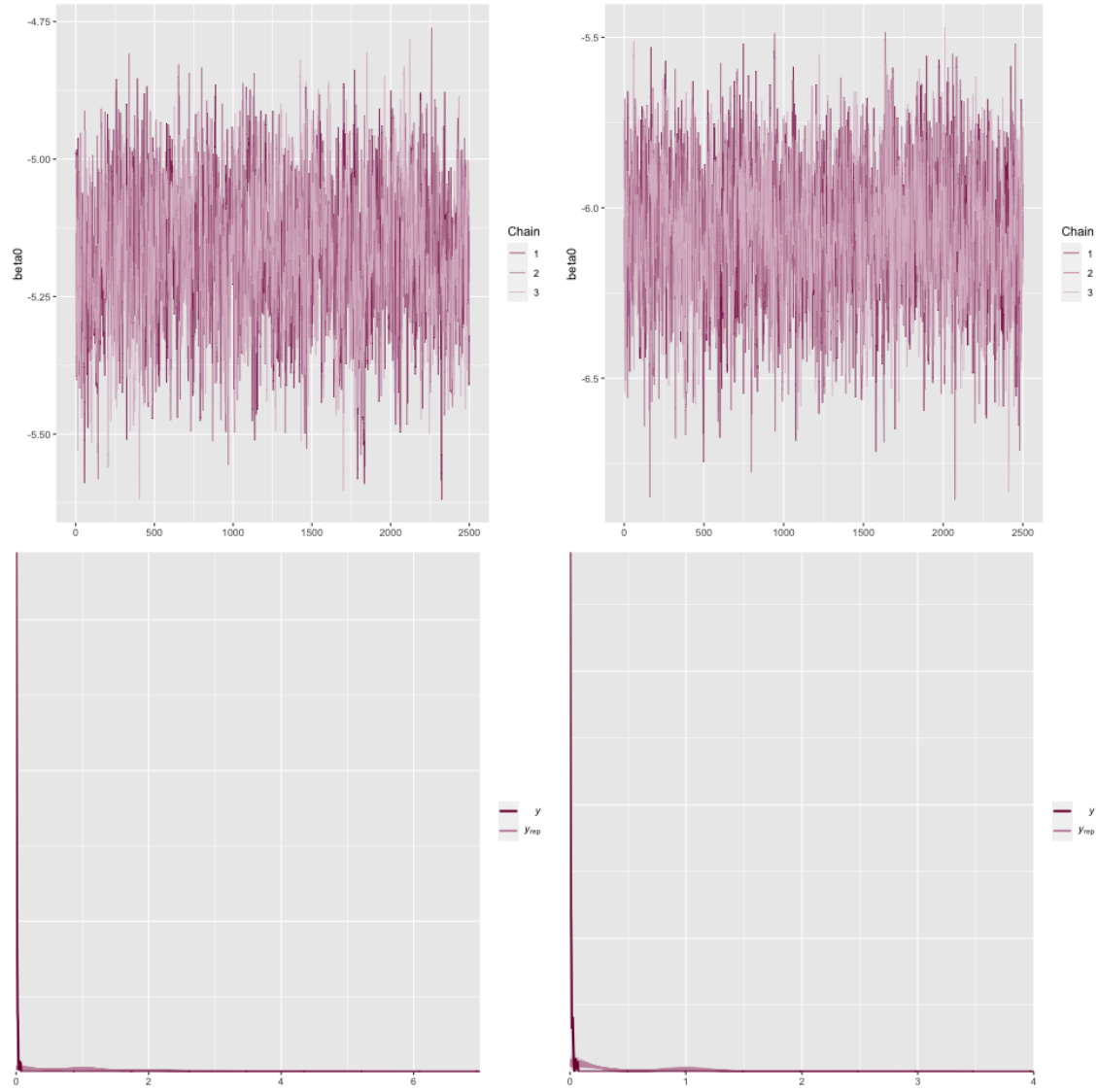


Figure 6: The a-b) posterior convergence of the parameters estimated by the germination from year one seedbank and germination from year two seedbank models respectively. The c-d) posterior distributions of floral viability estimates (pink lines) compared to the mean germination distribution (black line)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

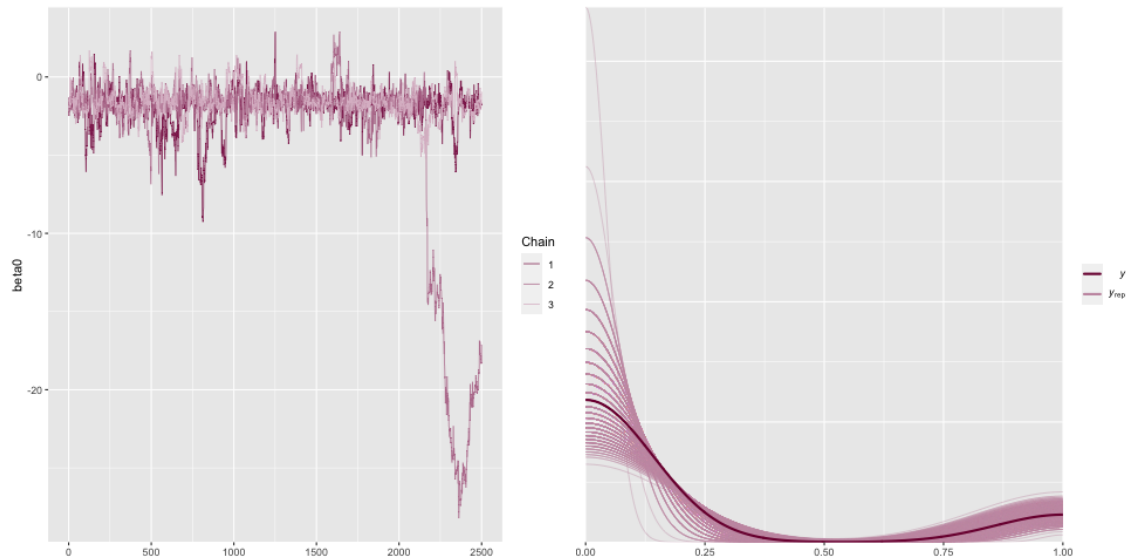


Figure 7: The a) posterior convergence of the parameters estimated by the pre-census survival model and the b) posterior distribution of the pre-census survival estimated (pink lines) compared to the mean distribution of observed pre-census survival (black line).

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

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

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

New recruits are expected to be between the sizes of 0.11 cm^3 and 0.38 cm^3 with a mean size of 0.20 cm^3 .³¹

³¹Move to an appendix. These results are not relevant for the questions at hand.