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# The intertwined population biology of two Amazonian myrmecophytes and their symbiotic ants

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*Abstract*. A major question in ecology is: how do mutualisms between species affect population dynamics? For four years, we monitored populations of two Amazonian myrmecophytes, *Cordia nodosa* and *Duroia hirsuta,* and their symbiotic ants. In this system, we investigated how positive feedback between mutualistic plants and ant colonies influenced population processes at two scales: (1) how modular organisms such as plants and ant colonies grew, or $\eta$-demography, and (2) how populations grew, or *N*-demography. We found evidence of positive feedback between ant colony and plant growth rates. Plants with mutualistic ants (*Azteca* spp. and *Myrmelachista schumanni*) grew in a geometric or autocatalytic manner, such that the largest plants grew the most. By contrast, the growth of plants with parasitic ants (*Allomerus octoarticulatus*) saturated. Ant colonies occupied new domatia as fast as plants produced them, suggesting that mutualistic ant colonies also grew geometrically or autocatalytically to match plant growth. Plants became smaller when they lost ants. While unoccupied, plants continued to become smaller until they had lost all or nearly all their domatia. Hence, the loss of mutualistic ants limited plant growth. *C. nodosa* and *D. hirsuta* live longer than their ant symbionts and were sometimes recolonized after losing ants, which again promoted plant growth. Plant growth had fitness consequences for ants and plants; mortality and fecundity depended on plant size. Positive feedback between ants and plants allowed a few plants and ant colonies to become very large; these probably produced the majority of offspring in the next generation.

*Key words: ant–plant interactions;* Cordia nodosa; *demography; domatia;* Duroia hirsuta; *modularity; mutualism; myrmecophytes; Peru; population dynamics; positive feedback; symbiosis.*

## INTRODUCTION

How do interactions between species affect the dynamics of natural populations? Over nearly a century, ecologists have made substantial progress toward understanding the population dynamics of competitive and trophic interactions. By comparison, the population dynamics of reciprocally beneficial interactions between species, or mutualisms, are not well understood (Holland et al. 2002), even though mutualisms are ubiquitous and ecologically important (Boucher et al. 1982, Bronstein 1994, Bruno et al. 2003).

Early efforts to model the population dynamics of mutualism quickly identified an important issue: positive feedback between mutualists tends to generate runaway population growth. The first models of mutualism began by taking the Lotka-Volterra competition equations and reversing the signs of the competition coefficients (Gause and Witt 1935). But in these models, if the effect of mutualism is sufficiently strong, populations grow to infinity in what May (1982) called "an orgy of reciprocal benefaction." This led many to suggest how explosive population growth might be kept under control (Goh 1979, Heithaus et al. 1980, Addicott 1981, May 1981, 1982, Boucher et al. 1982, Dean 1983, Wolin and Lawlor 1984, Pierce and Young 1986, Wright 1989). Three general solutions emerged: resource limitation may result in intraspecific competition that limits population growth (e.g., Goh 1979); a third species such as a predator or a competitor may limit population growth (e.g., Heithaus et al. 1980); or there may be diminishing returns to the mutualism as populations grow (e.g., Holland et al. 2002). Nonetheless, how the costs and benefits of mutualism shape population dynamics remains an open empirical question (Holland et al. 2002).

Symbiotic mutualisms pose a particular problem because they are spatially structured and highly variable from one interaction to the next. Symbioses are intimate associations between species that involve protracted physical contact between partners (Boucher et al. 1982, Saffo 1992). Many mutualisms are symbiotic, such as corals and dinoflagellates, or plants and mycorrhizal fungi, though many are not, such as plants and pollinators, or plants and seed dispersers. The mean-field assumption of models based on the Lotka-Volterra equations is a good approximation when populations are well mixed, but breaks down when individuals live in

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spatially structured environments (Dieckmann et al. 2000, Pascual 2005). Symbiotic organisms interact in local "neighborhoods" often comprised of only two individuals, host and symbiont. In symbioses, the benefits of mutualism are repeatedly exchanged between the same two partners, with the result that survival and reproduction depend more on the traits of the individual partners, than on their population densities. Many studies have investigated the effects of spatial structure and individual variability in competitive and trophic interactions (Huston et al. 1988, Dieckmann et al. 2000, and references therein). Here we consider the effects of spatial structure and individual variability on the population dynamics of mutualism.

Many symbiotic mutualisms occur between organisms with modular growth. Such organisms grow by the iteration of modules, permitting indeterminate growth. The modules may or may not become physically separate units. Corals and dinoflagellates, plants and mycorrhizal fungi, fungi and algae, termites and their gut protozoa, plants and ants, and ants and fungi are all examples of symbiotic mutualisms involving modular organisms (Wulff 1985). Demographic processes occur at two levels in modular organisms: individual organisms grow as modules are born and die, producing $\eta$-demography; and populations grow as individuals are born and die, producing $N$-demography (Harper 1977, 1981, Dirzo 1984, Watkinson and White 1986). Thus the population dynamics of modular organisms have a nested structure, with $\eta$-demography nested in $N$-demography. When a symbiotic mutualism occurs between modular organisms, the interaction tends to directly affect the $\eta$-demography of the participants, and in so doing, indirectly affects $N$-demography.

Here we consider a symbiotic mutualism between a plant and an ant colony in which the ant colony nests inside the plant's hollow stems. Plants are modular because they grow by the serial repetition of shoots; ant colonies are modular because they grow by the addition of sterile workers. Changes in the size of plants or ant colonies can be positive or negative, depending on the birth and death rates of shoots and workers, respectively (Watkinson and White 1986, Tschinkel 1993). This is the $\eta$-demography of plants and ant colonies, while $N$-demography involves the births and deaths of whole plants and whole ant colonies. In symbiotic mutualisms between ants and plants, the benefits of mutualism generally accrue at the level of $\eta$-demography and in turn, $\eta$-demography generates $N$-demography. Ant workers usually defend their host plant against herbivores (Heil and McKey 2003), which affects the $\eta$-demography of plants by reducing the death rates of plant modules/shoots. From the plant, the ant colony receives nest sites in the form of hollow stems, which should both increase the birth rate and decrease the death rate of ant modules/workers. These effects translate to $N$-demography. First, when all the shoots on a plant die, the plant dies as well, and the same is true for workers and ant colonies. Similarly, though by more complex processes, births of plant shoots or ant workers are converted into reproduction, the births of new plants or new ant colonies.

Few time-series data are available with which to evaluate population-dynamical models of mutualism. Here we report time-series data on the $\eta$- and $N$-demography of two plant species and four ant species that interact as mutualists in the Amazonian rain forest; and for comparison, we report on an ant species that is a parasite of these mutualisms. To explore how positive feedback, symbiosis, and modularity shape the population dynamics of these ant–plant interactions, we investigate how the growth rate of a plant (i.e., $\eta$-demography) changes over the course of its symbiotic association with an ant colony and following the death or desertion of the ant colony. We also consider the $\eta$-demography of ant colonies. We then examine how changes in $\eta$-demography, especially those changes that result from positive feedback between mutualists, affect the $N$-demography of ant colonies and plants.

## Study System

We studied two species of myrmecophytic plants, *Cordia nodosa* Lam. (Boraginaceae) and *Duroia hirsuta* [Poeppig and Endl.] K. Schum (Rubiaceae), and their ant symbionts. Myrmecophytes are plants that bear specialized structures, called domatia, to house ants. Most myrmecophytes produce domatia constitutively (Blüthgen and Wesenberg 2001), and both *C. nodosa* and *D. hirsuta* produce hollow, swollen stem domatia, whether or not ants are present (see Plate 1). Both *C. nodosa* and *D. hirsuta* produce one domatium per internode, so individual plants can be considered to grow as populations of domatia. Plants add domatia as they grow and lose domatia when branches die and fall off. Hence, the $\eta$-demography of these plants can be described as changes over time in the number of domatia per plant.

Phytoecious ants nest inside the domatia of myrmecophytic plants (Quek et al. 2004). *C. nodosa* and *D. hirsuta* associate with two or more phytoecious ant species each. Two ant species associate with both plants: *Azteca depilis* Emery (Dolichoderinae) and *Myrmelachista schumanni* Emery (Formicinae). These two species are the only ants that associate with *D. hirsuta*. *C. nodosa* also associates with two undescribed species in the genus *Azteca,* and with *Allomerus octoarticulatus* Mayr (Myrmicinae). Workers are often seen walking between domatia along plant stems, but reproductives are rarely observed outside domatia. All of these ant species tend scale insects (Hemiptera: Sternorrhyncha: Coccoidea) inside plant domatia; the scale insects provide food to the ant colony in the form of honeydew.

The ant species differ in how they treat their host plants. *Azteca* spp. and *M. schumanni* behave as mutualists, protecting their host plants against herbivores (Frederickson 2005). *M. schumanni* also provides an extra benefit; workers of this species kill heterospecific plants (potential competitors) near their host plants, thereby creating large stands of host plants called "devil's gardens" (Frederickson et al. 2005). *Al. octoarticulatus* behaves as a parasite. Although worker *Al. octoarticulatus* ants protect *C. nodosa* leaves against herbivores, they do not protect plant stems (Yu and Pierce 1998, Frederickson 2005). As a result, *C. nodosa* with *Al. octoarticulatus* ants are more frequently girdled by *Trachysomus* beetles than *C. nodosa* with other ant species (Yu and Pierce 1998, Frederickson 2005). Furthermore, *Al. octoarticulatus* sterilizes *C. nodosa* by destroying flowers (Yu and Pierce 1998).

*Azteca* spp. and *Al. octoarticulatus* colonies are monogynous, meaning each colony has a single egg-laying queen. One *Azteca* spp. or *Al. octoarticulatus* colony nests in a single host tree. In contrast, *M. schumanni* colonies are polygynous, meaning they have multiple egg-laying queens, and these colonies can occupy many host plants (Frederickson et al. 2005, Frederickson and Gordon 2007). All these ant species found colonies independently; queens fly to plants to colonize them. A colony of *M. schumanni* begins in the same way as an *Azteca* spp. or *Al. octoarticulatus* colony; a queen colonizes a single host tree, lays eggs, and produces workers. However, unlike the other ants, *M. schumanni* workers kill heterospecific plants growing near their host plant, thereby creating a bare patch where, over time, more *D. hirsuta* and *C. nodosa* trees establish. The *M. schumanni* colony expands to occupy the new plants and continues to enlarge the patch. As the *M. schumanni* colony grows, it adds queens, although it is not known by what mechanism. The *M. schumanni* colony can occupy any number of trees from one to several hundred; when the colony occupies many trees, the trees are clumped together to form a devil's garden.

## Methods

For four years, we monitored populations of *Cordia nodosa* and *Duroia hirsuta* in a 4-ha plot at Madre Selva Biological Station (MSBS; 3.63° S, 72.24° W) on the Rio Orosa in the Department of Loreto, Peru. The 4-ha plot was oriented along cardinal directions and divided into 16 $50 \times 50$ m squares. In July–August of 2002, 2003, 2004, and 2005, we exhaustively searched each square for all domatia-bearing *C. nodosa* and *D. hirsuta* plants by walking each square back and forth in a series of 2.5-m transects. Every year, we numbered, tagged, and mapped each new (i.e., unmarked) plant that we found, and we visited every plant that had been marked in previous years. Every year, we counted the number of domatia on every plant in the plot, except in 2005, when we counted domatia only on new plants and on plants without ants. We also recorded whether plants were producing flowers and fruit, and which species of symbiotic ant, if any, occupied each plant. A plant was considered to be occupied by ants if workers were observed on the plant. For *Azteca* spp. inhabiting *C. nodosa*, ants were identified only to genus because species are difficult to distinguish based on worker morphology alone, and we rarely observed reproductives.

In 2004–2005, we collected ant colonies at a second site, the Reserva Nacional Allpahuayo-Mishana (RNAM; 3.96° S, 73.4° W), located about 130 km west of MSBS on the Iquitos-Nauta highway in Loreto, Peru. Of the three species of *Azteca* that occupy *C. nodosa,* we focused only on *Azteca depilis*. We collected a total of 181 *Allomerus octoarticulatus* colonies and 97 *Az. depilis* colonies (40 from *C. nodosa* and 57 from *D. hirsuta*). We also collected the ants inhabiting 21 *D. hirsuta* trees from 10 *Myrmelachista schumanni* colonies. To collect the ants, we removed all domatia from each tree using tree pruners and then sealed the domatia in Ziploc bags. We could not prevent workers from escaping during collection, but we could collect nearly all reproductives because they rarely leave domatia, even when disturbed. Bags of domatia were stored in an ice chest after collection. Within 48 hours of collection, each domatium was cut open and the contents examined. Each domatium was scored as containing reproductives (with or without workers), containing workers only, or being empty. We recorded the number of female alates and female alate pupae for each domatium containing reproductives.

For the ant species, we define $\eta$ as the number of workers in an ant colony, and $N$ as the number of ant colonies in the population. Similarly, for the plants, we define $\eta$ as the number of domatia on a tree and $N$ as the number of trees in the population.

### $\eta$-*demography of myrmecophytic plants*

We considered plants to be growing as populations of domatia, such that $\eta_t$ is the number of domatia on a plant at time $t$. We used geometric growth as a null model; we chose a discrete-time model because we counted domatia on trees at discrete time intervals of one year. The branching pattern of many trees is evocative of geometric growth (i.e., one branch splits to become two, which split to become four, etc.). If a plant is growing geometrically, then $\eta_{t+1} = R\eta_t$. $R$ is the geometric growth factor; if $R < 1$, the plant is getting smaller by losing more domatia than it adds, and if $R > 1$, the plant is getting bigger by adding more domatia than it loses. Geometric growth assumes that $R$ does not depend on $\eta$ (Roughgarden 1998, Turchin 2003). This property of geometric growth is usually called "density independence" in population biology. Here we call it "size independence" because the concept of population density does not translate well from $N$-demography to $\eta$-demography.

We tested whether the growth of *C. nodosa* and *D. hirsuta* is size independent by analyzing the relationship between $R$ and $\eta$ using linear regression. We used data from the 2003–2004 census interval to calculate $R$, or $\eta_{2004}/\eta_{2003}$, and to investigate the relationship between

$R$ and $\eta_{2003}$. We used the data from the 2003–2004 census interval because we did not count the number of domatia on all plants in 2005, and sample sizes were larger in 2003–2004 than in 2002–2003. To investigate whether the nonindependence of $R$ and $\eta$ inflated the significance of the regression analyses, we created our own null distributions by recalculating regressions for random re-pairings of $R$ and $\eta_{2003}$. We compared the observed regression coefficients against the distribution of regression coefficients generated by 10 000 iterations of the randomization procedure. $P$ values were calculated by counting the number of times the regression coefficients of the randomized data were greater than the observed regression coefficient and dividing by 10 000.

In general, there are three possible relationships between $R$ and $\eta$: (1) No relationship between $R$ and $\eta$ means that plant growth is size independent; we cannot reject the null model that *C. nodosa* and *D. hirsuta* grow geometrically. If $R > 1$, then plants continue to grow larger, becoming infinitely large in infinite time and plant growth does not slow down as plants get large. (If $R < 1$, then plants become smaller and smaller, becoming infinitely small in infinite time.) (2) A positive relationship between $R$ and $\eta$ means that plant growth is positively size dependent, and we reject the null model that plants grow geometrically. Growth is autocatalytic, and plants grow faster, not slower, as trees get large. If autocatalytic growth continues indefinitely, plants will become infinitely large in finite time (Roughgarden 1998). (3) A negative relationship between $R$ and $\eta$ means that plant growth is negatively size dependent. Again, we reject the null model that plants grow geometrically. Instead, plant growth slows down or even becomes negative as plants get large.

We investigated what happens to plant growth when a plant loses its ants. We compared plant growth rate, $R$, between (1) plants whose ants survived the 2003–2004 census interval, and (2) plants whose ants died or abandoned plants in any census interval. The former group included plants whose ants survived through all censuses (2002–2005), and also plants that were colonized by ants between 2002 and 2003 and whose ants survived to 2005. Plants whose ants survived from 2003–2004, but died or abandoned the plant in 2004–2005, were included only in the latter group, so no plant was included in the analysis twice. Plants lost ants when ant colonies died and also when *M. schumanni* colonies abandoned trees. When an ant colony died or abandoned a tree, the plant typically remained unoccupied by ants for at least one census, with few exceptions (Appendix E). Thus we restricted the second group to plants that were occupied by ants in one census but did not have ants in the following census. In general, there were too few data points (i.e., $n \leq 5$) to also compare the growth rate of plants that switched ant species between censuses. Only *Az. depilis* frequently replaced *M. schumanni* on *D. hirsuta* trees within one census interval ($n = 50$); we included these trees as a separate group in the analysis. For plants that retained ants, $R$ was measured as $\eta_{2004}/\eta_{2003}$. For plants that lost ants, $R$ was measured as $\eta_{t+1}/\eta_t$, where $t$ was the census before the ant colony died or deserted the plant, and $t + 1$ was the first census after. We analyzed the data using two-tailed $t$ tests assuming unequal variances or using ANOVA followed by Tukey post hoc tests.

### $\eta$-*demography of phytoecious ant colonies*

We used the data from RNAM to investigate the $\eta$-demography of phytoecious ant colonies. Because we could not prevent workers from escaping during collection, we did not count the number of workers in the ant colonies we collected. Instead we used the number of domatia occupied by ants as an indirect measure of colony size. We analyzed the relationship between the number of domatia occupied by ants and the total number of domatia on a plant, square-root transforming both variables.

### *N-demography of plants and ant colonies*

To evaluate the $N$-demography of ant colonies and plants, we chose the following measures of recruitment and death of ant colonies and host plants. A plant was considered to have recruited into the population if it bore domatia and had not been previously censused, and to have died if all its aboveground tissue was dead. An ant colony was considered to have colonized a plant between censuses if its host plant was not occupied or was occupied by a colony of a different ant species in the previous census. An ant colony was considered to have died between censuses if the host plant that it occupied in one census was not occupied or was occupied by a colony of a different ant species in the next census. For *M. schumanni* colonies that occupied many host plants, we considered a colony to have died when all the host plants previously occupied by the colony were unoccupied or occupied by other ant species. When only some of the host plants previously occupied by a *M. schumanni* colony were unoccupied or occupied by other ants, we considered the *M. schumanni* colony to have abandoned these trees. Our methodology underestimates both ant colony deaths and ant colony colonizations, because we did not count colonies that died and had their host plants colonized by a new colony of the same species before the next census. However, since the numbers of ant colony deaths and ant colony colonizations are underestimated by exactly the same amount, estimates of net population growth rate are not affected.

Since plants were counted in the yearly census only after they produced domatia, and ant colonies were counted only after they produced their first workers, the rates at which plants and ant colonies were added to the population each year represent colonization rates instead of true birth rates. The colonization rate of ant colonies and plants ($b$) was calculated as $b = \ln(N_{t+1}) - \ln(N_t - D)$, the death rate ($d$) as $d = \ln(N_t) - \ln(N_t - D)$, and the net growth rate ($r$) as $r = \ln(N_{t+1}) - \ln(N_t)$, where

TABLE 1. Dependence of plant growth rate, $R$, on plant size, $\eta$, for two species of Amazonian myrmecophytes with or without various ant species.

| Host tree and ant interaction | df | Regression equation | $R^2$ | $P$ | Size dependence |
|---|---|---|---|---|---|
| *Cordia nodosa* | | | | | |
| No interaction (no ants) | 45 | $R = -0.139\eta + 1.517$ | 0.176 | 0.004 | negative |
| Parasitic (*Allomerus octoarticulatus*) | 137 | $R = -0.027\eta + 1.643$ | 0.115 | $\ll 0.001$ | negative |
| Mutualistic (*Azteca* spp.) | 53 | $R = -0.002\eta + 1.341$ | 0.042 | 0.137 | size independent |
| Mutualistic (*Myrmelachista schumanni*) | 15 | $R = -0.004\eta + 1.310$ | 0.027 | 0.541 | size independent |
| *Duroia hirsuta* | | | | | |
| No interaction (no ants) | 107 | $R = -0.003\eta + 0.887$ | 0.009 | 0.327 | size independent |
| Mutualistic (*Azteca depilis*) | 68 | $R = 0.001\eta + 1.097$ | 0.052 | 0.058† | marginally positive |
| Mutualistic (*Myrmelachista schumanni*) | 376 | $R = 0.001\eta + 1.002$ | 0.058 | $\ll 0.001$ | positive |

† The statistical significance of the relationship between $R$ and $\eta$ for *D. hirsuta* with *Az. depilis* was marginal. However, when we excluded one outlier, there was a significant positive relationship, with $P = 0.01$. See also Appendix B: Fig. B1b.

$N_t$ was the number of plants or colonies at the start of the census interval, $N_{t+1}$ was the number of plants or colonies at the end of the census interval, and $D$ was the number of deaths during the census interval (Chew 1987). This model assumes that all deaths occur before any new plants or colonies are added to the population. The geometric mean was used to calculate average rates (Carey 1993). Life expectancy at birth was calculated as the inverse of the average death rate (Carey 2001).

### *Links between $\eta$-demography and N-demography*

We investigated the size dependence of mortality and fecundity for both plants and ant colonies. To investigate the effect of plant size on plant mortality, we compared the initial size of plants that survived the 2003–2004 census interval to the initial size of plants that died in any census interval. To make these comparisons, we used two-sided $t$ tests, assuming unequal variances. The first group included plants that survived through all censuses (2002–2005) and also plants that recruited into the population between 2002 and 2003 and survived to 2005. Plants that survived from 2003–2004, but died in 2004–2005 were included in the latter group, so no plant was included twice. For plants that survived, plant size was measured as the number of domatia in the 2003 census. For plants that died, plant size was measured as the number of domatia in the census before the plant died. To investigate the effects of plant size on ant colony mortality, we performed the same analysis, except we compared plants whose ant colonies survived the 2003–2004 interval to plants that lost ants in any census interval (see *Methods*: $\eta$-*demography of myrmecophytic plants*). We square-root transformed the number of domatia to improve normality. For *M. schumanni,* we also investigated the effect of devil's garden (i.e., patch) size on the survival of *M. schumanni* colonies by comparing the number of trees occupied by a colony that survived the 2003–2004 census interval to the number of trees initially occupied by a colony that died in any census interval. Because the number of trees in devil's gardens was not normally distributed, we used a nonparametric test to make this last comparison.

To determine whether plant fecundity is size dependent, we analyzed the relationship between fruit production and domatia number for *D. hirsuta*. We did not conduct the same analysis for *C. nodosa* because only four out of the 346 *C. nodosa* in our plot were observed to produce fruit during our censuses. We used the data from RNAM to determine the size dependence of ant colony fecundity. We analyzed the relationship between the number of female alates (including both eclosed alates and alate pupae) in an ant colony and the number of domatia on a plant, square-root transforming both variables.

Finally, we investigated the size and age of plants colonized by ants. We divided plants into different age classes and calculated what percentage of unoccupied plants in each age class was colonized by ants. In the first year of our study (2002–2003), we could divide plants into only two age classes: plants more than one year old were present in the initial census in 2002, while plants less than one year old recruited into the population between 2002 and 2003. The next year, we could divide plants into three age classes: plants more than two years old, one to two years old, and less than one year old. Finally, in 2004–2005, we could divide plants into four age classes: plants more than three years old, two to three years old, one to two years old, and less than one year old.

## RESULTS

### $\eta$-*demography of myrmecophytic plants*

Plants with mutualistic ants grew geometrically or autocatalytically for as long as the mutualism persisted, while other plants inevitably reached a size beyond which no further growth was possible. Linear regression and randomization tests produced nearly identical results (Appendix A); only linear regression results are discussed. All three types of size dependence occurred in this system (Table 1). *Cordia nodosa* without ants or with *Allomerus octoarticulatus* exhibited negatively size-dependent growth; there was a significant negative relationship between $R$ and $\eta$ (Table 1; Appendix B). These plants tended to grow when small; the 95% CI around the $y$-intercept was >1 (no ants, 1.174–1.859; *Al.*

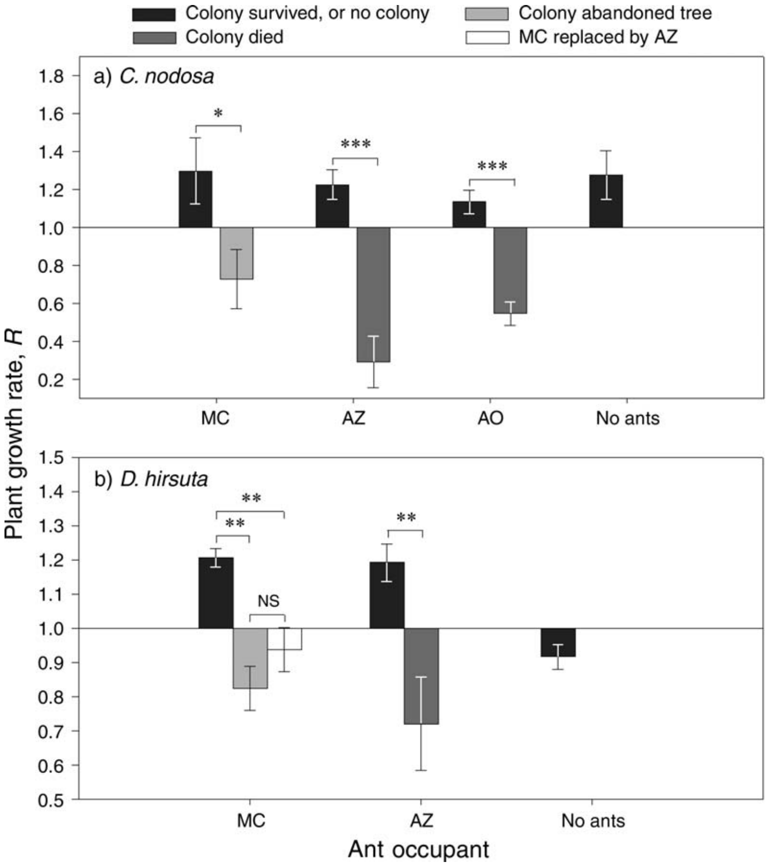

FIG. 1. Plant geometric growth rate, $R$ (mean ± SE), for Amazonian host trees (a) *Cordia nodosa* and (b) *Duroia hirsuta* with different ant partners (MC = *Myrmelachista schumanni,* AZ = *Azteca* spp., AO = *Allomerus octoarticulatus*) or without ants. Black bars represent plants with ant colonies that survived from one census to the next or plants that did not have ants. These plants did not change their occupation status from one census to the next. If they had ants in 2003, they were occupied by the same ant species in 2004, and if they did not have ants in 2003, they still did not have ants in 2004. Dark gray bars represent plants with ant colonies that died between censuses, light gray bars represent plants that were abandoned by *M. schumanni,* and white bars represent plants that were occupied by *M. schumanni* in one census and by *Az. depilis* in the next census. Significance of means is indicated.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, not significant.

*octoarticulatus*, 1.388–1.899). But beyond a certain size, these plants tended to lose domatia overall. This size (i.e., the value of $\eta$ at which $R = 1$) was four domatia for *C. nodosa* without ants and 24 domatia for *C. nodosa* with *Al. octoarticulatus*. By contrast, *Duroia hirsuta* plants without ants did not grow when small. Instead, these plants tended to lose domatia regardless of their initial size; the 95% CI around the $y$-intercept was $<1$ (0.808–0.965). They lost domatia in an approximately geometric fashion; there was no relationship between $R$ and $\eta$ (Table 1, Appendix B). Thus although the two plant species did not have the same growth pattern, in the absence of mutualistic ants, neither *C. nodosa* nor *D. hirsuta* continued to grow after reaching a certain size.

The growth of plants with mutualistic ants did not taper off even at the largest sizes, but continued unabated or even accelerated as plants grew. The growth of *C. nodosa* with mutualistic ants was statistically indistinguishable from geometric growth; $R$ did not depend on $\eta$ (Table 1; Appendix B). For as long as the mutualism persisted, these plants increased in size, and there was no evidence of an upper limit to plant growth. The growth of *D. hirsuta* with mutualistic ants was positively size dependent; these plants grew faster the larger they became (Table 1; Appendix B). The statistical significance was marginal for *D. hirsuta* with *Azteca depilis,* but became highly significant when we excluded one outlier. For both *Myrmelachista schumanni*- and *Az. depilis*-occupied *D. hirsuta*, the effect of the positive slope of the relationship between $R$ and $\eta$ was negligible at small sizes but substantial for large plants. We calculated that, as a result of the positive feedback between $R$ and $\eta$, a *D. hirsuta* plant with 32 domatia gains only one extra domatium in a year, but a *D. hirsuta* plant with 200 domatia gains 40 extra domatia, and a *D. hirsuta* plant with 400 domatia gains 160 extra domatia in a year.

Plants grew for as long as they were occupied by mutualistic ants, but became smaller when they lost ants (Fig. 1). In the case of plants with *Azteca* spp. or *Al.*

PLATE 1. *Cordia nodosa* (left) and *Duroia hirsuta* (right) branches, showing the stem swellings (domatia) that house ants. Photo credit: M. E. Frederickson.

*octoarticulatus* ants, mean plant growth was significantly greater for plants with ant colonies that survived than for plants with ant colonies that died between censuses (Fig. 1; *C. nodosa* with *Azteca* spp., $t_{14} = 5.94$, $P < 0.0001$; *C. nodosa* with *Al. octoarticulatus*, $t_{135} = 6.78$, $P < 0.0001$; *D. hirsuta* with *Az. depilis*, $t_{12} = 3.20$, $P = 0.008$). Most of the *C. nodosa* plants that lost *M. schumanni* ants were abandoned by the colony and did not have ants in the next census ($n = 8$). Three *C. nodosa* trees were inhabited by other ants after losing *M. schumanni,* and one *M. schumanni* colony inhabiting a single, isolated *C. nodosa* tree died; these trees were not included in the analysis. *C. nodosa* plants abandoned by *M. schumanni* grew significantly less than *C. nodosa* plants that kept *M. schumanni* (Fig. 1; $t_{19} = 2.43$, $P = 0.03$). Similarly, most of the *D. hirsuta* trees that lost *M. schumanni* ants were abandoned by the colony and did not have ants in the next census ($n = 103$). However, a large number of *D. hirsuta* trees were occupied by *M. schumanni* ants in one census, but by *Az. depilis* in the next ($n = 50$). Both of these groups of trees grew significantly less than *D. hirsuta* that kept *M. schumanni* (Fig. 1; ANOVA, $F_{2,386} = 24.00$, $P < 0.0001$). Five *M. schumanni* colonies occupying only one or a few *D. hirsuta* trees died during the study; in three cases, a *M. schumanni* colony on an isolated *D. hirsuta* was replaced by an *Az. depilis* colony between censuses. Again, these trees were not included in the analysis of plant growth rate because of the very small sample sizes.

### η-*demography of phytoecious ant colonies*

Ants occupied nearly all the available domatia on a host plant, no matter how large a plant became. The number of occupied domatia and the total number of domatia were strongly and significantly correlated for all ant–plant associations (Appendix C; *C. nodosa* with *Al. octoarticulatus*, $r^2 = 0.996$, $P < 0.0001$; *C. nodosa* with *Az. depilis*, $r^2 = 0.995$, $P < 0.0001$; *D. hirsuta* with *Az. depilis*: $r^2 = 0.991$, $P < 0.0001$; *D. hirsuta* with *M. schumanni*, $r^2 = 1.000$, $P < 0.0001$). The number of occupied domatia did not saturate as plants became large.

### *N-demography of plants and ant colonies*

On average, *C. nodosa* and *D. hirsuta* plants lived longer than their ant colonies. Per capita annual mortality of *C. nodosa* and *D. hirsuta* averaged 0.013 and 0.017, respectively (Appendix D). Thus life expectancies at birth for *C. nodosa* and *D. hirsuta* are approximately 77 years and 59 years, respectively. Ant colony mortality exceeded plant mortality, averaging 0.128 for *Al. octoarticulatus* colonies, 0.072 for colonies of *Azteca* spp. inhabiting *C. nodosa*, 0.074 for *Az. depilis* colonies inhabiting *D. hirsuta*, and 0.093 for *M. schumanni* colonies (Appendix D). Thus life expectancy is approximately 7.8 years for *Al. octoarticulatus* colonies, 14 years for *Azteca* spp. colonies, and 11 years for *M. schumanni* colonies.

There was little evidence that one ant colony ever invades and expels another colony that is already established on a host plant. Ants generally colonized plants that were unoccupied at the previous census (Appendix E). There was one major exception: *Az. depilis* colonized 50 *D. hirsuta* plants that were occupied by *M. schumanni* at the previous census (Appendix E). These were located mostly around the margins of devil's gardens. It was not possible to determine whether *M. schumanni* vacated these plants before they were colonized by *Az. depilis*, or whether *Az. depilis* actively cast out *M. schumanni* from these plants. However, four of the six *M. schumanni* colonies that died (Appendix D2) were immediately replaced by *Az. depilis* colonies, suggesting that if they occur, *Az. depilis* takeovers of *M. schumanni* colonies may be an important source of mortality for *M. schumanni* colonies.

Because *C. nodosa* and *D. hirsuta* live longer than their ant symbionts, these plants can be repeatedly colonized by ants throughout their lives. Ninety-eight out of a total of 174 ant colonizations of plants, or 56%, occurred on plants that had previously been occupied by ants, even though most plants were unoccupied immediately before colonization. In addition to the 50 *D. hirsuta* that were occupied by *M. schumanni* at the

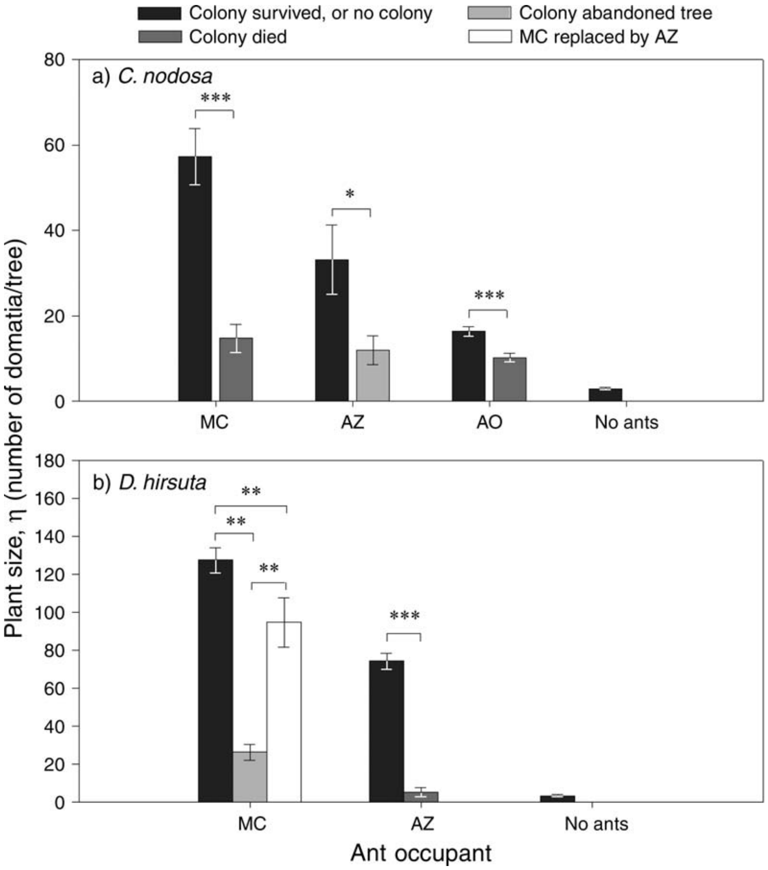

FIG. 2. Initial plant size, η (mean ± SE), for Amazonian host trees (a) *Cordia nodosa* and (b) *Duroia hirsuta* with different ant partners (MC = *Myrmelachista schumanni*, AZ = *Azteca* spp., AO = *Allomerus octoarticulatus*) or without ants. Plant size is measured as the number of domatia per tree. Explanations of bar shading are the same as in Fig. 1. Significance of means is indicated as * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, not significant.

census before they were colonized by *Az. depilis*, another 13 plants were occupied by a different ant species the year before they were colonized (Appendix E). An additional 32 plants were colonized by ants after losing ants and being unoccupied in one census, and three were colonized by ants after losing ants and being unoccupied in two consecutive censuses.

### *Links between η- and N-demography*

Plants that died were significantly smaller than plants that survived. *C. nodosa* that died had 6.77 ± 1.45 (mean ± SE) domatia, while *C. nodosa* that survived had 20.9 ± 1.62 domatia ($t_{19} = 4.93$, $P < 0.0001$). *D. hirsuta* that died had 35.5 ± 10.9 domatia, while *D. hirsuta* that survived had 81.7 ± 3.82 domatia ($t_{32} = 3.96$, $P = 0.0003$). Ant colonies that died inhabited significantly smaller plants than ant colonies that survived (Fig. 2; *C. nodosa* with *Al. octoarticulatus*, $t_{116} = 3.95$, $P = 0.0001$; *C. nodosa* with *Azteca* spp., $t_{21} = 5.44$, $P < 0.0001$; *D. hirsuta* with *Az. depilis*, $t_{54} = 8.09$, $P < 0.0001$). *C. nodosa* abandoned by *M. schumanni* were significantly smaller than *C. nodosa* that retained *M. schumanni* (Fig. 2; *C. nodosa* with *M. schumanni*, $t_{19} = 2.43$, $P = 0.03$). Similarly, *D. hirsuta* abandoned by *M. schumanni* were significantly smaller than *D. hirsuta* that kept *M. schumanni*; *D. hirsuta* on which *M. schumanni* was replaced by *Az. depilis* were intermediate in size between these two groups (Fig. 2; ANOVA, $F_{2,386} = 70.85$, $P < 0.0001$). Only six *M. schumanni* colonies died during our study, and these colonies occupied significantly fewer plants than the *M. schumanni* colonies that survived ($U_{6,20} = 30$, $P = 0.04$); in four cases, *M. schumanni* colonies that died had occupied just one host plant. Thus small plants are more likely to lose ants than large plants, and the same is true for small devil's gardens.

Larger *D. hirsuta* plants produced more fruit (in 2004, $r^2 = 0.093$, $P < 0.0001$). Similarly, ant colonies that lived in larger plants produced more female alates (Appendix F; *C. nodosa* with *Al. octoarticulatus*, $r^2 = 0.223$, $P < 0.0001$; *C. nodosa* with *Az. depilis*, $r^2 = 0.316$, $P = 0.0002$; *D. hirsuta* with *Az. depilis*, $r^2 = 0.311$, $P < 0.0001$), except for *D. hirsuta* with *M. schumanni*. The number of female *M. schumanni* alates in a *D. hirsuta* tree was not correlated with the number of domatia on the tree ($r^2 = 0.075$, $P = 0.23$), but instead with the number of *D.*

*hirsuta* trees in the devil's garden where the tree was located ($r^2 = 0.823$, $P = 0.0003$).

Ants generally colonized small plants, irrespective of plant age. With the exception of *Az. depilis* that colonized *D. hirsuta* previously occupied by *M. schumanni*, plants bore an average of 11 or fewer domatia at the census before they were colonized by ants and belonged to any age class (Appendix E).

## DISCUSSION

### $\eta$-*demography: positive feedback between mutualistic ant colonies and plants*

Our results suggest that ants affect the $\eta$-demography of their host plants. Plants with mutualistic ants grew in a geometric (*Cordia nodosa*) or autocatalytic (*Duroia hirsuta*) manner. The growth of these plants did not taper off, but instead continued unabated or even accelerated as plants grew large, such that the largest plants grew the most. By contrast, plants without ants or plants with parasitic ants reached sizes beyond which no further growth was possible; plants not inhabited by mutualistic ants tended to become smaller once they had more than 24 domatia in the case of *C. nodosa* with *Al. octoarticulatus*, more than four domatia in the case of *C. nodosa* without ants, or any domatia at all in the case of *D. hirsuta* without ants. Ants occupied new domatia as fast as plants produced them. Thus either colony growth keeps pace with plant growth, or the number of workers occupying each domatium declines as a plant grows. If the first alternative is true, then mutualistic ant colonies also grow geometrically or autocatalytically to match the growth of *C. nodosa* and *D. hirsuta*.

We expected to find that plant and ant colony growth eventually tapered off, regardless of the type of ant–plant interaction, because this is the way most modular organisms grow. Modular organisms like trees and ant colonies usually grow quickly when small and more slowly as they become large (Oster and Wilson 1978, Sebens 1987, Gordon 1992, 1995, Tschinkel 1993, Ryan and Yoder 1997). All organisms consume resources as they grow, depleting the resources available locally for further growth. Since most modular organisms have limited mobility, local resource depletion should cause the growth of modular organisms to slow down over time. Moreover, many modular organisms are prevented from growing to the point that resources become limiting by other factors, such as physiological constraints that increase with size (e.g., transporting water to the top of a tall tree; Koch et al. 2004). However, there was no evidence that growth attenuated at large sizes for plants inhabited by mutualistic ant species.

Our results suggest that in these mutualisms, positive feedback between ant colony and plant growth allows the partners to overcome factors that would otherwise limit growth. Herbivory is probably one such factor limiting the growth of *C. nodosa* and *D. hirsuta* in the absence of ants. All the ant species we studied protect the leaves of their host plants against foliovores, even the parasite, *Allomerus octoarticulatus*. In a previous study at Madre Selva Biological Station (MSBS), naturally occurring *C. nodosa* and *D. hirsuta* without ants sustained roughly twice the folivory as *C. nodosa* and *D. hirsuta* with ants, and folivory increased severalfold when ants were experimentally excluded (Frederickson 2005). At a different site, simulated folivory on *C. nodosa* led to increased mortality of domatia (Edwards et al. 2006).

Studies of other ant–plant interactions have found that as an ant colony grows, it provides more protection from herbivory to its host plant (Duarte Rocha and Godoy Bergallo 1992, Gaume et al. 1998, Heil et al. 2001). It seems likely that the more ants can lower the burden of herbivory, the more resources a plant can devote to growth, and especially to the production of domatia. Domatia are often a limiting resource for phytoecious ants (Fonseca 1993, 1999, Gaume et al. 1998), but as an ant colony grows, it increases the amount of available resources by promoting plant growth. For ant species not involved in a mutualism, this positive relation between colony growth and resource abundance does not hold; though a larger colony may be able to obtain more resources, e.g., because it has more foragers, larger colonies are also more likely to deplete available resources. Because phytoecious ant colonies use their mutualistic partners as resources, and promote the growth of their partners, there is an opportunity for geometric or even autocatalytic growth.

### $\eta$-*demography: what limits positive feedback between mutualistic ant colonies and plants?*

Positive feedback between mutualists must eventually be countered by a negative effect, or else plants and ant colonies would grow to be infinitely large. Several researchers have proposed that the growth of mutualistic populations may be curbed by diminishing returns to the mutualism as populations grow (Breton and Addicott 1992, Holland et al. 2002, Bronstein et al. 2003). Fonseca (1993) suggested that as an ant colony inhabiting a plant grows, the protective benefit the colony provides to the plant may saturate because the contribution each ant worker makes to plant defense may be greater in a small than a large colony, while the cost of each worker to the plant remains the same. If herbivore pressure on a plant remains constant as the plant and its ant colony grow, eventually there should be enough ants in the colony to reduce herbivory on the plant to zero. Any further ant colony growth cannot benefit the plant, but ant colony growth may still bear a cost. Diminishing returns such as this should produce negative size dependence, and plant growth should slow as plants and ant colonies become large.

Because we did not find any evidence of negative size dependence, even at very large plant sizes, we doubt that the ant–plant mutualisms we studied are subject to diminishing returns of this type. It is possible that herbivore pressure does not remain constant, but instead increases as plants grow; larger plants may be bigger targets and provide more abundant resources for herbivores. For *D. hirsuta* with mutualistic ants, which exhibited positive size-dependent growth, the benefits of mutualism may be subject not to diminishing but to increasing returns as the plant grows. For example, twice as many ant workers could be more than twice as good at defending the plant against herbivores, perhaps because large colonies are more efficient at organizing work than small colonies (Gordon 1987, 1992, Anderson and Ratnieks 1999).

However, protection against herbivory is not the only benefit ants can provide to plants. The best evidence for autocatalytic growth came from *D. hirsuta* trees with *Myrmelachista schumanni* ants. These ants provide at least two benefits to their host plants; not only do they defend their host plants against herbivores, they also kill heterospecific plants to create large patches of mostly *D. hirsuta* trees and the occasional *C. nodosa* (Frederickson et al. 2005). In so doing, *M. schumanni* alters the local environment in many ways, reducing canopy cover (Frederickson 2005) and presumably decreasing interspecific competition for light and other resources. The positive size dependence of *D. hirsuta* trees with *M. schumanni* ants may be related to these factors, and not to herbivory. Yet another explanation for the growth pattern of *D. hirsuta* with *M. schumanni* is that *M. schumanni* abandons slow-growing trees. Further research and manipulative experiments are needed to understand how the myriad benefits and costs of mutualism change with plant and ant colony size, and how the size dependence of benefits and costs varies among partners and among local environments, including that created by *M. schumanni*.

Ultimately, the reason we did not find evidence of negative size dependence among plants with mutualistic ants was that plants lost their ants before resources or other constraints limited plant growth. Hence, the loss of mutualistic ants limits the growth of *C. nodosa* and *D. hirsuta*. Plants grew when occupied by mutualistic ants, but became smaller when the ant colony died or, in the case of *M. schumanni*, when ant colony fragments abandoned trees. (Our data set did not allow us to determine whether plants became smaller and then lost ants as a result, or plants became smaller after losing their ants, or both.) Host plants grow much like investments earning compound interest. The size of the host plant (or investment) at maturity depends on how fast the plant grows (the interest rate) and how long the plant grows (the term of investment). The term of investment, or how long the plant grows, is often a consequence of the life span of its partner, or in the case of *M. schumanni*, the residence time of the ants on a tree. Because both the interest rate and the term of investment vary among ant species, the maximum size of *C. nodosa* and *D. hirsuta* is highly variable, depending on the ant species occupying the plant. In 2004, the 95th percentile of plant size was: 31 domatia for *Al. octoarticulatus*-occupied *C. nodosa* ($n = 164$), 152 domatia for *Azteca* spp.-occupied *C. nodosa* ($n = 61$), 40 domatia for *M. schumanni*-occupied *C. nodosa* ($n = 19$), 231 domatia for *Az. depilis*-occupied *D. hirsuta* ($n = 89$), and 383 domatia for *M. schumanni*-occupied *D. hirsuta* ($n = 385$).

### η-*demography: the special case of* Allomerus octoarticulatus

What causes the negative size dependence observed for *C. nodosa* with *Al. octoarticulatus*? Small *Al. octoarticulatus*-occupied *C. nodosa* grew, but large *Al. octoarticulatus*-occupied *C. nodosa* lost domatia and became smaller. *Al. octoarticulatus* is a parasite of *C. nodosa*, but its parasitic behaviors are apparent only at large plant sizes. *Al. octoarticulatus* protects *C. nodosa* leaves, but not stems, against herbivores. As a result, the stems of *Al. octoarticulatus*-occupied *C. nodosa* are more frequently girdled by *Trachysomus* beetles than are those of *C. nodosa* with other ants (Yu and Pierce 1998, Frederickson 2005). Domatia on girdled stems rot and fall off shortly after being attacked. Because the beetles tend to girdle larger plants (Yu and Pierce 1998, Frederickson 2005), the fact that *Al. octoarticulatus* does not protect plant stems becomes increasingly important to plant growth as plants grow large.

An alternate explanation for the growth pattern of *Al. octoarticulatus*-occupied *C. nodosa* comes from the sterilization behavior of *Al. octoarticulatus*. *Al. octoarticulatus* destroys *C. nodosa* flowers (Yu and Pierce 1998), but only once the plant is large enough to reproduce. If plants "punish" ants for destroying flowers by losing domatia, this could also explain why *Al. octoarticulatus*-occupied *C. nodosa* grow when small but lose domatia when large. Yu and Pierce (1998) proposed the opposite, however; they hypothesized that *Al. octoarticulatus* sterilizes *C. nodosa* so that the plant continues to invest resources in growth, resources that would otherwise be diverted to reproduction. It is difficult to reconcile this hypothesis with the observed growth pattern of *Al. octoarticulatus*-occupied *C. nodosa*, and future work will investigate the growth consequences of *Al. octoarticulatus* sterilization of *C. nodosa*.

### *Links between* η- *and N-demography*

Because the plants in this system live longer than their ant symbionts, they are probably occupied by several different ant colonies over the course of their lives. For the most part, ants colonized plants that were not already occupied by ants, and most of these plants were small, bearing just a few domatia. However, many of these small, unoccupied plants were not juveniles; as in many modular organisms (Watkinson and White 1986), size and age are not well correlated for *C. nodosa* and *D. hirsuta*. There are several situations in which plants can become smaller (e.g., the death or abandonment of an ant colony, the presence of *Al. octoarticulatus* on a large plant, and time spent without ants), so plant size is not a good measure of plant age. The relationship between age and size is asymmetric; large plants must be old because it takes time to grow large, but small plants can be old or young. Ants frequently colonized plants in the oldest age class, most of which had regressed to the size of saplings because they did not have ants.

We found that the more a plant grew, the more likely it was to retain its ant colony, thus encouraging further growth. In such positive-feedback processes, it is difficult to disentangle cause and effect; ant colony survival may be both a cause and an effect of plant growth. Such a "runaway" process probably explains why a small number of *C. nodosa* and *D. hirsuta* reach enormous sizes; most plants are small, but a few are very large, such that the size distributions of *C. nodosa* and *D. hirsuta* have very long tails to the right (Appendix G).

A runaway process may also explain why a small number of devil's gardens become very large and very old. An interesting difference between *Azteca* spp., *Al. octoarticulatus*, and *M. schumanni* is that *Azteca* spp. and *Al. octoarticulatus* affect only the $\eta$-demography of their host plants directly; when ant workers defend their host plant against herbivores they promote plant growth. But *M. schumanni* directly affects both the $\eta$- and the $N$-demography of its host plants. The benefits that a *M. schumanni* colony provides to its host plants promote the growth of individual trees ($\eta$-demography) and also promote the recruitment of new trees into the population ($N$-demography). The average *M. schumanni* colony at MSBS inhabited 23 *D. hirsuta* trees in 2004, but one large colony at the Reserva Nacional Allpahuayo-Mishana inhabited 594 *D. hirsuta* trees. Similarly, the average life expectancy of *M. schumanni* colonies is 11 years, but previous work estimated that one colony at MSBS may be 800 years old (Frederickson et al. 2005).

Plant growth had fitness consequences for both plant and ant partners, because for both, mortality and fecundity were significantly size dependent. Plants that died were significantly smaller than plants that survived. *Al. octoarticulatus* and *Azteca* spp. colonies that died lived in plants that were significantly smaller than plants occupied by colonies that survived, and *Al. octoarticulatus* and *Az. depilis* colonies living in larger plants produced more female alates. Larger *D. hirsuta* bore more fruit, although plant size explained only a small proportion of the variation in fruit number. Most *D. hirsuta* and *C. nodosa* were not producing fruit in July and August when we conducted our censuses, making it difficult to evaluate the strength of the relationship between plant size and fruit production, especially for *C. nodosa*. However, another study measured fruit production by *Azteca* spp.-occupied *C. nodosa* over an 11-month period and found that fruit production was highly correlated with the number of domatia on a plant (Yu and Pierce 1998). For *M. schumanni* colonies, which can occupy many host plants, the size of the devil's garden or host plant patch occupied by a colony determined mortality and fecundity. The number of female *M. schumanni* alates in a *D. hirsuta* tree was correlated with the number of *D. hirsuta* trees occupied by the ant colony, not with the number of domatia on the tree. *M. schumanni* colony mortality also depended on the number of trees occupied by the colony; *M. schumanni* colonies that died occupied significantly fewer trees than colonies that survived.

Because fecundity and mortality are correlated with plant growth (or patch growth, for *M. schumanni*), the few enormous plants (or plant patches) in the population probably produce the majority of plant and ant offspring in the next generation. As a result, selection on traits that promote runaway growth should be strong. Because plant growth is limited by the loss of mutualistic ants, natural selection on the plants should promote traits that increase ant colony survival. Similarly, natural selection on the ants should promote ant traits that increase plant growth, or plant patch growth for *M. schumanni* colonies. Thus positive feedback between ants and plants should result in increased adaptation of partner species to one another.

Positive feedback between ant colony and plant growth may explain how these mutualisms persist despite the risk of exploitation by cheaters, individuals that take the benefits of mutualism without reciprocating. In most of the ant–plant interactions we studied, natural selection has probably favored mutualism because an individual (or colony) that fails to cooperate reduces its own fitness. If ant workers do not protect their host plant, the plant cannot produce the domatia necessary for the colony to grow and to produce reproductives. Even the parasite *Al. octoarticulatus* defends the leaves of *C. nodosa*, although it is still an open question why *Al. octoarticulatus* destroys flowers and fails to protect plant stems. Many, perhaps most, mutualisms involve repeated or persistent interactions among individuals. Positive feedback between partners may be a general mechanism that helps maintain such mutualisms in natural populations (i.e., "partner fidelity feedback"; Sachs et al. 2004). The present study contributes to a growing body of evidence that positive-feedback processes shape the ecological and evolutionary dynamics of mutualisms.

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## Literature Cited

Addicott, J. F. 1981. Stability properties of 2-species models of mutualism: simulation studies. Oecologia 49:42–49.

Anderson, C., and F. L. W. Ratnieks. 1999. Task partitioning in insect societies. I. Effect of colony size on queueing delay and colony ergonomic efficiency. American Naturalist 154: 521–535.

Blüthgen, N., and J. Wesenberg. 2001. Ants induce domatia in a rain forest tree (*Vochysia vismiaefolia*). Biotropica 33:637–642.

Boucher, D. H., S. James, and K. H. Keeler. 1982. The ecology of mutualism. Annual Review of Ecology and Systematics 13: 315–347.

Breton, L. M., and J. F. Addicott. 1992. Density-dependent mutualism in an aphid–ant interaction. Ecology 73:2175–2180.

Bronstein, J. L. 1994. Our current understanding of mutualism. Quarterly Review of Biology 69:31–51.

Bronstein, J. L., W. G. Wilson, and W. F. Morris. 2003. Ecological dynamics of mutualist/antagonist communities. American Naturalist 162:S24–S39.

Bruno, J. F., J. J. Stachowicz, and M. D. Bertness. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

Carey, J. R. 1993. Applied demography for biologists: with special emphasis on insects. Oxford University Press, New York, New York, USA.

Carey, J. R. 2001. Insect biodemography. Annual Review of Entomology 46:79–110.

Chew, R. M. 1987. Population dynamics of colonies of three species of ants in desertified grassland, southeastern Arizona, 1958–1981. American Midland Naturalist 118:177–188.

Dean, A. M. 1983. A simple model of mutualism. American Naturalist 121:409–417.

Dieckmann, U., R. Law, and J. A. J. Metz. 2000. The geometry of ecological interactions: simplifying spatial complexity. Cambridge University Press, Cambridge, UK.

Dirzo, D. 1984. Herbivory: a phytocentric overview. Pages 141–165 *in* R. Dirzo and J. Sarukhán, editors. Perspectives on plant population ecology. Sinauer Associates, Sunderland, Massachusetts, USA.

Duarte Rocha, C. F., and H. Godoy Bergallo. 1992. Bigger ant colonies reduce herbivory and herbivore residence time on leaves of an ant-plant: *Azteca muelleri* vs. *Coelomera ruficornis* on *Cecropia pachystachya*. Oecologia 91:249–252.

Edwards, D. P., M. Hassall, W. J. Sutherland, and D. W. Yu. 2006. Selection for protection in an ant–plant mutualism: host sanctions, host modularity, and the principal agent-game. Proceedings of the Royal Society B 273:595–602.

Fonseca, C. R. 1993. Nesting space limits colony size of the plant–ant *Pseudomyrmex concolor*. Oikos 67:473–482.

Fonseca, C. R. 1999. Amazonian ant–plant interactions and the nesting space limitation hypothesis. Journal of Tropical Ecology 15:807–825.

Frederickson, M. E. 2005. Ant species confer different partner benefits on two neotropical myrmecophytes. Oecologia 143: 387–395.

Frederickson, M. E., and D. M. Gordon. 2007. The devil to pay: a cost of mutualism with *Myrmelachista schumanni* ants in 'devil's gardens' is increased herbivory on *Duroia hirsuta* trees. Proceedings of the Royal Society B 274:1117–1123.

Frederickson, M. E., M. J. Greene, and D. M. Gordon. 2005. 'Devil's gardens' bedevilled by ants. Nature 437:495–496.

Gaume, L., D. McKey, and S. Terrin. 1998. Ant–plant–homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. Proceedings of the Royal Society B 265:569–575.

Gause, G. F., and A. A. Witt. 1935. Behavior of mixed populations and the problem of natural selection. American Naturalist 69:596–609.

Goh, B. S. 1979. Stability in models of mutualism. American Naturalist 113:261–275.

Gordon, D. M. 1987. Group-level dynamics in harvester ants: young colonies and the role of patrolling. Animal Behaviour 35:833–843.

Gordon, D. M. 1992. How colony growth affects forager intrusion between neighboring harvester ant colonies. Behavioral Ecology and Sociobiology 31:417–427.

Gordon, D. M. 1995. The development of an ant colony's foraging range. Animal Behaviour 49:649–659.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Harper, J. L. 1981. The concept of population in modular organisms. Pages 53–77 *in* R. M. May, editor. Theoretical ecology: principles and applications. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Heil, M., A. Hilpert, B. Fiala, and K. E. Linsenmair. 2001. Nutrient availability and indirect (biotic) defence in a Malaysian ant-plant. Oecologia 126:404–408.

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.

Heithaus, E. R., D. C. Culver, and A. J. Beattie. 1980. Models of some ant–plant mutualisms. American Naturalist 116:347–361.

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.

Huston, M., D. L. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. Bioscience 38: 682–691.

Koch, G. W., S. C. Sillett, G. M. Jennings, and D. M. Davis. 2004. The limits to tree height. Nature 428:851–854.

May, R. M. 1981. Models for two interacting populations. Pages 78–104 *in* R. M. May, editor. Theoretical ecology: principles and applications. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

May, R. M. 1982. Mutualistic interactions among species. Nature 296:803–804.

Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in the social insects. Princeton University Press, Princeton, New Jersey, USA.

Pascual, M. 2005. Computational ecology: from the complex to the simple and back. PLOS Computational Biology 1:e18.

Pierce, N. E., and W. R. Young. 1986. Lycaenid butterflies and ants: two species stable equilibria in mutualistic, commensal, and parasitic interactions. American Naturalist 128:216–227.

Quek, S. P., S. J. Davies, T. Itino, and N. E. Pierce. 2004. Codiversification in an ant–plant mutualism: stem texture and the evolution of host use in *Crematogaster* (Formicidae: Myrmicinae) inhabitants of *Macaranga* (Euphorbiaceae). Evolution 58:554–570.

Roughgarden, J. 1998. Primer of ecological theory. Prentice Hall, Upper Saddle, New Jersey, USA.

Ryan, M. G., and B. J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience 47:235–242.

Sachs, J. L, U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. The evolution of cooperation. Quarterly Review of Biology 79:135–160.

Saffo, M. B. 1992. Coming to terms with a field: words and concepts in symbiosis. Symbiosis 14:17–31.

Sebens, K. P. 1987. The ecology of indeterminate growth in animals. Annual Review of Ecology and Systematics 18:371–407.

Tschinkel, W. R. 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. Ecological Monographs 63:425–457.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. Princeton University Press, Princeton, New Jersey, USA.

Watkinson, A. R., and J. White. 1986. Some life-history consequences of modular construction in plants. Philosophical Transactions of the Royal Society B 313:31–51.

Wolin, C. L., and L. R. Lawlor. 1984. Models of facultative mutualism: density effects. American Naturalist 124:843–862.

Wright, D. H. 1989. A simple, stable model of mutualism incorporating handling time. American Naturalist 134:664–667.

Wulff, J. L. 1985. Clonal organisms and the evolution of mutualism. Pages 437–466 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution in clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Yu, D. W., and N. E. Pierce. 1998. A castration parasite of an ant–plant mutualism. Proceedings of the Royal Society B 265:375–382.

## APPENDIX A

Comparison of results of linear regression and randomization analyses (*Ecological Archives* E090-110-A1).

## APPENDIX B

Plant growth pattern (*Ecological Archives* E090-110-A2).

## APPENDIX C

Ant colony growth pattern (*Ecological Archives* E090-110-A3).

## APPENDIX D

*N*-demography of plants and ant colonies (*Ecological Archives* E090-110-A4).

## APPENDIX E

Characteristics of plants colonized by ants (*Ecological Archives* E090-110-A5).

## APPENDIX F

Ant colony fecundity (*Ecological Archives* E090-110-A6).

## APPENDIX G

Plant size distributions (*Ecological Archives* E090-110-A7).