A comparison of *A. collinsii* reproductive facilitation by obligate vs. facultative mutualist ant species

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Abstract: Obligate mutualists should provide greater benefits to their hosts than facultative mutualists because they have a more vested interest in the persistence of their partner species. We tested this hypothesis by comparing the occurrence of *Acacia collinsii* and non-*A. collinsii* vegetation growing under large *A. collinsii* trees inhabited by the obligate mutualist *Pseudomyrmex spinicola* versus the facultative mutualist *Crematogaster brevispinosa*. We found significantly less foreign vegetation but more *A. collinsii* shoots and saplings (young growth) under mature *A. collinsii* trees inhabited by *P. spinicola* than under trees with *C. brevispinosa*. Most (88%) young *A. collinsii* growth was occupied by the ant species found on the nearest mature tree for both species; no ants occupied the remaining 12%. These findings suggest that both ant species make use of young growth, but because *A. collinsii* growth is more abundant under trees with *P. spinicola*, these ants have more opportunities to colonize new growth. We propose that the obligate mutualist *P. spinicola* may facilitate the propagation of its host, and at the same time expand its own resource base more than does the facultative mutualist *C. brevispinosa*.

Key Words: Crematogaster brevispinosa, *plant-insect coevolution,* Pseudomyrmex spinicola

Introduction

When two species form a mutualistic relationship, it is in their best interest to promote the health and persistence of their partner. Because the association has formed through tight coevolution, self-promoting actions of one organism such as collecting food or defending resources may indirectly facilitate the success of the other organism. We examined mechanisms that facilitate the propagation of the acacia, *A. collinsii,* by two ant species that vary in their mutualistic dependency on this tree. *Pseudomyrmex spinicola* and *A. collinsii* form an obligate mutualism in which the tree provides food and habitat, and the ant provides critical defense against herbivores and competitors. Janzen (1966, 1983) found that *P. spinicola* kills any foreign vegetation within a 1-4 m diameter around the tree they inhabit. While we do not know what motivates the ant to invest energy in clearing the area around its tree, Janzen (1966) found that mating queens often colonize the nearest new, or unoccupied habitat, suggesting that promoting new growth of *A. collinsii* would benefit both the host tree and the ant.

Crematogaster brevispinosa is not dependent on *A. collinsii*, but both species benefit from their facultative association. Wickre et al. (2003) found that *C. brevispinosa* offers defense against herbivory comparable to protection provided by *P. spinicola*. However, because *C. brevispinosa* is not fully dependent on its association with *A. collinsii*, it may not invest the same amount of energy in promoting its host.

We hypothesized that there would be differences in the vegetative growth under *A. collinsii* trees inhabited by *P. spinicola* and *C. brevispinosa*. We predicted that other (non-*A. collinsii*) vegetation would cover less area under trees with *P. spinicola* than under those with *C. brevispinosa*, that more young *A. collinsii* growth would occur under focal trees inhabited by *P. spinicola* than trees with *C. brevispinosa*, and that ants would use the young growth as new habitat. The last prediction is based on the idea that if either ant spends time clearing space, it should take advantage of any young *A. collinsii* growth that is able to grow in this space.

Methods

We conducted our study on 13 January 2003 along the road east of the OTS

Station in Palo Verde National Park, Guanacaste Province, Costa Rica. We collected data from 20 *A. collinsii* trees inhabited by *P. spinicola* and 19 trees with *C. brevispinosa*. All *A. collinsii* sampled were judged to be in moderate to good health and had a diameter at breast height between 5 and 10 cm.

We estimated the percentage of non-*A. collinsii* vegetative cover within a 2 m diameter circle around the base of each tree, not including detritus. We recorded the number of young *A. collinsii* shoots and saplings (young growth) with thorns within the circle and the number of young growth inhabited by ants. We did not distinguish between vegetative shoots and saplings or seedlings of *A. collinsii.*

Because the data did not meet the assumptions of normality or equal variance after arcsine-transformation, we used the non-parametric Kruskal-Wallis test to compare the percent vegetative cover under *C. brevispinosa*- and *P. spinicola*-inhabited trees. We performed a one-way ANOVA on log-transformed data for the number of young growth under *C. brevispinosa*- and *P. spinicola*-inhabited trees.

Results

The mean percentage of non-*A. collinsii* vegetative cover was significantly greater under *C. brevispinosa*-inhabited trees than under *P. spinicola*-inhabited trees (Fig. 1; $X^2 = 25.82$, df = 1, $P < 0.01$). There was also significantly more *A. collinsii* young growth under *P. spinicola* -inhabited trees than *C. brevispinosa* -inhabited trees (Fig. 2, $F = 59.99$, df = 1, 38, $P < 0.01$). *P. spinicola* and *C. brevispinosa* used 88% of the young growth beneath trees they inhabited; the remaining 12% of young growth was not occupied by ants.

Discussion

In this study we found that the obligate mutualist *P. spinicola* provided greater reproductive benefits to its partner than did the facultative mutualist *C. brevispinosa*. Vegetative cover was 17 times greater under focal acacias inhabited by *C. brevispinosa* than under trees with *P. spinicola*. Based on this finding and previous studies that noted the clearing actions of *P. spinicola*, we speculate that this ant effec

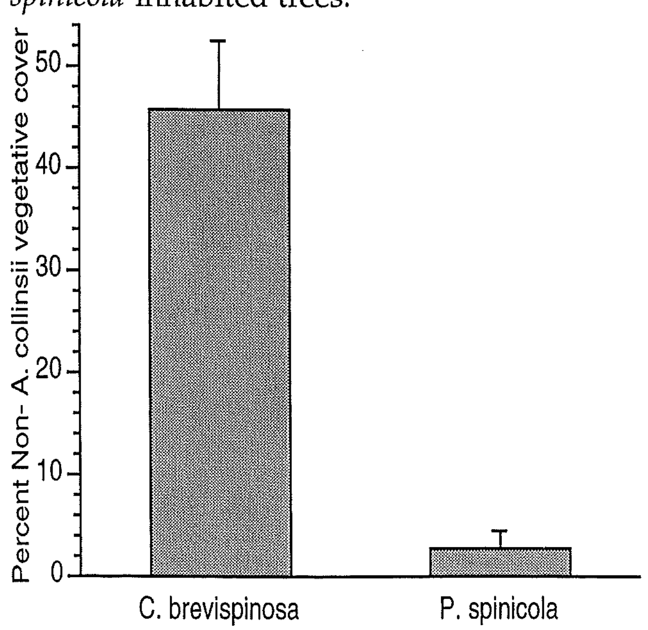

FIG. 1. Percentage (mean ± SE) of non-*A. collinsii* vegetative cover within a 1-m radius under focal *A. collinsii* trees inhabited by C. *brevispinosa* (n = 19) and *P. spinicola* (n = 20).

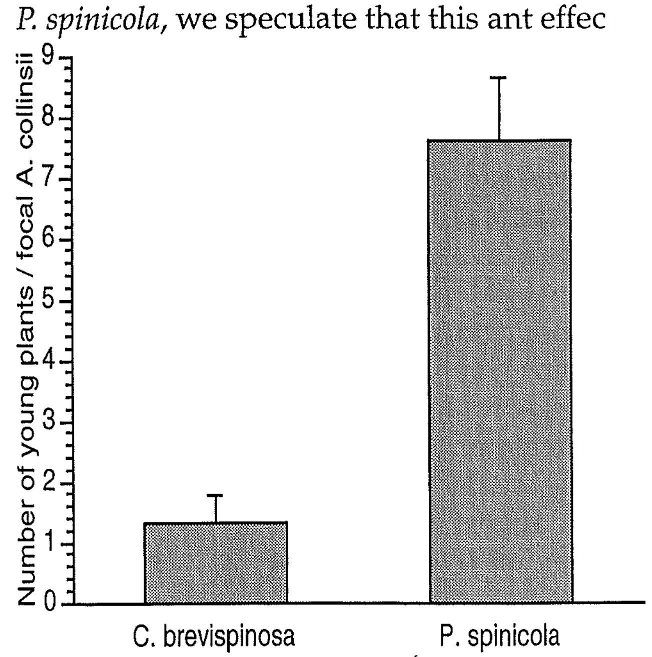

FIG. 2. Abundance (mean ± SE) of young *A. collinsii* plants under focal *A. collinsii* trees inhabited by *C. brevispinosa* (n = 19) and *P. spinicola* (n = 20).

tively clears non-*A. collinsii* vegetation under trees it occupies, increasing the space, nutrients, and water quantity available to young growth of its host. Further support for this idea comes from our finding of nearly six times more young *A. collinsii* growth under trees inhabited by *P. spinicola* than those inhabited by *C. brevispinosa*. The cleared space thus appears to facilitate the growth of *A. collinsii*, while simultaneously expanding *P. spinicola* resources.

Both ant species utilize new growth below trees they inhabit. Because we found that there was more young growth under trees inhabited by *P. spinicola*, this ant might have greater access to suitable habitat than *C. brevispinosa*. Perhaps the observation that it was easier for us to find *P. spinicola*- than *C. brevispinosa*-inhabited trees can be explained by clearing activity under host trees, which opened up space for new *A. collinsii* growth and increases *P. spinicola* resources.

Our study found that *P. spinicola* reduces the cover of foreign vegetation around *A. collinsii*, which may facilitate the reproduction of its host plant and simultaneously expand the availability of resources important to the ant. This obligate mutualism can be summarized in the form of a positive feedback loop (Fig. 3), in which the actions of the ant promote the reproductive success of the tree, which in turn provides the ant with more resources to exploit. This model may have implications for understanding the evolution of this mutualism. While one organism may appear to promote the success of its partner, the model demonstrates that the energy it invests will eventually return as benefits to itself. Because mutualists are interdependent, actions that benefit one increase the fitness of the other.

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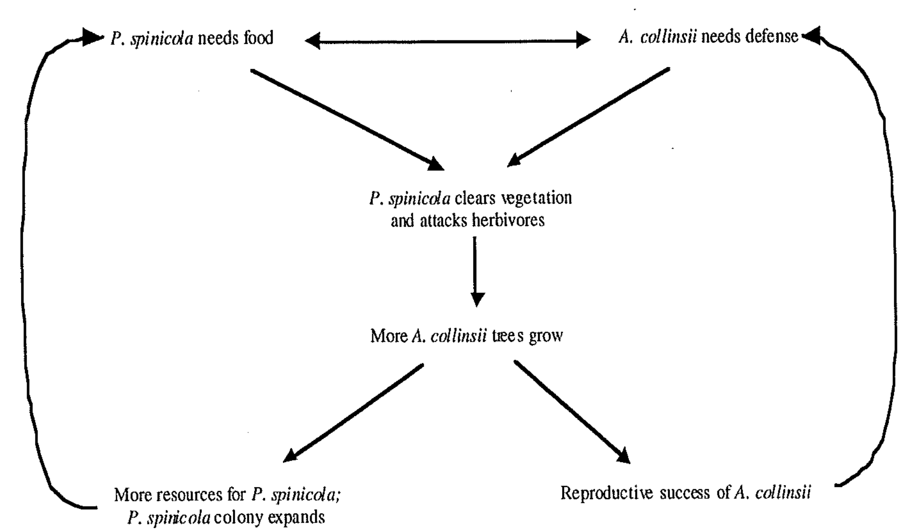

FIG 3. Positive feedback loop between the obligate mutualist *P. spinicola* and its *A. collinsii* host.