

Thank you, next: partner turnover elevates benefits of mutualism for an ant-tended plant

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Abstract

Introduction

Mutualisms are species interactions where all participants benefit, leading to higher individual fitness and increased population growth rates. They are among the most widespread species interactions (Bronstein, 1994; Chamberlain et al., 2014; Frederickson, 2013), but can deteriorate into commensalism or parasitism (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.

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; 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). Even 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 (?). Whether and how partner diversity modifies the demographic effects of mutualistic interactions remain open questions within relevance in applied settings such as agriculture (Rogers et al., 2014), restoration (cite), and pest management (cite).

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 (BEF chapter). 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 then partner diversity may impose opportunity costs, leading to negative effects of a diverse mutualist assemblage relative to exclusive association with the 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); ?. For example, [give example]. 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 (cite). Third, partner species can have species-specific responses to the environment, either spatially (Ollerton et al., 2006) or temporally (Alarcón et al., 2008). Multiple partners can therefore act as a 'portfolio' that stabilizes fitness benefits across environmental stochasticity or temporal heterogeneity, leading to positive effects of partner diversity through the portfolio effect Batstone (2018); Lázaro et al. (2022).

Partner diversity can have different effects depending on whether partners are present all at once or sequentially (partner turnover) (Bruna et al., 2014; Djiéto-Lordon et al., 2005; Ness et al., 2006). Sequential associations are likely when alternative partners engage in interference competition for access to a shared mutualist (cite examples, including non-ant-plant examples). 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 (e.g., when sequential partners provide complementary functions) or if they saturate over time (Sachs et al., 2004). Directionality of turnover can also influence diversity effects, particularly if partner identity changes consistently across ontogeny of a focal mutualist (Fonseca et al., 2003). 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 (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). Ant-plant mutualisms are commonly multi-species, where a guild of ant partner species share, and often compete for, a plant mutualist (examples), including dynamic turnover patterns between partners that may differ in quantity and quality of defensive services (cite). While these interactions have been well studied (Beattie, 1985; Ness et al., 2006; Schultheiss et al., 2022), few have considered how diversity within ant defender guilds (Stanton, 2013) or temporal fluctuations in partner interactions (Trøjelsgaard et al., 2015) affect the overall benefits of mutualism for the plant partner.

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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 at the scale of meters, 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 and *Crematogaster opuntiae* actually having net negative fitness effects though deterrence of pollinators (Miller, 2007; Ohm and Miller, 2014). However, those studies did not consider variation in ant defense across the plant life cycle, nor did they account for inter-annual fluctuations, and

¹It is noticeable to anyone who knows this literature that you do not cite Palmer et al. 2010 in this paragraph. I think this paragraph gives a nice intro to ant-plant studies but I think you need a more thorough summary of what is known about effects of partner diversity in these systems (including Palmer), and what outstanding gaps in knowledge this study will fill.

78 therefore may have missed important mechanisms through which different partner species, and
their combination, may be beneficial.

In this study we used a unique long-term data set that allows us to explore mutualistic as-
81 sociations with multiple partner species and how the demographic effects of alternative partner
species varied across the range of plant size structure and nearly 20 years of inter-annual fluc-
tuations. We used this observational data set, contextualized by previous experiments, to ask
84 whether and through which mechanism(s) partner diversity affects the fitness benefits of mutu-
alism for the focal plant partner. Specifically, we asked:

1. What are the demographic effects of association with alternative partners and how do they
87 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
90 this effect?

To answer these questions, we used a 20-year long-term dataset of individual-level demo-
graphic information and ant partner identity and quantity data to track the structure of the
93 population across time as well as individual level impacts of ant partners on the cacti. We used
vital rate functions to evaluate the first two questions. We then used the composite integral pro-
jection model (IPM) to evaluate how vital rate differences affect intrinsic population growth rates
96 and identify mechanisms at play.

Methods

Results

Discussion

Conclusion

Acknowledgments

Data and Code Availability

Appendix A: Additional Methods and Parameters

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Tables

Figure legends