

Distribution of acacia-ant species among successional habitats

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Abstract: Swollen-thorn acacias (*Acacia collinsii*) in Central American lowlands often occur in recently disturbed habitats. Such habitats, however, are not static and the vegetation often changes over time due to physical disturbances and competitive interactions among the plants. Such gradual changes in the size, health, and/or immediate surroundings of the acacias could affect the occurrence and persistence of the associated ant species. In this study, we examined the occurrence of acacia-ant species in early and late successional habitats. Acacias in these two sites differed significantly in canopy cover, height and ant species composition, but not in acacia health. *Crematogaster brevispinosa* and *Pseudomyrmex flavicornis* were found more frequently in the early successional site, whereas *P. spinicola* and *P. nigrocincta* were the most abundant ant species in the late successional habitat. These findings indicate that different ant species predominate at different stages of succession, and suggest that the composition of acacia-ant species may change in response to habitat alterations due to fires, grazing, and other events. The mechanisms leading to these changes in ant species composition over time, however, remain unknown.

Key Words: *Acacia collinsii*, *Crematogaster brevispinosa*, *Pseudomyrmex flavicornis*, *P. gracilis*, *P. nigrocincta*, *P. nigropilosa*, *P. spinicola*

INTRODUCTION

Swollen-thorn acacias (*Acacia collinsii*) are lowland trees that frequently occur in disturbed areas throughout Central America. This species supports a number of ant species that occupy the tree's large thorns and feed on nectaries at the base of each leaf. In exchange for food and shelter, the ants provide defense for the tree by stinging potential herbivores and eliminating potential plant competitors around the base of the acacias. The ant species that exist in this mutualistic relationship with the acacias appear to vary in distribution across the landscape (R. T. Holmes, pers. comm). Spatial and temporal patterns in ant species distributions on acacias within specific sites, however, are poorly understood.

The elimination of commercial cattle grazing and the suppression of fire at Palo Verde National Park in Guanacaste Province, Costa Rica during the last twenty years has led to a change in plant community composition and structure. The overall canopy cover and forest age of ant-acacia habitat has increased, shifting from a predominantly early successional habitat to a

late successional habitat. During this period, the distribution of acacia-ant species may also have changed, suggesting that some ant species may have replaced others over time (R. T. Holmes, pers. comm.). For example, it has been reported that *Pseudomyrmex flavicornis* occurs more frequently in open sunlit areas than in shady closed habitats, *P. nigrocincta*, in deeply shaded acacias, and *P. spinicola* in a wide variety of habitats from open to closed canopies (Janzen 1983). Finally, a fourth species, *Crematogaster brevispinosa*, a small, black, less aggressive ant has been observed commonly in dead or dying acacias (Janzen 1983).

In this study we tested the hypothesis that acacia-ant species distribution changes over the course of forest succession by comparing the occurrence of ant species in an early and a late successional habitat. We anticipated that sites that experienced more recent disturbance events, such as cattail removal or grazing, would have more open canopies and younger, smaller trees. Based on Janzen (1983) and our own observations, we predicted a greater overall proportion of *P. flavicornis* in the early successional site, a

higher proportion of *P. nigrocincta* and *C. brevispinosa* in the older site, and an even distribution of *P. spinicola* at both sites.

METHODS

STUDY SITES: We studied acacia-ant distribution in Palo Verde National Park, Guanacaste Province, Costa Rica. We selected two sites for study that differed in disturbance history. Site A was burned eight years ago (1994-95) and is currently actively grazed by cattle. Site B was grazed extensively until 1981, when most of the cattle were removed. Since then, a dense canopy of overstory trees has developed, shading the understory acacias. Site A was approximately 6 km southeast of the OTS field station (4 km along the entrance road and then 2 km along the La Carreta road, GPS coordinates: 16P 068 5939, 1147437), and site B was 1 km east of the station, about 30 m south of the entrance and road.

SAMPLING: At each site, we laid out a line along the edge of the selected study area and established three transects at approximately 12 m intervals parallel to each other and through the stands of acacia trees. We sampled all acacias within 2 m of each side of the transect line to a distance of 50 m

(site A) or 40 m (site B). We permanently marked the end of each transect line with metal stakes.

We inventoried all acacias within these transects and attached an individually numbered aluminum tag to the base of each tree. Additionally, we measured height of each acacia as an indicator of size, and estimated the health status of each acacia on a scale of 0-2; where 0 = sparse or dead foliage, 1 = scattered foliage, and 2 = lush, dense foliage. We also noted canopy cover on a graded scale ranging from 0-3, where 0 = 0-10% cover, 1 = 10-30% cover, 2 = 30-70% cover and 3 = 70-100% cover. Finally, we recorded the species of ants that inhabited each acacia tree. Because a single colony of acacia-ants may inhabit multiple acacia plants, we recorded whether or not each acacia was part of a cluster. We defined a cluster as two or more acacias with overlapping canopies or two or more acacias that shared a single, cleared, basal area. In large clusters we sampled the largest tree and a random selection of smaller ones. We measured the largest tree in a cluster, even if it fell outside the 4 m-wide belt. We included only the characteristics of the tallest tree in each cluster and independent trees not in a cluster for analysis.

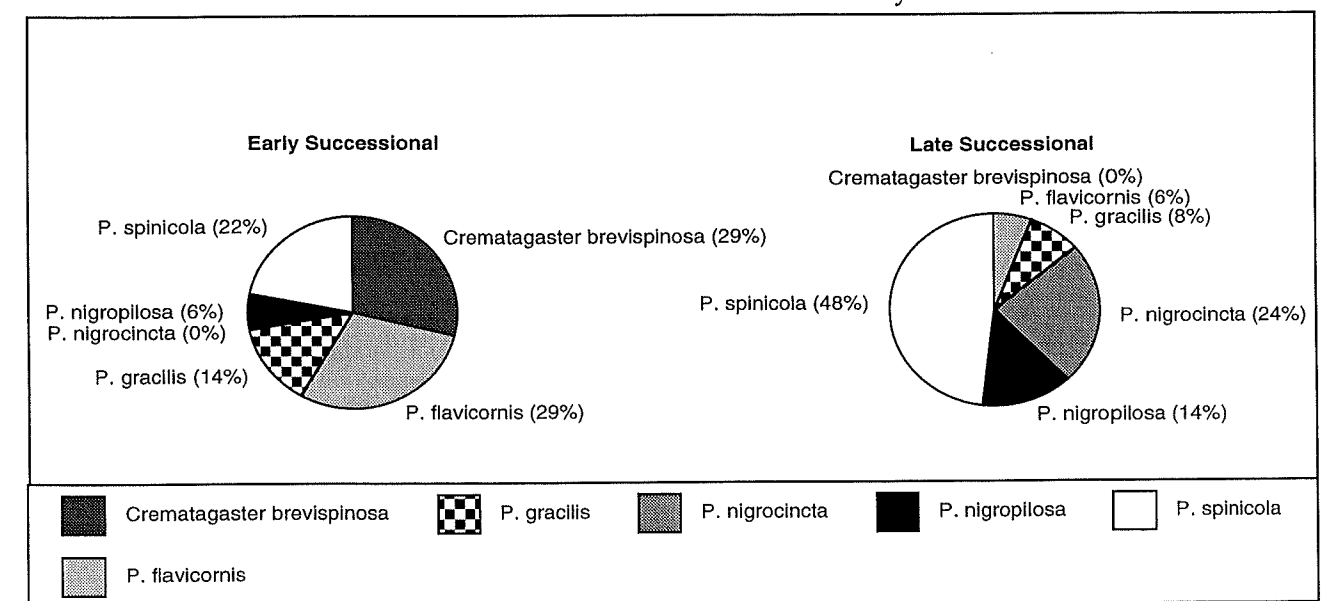


FIG. 1. Proportion of ant species inhabiting *Acacia collinsii* trees in one early and one late successional site in Palo Verde National Park, Costa Rica ($\chi^2=42.24$, $df=5$, 91 , $P<0.0001$).

data analysis: We tested for differences in acacia health and canopy cover between sites, and we compared ant species between sites with X^2 tests. We determined whether tree heights were significantly different between sites with a one-way ANOVA. Data are presented as means \pm SE.

RESULTS

Acacia height in site A ($1.88 \text{ m} \pm 0.18$) and site B ($2.83 \text{ m} \pm 0.27$) differed significantly ($t = -2.90$, $df = 191$, $P = 0.004$). Canopy cover between site A (0.16 ± 0.06) and site B (2.60 ± 0.09) was also significantly different ($X^2 = 171.62$, $df = 3$, 189 , $P < 0.001$). However, acacia health did not differ significantly between site A (1.47 ± 0.07) and site B (1.30 ± 0.07) ($X^2 = 1.27$, $df = 2$, 190 , $P = 0.53$).

As predicted, ant species composition differed significantly between the two sample sites (Fig. 1). Site A contained large numbers of *C. brevispinosa* (29%) and *P. flavicornis* (29%); *P. spinicola* was also common (22%) in site A (Fig. 1). In contrast, site B was largely dominated by *P. spinicola* and *P. nigrocincta*, which comprised 48% and 24% of the sampled acacias respectively (Fig. 1). *P. nigrocincta* was absent in the sample from the early successional site, and *C. brevispinosa* was absent from the late successional site (Fig. 1). *Pseudomyrmex gracilis* shared an acacia with another acacia-ant species on 10 occasions, and *P. flavicornis* and *P. spinicola* were found to simultaneously inhabit the same acacia twice.

We computed the mean health and height of trees inhabited by each species for site A and site B (Table 1). In site A, *C. brevispinosa* occupied trees with a health index of 1.22 ± 0.11 . This health index was significantly lower than those for trees inhabited by the more aggressive ant species (*P. flavicornis*, *P. spinicola*, and *P. nigropilosa*) ($F = 3.97$, $df = 208$, $P < 0.001$), but not significantly different from trees with the non-aggressive *P. gracilis* or trees without ants ($F = 0.36$, $df = 71$, $P = 0.70$).

DISCUSSION

Ant species composition differed between the early and late successional sites, and it appears that the differences in site structure and acacia qualities may influence the ant species composition. While tree health did not differ significantly between sites, site B had taller and presumably older acacias with more canopy cover than site A. Our results confirm previous observations that *P. flavicornis* occurs more frequently on acacias in open sun, *P. spinicola* in both sunny and shady patches, and *P. nigrocincta* in deep shade (Janzen 1983). *Pseudomyrmex flavicornis* constituted a higher proportion of the ant species in site A than in site B. *Pseudomyrmex spinicola* was relatively common in both sites, while *P. nigrocincta* occurred exclusively in site B. The fact that *P. flavicornis* occurs more often on acacias in the site with a sparse canopy and smaller trees suggests that it may be

highly successful in colonizing young, unoccupied trees following a disturbance event. It may then be out-competed by later successional ant species, such as *P. spinicola* or *P. nigrocincta*. While *P. spinicola* was prevalent in both sites, as predicted, this species occurred much more frequently in site B. Ginsburg and Kaveeshwar (1995) showed that *P. spinicola* was competitively dominant over ant species at high levels of canopy cover and low ambient temperatures. They reported that *P. spinicola* became less active and potentially less competitive at higher temperatures, such as midday in sunny locations. This response to higher temperatures may explain the slightly lower proportion of *P. spinicola* in the open canopy site, as found in our study.

Contrary to our prediction, *C. brevispinosa* was not found in the later successional site, where acacias were older and presumably at an early stage of senescence. This prediction had been based on the observation that *C. brevispinosa* occurs often on dead or dying acacias (Janzen 1983). We did find that the trees inhabited by *C. brevispinosa* in site A had a lower mean health index than trees inhabited by other ant species. Thus, even within early successional sites with smaller and presumably younger acacias, those that are less healthy are often occupied by *C. brevispinosa*. The less aggressive *C. brevispinosa* (Simon 1983) may be unable to establish colonies in healthy trees occupied by the more aggressive species, or may simply be out-competed.

Our results confirm observations from previous studies that *P. gracilis* is found relatively more often, but never frequently, in early successional sites (Janzen 1984). *P. gracilis* are non-aggressive, facultative mutualists (Simon 1983), and therefore may have been out-competed by more aggressive, obligate species at site B.

Pseudomyrmex flavicornis, *P. nigrocincta*, and *P. spinicola* are all very

aggressive in their defense of the acacia against herbivory (Simon 1983). Therefore, it is reasonable to expect that acacias will benefit more when inhabited by these species. Given a greater proportion of non-aggressive and facultative mutualists in the early successional sites, it is logical to expect that trees in these sites might suffer the effects of increased herbivory. These conclusions suggest how future disturbances (i.e., fire, grazing, or tree-fall gaps) may shift ant species distribution and herbivory levels.

The results of this study raise questions regarding the rate of ant species turnover on individual acacias. We occasionally observed trees occupied by more than one ant species. *Pseudomyrmex gracilis* was most likely to share an acacia with another species, and *P. flavicornis* and *P. spinicola* occasionally simultaneously inhabited large trees. The latter suggests a possible transition from occupation by *P. flavicornis* to *P. spinicola*. This study represents the first year of a long-term study at Palo Verde to document the changes in ant species composition as forests develop and mature. Measuring changes in a site over time will give more insight into the pattern and rates of succession of both trees and ants in this tropical dry forest. An important caveat worth mentioning is that our analysis is based on data from only two sites in one year. A more comprehensive study should include sites over a greater range of successional stages as well as more replication of site ages.

LITERATURE CITED

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TABLE 1. Tree height and tree health of *Acacia collinsii* inhabited by acacia ant species in early (A) and later successional (B) sites in Palo Verde National Park, Costa Rica. Data are means \pm SE. See text for description of health index.

Site A Species	Height (m)	Health Index	Site B Species	Height (m)	Health Index
<i>C. brevispinosa</i>	2.5 ± 0.2	1.2 ± 0.1	<i>P. flavicornis</i>	5.8 ± 2.2	$1.3 \pm .3$
<i>P. flavicornis</i>	$2.2 \pm .2$	$1.6 \pm .2$	<i>P. spinicola</i>	$3.2 \pm .2$	$1.3 \pm .1$
<i>P. spinicola</i>	$1.5 \pm .1$	$1.7 \pm .2$	<i>P. gracilis</i>	4.2 ± 1.3	$1.3 \pm .3$
<i>P. gracilis</i>	$2.8 \pm .7$	$1.1 \pm .2$	<i>P. nigropilosa</i>	1.5 ± 1.0	$1.0 \pm .3$
<i>P. nigropilosa</i>	1.6 ± 1.1	$1.5 \pm .3$	<i>P. nigrocincta</i>	$2.4 \pm .2$	$1.6 \pm .1$
None	$.6 \pm .2$	$1.1 \pm .1$	None	$1.5 \pm .2$	$1.0 \pm .3$

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