

1 **EFFECT OF MUTUALIST PARTNER IDENTITY ON PLANT DEMOGRAPHY**

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23 **ABSTRACT**

24 Mutualisms play a central role in the origin and maintenance of biodiversity. Because many
25 mutualisms have strong demographic effects, interspecific variation in partner quality could have
26 important consequences for population dynamics. Nevertheless, few studies have quantified how
27 a mutualist partner influences population growth rates, and still fewer have compared the
28 demographic impacts of multiple partner species. We used integral projection models
29 parameterized with three years of census data to compare the demographic effects of two ant
30 species – *Crematogaster laevis* and *Pheidole minutula* – on populations of the Amazonian ant-
31 plant *Maieta guianensis*. Estimated population growth rates were positive (i.e., $\lambda > 1$) for all ant-
32 plant combinations. However, populations with only *Pheidole minutula* had the highest
33 asymptotic growth rate ($\lambda = 1.23$), followed by those colonized by *Crematogaster laevis* ($\lambda = 1.16$),
34 and in which the partner ant alternated between *C. laevis* and *P. minutula* at least once during our
35 study ($\lambda = 1.15$). Our results indicate that the short-term superiority of a mutualist partner – in this
36 system *P. minutula* is a better defender of plants against herbivores than *C. laevis* – can have
37 long-term demographic consequences. Furthermore, the demographic effects of switching among
38 alternative partners appear to be context-dependent, with no benefits to plants hosting *C. laevis*
39 but a major cost of switching to plants hosting *P. minutula*. Our results underscore the
40 importance of expanding the study of mutualisms beyond the study of pair-wise interactions to
41 consider the demographic costs and benefits of interacting with different, and multiple, potential
42 partners.

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44 **Key words:** *Azteca*, *Crematogaster*, Integral projection model, lambda, Life-table response
45 experiment, *Maieta*

INTRODUCTION

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Mutualisms play a central role in the origin and maintenance of biological diversity (Boucher 1985, Bronstein 1994, Aslan et al. 2013). Plants can be involved in several categories of mutualisms over the course of their life, including pollination, seed dispersal, and nutritional symbioses. In all of these mutualisms plants typically interact with multiple partner species (Stanton 2003), which can differ significantly in the quality of services they provide (Schemske and Horvitz 1984, Hoeksema et al. 2010, Schupp et al. 2010). Since many mutualisms exert strong effects on demographic processes such as growth, survivorship, and reproduction (e.g., Janzen 1966, Vasconcelos 1991), it has been posited that interspecific variation in partner quality could have important consequences for plant population dynamics (reviewed in Stanton 2003). However, few empirical studies have quantified the way in which a mutualist partner species influences plant population growth rates (sensu Geib and Galen 2012); still more rare are those that compare the demographic benefits provided by multiple partner species (but see Loayza and Knight 2010, Palmer et al. 2010, Ohm and Miller 2014). Without such comparisons, a general understanding of the evolution and maintenance of mutualist interactions, including the emergence of cheaters, will continue to prove elusive (Stanton 2003).

Myrmecophytic plants have emerged as model systems with which to evaluate how mutualist partner identity influences plant demography (Yu et al. 2001, Frederickson and Gordon 2009, Palmer et al. 2010). Hundreds of tropical plant species have specialized structures such as swollen thorns or hollow stems, known as domatia, in which ant species establish colonies (Benson 1985). The resident ant species are typically obligate mutualists that defend their host-plants from herbivores; the loss of ant partners can lead to severe defoliation, reduced fruit production, and host-plant mortality (reviewed in Heil and McKey 2003). Although individuals

69 of some myrmecophytic plant species can be occupied simultaneously by multiple ant species
70 (e.g., Trager and Bruna 2006), many are occupied by a colony of a single ant species at a time
71 (Vasconcelos and Davidson 2000, Palmer et al. 2010). Experimental work has demonstrated that
72 these different ant species can vary substantially in their defense of plants, resulting in
73 differential rates of plant growth, reproduction, and survivorship (e.g., Bruna et al. 2004,
74 Frederickson 2005, Stanton and Palmer 2011). While these studies are mostly short-term in
75 nature, they suggest there could be demographic consequences to long-term colonization by less
76 effective mutualists.

77 We used demographic models parameterized with multi-year census data to isolate and
78 compare the effects of individual mutualist partners on plant population growth rates. Our focal
79 system was the Amazonian ant-plant *Maieta guianensis* (Melastomataceae), which has
80 specialized leaf domatia in which the ant species *Crematogaster laevis* and *Pheidole minutula*
81 establish colonies (described in Vasconcelos 1993, Vasconcelos and Davidson 2000). Prior work
82 indicates plants inhabited by *Crematogaster laevis* are much smaller than those inhabited by
83 *Pheidole minutula* (Vasconcelos and Davidson 2000), presumably because *C. laevis* is an
84 inferior defender of plants against herbivores (Lapola et al. 2003), or tends four-fold more
85 herbivorous trophobionts in domatia than *P. minutula* does (Lapola et al. 2005). Plants inhabited
86 by *C. laevis* also have greater rates of colony loss than those colonized by *P. minutula*, and plants
87 without colonies are often severely defoliated and have lower survival (Vasconcelos and
88 Davidson 2000). Our hypothesis was therefore that the rate of population growth (i.e., λ) would
89 be highest for populations of plants colonized by *P. minutula* and lowest for those colonized by
90 *C. laevis*. Populations in which individuals alternated partners between *C. laevis* and *P. minutula*
91 should have intermediate values of λ .

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MATERIALS AND METHODS

Study site and system

95 Field work was conducted from January 2006 to January 2009 in Reserve 1501 of the
96 Biological Dynamics of Forest Fragments Project (BDFFP; 2°30' S, 60° W). The habitat is non-
97 flooded primary lowland forest with a 30- 35 m tall canopy and an understory dominated by
98 stemless palms. Annual rainfall ranges from 1,900-3,500 mm, with a pronounced dry season
99 from June-October (Bierregaard et al. 2002).

100 *Maieta guianensis* (Melastomataceae) is an understory shrub that grows to a height of 1.5
101 m (Vasconcelos 1993, Vasconcelos and Davidson 2000). It has highly dimorphic paired leaves
102 with a pair of foliar pouches at the base of the larger leaves in which ants nest. Seedlings can
103 harbor more than one incipient (i.e., non-reproductive) colony, however adult plants house a
104 single colony of only one species (Izzo et al. 2009, Bruna et al. 2011a). In addition to scavenging
105 for insects on the leaf surface, resident ants tend coccids for honeydew inside domatia
106 (Vasconcelos 1991, Lapola et al. 2005).

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Sampling design and data collection

109 In January 2006 we used the trail system that bisects Reserve 1501 to find 10 gaps in the
110 upland plateaus and 10 gaps adjacent to streams. We measured the length and width of each of
111 these gaps, calculated the area of each gap with the formula for an ellipse, and used these
112 measurements to mark an area of comparable size in adjacent closed canopy forest. Gap and
113 paired closed canopy sites (hereafter, plots) were separated by ~50 m (Forest plots: $405.11 \text{ m}^2 \pm$
114 150.48 SD , Gap plots: $514.05 \text{ m}^2 \pm 188.90 \text{ SD}$). We then surveyed each plot and marked all

115 *Maieta guianensis* with a permanent tag. We recorded the identity of any ant occupants and
 116 measured the size of each plant by counting the number of domatia and branches each plant had.
 117 These two proxies of plant size are highly correlated (results not shown); we therefore use
 118 domatia number as the unit of plant size because it is directly related to ant colony size. The plots
 119 were censused at 6 month intervals, at which time we recorded whether marked plants had died,
 120 the size of surviving plants, and the identity of ant residents. We also marked and measured any
 121 newly established seedlings. In the fourth, fifth, and sixth censuses we quantified plant
 122 reproductive effort by counting the number of fruits or flowers on each plant.

123 124 *Demographic modeling and analysis*

125 To test our hypothesis we used the demographic survey data to build integral projection
 126 models. In contrast to matrix-based demographic models (Caswell 2001), integral projection
 127 models (IPM, Easterling et al. 2000, Ellner and Rees 2006) do not require that individuals be
 128 assigned to discrete size or stage classes. Instead, they use continuous functions to describe size-
 129 dependent growth, survivorship, and fecundity (Coulson 2012, Merow et al. 2013). Our IPM
 130 describes the change in population size (n) over the course of six intervals of six months each.

131 Our full model takes the form:
$$n(y, t + 1) = \int_L^U [p(x, y) + f(x, y)]n(x, t)dx$$
. The $p(x, y)$ kernel
 132 represents transitions of an individual of size x to size y attributable to survival, s , and growth, g ,
 133 $p(x, y) = s(x)g(x, y)$. The $f(x, y)$ kernel describes per-capita production of y sized individuals in
 134 the next census by reproductive individuals of size x (i.e., the recruit density function at the next
 135 census), $f(x, y) = s(x)f_n(x)p_E f_d(y)$. Here $s(x)$ is again size-specific survival, $f_n(x)$ is the number
 136 of fruits or flowers produced by a plant of size x , p_E is a constant for the number of seedlings

137 resulting per fruit, and $f_d(y)$ is the size distribution of seedlings. The growth, survival, and
138 fertility functions are obtained from statistical models of the census data (described below). To
139 test our hypothesis we constructed IPMs for three hypothetical populations: one pooling plants
140 that were occupied solely by *P. minutula* over the course of all six surveys, one for plants
141 occupied solely by *C. laevis*, and one for plants occupied in every survey but whose resident ant
142 partner changed at least once. Because the low densities of some ant-plant combinations in some
143 plots made determining plot-specific demographic functions impossible, we pooled plants from
144 all plots to conduct our analyses; a landscape-scale analysis such as this is equivalent to
145 constructing ‘summary matrices’ in matrix models (sensu Horvitz and Schemske 1995, Caswell
146 2001) to correct for the disproportionate weight that low sample sizes can give to some transition
147 probabilities (e.g., Bruna 2003). Because we had insufficient data to build a robust stochastic
148 model, we also pooled data across all years of our study to represent a single average time step
149 (sensu Miller et al. 2009). Models were built and analyzed with the IPMpack (Metcalf et al.
150 2013) and popbio (Stubben and Milligan 2007) packages for R (R Core Development Team
151 2014).

152 IPM functions were fit using the natural logarithm of domatia number as the size
153 variable. We first calculated alternative statistical relationships for growth, survivorship, and
154 fecundity as functions of plant size (Table 1), then used model selection methods based on the
155 Akaike Information Criterion (AIC) to determine which provided the best fit to the data. Because
156 individual *M. guianensis* fruits have thousands of dust-like seeds, we were unable to count
157 accurately the number of seeds per fruit or estimate seed germination rates. Instead we estimated
158 the proportion of fruits becoming seedlings (p_E) by counting the number of newly established
159 seedlings we counted during the surveys, dividing this number by the number of fruits produced

160 by all plants in the previous reproductive season (all seasons pooled). This constant was used in
161 all IPMs because there is no reason to believe that ant identity of the maternal plants influences
162 the germination success of host-plant seeds.

163 After initial analyses we were concerned that the very small number of seedlings in our
164 study plots that were colonized by *Crematogaster laevis* was leading to inaccurate demographic
165 functions for survivorship. To increase the number of seedlings in our demographic dataset, we
166 complemented our survey data with data from an experiment investigating the colonization rates
167 of *M. guianensis* seedlings by queens of *P. minutula* and *C. laevis* (Bruna et al. 2011a). This
168 study was conducted contemporaneously (2007) and the closest demographic plots were less
169 than a kilometer away. The study provided data on how survivorship of *M. guianensis* seedlings
170 over 90 days was influenced by the identity of ant occupant (Bruna et al. 2011b).

171 Each IPM was used to calculate lambda by discretizing the kernel using the midpoint rule
172 with 50 mesh points. The upper limit for each integration was based on the maximum size of
173 plants in the populations being modeled, and the lower limit was constant for all populations. We
174 also calculated the bias-corrected 95% confidence intervals for each estimate of lambda by
175 bootstrapping (n = 1000 simulations) and used randomization tests (n = 1000 permutations) to
176 determine if estimates of λ for populations with different ant partners were significantly different
177 from each other (Caswell 2001).

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179 *Life-table response experiments*

180 To elucidate the demographic mechanisms underlying differences among populations we
181 used Life Table Response Experiments (LTRE), which decompose differences in λ into the

182 contributions from different demographic variables (Caswell 1989). We used a fixed-design
 183 LTRE (Caswell 2001), in which the difference in λ between two treatments, $\Delta\lambda$, is given by:

$$184 \quad \Delta\lambda = \lambda^{(t)} - \lambda^{(c)} \approx \sum_{ij} (a_{ij}^{(t)} - a_{ij}^{(c)}) \times \left(\frac{\partial\lambda}{\partial a_{ij}} \right) \bigg|_{\frac{(\mathbf{A}^{(t)} + \mathbf{A}^{(c)})}{2}}, \text{ where } (a_{ij}^{(t)} - a_{ij}^{(c)}) \text{ is the difference in } a_{ij}$$

185 between the two matrices, and $\partial\lambda / \partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} evaluated at the
 186 average of $a_{ij}^{(1)}$ and $a_{ij}^{(2)}$. Close correspondence between values of $\Delta\lambda$ and LTRE contributions
 187 indicates the suitability of the LTRE models.

188 189 RESULTS

190 We sampled 706 *Maieta guianensis* plants over the course of our study. Plant density was
 191 significantly greater in lowlands than plateaus, although there was no difference between gaps
 192 and adjacent areas of forest within a canopy-cover type (Appendix A). Because we were
 193 attempting to isolate the effect of ant identity on plant demography, we excluded 208 plants that
 194 had no ant resident in one or more of the surveys (the effect of how long plants remain without
 195 ant partners on demography is the subject of future manuscript). Of the remaining 498 plants, 42
 196 were colonized throughout solely by *Crematogaster laevis* and 398 were colonized exclusively
 197 by *Pheidole minutula*. We had 58 plants that were colonized in every survey but switched ant
 198 partners at least once (i.e, the ant resident was different in subsequent surveys). Most of these
 199 plants (74%) had only one change in resident ant species over the course of our study (single
 200 change: N=43; two changes: N=12; three changes, N=3).

201 Plant size at a survey depended on size in the previous survey, with a linear function
 202 providing the best fit to the ln-transformed size data (Appendix B, Fig. 1). The growth functions,

203 $g(x,y)$, for plants occupied by the different ant species were not significantly different. The
204 probability of individual survival, $s(x)$, increased with plant size (Fig. 1). Overall plant survival
205 was high (98%), but the smallest plants had a higher risk of mortality when colonized by *C.*
206 *laevis* (Fig. 1F) or alternating partners (Fig. 1J), than when colonized by *P. minutula*. Both the
207 likelihood of flowering and per-individual fruit production were also size-dependent (Fig. 1).
208 However, very few plants colonized by *C. laevis* reproduced (Fig. 1G), and those that did were
209 generally plants in size classes that produced few fruits (Fig. 1H). When plants colonized by *C.*
210 *laevis* or by alternating partners did reproduce, they produce far fewer fruits than comparably
211 sized plants colonized by *P. minutula* (Fig. 1D, 1H, 1L).

212 Asymptotic rates of population growth were positive (i.e., $\lambda > 1$) for all three hypothetical
213 *Maieta guianensis* populations (Table 1). However, the population associated with *P. minutula*
214 had the highest growth rate ($\lambda = 1.23$), followed by *C. laevis* ($\lambda = 1.16$) and the population made up
215 of plants that at some point in our survey alternated between partner species ($\lambda = 1.15$).
216 Randomization tests indicated λ of populations always colonized by *P. minutula* was
217 significantly greater than that of populations colonized by either *C. laevis* ($P = 0.04$) or switching
218 partners ($P = 0.03$). There was no significant difference in the λ values of populations always
219 colonized by *C. laevis* and those switching partners ($P = 0.26$).

220 Our LTRE analysis revealed similar demographic mechanisms were responsible for the
221 differences in λ between all three comparisons (*P. minutula* vs. *C. laevis*, *P. minutula* vs. partner
222 switching, and *C. laevis* vs. partner switching; Appendix C). For instance, differences in λ
223 between populations associated with *P. minutula* and those colonized by *C. laevis* were due
224 primarily to reduced stasis by intermediate to larger plants colonized by *C. laevis* (Appendix C).

225 The negative contributions to $\Delta\lambda$ along the principal diagonal, representing stasis in the largest
226 (and reproductive) size classes far outweighed the positive ones from other regions of the matrix.

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DISCUSSION

229 Despite an increasingly robust theoretical literature exploring how variation among
230 mutualists in the benefits they provide influences the population dynamics of partners (Boucher
231 1985, Hoeksema and Bruna 2000, Holland et al. 2002, Ohm and Miller 2014), few empirical
232 studies address this topic. We found that associations with different mutualist partners resulted in
233 different population growth rates for an Amazonian host plant. Although all projections of λ
234 were greater than one, λ was significantly greater for plants associated with one of the ant species
235 than with the other. Furthermore, plants that switched partners during our study had net benefits
236 similar to those of always associating with the poorer mutualist partner, as opposed to an
237 intermediate value as predicted by Stanton (2003). Because we used deterministic models,
238 caution must be taken not to assume our results would be identical had we conducted our study
239 in different years (Caswell 2001), and additional survey data would allow us to estimate
240 temporal stochasticity in λ . Nevertheless, our results underscore the importance of expanding the
241 study of mutualisms beyond the “pair-wise perspective” (sensu Stanton 2003) to consider the
242 costs and benefits of interacting with different putative partners. Considering the long-term
243 demographic consequences of these costs and benefits will greatly enhance our ability to
244 generalize about how mutualisms evolve and persist (Bruna et al. 2008, Palmer et al. 2010).

245 What are the demographic mechanisms underlying the lower growth rates of populations
246 housing *C. laevis* or switching partners? Life-table response experiments indicate that the
247 differences in λ are due primarily to differences in the probability of growing into or remaining

248 in large size classes (Appendix C), which are those that are most likely to reproduce and produce
249 the most fruit when they do (Fig. 1). These results are consistent with those of short-term
250 experiments and previous observations. Plants with *C. laevis* are smaller than those with *P.*
251 *minutula* (Vasconcelos and Davidson 2000), and *C. laevis* respond more slowly and at lower
252 intensity to cues associated with herbivory (Lapola et al. 2003). They also house more
253 trophobionts inside domatia (Lapola et al. 2005), which at high densities could conceivably
254 reduce the growth of plants (Heil and McKey 2003). Finally, experimental removal of ants from
255 *M. guianensis* greatly increased herbivory and reduced fruit set (Vasconcelos 1991), which is
256 consistent with results from sympatric and closely related systems (Bruna et al. 2004). Although
257 recent meta-analyses have argued that herbivore damage is not a reliable surrogate for fitness
258 consequences of ant-protection (Trager et al. 2010), our results suggest that differences among
259 ant species in the costs and benefits they provide – even small ones – can indeed interact in
260 subtle ways that affect λ .

261 Finally, we provide some of the first demographic evidence to date that associating with
262 multiple partners reduces the net benefits to host plants. While prior simulation studies have
263 provided support for this idea (Bronstein et al. 2003, Miller 2007), the most comprehensive
264 empirical work to date has found the opposite to be true. Palmer et al. (2010) found that for
265 African *Acacia drepanolobium* trees λ was lower for hypothetical populations interacting with
266 only one ant partner than for populations successively colonized by four different ant species,
267 even though one ant species is a sterilization parasite that inhibits reproduction and another
268 reduces tree survivorship. They argued that this counter-intuitive effect is due to tradeoffs
269 between survivorship and fecundity at different stages of the tree life-cycle facilitated by the
270 different life-spans of the trees and their partners. Our results suggest the extent to which

271 multiple sequential partners are detrimental or beneficial in ant-plant mutualisms varies among
272 ant-plant systems. In our study system there is no sterilizing ant partner that enhances plant
273 growth at the expense of reproduction; mutualists that sterilize a partner species have garnered
274 considerable interest (e.g., Izzo and Vasconcelos 2002, Frederickson 2009) but appear rare
275 among ant-plant mutualisms. Indeed, there is no *a priori* reason to expect that the effects of
276 temporal changes in partner identity should be inherently beneficial or detrimental. Instead,
277 Jensen's Inequality (Karban et al. 1997, Inouye 2005) predicts that the mean benefits will depend
278 on the functional form of the relationship between frequency of partner identity and λ , and this
279 relationship is likely to vary among plant species as the number and quality of mutualist partners
280 changes.

281 We used an estimated constant for the number of seedlings resulting from each fruit.
282 While an over- or underestimate of this value could influence our projections of lambda, there is
283 no reason to expect that the recruitment rate varies with the maternal plant's ant symbiont, and
284 hence the relative rankings of lambda for plants colonized by each species are likely to be similar
285 in good and bad recruitment years. It is also important to note that *Maieta guianensis* is more
286 common in gaps (Appendix A) and that the dynamics of ant-plant associations can vary as a
287 function of both local myrmecophyte density and habitat type (Schupp and Feener 1991,
288 Vasconcelos 1993, Yu and Davidson 1997, Nery and Vasconcelos 2003, Bruna et al. 2011a).
289 Because such variation could alter key demographic vital rates (e.g., plant growth or
290 reproduction could be greater in gaps, the likelihood of colonization by *P. minutula* could be
291 density-dependent), it could influence the population dynamics of both ants and plants at the
292 landscape scale – an issue we are addressing in a subsequent paper. Finally, our study included
293 only plants that were colonized in every survey. Partner switching necessarily means plants

294 were temporarily vacant, and though we have previously shown colonization of vacant *M.*
295 *guianensis* can be extremely fast (Bruna et al. 2011a), some plants in our survey were vacant for
296 more extended time periods. While we focused our analyses on the effects of partner identity
297 rather than partner loss, subsequent work will address the demographic costs of partner loss and
298 the length of time plants remain without the benefits of the services they provide – another
299 important but little explored factor influencing the origin and maintenance of interspecific
300 mutualisms.

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LITERATURE CITED

308

309 Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption threatens
310 global plant biodiversity: a systematic review. *Plos One* **8**.

311 Benson, W. W. 1985. Amazon ant-plants. Pages 239-266 in G. T. Prance and T. E. Lovejoy,
312 editors. *Amazonia*. Pergamon Press, New York.

313 Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2002. Lessons from
314 Amazonia: the ecology and conservation of a fragmented forest. Yale University Press,
315 New Haven.

316 Boucher, D. H., editor. 1985. *The biology of mutualism*. Oxford University Press, New York.

317 Bronstein, J. L. 1994. Our current understanding of mutualism. *Quarterly Review of Biology*
318 **69**:31-51.

319 Bronstein, J. L., W. G. Wilson, and W. E. Morris. 2003. Ecological dynamics of
320 mutualist/antagonist communities. *American Naturalist* **162**:S24-S39.

321 Bruna, E. M. 2003. Are plants in rain forest fragments recruitment limited? Tests with an
322 Amazonian herb. *Ecology* **84**:932-947.

323 Bruna, E. M., M. R. Darrigo, A. M. F. Pacheco, and H. L. Vasconcelos. 2008. Interspecific
324 variation in the defensive responses of ant mutualists to plant volatiles. *Biological Journal*
325 *of the Linnean Society* **94**:241-249.

326 Bruna, E. M., T. J. Izzo, B. D. Inouye, M. Uriarte, and H. L. Vasconcelos. 2011a. Asymmetric
327 dispersal and colonization success of Amazonian plant-ants queens. *Plos One* **6**:e22937.

328 Bruna, E. M., T. J. Izzo, B. D. Inouye, M. Uriarte, and H. L. Vasconcelos. 2011b. Data from:
329 Asymmetric dispersal and colonization success of Amazonian plant-ants queens. . Dryad
330 Digital Repository. doi:10.5061/dryad.h6t7g.

- 331 Bruna, E. M., D. M. Lapola, and H. L. Vasconcelos. 2004. Interspecific variation in the
332 defensive responses of obligate plant-ants: experimental tests and consequences for
333 herbivory. *Oecologia* **138**:558-565.
- 334 Caswell, H. 1989. Analysis of life table response experiments 1: Decomposition of effects on
335 population growth rate. *Ecological Modelling* **46**:221-237.
- 336 Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer
337 Associates, Sunderland.
- 338 Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in
339 ecology. *Oikos* **121**:1337-1350.
- 340 Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new
341 structured population model. *Ecology* **81**:694-708.
- 342 Ellner, S. P., and M. Rees. 2006. Integral projection models for species with complex
343 demography. *American Naturalist* **167**:410-428.
- 344 Frederickson, M. E. 2005. Ant species confer different partner benefits on two Neotropical
345 myrmecophytes. *Oecologia* **143**:387-395.
- 346 Frederickson, M. E. 2009. Conflict over Reproduction in an Ant-Plant Symbiosis: Why
347 *Allomerus octoarticulatus* Ants Sterilize *Cordia nodosa* Trees. *American Naturalist*
348 **173**:675-681.
- 349 Frederickson, M. E., and D. M. Gordon. 2009. The intertwined population biology of two
350 Amazonian myrmecophytes and their symbiotic ants. *Ecology* **90**:1595-1607.
- 351 Geib, J. C., and C. Galen. 2012. Tracing impacts of partner abundance in facultative pollination
352 mutualisms: from individuals to populations. *Ecology* **93**:1581-1592.

- 353 Heil, M., and D. McKey. 2003. Protective ant-plant interactions as model systems in ecological
354 and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics*
355 **34**:425-453.
- 356 Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A.
357 Pringle, C. Zabinski, J. D. Bever, J. C. Moore, G. W. T. Wilson, J. N. Klironomos, and J.
358 Umbanhowar. 2010. A meta-analysis of context-dependency in plant response to
359 inoculation with mycorrhizal fungi. *Ecology Letters* **13**:394-407.
- 360 Hoeksema, J. H., and E. M. Bruna. 2000. Pursuing the big questions about interspecific
361 mutualisms: a review of theoretical approaches. *Oecologia* **125**:321-330.
- 362 Holland, J. N., D. L. DeAngelis, and J. L. Bronstein. 2002. Population dynamics and mutualism:
363 Functional responses of benefits and costs. *American Naturalist* **159**:231-244.
- 364 Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions
365 of a tropical understory herb: Projection matrix analysis. *Ecological Monographs* **65**:155-
366 192.
- 367 Inouye, B. D. 2005. The importance of the variance around the mean effect size of ecological
368 processes: Comment. *Ecology* **86**:262-265.
- 369 Izzo, T., and H. L. Vasconcelos. 2002. Cheating the cheater: domatia loss minimizes the effects
370 of ant castration in an Amazonian ant-plant. *Oecologia* **133**:200-205.
- 371 Izzo, T. J., E. M. Bruna, H. L. Vasconcelos, and B. D. Inouye. 2009. Cooperative colony
372 founding alters the outcome of interspecific competition between Amazonian plant-ants.
373 *Insectes Sociaux* **56**:341-345.
- 374 Janzen, D. H. 1966. Coevolution of a mutualisms between ants and Acacias in Central America.
375 *Evolution* **20**:249-275.

- 376 Karban, R., A. A. Agrawal, and M. Mangel. 1997. The benefits of induced defenses against
377 herbivores. *Ecology* **78**:1351-1355.
- 378 Lapola, D. M., E. M. Bruna, C. G. de Willink, and H. L. Vasconcelos. 2005. Ant-tended
379 hemiptera in Amazonian myrmecophytes: patterns of abundance and implications for
380 mutualism function. *Sociobiology* **46**:433-442.
- 381 Lapola, D. M., E. M. Bruna, and H. L. Vasconcelos. 2003. Contrasting responses to induction
382 cues by ants inhabiting *Maieta guianensis* (Melastomataceae). *Biotropica* **35**:295-300.
- 383 Loayza, A. P., and T. Knight. 2010. Seed dispersal by pulp consumers, not "legitimate" seed
384 dispersers, increases *Guettarda viburnoides* population growth. *Ecology* **91**:2684-2695.
- 385 Merow, C., J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. K. Evans, E. Jongejans, S.
386 Record, M. Rees, R. Salguero-Gómez, and S. M. McMahon. 2013. Advancing population
387 ecology with integral projection models: a practical guide. *Methods in Ecology and*
388 *Evolution*:n/a-n/a.
- 389 Metcalf, C. J. E., S. M. McMahon, R. Salguero-Gomez, and E. Jongejans. 2013. IPMPack: an R
390 package for integral projection models. *Methods in Ecology and Evolution* **4**:195-200.
- 391 Miller, T. E. X. 2007. Does having multiple partners weaken the benefits of facultative
392 mutualism? A test with cacti and cactus-tending ants. *Oikos* **116**:500-512.
- 393 Miller, T. E. X., S. M. Louda, K. A. Rose, and J. O. Eckberg. 2009. Impacts of insect herbivory
394 on cactus population dynamics: experimental demography across an environmental
395 gradient. *Ecological Monographs* **79**:155-172.
- 396 Nery, A. S., and H. L. Vasconcelos. 2003. Growth and survival of incipient ant-colonies in two
397 Amazonian ant-plants: effects of host plant, habitat, and mode of colony founding
398 (Hymenoptera: Formicidae). *Sociobiology* **42**:151-162.

- 399 Ohm, J. R., and T. E. X. Miller. 2014. Balancing anti-herbivore benefits and anti-pollinator costs
400 of defensive mutualists. *Ecology*.
- 401 Palmer, T. M., D. F. Doak, M. L. Stanton, J. L. Bronstein, E. T. Kiers, T. P. Young, J. R.
402 Goheen, and R. M. Pringle. 2010. Synergy of multiple partners, including freeloaders,
403 increases host fitness in a multispecies mutualism. *Proceedings of the National Academy
404 of Sciences of the United States of America* **107**:17234-17239.
- 405 R Core Development Team. 2014. R: A language and environment for statistical computing. *in* R
406 Foundation for Statistical Computing, editor., Vienna, Austria.
- 407 Schemske, D. W., and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability:
408 a precondition for mutualism specialization. *Science* **225**:519-521.
- 409 Schupp, E. W., and D. H. Feener. 1991. Phylogeny, lifeform, and habitat dependence of ant-
410 defended plants in a Panamanian forest. Pages 175-197 *in* C. R. Huxley and D. F. Cutler,
411 editors. *Ant-plant interactions*. . Oxford Univ. Press, Oxford.
- 412 Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a
413 conceptual review. *New Phytologist* **188**:333-353.
- 414 Stanton, M. L. 2003. Interacting guilds: Moving beyond the pairwise perspective on mutualisms.
415 *American Naturalist* **162**:S10-S23.
- 416 Stanton, M. L., and T. M. Palmer. 2011. The high cost of mutualism: effects of four species of
417 East African ant symbionts on their myrmecophyte host tree. *Ecology* **92**:1073-1082.
- 418 Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the
419 popbio package in R. *Journal of Statistical Software* **22**:1-23.

- 420 Trager, M. D., S. Bhotika, J. A. Hostetler, G. V. Andrade, M. A. Rodriguez-Cabal, C. S.
421 McKeon, C. W. Osenberg, and B. M. Bolker. 2010. Benefits for plants in ant-plant
422 protective mutualisms: A meta-analysis. *Plos One* **5**:e14308.
- 423 Trager, M. D., and E. M. Bruna. 2006. Effects of plant age, experimental nutrient addition and
424 ant occupancy on herbivory in a neotropical myrmecophyte. *Journal of Ecology* **94**:1156-
425 1163.
- 426 Vasconcelos, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmecophytic
427 melastome, and one of its ant inhabitants: ant protection against insect herbivores.
428 *Oecologia* **87**:295-298.
- 429 Vasconcelos, H. L. 1993. Ant colonization of *Maieta guianensis* seedlings, an Amazon ant-plant.
430 *Oecologia* **95**:439-443.
- 431 Vasconcelos, H. L., and D. W. Davidson. 2000. Relationship between plant size and ant
432 associates in two Amazonian ant-plants. *Biotropica* **32**:100-111.
- 433 Yu, D. W., and D. W. Davidson. 1997. Experimental studies of species-specificity in Cecropia-
434 ant relationships. *Ecological Monographs* **67**:273-294.
- 435 Yu, D. W., H. B. Wilson, and N. E. Pierce. 2001. An empirical model of species coexistence in a
436 spatially structured environment. *Ecology* **82**:1761-1771.

437

Table 1. Asymptotic growth rates (λ) and 95% confidence intervals of hypothetical *Maieta guianensis* populations with different mutualist ant partners.

Mutualist partner	λ (95% Confidence Intervals)
Always occupied by <i>Pheidole minutula</i>	1.23 (1.21-1.25)
Always occupied by <i>Crematogaster laevis</i>	1.16 (1.04-1.24)
Occupied every survey; partner changed at least once	1.15 (1.008-1.21)

FIGURE LEGENDS

Figure 1. Size dependent growth, survivorship, flowering, and fruit production of plants occupied continuously by *Pheidole minutula* during our study, continuously by *Crematogaster laevis* during our study, or switching partners at least once during our demographic surveys.

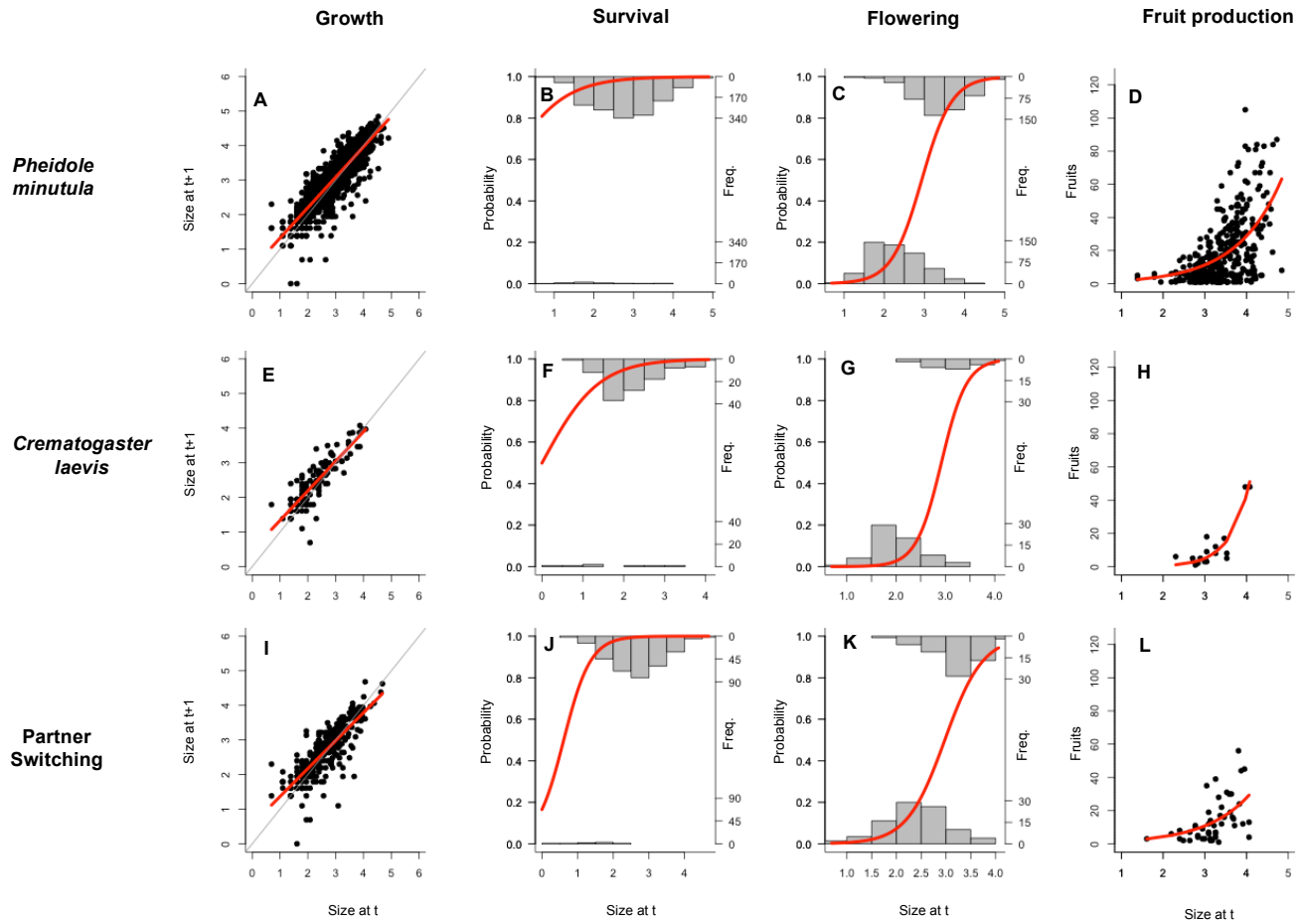
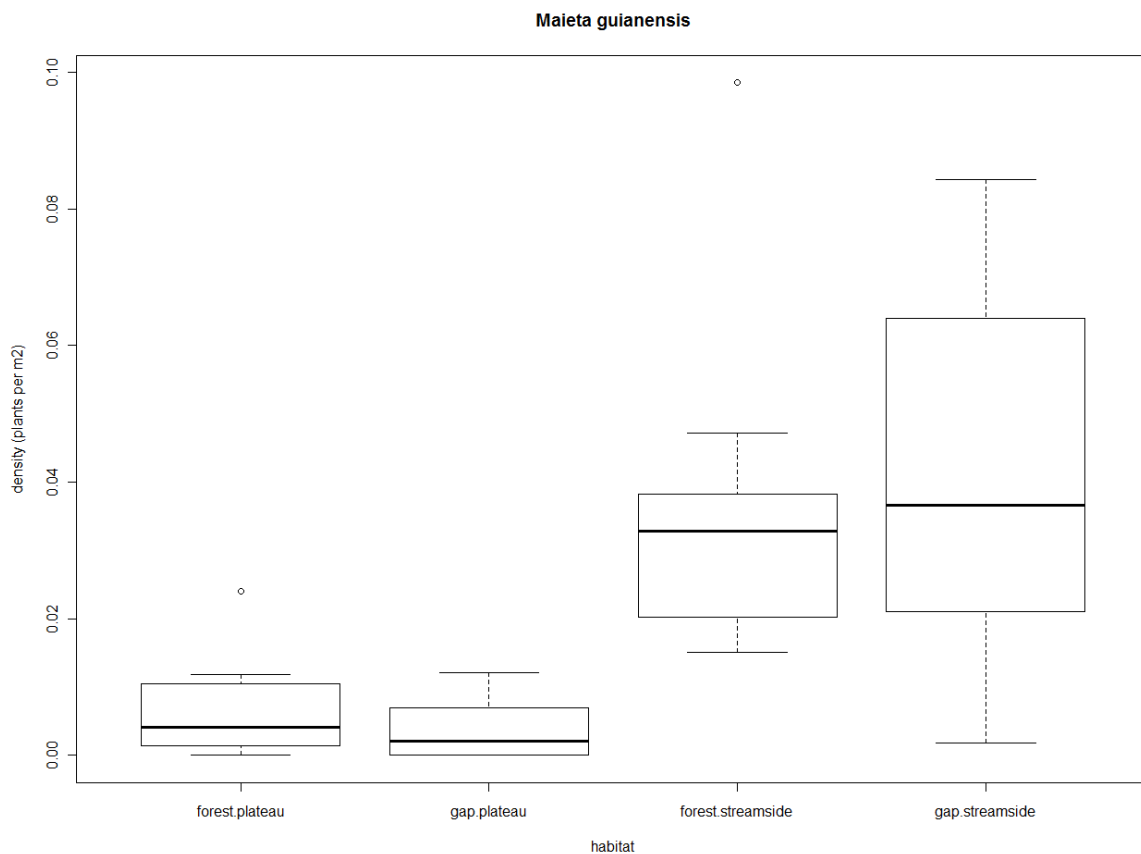


Figure 1

APPENDIX A: The number of *Maieta guianensis* plants in each combination of canopy cover and topography and the median density of plants per plot in each topography x canopy cover combination. There is a strong effect of topography on plant density but no effect of canopy cover or canopy cover x topography interaction and no effect of block (Split plot ANOVA with topography (upland plateau or streamside) as the whole plot treatment, canopy cover (gap or understory) as the within plot treatment, and each paired gap-understory site (n = 20) as a block.

<u>Topography</u>	<u>Canopy cover</u>	
	<u>forest</u>	<u>Gap</u>
Plateau	31	19
Streamside	124	187



Appendix B. Candidate models of *Maieta guianensis* demographic functions and the results of model fitting. ΔAICc values indicate the difference between the best fit model (in bold) and the alternative model. We used the best-fit model in all cases except for fruit production in partner-switching populations, in which diagnostic tools to assess suitability of the IPMs indicated the alternative model was superior for IPM construction. We felt this was acceptable given the very low ΔAICc value in this case.

Model	ΔAICc
Always <i>Pheidole minutula</i>	
Survival	
Logit(survival) = $a + b * \text{size}_t$	1.3
Logit(survival) = $a + b * \text{size}_t + c * \text{size}_t^2$	
Growth	
Size_{t+1} = $a + b * \text{size}_t$	
Size _{t+1} = $a + b * \text{size}_t + c * \text{size}_t^2$	0.78
Flowering	
Logit(flowering) = $a + b * \text{size}_t$	
Logit(flowering) = $a + b * \text{size}_t + c * \text{size}_t^2$	1.91
Fruit production	
Fruits _{t+1} = $a + b * \text{size}_t$	10.6
Fruits_{t+1} = $a + b * \text{size}_t + c * \text{size}_t^2$	
Always <i>Crematogaster laevis</i>	
Survival	
Logit(survival) = $a + b * \text{size}_t$	2.89
Logit(survival) = $a + b * \text{size}_t + c * \text{size}_t^2$	
Growth	
Size_{t+1} = $a + b * \text{size}_t$	
Size _{t+1} = $a + b * \text{size}_t + c * \text{size}_t^2$	0.54
Flowering	
Logit(flowering) = $a + b * \text{size}_t$	
Logit(flowering) = $a + b * \text{size}_t + c * \text{size}_t^2$	1.59
Fruit production	
Fruits _{t+1} = $a + b * \text{size}_t$	12.12
Fruits_{t+1} = $a + b * \text{size}_t + c * \text{size}_t^2$	

APPENDIX B, Cont.

Partner switching

Survival

$$\text{Logit}(\text{survival}) = a + b * \text{size}_t \quad 0.93$$

$$\text{Logit}(\text{survival}) = a + b * \text{size}_t + c * \text{size}_t^2$$

Growth

$$\text{Size}_{t+1} = a + b * \text{size}_t$$

$$\text{Size}_{t+1} = a + b * \text{size}_t + c * \text{size}_t^2 \quad 0.02$$

Flowering

$$\text{Logit}(\text{flowering}) = a + b * \text{size}_t \quad 3.92$$

$$\text{Logit}(\text{flowering}) = a + b * \text{size}_t + c * \text{size}_t^2$$

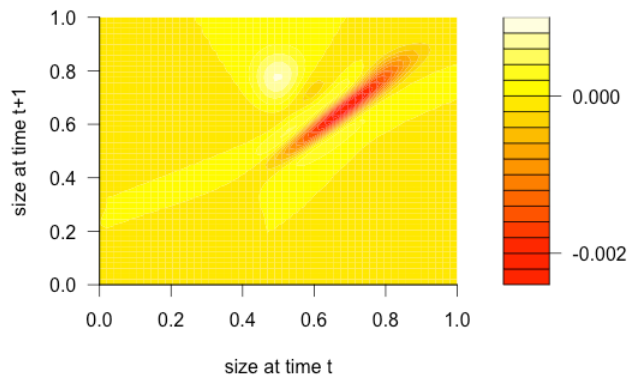
Fruit production

$$\text{Fruits}_{t+1} = a + b * \text{size}_t$$

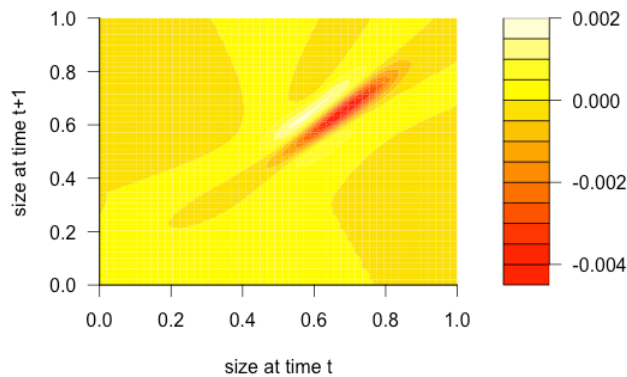
$$\text{Fruits}_{t+1} = a + b * \text{size}_t + c * \text{size}_t^2 \quad 0.84$$

APPENDIX C: Results of Life Table Response Experiments. The figures show the contribution to each size class to differences in population growth rate (i.e., $\Delta\lambda$) for each ant-plant partner combination. (A) *Pheidole minutula* vs. *Crematogaster laevis*, (B) *Pheidole minutula* vs. partner switching, (C) *Crematogaster laevis* vs. Partner switching. The first of the pair being compared is the “control matrix” in the LTRE. Note the different scales of the three figures.

A) *Pheidole minutula* vs. *Crematogaster laevis*



B) *Pheidole minutula* vs. Partner switching



C) *Crematogaster laevis* vs. Partner switching

