

1 **EFFECT OF MUTUALIST PARTNER IDENTITY AND FIDELITY**
2 **ON PLANT DEMOGRAPHY**

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ABSTRACT

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Mutualisms play a central role in the origin and maintenance of biodiversity. Because many

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mutualisms have strong demographic effects, interspecific variation in partner quality could have

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important consequences for population dynamics. Nevertheless, few studies have quantified how

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a mutualist partner influences population growth rates; still fewer have compared the

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demographic impacts of multiple partner species. We used integral projection models

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parameterized with multi-year census data to compare the demographic effects of two ant species

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– *Crematogaster laevis* and *Pheidole minutula* – on the Amazonian ant-plant *Maieta guianensis*.

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Estimated population growth rates were positive (i.e., $\lambda > 1$) for all ant-plant combinations.

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However, populations with only *Pheidole minutula* had the highest asymptotic growth rate

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($\lambda = 1.23$), followed by those colonized by *Crematogaster laevis* ($\lambda = 1.16$), and in which the

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partner ant alternated between *C. laevis* and *P. minutula* at least once during our study ($\lambda = 1.15$).

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Our results indicate that the short-term superiority of a particular mutualist partner can translate

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into long-term demographic benefits, and that there is a demographic cost to switching between

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alternative mutualist partners. Our results underscore the importance of expanding the study of

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mutualisms beyond the study of pair-wise interactions to consider the demographic costs and

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benefits of interacting with different potential partners.

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Key words: *Azteca*, *Crematogaster*, Integral projection model, lambda, Life-table response

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experiment, *Maieta*

INTRODUCTION

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

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

67 McKey 2003). Although individuals of some myrmecophytic plant species can be occupied
68 simultaneously by multiple ant species (e.g., Trager and Bruna 2006), many are occupied by a
69 colony of a single ant species at a time (Vasconcelos and Davidson 2000, Palmer et al. 2010).
70 Experimental work has demonstrated that these different ant species can vary substantially in
71 their defense of plants, resulting in differential rates of plant growth, reproduction, and
72 survivorship (e.g. Bruna et al. 2004, Frederickson 2005, Stanton and Palmer 2011). While these
73 studies are mostly short-term in nature, they suggest there could be demographic consequences
74 to long-term colonization by less effective mutualists.

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

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MATERIALS AND METHODS

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

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

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Sampling design and data collection: In January 2006 we used the trail system that bisects Reserve 1501 to find 10 gaps in the upland plateaus and 10 gaps adjacent to streams. We measured the length and width of each of these gaps, calculate the area of each gap with the formula for an ellipse, and used these measurements to mark an area of comparable size in adjacent closed canopy forest. Gap and paired closed canopy sites (hereafter, plots) were separated by ~50 meters (Forest plots: 405.11 m² ± 150.48 SD, Gap plots: 514.05 m² ± 188.90 SD). We then surveyed each plot and marked all *Maieta guianensis* with a permanent tag. We recorded the identity of any ant occupants and measured the size of each plant by counting the number of domatia and branches each plant had. These two proxies of plant size are highly

113 correlated (results not shown); we therefore use domatia number as the unit of plant size because
 114 it is directly related to ant colony size. The plots were censused at 6 month intervals, at which
 115 time we recorded if any marked plants had died, the size of surviving plants, and the identity of
 116 ant residents. We also marked and measured any newly established seedlings. In the fourth, fifth,
 117 and sixth censuses we quantified plant reproductive effort by counting the number of fruits or
 118 flowers on each plant.

119 *Demographic modeling and analysis:* To test our hypothesis we used the data from
 120 demographic surveys to build integral projection models. Integral projection models (IPM,
 121 Easterling et al. 2000, Ellner and Rees 2006) do not require that individuals be assigned to
 122 discrete size or stage classes in the way matrix models do, rather, they use continuous functions
 123 of describe size dependent growth, survivorship, and fecundity (Coulson 2012, Merow et al.
 124 2013). Our IPM describes the change in population size (n) over the course of six intervals of six
 125 months each. Our full model takes the form:

$$126 \quad n(y, t + 1) = \int_L^U [p(x, y) + f(x, y)]n(x, t)dx \quad (\text{eqn. 1})$$

127 Where the $P(y,x)$ kernel represents transitions of an individual of size x attributable to survival
 128 and growth, $p(x, y) = s(x)g(x, y)$ (eqn. 2)

129 The $F(y,x)$ kernel describes per-capita production of y sized individuals in the next census by
 130 reproductive individuals of size x (i.e., the recruit density function at the next census),

$$131 \quad f(x, y) = s(x)f_n(x)p_E f_d(y) \quad (\text{eqn. 3})$$

132 Where $s(x)$ is size-specific survival, $f_n(x)$ is the number of fruits or flowers produced by a plant of
 133 size x , p_E is a constant for the number of seedlings resulting per fruit, and $f_d(y)$ is the size
 134 distribution of seedlings. The growth, survival, and fertility functions are obtained from

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

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

157 constant was used in all IPMs because there is no reason to believe that ant identity of the
158 parental plants influences the germination success of host-plant seeds.

159 After initial analyses we were concerned that the very small number of seedlings in our
160 study plots that were colonized by *Crematogaster laevis* was leading to inaccurate demographic
161 functions for survivorship. We therefore supplemented our survey data with data from a
162 contemporaneous study conducted less than a kilometer from the demography plots on the rates
163 of seedling colonization by queens of *P. minutula* and *C. laevis* (Bruna et al. 2011a); this
164 provided additional data for colonization and survivorship of *M. guianensis* seedlings over 90
165 days (Bruna et al. 2011b).

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

173 *Life-table response experiments:* To elucidate the demographic mechanisms underlying
174 differences among populations we used Life Table Response Experiments (LTRE), which
175 decompose differences in λ into the contributions from different demographic variables (Caswell
176 1989). We used a fixed-design LTRE (Horvitz et al. 1996, Caswell 2001), in which the
177 difference in λ between the ‘control’ and ‘experimental’ treatments, $\Delta\lambda$, is given by:

$$178 \quad \Delta\lambda = \lambda^{(t)} - \lambda^{(c)} \approx \sum_j (a_{ij}^{(t)} - a_{ij}^{(c)}) \times \left(\frac{\partial \lambda}{\partial a_{ij}} \right) \bigg|_{\frac{(\mathbf{A}^{(t)} + \mathbf{A}^{(c)})}{2}} \quad (\text{eqn. 4})$$

179 where $(a_{ij}^{(t)} - a_{ij}^{(c)})$ is the difference in a_{ij} between the ‘treatment’ matrix and the ‘control’ matrix,
 180 and $\partial\lambda / \partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} evaluated at the mean value (i.e., the matrix
 181 that is an average of the matrices being compared, Caswell 2001). Close correspondence
 182 between values of $\Delta\lambda$ and LTRE contributions indicates the suitability of the LTRE models.

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RESULTS

185 We sampled 706 *Maieta guianensis* plants over the course of our study. Of those 42 were
 186 colonized throughout solely by *Crematogaster laevis*, 398 were colonized exclusively by
 187 *Pheidole minutula*, and 58 were colonized in every survey but had switched ant partners at least
 188 once from one survey to the next. Plant density was significantly greater in lowlands than
 189 plateaus, although there was no difference between gaps and adjacent areas of forest within a
 190 canopy-cover type (Appendix A).

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Plant size at a survey depended on size in the previous survey, with a linear function
 providing the best fit to the data (Appendix B, Fig. 1). The growth functions, $g(x,y)$, for plants
 occupied by the different ant species were not significantly different. The probability of
 individual survival, $s(x)$, increased with plant size (Fig. 1). Overall plant survival was high
 (98%), but the smallest plants had a higher risk of mortality when colonized by *C. laevis* (Fig.
 1F) or alternating partners (Fig. 1J), than when colonized by *P. minutula*. Both the likelihood of
 flowering and per-individual fruit production were also size-dependent (Fig. 1). However, very
 few plants colonized by *C. laevis* reproduced (Fig. 1G), and those that did were generally plants
 in size classes that produced few fruits (Fig. 1H). When plants colonized by *C. laevis* or by
 alternating partners did reproduce, they produce far fewer fruits than comparably sized plants
 colonized by *P. minutula* (Fig. 1D, 1H, 1L).

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

210 Our LTRE analysis revealed similar demographic mechanisms were responsible for the
211 differences in λ between all three comparisons (*P. minutula* vs. *C. laevis*, *P. minutula* vs. partner
212 switching, and *C. laevis* vs. partner switching; Appendix C), for populations associated with *P.*
213 *minutula* and those colonized by *C. laevis* were due primarily to reduced stasis by intermediate to
214 larger plants colonized by *C. laevis* (Appendix C). The negative contributions to $\Delta\lambda$ along the
215 principal diagonal, representing stasis in the largest (and reproductive) size classes far
216 outweighed the positive ones from other regions of the matrix.

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DISCUSSION

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Despite an increasingly robust theoretical literature exploring how variation among
mutualists in the benefits they provide influences the population dynamics of partners (Boucher
1985, Hoeksema and Bruna 2000, Holland et al. 2002), few empirical studies address this topic.
We found that associations with different mutualist partners would result in different population
growth rates for an Amazonian host plant. Although all projections of λ were greater than one, λ
was significantly greater for plants associated with one of the ant species than with the other.

225 Furthermore, plants that switched partners during our study had net benefits similar to those of
226 always associating with the poorer mutualist partner, as opposed to an intermediate value as
227 predicted by Stanton (2003). Our results underscore the importance of expanding the study of
228 mutualisms beyond the “pair-wise perspective” (sensu Stanton 2003) to consider the costs and
229 benefits of interacting with different putative partners. Considering the long-term demographic
230 consequences of these costs and benefits will greatly enhance our ability to generalize about how
231 mutualisms evolve and persist (Bruna et al. 2008, Palmer et al. 2010).

232 What are the demographic mechanisms underlying the lower growth rates of populations
233 housing *C. laevis* or switching partners? Life-table response experiments indicate that the
234 differences in λ are due primarily to differences in the probability of growing into or remaining
235 in large size classes (Appendix C), which are those that are most likely to reproduce and produce
236 the most fruit when they do (Fig. 1). These results are consistent with those of short-term
237 experiments and previous observations. Plants with *C. laevis* are smaller than those with *P.*
238 *minutula* (Vasconcelos and Davidson 2000), and *C. laevis* respond more slowly and at lower
239 intensity to cues associated with herbivory (Lapola et al. 2003). They also house more
240 trophobionts inside domatia (Lapola et al. 2005), which at high densities could conceivably
241 reduce the growth of plants (Heil and McKey 2003). Finally, experimentally removing ants from
242 *M. guianensis* greatly increased herbivory and reduced fruit set (Vasconcelos 1991), which is
243 consistent with results from sympatric and closely related systems (Bruna et al. 2004). Although
244 recent meta-analyses have argued that herbivore damage is not a reliable surrogate for fitness
245 consequences of ant-protection (Trager et al. 2010), our results suggest that differences among
246 ant species in the costs and benefits they provide – even small ones – can indeed interact in
247 subtle ways that affect λ .

248 Finally, we provide some of the first demographic evidence to date that associating with
249 multiple partners reduces the net benefits to host plants. While prior simulation studies have
250 provided support for this idea (Bronstein et al. 2003, Miller 2007), the most comprehensive
251 empirical work to date has found the opposite to be true. Palmer et al. (2010) found that for
252 African *Acacia drepanolobium* trees λ was lower for hypothetical populations interacting with
253 only one ant partner than for populations successively colonized by four different ant species,
254 even though one ant species is a sterilization parasite that inhibits reproduction and another
255 reduces tree survivorship. They argued that this counter-intuitive effect is due to tradeoffs
256 between survivorship and fecundity at different stages of the tree life-cycle facilitated by the
257 different life-spans of the trees and their partners. Our results suggest the extent to which
258 multiple sequential partners are detrimental or beneficial in ant-plant mutualisms varies among
259 ant-plant systems. In our study system there is no sterilizing ant partner that enhances plant
260 growth at the expense of reproduction; mutualists that sterilize a partner species have garnered
261 considerable interest (e.g., Izzo and Vasconcelos 2002, Frederickson 2009) but appear rare
262 among ant-plant mutualisms. Indeed, there is no *a priori* reason to expect the effects of temporal
263 changes in partner identity should be inherently beneficial or detrimental. Instead, Jensen's
264 inequality (Karban et al. 1997, Inouye 2005) predicts that the mean benefits will depend on the
265 functional form of the relationship between frequency of partner identity and λ , and this
266 relationship is likely to vary among plant species as the number and quality of mutualist partners
267 changes.

268 It is important to recognize that we used an estimated constant for the number of
269 seedlings resulting from each fruit. While an over- or underestimate of this value could influence
270 our projections of λ , there is no reason to expect the recruitment rate varies with ant

271 symbiont, and hence the relative rankings of lambda for plants colonized by each species are
272 likely to be similar in good and bad recruitment years. It is also important to note that *Maieta*
273 *guianensis* is more common in gaps (Appendix A) and that the dynamics of ant-plant
274 associations can vary by habitat (Schupp and Feener 1991, Yu and Davidson 1997, Nery and
275 Vasconcelos 2003, Bruna et al. 2011a). Habitat-specific differences in demography could
276 influence the dynamics of these interactions at the landscape scale, and we plan to test this
277 hypothesis in a future study. It is also important to recognize that our study included only plants
278 that were colonized in every survey. Partner switching necessarily means plants were
279 temporarily vacant, and though we have previously shown colonization of vacant *M. guianensis*
280 can be extremely fast (Bruna et al. 2011a) some plants in our survey were vacant for more
281 extended time periods. While we focused our analyses on the effects of partner identity rather
282 than partner loss, subsequent work will address the demographic costs of partner loss and the
283 length of time plants remain without the benefits of services provided by mutualists – another
284 important but little explored factor influencing the origin and maintenance of interspecific
285 mutualisms.

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LITERATURE CITED

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421

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.

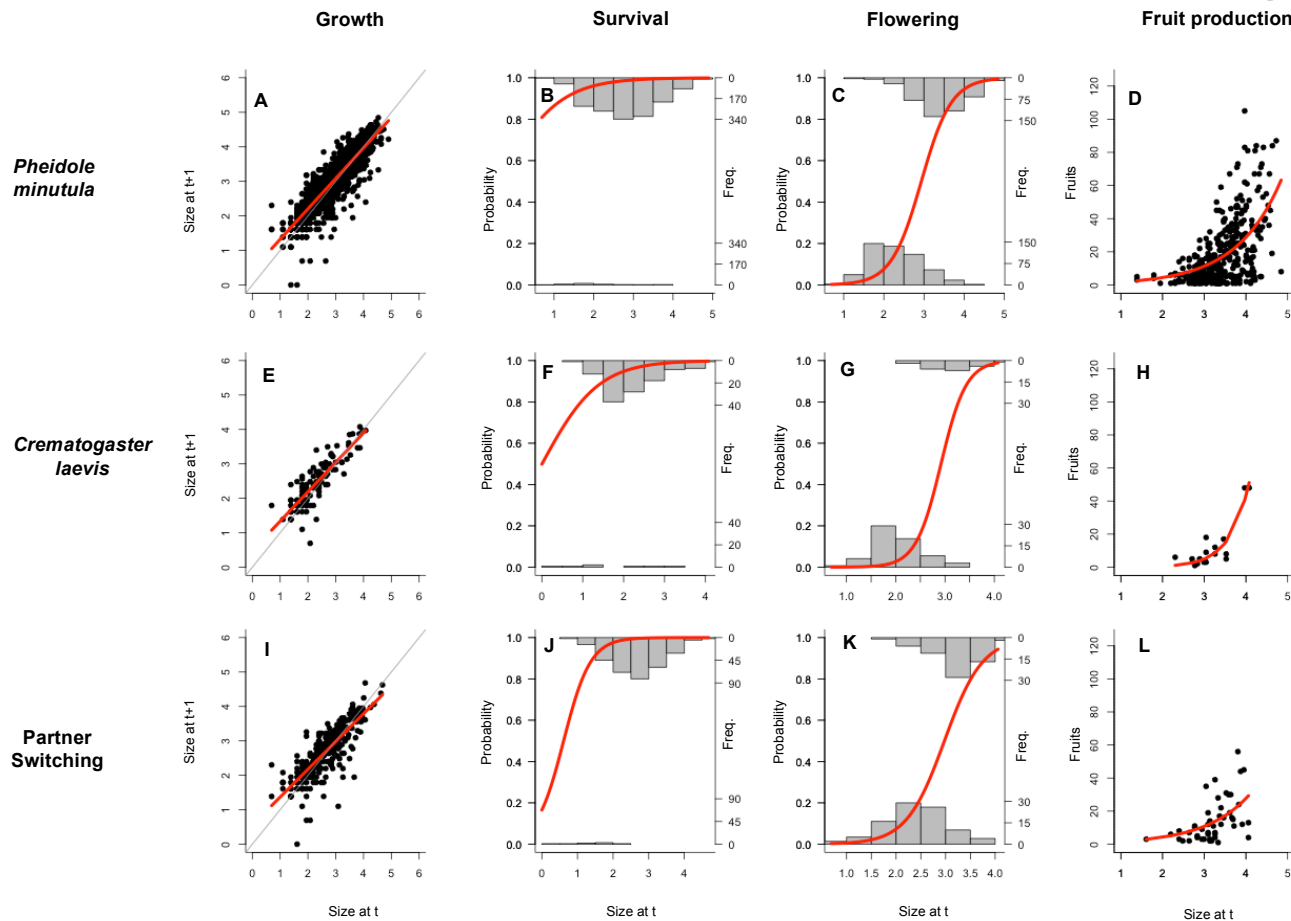
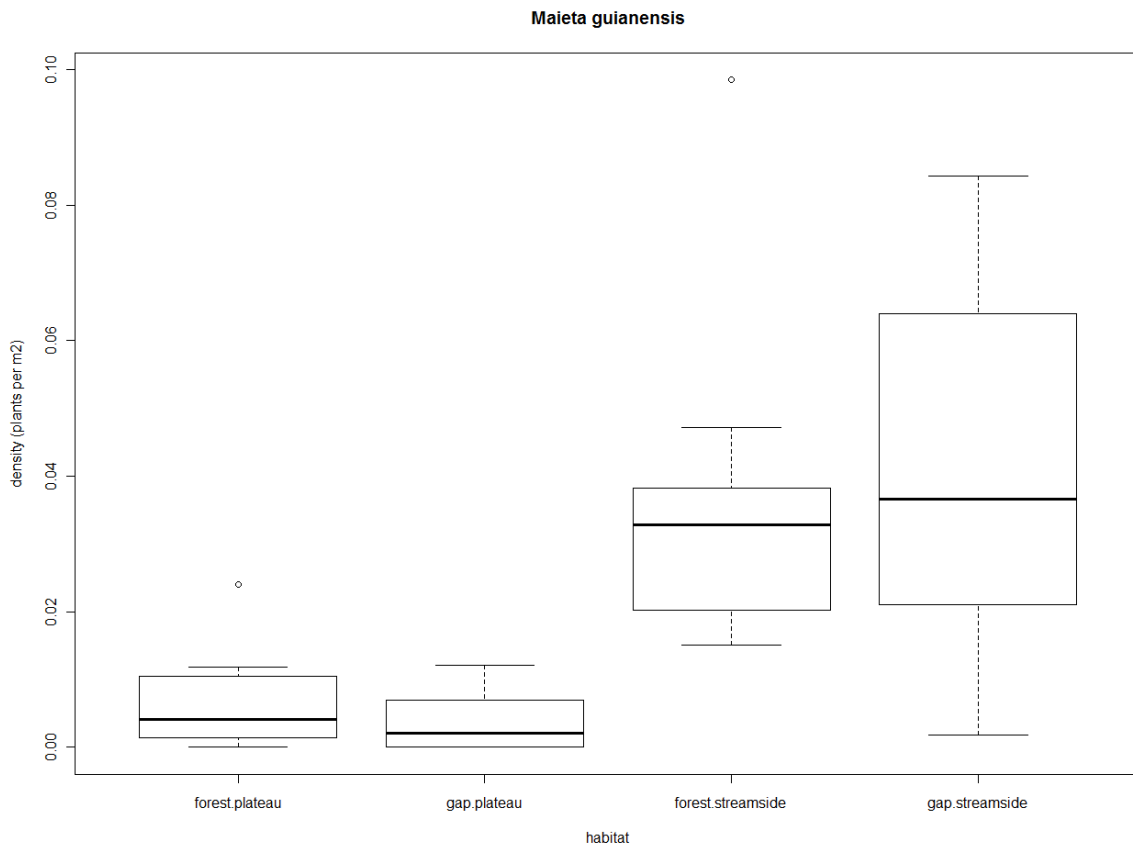


Figure 1

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. $\Delta AICc$ 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 $\Delta AICc$ value in this case.

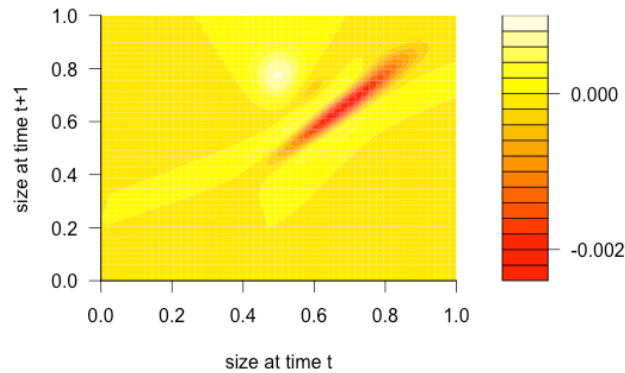
Model	$\Delta AICc$
Always <i>Pheidole minutula</i>	
Survival	
Logit(survival) = $a + b * size_t$	1.3
Logit(survival) = $a + b * size_t + c * size_t^2$	
Growth	
Size_{t+1} = $a + b * size_t$	
Size _{t+1} = $a + b * size_t + c * size_t^2$	0.78
Flowering	
Logit(flowering) = $a + b * size_t$	
Logit(flowering)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

APPENDIX B, Cont.

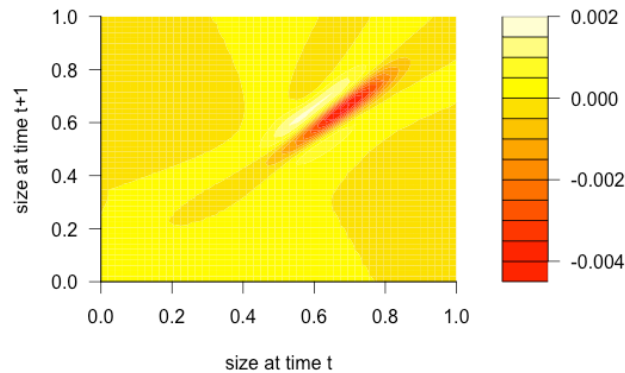
Partner switching		
Survival		
	$\text{Logit}(\text{survival}) = a + b * \text{size}_t$	0.93
	$\text{Logit}(\text{survival}) = a + b * \text{size}_t + c * \text{size}_t^2$	
Growth		
	$\text{Size}_{t+1} = a + b * \text{size}_t$	
	$\text{Size}_{t+1} = a + b * \text{size}_t + c * \text{size}_t^2$	0.02
Flowering		
	$\text{Logit}(\text{flowering}) = a + b * \text{size}_t$	3.92
	$\text{Logit}(\text{flowering}) = a + b * \text{size}_t + c * \text{size}_t^2$	
Fruit production		
	$\text{Fruits}_{t+1} = a + b * \text{size}_t$	
	$\text{Fruits}_{t+1} = a + b * \text{size}_t + c * \text{size}_t^2$	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

