

December 2014

esa

Volume 95 No. 12

ECOLOGY

A PUBLICATION OF THE ECOLOGICAL SOCIETY OF AMERICA



Reports

Effect of mutualist partner identity on plant demography

Concepts and Synthesis

Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition

Articles

Coastal wetland stability maintained through counterbalancing accretionary responses to chronic nutrient enrichment

Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics

Reports

Ecology, 95(12), 2014, pp. 3237–3243
© 2014 by the Ecological Society of America

Effect of mutualist partner identity on plant demography

EMILIO M. BRUNA,^{1,2,6,7} THIAGO J. IZZO,^{3,6} BRIAN D. INOUE,^{4,6} AND HERALDO L. VASCONCELOS^{5,6}

¹*Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611-0430 USA*

²*Center for Latin American Studies, University of Florida, Gainesville, Florida 32611-5530 USA*

³*Universidade Federal do Mato Grosso, I.B., Departamento de Botânica e Ecologia, Avenida Fernando Correia da Costa, s/n, Cuiabá, MT 78060 900 Brazil*

⁴*Department of Biological Science, Florida State University, Tallahassee, Florida 32306-4295 USA*

⁵*Instituto de Biologia, Universidade Federal de Uberlândia (UFU), C.P. 593, 38400 902, Uberlândia, MG Brazil*

⁶*Biological Dynamics of Forest Fragments Project, (INPA-STRI), C.P. 478, Manaus, AM 69011 970 Brazil*

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

Key words: Azteca; *Crematogaster*; *integral projection model*; *lambda*; *life-table response experiment*; *Maieta*; *Melastomataceae*.

INTRODUCTION

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

Manuscript received 10 March 2014; revised 10 July 2014; accepted 14 August 2014; final version received 22 September 2014. Corresponding Editor: N. J. Sanders.

⁷ E-mail: embruna@ufl.edu

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

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

MATERIALS AND METHODS

Study site and system

Field work was conducted from January 2006 to January 2009 in Reserve 1501 of the Biological Dynamics of Forest Fragments Project (BDFFP), which is located approximately 60 km north of Manaus, Brazil (2°30' S, 60° W). The habitat is non-flooded primary lowland forest with a 30–35 m tall canopy and an

understory dominated by stemless palms. Annual rainfall ranges from 1900–3500 mm, with a pronounced dry season from June to October (Bierregaard et al. 2002).

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., nonreproductive) 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).

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, calculated 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 m (forest plots, $405.11 \pm 150.48 \text{ m}^2$ [mean \pm SD]; gap plots, $514.05 \pm 188.90 \text{ m}^2$). 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 correlated (results not shown); we therefore use domatia number as the unit of plant size because it is directly related to ant colony size. The plots were censused at six-month intervals, at which time we recorded whether marked plants had died, the size of surviving plants, and the identity of ant residents. We also marked and measured any newly established seedlings. In the fourth, fifth, and sixth censuses we quantified plant reproductive effort by counting the number of fruits or flowers on each plant. These data are available from the Dryad Digital Repository (see Data Availability).

Demographic modeling and analysis

To test our hypothesis we used the demographic survey data to build integral projection models. In contrast to matrix-based demographic models (Caswell 2001), integral projection models (IPM; Easterling et al. 2000, Ellner and Rees 2006) do not require that individuals be assigned to discrete size or stage classes. Instead, they use continuous functions to describe size-dependent growth, survivorship, and fecundity (Coulson 2012, Merow et al. 2014). Our IPM describes the change in population size (n) over the course of six intervals of six months each. We chose to build models based on six-month intervals rather than the more

common one-year intervals typically used in studies of plant demography because our preliminary observations suggested that ant turnover in this system (i.e., colony loss and subsequent recolonization) was more rapid than previously observed (Vasconcelos and Davidson 2000). Longer census and model intervals would therefore fail to capture the potential impacts of this rapid turnover on *M. guianensis* demography. In addition, because *M. guianensis* in our sites grow and reproduce year round instead of in discrete seasons (Vasconcelos 1991), a six-month interval captures all demographic processes.

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 represents transitions of an individual of size x to size y attributable to survival, s , and growth, g , $p(x, y) = s(x)g(x, y)$. The $f(x, y)$ kernel describes per-capita production of y -sized individuals in the next census by reproductive individuals of size x (i.e., the recruit density function at the next 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 of fruits or flowers produced by a plant of size x , p_E is a constant for the estimated number of seedlings resulting per fruit, and $f_d(y)$ is the size distribution of seedlings. The growth, survival, and fertility functions are obtained from statistical models of the census data. To test our hypothesis, we constructed IPMs for three hypothetical populations: one pooling plants that were occupied solely by *P. minutula* over the course of all six surveys, one for plants occupied solely by *C. laevis*, and one for plants occupied in every survey but whose resident ant partner changed at least once. Because the low densities of some ant-plant combinations in some plots made determining plot-specific demographic functions impossible, we pooled plants from all plots to conduct our analyses; a landscape-scale analysis such as this is equivalent to constructing “summary matrices” in matrix models (sensu Horvitz and Schemske 1995, Caswell 2001) to correct for the disproportionate weight that low sample sizes can give to some transition probabilities (e.g., Bruna 2003). Because we had insufficient data to build a robust stochastic model, we also pooled data across all years of our study to represent a single average time step (sensu Miller et al. 2009). Data were prepared for analysis and models were built and analyzed with modified versions (Bruna 2014) of the IPMpack (Metcalfe et al. 2013) and popbio (Stubben and Milligan 2007) packages for R (R Development Core Team 2014).

IPM functions were fit using the natural logarithm of domatia number as the size variable. We first calculated alternative statistical relationships for growth, survivorship, and fecundity as functions of plant size (Table 1), then used model selection methods based on the Akaike information criterion (AIC) to determine which provided the best fit to the data. Because individual *M.*

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

Mutualist partner	λ
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)

guianensis fruits have thousands of dust-like seeds, we were unable to count accurately the number of seeds per fruit or estimate seed germination rates. Instead we estimated the proportion of fruits becoming seedlings (p_E) by counting the number of newly established seedlings we counted during the surveys, dividing this number by the number of fruits produced by all plants in the previous reproductive season (all seasons pooled, see Bruna [2014]). This constant was used in all IPMs because there is no reason to believe that ant identity of the maternal plants influences the germination success of host-plant seeds.

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

Each IPM was used to calculate lambda by discretizing the kernel using the midpoint rule with 50 mesh points. The upper limit for each integration was based on the maximum size of plants in the populations being modeled, and the lower limit was constant for all populations. We also calculated the bias-corrected 95% confidence intervals for each estimate of lambda by bootstrapping ($n = 1000$ simulations) and used randomization tests ($n = 1000$ permutations) to determine if estimates of λ for populations with different ant partners were significantly different from each other (Caswell 2001, Bruna 2014).

Life-table response experiments

To elucidate the demographic mechanisms underlying differences among populations we used life table response experiments (LTRE), which decompose differences in λ into the contributions from different demographic variables (Caswell 1989). We used a fixed-design LTRE (Caswell 2001), in which the difference in λ between two treatments, $\Delta\lambda$, is given by

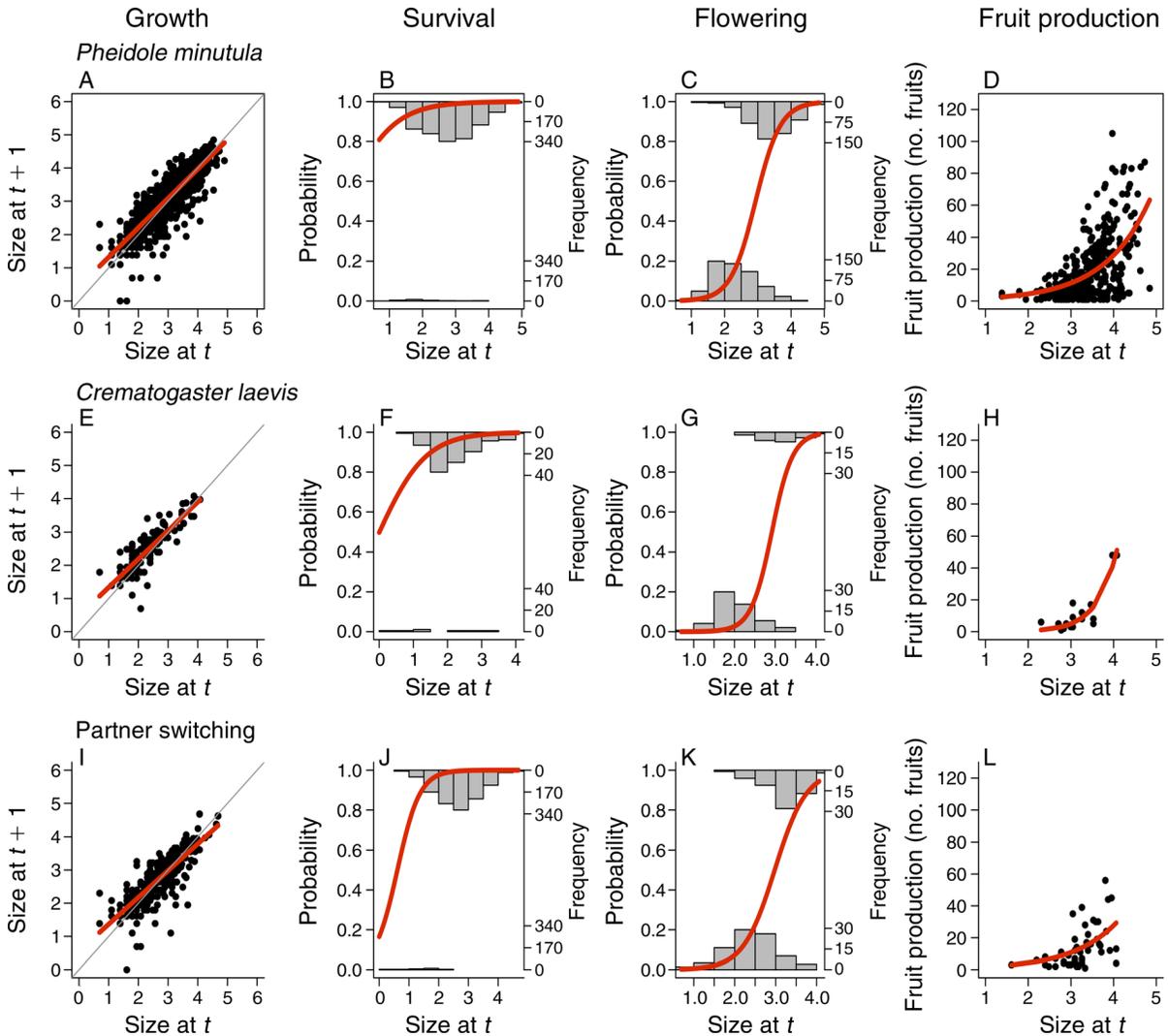


FIG. 1. Size-dependent growth, survivorship, flowering, and fruit production of plants during initial (t) and subsequent ($t + 1$) surveys. Plants were either occupied throughout our study by *Pheidole minutula* (A–D), continuously by *Crematogaster laevis* (E–H), or switched partners at least once (i.e., from a given survey t to the subsequent survey $t + 1$) during the study period (I–L). Size is measured as $\ln(\text{number of domatia})$.

$$\Delta\lambda = \lambda^{(t)} - \lambda^{(c)} \approx \sum_{ij} (a_{ij}^{(t)} - a_{ij}^{(c)}) \times \left(\frac{\partial\lambda}{\partial a_{ij}} \right) \bigg|_{\left(\frac{\lambda^{(t)} + \lambda^{(c)}}{2} \right)}$$

where $(a_{ij}^{(t)} - a_{ij}^{(c)})$ is the difference in a_{ij} between the arbitrarily defined treatment (t) and control (c) matrices, and $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} evaluated at the average of $a_{ij}^{(t)}$ and $a_{ij}^{(c)}$. Close correspondence between values of $\Delta\lambda$ and LTRE contributions indicates the suitability of the LTRE models. LTRE analyses were also conducted with the popbio package (Stubben and Milligan 2007).

RESULTS

We sampled 706 *Maieta guianensis* plants over the course of our study. Plant density was significantly

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

Plant size at a survey depended on size in the previous survey, with a linear function providing the best fit to the ln-transformed size 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).

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

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

DISCUSSION

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, Ohm and Miller 2014), few empirical studies address this topic. We found that associations with different mutualist partners resulted 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. In addition, plants that switched partners during

our study had net benefits similar to those of always associating with the poorer mutualist partner, as opposed to an intermediate value as predicted by Stanton (2003). These differences are even more striking when considering that our values for λ are for six-month intervals as opposed to the one-year intervals more typical in studies of plant demography. Because we used deterministic models, caution must be taken not to assume our results would be identical had we conducted our study in different years (Caswell 2001), and additional survey data would allow us to estimate temporal stochasticity in λ . Nevertheless, our results underscore the importance of expanding the study of mutualisms beyond the “pair-wise perspective” (sensu Stanton 2003) to consider the costs and benefits of interacting with different putative partners. Considering the long-term demographic consequences of these costs and benefits will greatly enhance our ability to generalize about how mutualisms evolve and persist (Bruna et al. 2008, Palmer et al. 2010).

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

Finally, we provide some of the first demographic evidence to date that associating with multiple partners reduces the net benefits to host plants. While prior simulation studies have provided support for this idea (Bronstein et al. 2003, Miller 2007), the most comprehensive empirical work to date has found the opposite to be true. Palmer et al. (2010) found that, for African *Acacia drepanolobium* trees, λ was lower for hypothetical populations interacting with only one ant partner than for populations successively colonized by four different ant species, even though one ant species is a sterilization parasite that inhibits reproduction and another reduces

tree survivorship. They argued that this counterintuitive effect is due to trade-offs between survivorship and fecundity at different stages of the tree life-cycle facilitated by the different life spans of the trees and their partners. Our results suggest the extent to which multiple sequential partners are detrimental or beneficial in ant-plant mutualisms varies among ant-plant systems. In our study system, there is no sterilizing ant partner that enhances plant growth at the expense of reproduction; mutualists that sterilize a partner species have garnered considerable interest (e.g., Izzo and Vasconcelos 2002, Frederickson 2009) but appear rare among ant-plant mutualisms. Indeed, there is no a priori reason to expect that the effects of temporal changes in partner identity should be inherently beneficial or detrimental. Instead, Jensen's inequality (Karban et al. 1997, Inouye 2005) predicts that the mean benefits will depend on the functional form of the relationship between frequency of partner identity and λ , and this relationship is likely to vary among plant species as the number and quality of mutualist partners changes.

We used an estimated constant for the number of seedlings resulting from each fruit. While an over- or underestimate of this value could influence our projections of lambda, there is no reason to expect that the recruitment rate varies with the maternal plant's ant symbiont, and hence the relative rankings of lambda for plants colonized by each species are likely to be similar in good and bad recruitment years. It is also important to note that *Maieta guianensis* is more common in gaps (Appendix A) and that the dynamics of ant-plant associations can vary as a function of both local myrmecophyte density and habitat type (Schupp and Feener 1991, Vasconcelos 1993, Yu and Davidson 1997, Nery and Vasconcelos 2003, Bruna et al. 2011a). Because such variation could alter key demographic vital rates (e.g., plant growth or reproduction could be greater in gaps, the likelihood of colonization by *P. minutula* could be density dependent), it could influence the population dynamics of both ants and plants at the landscape scale: an issue we are addressing in a subsequent paper. Finally, our study included only plants that were colonized in every survey. Partner switching necessarily means plants were temporarily vacant, and though we have previously shown colonization of vacant *M. guianensis* can be extremely fast (Bruna et al. 2011a), some plants in our survey were vacant for more extended time periods. While we focused our analyses on the effects of partner identity rather than partner loss, subsequent work will address the demographic costs of partner loss and the length of time plants remain without the benefits of the services they provide: another important but little-explored factor influencing the origin and maintenance of interspecific mutualisms.

ACKNOWLEDGMENTS

We thank T. Caughlin and two anonymous reviewers for comments on the manuscript and E. Z. de Albuquerque and O. F. da Silva for assistance in the field. Financial support was

provided by Brazil's CNPq (Grants 552680/2006-0 and 490518/2006-0), and the U.S. NSF (grants DEB-0452720 and DEB-0453631). This is publication number 650 in the BDFFP technical series.

LITERATURE CITED

- Aslan, C. E., E. S. Zavaleta, B. Tershy, and D. Croll. 2013. Mutualism disruption threatens global plant biodiversity: a systematic review. *PLoS ONE* 8.
- Benson, W. W. 1985. Amazon ant-plants. Pages 239–266 in G. T. Prance and T. E. Lovejoy, editors. Amazonia. Pergamon Press, New York, New York, USA.
- Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2002. Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven, Connecticut, USA.
- Boucher, D. H., editor. 1985. The biology of mutualism. Oxford University Press, New York, New York, USA.
- Bronstein, J. L. 1994. Our current understanding of mutualism. *Quarterly Review of Biology* 69:31–51.
- Bronstein, J. L., W. G. Wilson, and W. E. Morris. 2003. Ecological dynamics of mutualist/antagonist communities. *American Naturalist* 162:S24–S39.
- Bruna, E. M. 2003. Are plants in rain forest fragments recruitment limited? Tests with an Amazonian herb. *Ecology* 84:932–947.
- Bruna, E. M. 2014. R code for analyses and in Bruna et al. Effect of mutualist partner identity on plant demography. <http://dx.doi.org/10.5281/zenodo.11650>
- Bruna, E. M., M. R. Darrigo, A. M. F. Pacheco, and H. L. Vasconcelos. 2008. Interspecific variation in the defensive responses of ant mutualists to plant volatiles. *Biological Journal of the Linnean Society* 94:241–249.
- Bruna, E. M., T. J. Izzo, B. D. Inouye, M. Uriarte, and H. L. Vasconcelos. 2011a. Asymmetric dispersal and colonization success of Amazonian plant-ants queens. *PLoS ONE* 6: e22937.
- Bruna, E. M., T. J. Izzo, B. D. Inouye, M. Uriarte, and H. L. Vasconcelos. 2011b. Data from: Asymmetric dispersal and colonization success of Amazonian plant-ants queens. *PLoS ONE*. Dryad Digital Repository. <http://doi:10.5061/dryad.h6t7g>
- Bruna, E. M., D. M. Lapola, and H. L. Vasconcelos. 2004. Interspecific variation in the defensive responses of obligate plant-ants: experimental tests and consequences for herbivory. *Oecologia* 138:558–565.
- Caswell, H. 1989. Analysis of life table response experiments I: decomposition of effects on population growth rate. *Ecological Modelling* 46:221–237.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.
- Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos* 121: 1337–1350.
- Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708.
- Ellner, S. P., and M. Rees. 2006. Integral projection models for species with complex demography. *American Naturalist* 167: 410–428.
- Frederickson, M. E. 2005. Ant species confer different partner benefits on two Neotropical myrmecophytes. *Oecologia* 143: 387–395.
- Frederickson, M. E. 2009. Conflict over reproduction in an ant-plant symbiosis: why *Allomerus octoarticulatus* ants sterilize *Cordia nodosa* trees. *American Naturalist* 173:675–681.
- Frederickson, M. E., and D. M. Gordon. 2009. The intertwined population biology of two Amazonian myrmecophytes and their symbiotic ants. *Ecology* 90:1595–1607.

- Geib, J. C., and C. Galen. 2012. Tracing impacts of partner abundance in facultative pollination mutualisms: from individuals to populations. *Ecology* 93:1581–1592.
- Heil, M., and D. McKey. 2003. Protective ant–plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics* 34:425–453.
- Hoeksema, J. D., et al. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters* 13:394–407.
- Hoeksema, J. D., and E. M. Bruna. 2000. Pursuing the big questions about interspecific mutualisms: a review of theoretical approaches. *Oecologia* 125:321–330.
- Holland, J. N., D. L. DeAngelis, and J. L. Bronstein. 2002. Population dynamics and mutualism: functional responses of benefits and costs. *American Naturalist* 159:231–244.
- Horvitz, C. C., and D. W. Schemske. 1995. Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. *Ecological Monographs* 65:155–192.
- Inouye, B. D. 2005. The importance of the variance around the mean effect size of ecological processes: comment. *Ecology* 86:262–265.
- Izzo, T. J., E. M. Bruna, H. L. Vasconcelos, and B. D. Inouye. 2009. Cooperative colony founding alters the outcome of interspecific competition between Amazonian plant–ants. *Insectes Sociaux* 56:341–345.
- Izzo, T., and H. L. Vasconcelos. 2002. Cheating the cheater: domatia loss minimizes the effects of ant castration in an Amazonian ant–plant. *Oecologia* 133:200–205.
- Janzen, D. H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* 20:249–275.
- Karban, R., A. A. Agrawal, and M. Mangel. 1997. The benefits of induced defenses against herbivores. *Ecology* 78:1351–1355.
- Lapola, D. M., E. M. Bruna, C. G. de Willink, and H. L. Vasconcelos. 2005. Ant-tended hemiptera in Amazonian myrmecophytes: patterns of abundance and implications for mutualism function. *Sociobiology* 46:433–442.
- Lapola, D. M., E. M. Bruna, and H. L. Vasconcelos. 2003. Contrasting responses to induction cues by ants inhabiting *Maieta guianensis* (Melastomataceae). *Biotropica* 35:295–300.
- Loayza, A. P., and T. Knight. 2010. Seed dispersal by pulp consumers, not “legitimate” seed dispersers, increases *Guetarda viburnoides* population growth. *Ecology* 91:2684–2695.
- Merow, C., J. P. Dahlgren, C. J. E. Metcalf, D. Z. Childs, M. E. K. Evans, E. Jongejans, S. Record, M. Rees, R. Salguero-Gómez, and S. M. McMahon. 2014. Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution* 5:99–110.
- Metcalf, C. J. E., S. M. McMahon, R. Salguero-Gomez, and E. Jongejans. 2013. IPMPack: an R package for integral projection models. *Methods in Ecology and Evolution* 4:195–200.
- Miller, T. E. X. 2007. Does having multiple partners weaken the benefits of facultative mutualism? A test with cacti and cactus-tending ants. *Oikos* 116:500–512.
- Miller, T. E. X., S. M. Louda, K. A. Rose, and J. O. Eckberg. 2009. Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecological Monographs* 79:155–172.
- Nery, A. S., and H. L. Vasconcelos. 2003. Growth and survival of incipient ant-colonies in two Amazonian ant-plants: effects of host plant, habitat, and mode of colony founding (Hymenoptera: Formicidae). *Sociobiology* 42:151–162.
- Ohm, J. R., and T. E. X. Miller. 2014. Balancing anti-herbivore benefits and anti-pollinator costs of defensive mutualists. *Ecology* 95:2924–2935.
- Palmer, T. M., D. F. Doak, M. L. Stanton, J. L. Bronstein, E. T. Kiers, T. P. Young, J. R. Goheen, and R. M. Pringle. 2010. Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *Proceedings of the National Academy of Sciences USA* 107:17234–17239.
- R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Schemske, D. W., and C. C. Horvitz. 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science* 225:519–521.
- Schupp, E. W., and D. H. Feener. 1991. Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. Pages 175–197 in C. R. Huxley and D. F. Cutler, editors. *Ant–plant interactions*. Oxford University Press, Oxford, UK.
- Schupp, E. W., P. Jordano, and J. M. Gómez. 2010. Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist* 188:333–353.
- Stanton, M. L. 2003. Interacting guilds: moving beyond the pairwise perspective on mutualisms. *American Naturalist* 162:S10–S23.
- Stanton, M. L., and T. M. Palmer. 2011. The high cost of mutualism: effects of four species of East African ant symbionts on their myrmecophyte host tree. *Ecology* 92:1073–1082.
- Stubben, C., and B. Milligan. 2007. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22:1–23.
- Trager, M. D., S. Bhotika, J. A. Hostetler, G. V. Andrade, M. A. Rodriguez-Cabal, C. S. McKeon, C. W. Osenberg, and B. M. Bolker. 2010. Benefits for plants in ant–plant protective mutualisms: a meta-analysis. *PLoS ONE* 5:e14308.
- Trager, M. D., and E. M. Bruna. 2006. Effects of plant age, experimental nutrient addition and ant occupancy on herbivory in a neotropical myrmecophyte. *Journal of Ecology* 94:1156–1163.
- Vasconcelos, H. L. 1991. Mutualism between *Maieta guianensis* Aubl., a myrmecophytic melastome, and one of its ant inhabitants: ant protection against insect herbivores. *Oecologia* 87:295–298.
- Vasconcelos, H. L. 1993. Ant colonization of *Maieta guianensis* seedlings, an Amazon ant–plant. *Oecologia* 95:439–443.
- Vasconcelos, H. L., and D. W. Davidson. 2000. Relationship between plant size and ant associates in two Amazonian ant-plants. *Biotropica* 32:100–111.
- Yu, D. W., and D. W. Davidson. 1997. Experimental studies of species-specificity in *Cecropia*–ant relationships. *Ecological Monographs* 67:273–294.
- Yu, D. W., H. B. Wilson, and N. E. Pierce. 2001. An empirical model of species coexistence in a spatially structured environment. *Ecology* 82:1761–1771.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/14-0481.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.h6t7g>