

An Ant Mosaic Revisited: Dominant Ant Species Disassemble Arboreal Ant Communities but Co-Occur Randomly

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ABSTRACT

The spatial distributions of many tropical arboreal ant species are often arranged in a mosaic such that dominant species have mutually exclusive distributions among trees. These dominant species can also mediate the structure of the rest of the arboreal ant community. Little attention has been paid to how diet might shape the effects of dominant species on one another and the rest of the ant community. Here, we take advantage of new information on the diets of many tropical arboreal ant species to examine the intra- and inter-guild effects of dominant species on the spatial distribution of one another and the rest of the tropical arboreal ant community in a cocoa farm in Bahia, Brazil. Using null model analyses, we found that all ant species, regardless of dominance status or guild membership, co-occur much less than expected by chance. Surprisingly, the suite of five dominant species showed random co-occurrence patterns, suggesting that interspecific competition did not shape their distribution among cocoa trees. Across all species, there was no evidence that competition shaped co-occurrence patterns within guilds. Co-occurrence patterns of subordinate species were random on trees with dominant species, but highly nonrandom on trees without dominant species, suggesting that dominant species disassemble tropical arboreal ant communities. Taken together, our results highlight the often complex nature of interactions that structure species-rich tropical arboreal ant assemblages.

Key words: assembly rules; Brazil; community structure; co-occurrence; null model; tropical diversity.

IN ANTS, THERE SEEMS TO BE LITTLE DOUBT THAT COMPETITION AMONG SPECIES CAN STRUCTURE COMMUNITIES (Hölldobler & Wilson 1990). Much of the evidence for the structuring role of competition in ant communities comes from examining spatial distributions of species (Jackson 1984, Adams 1994, Gotelli & McCabe 2002, Sanders *et al.* 2003) and the impact of competitively dominant species on community structure (Savolainen & Vepsäläinen 1988, Adams 1994, Andersen & Patel 1994, Human & Gordon 1997, Holway 1999, Dejean *et al.* 2003, Sanders *et al.* 2003). The spatial distributions of arboreal species, at least in some tropical systems, seem to be arranged in a mosaic (Room 1971, Majer 1972, Adams 1994), such that dominant arboreal ant species have mutually exclusive distributions among trees, which arise as a result of interspecific and intraspecific competition (Room 1971, 1975; Leston 1973, 1978; Majer 1976a, b, c). Furthermore, both behavioral studies and experimental removals of ant species indicate that these dominant species can mediate the structure of the rest of the arboreal ant community (Room 1971, Majer 1976c, Adams 1994, Blüthgen *et al.* 2004).

Where it has been studied, competition among tropical canopy ants is typically for food resources. At least some behaviorally dominant canopy ants defend these resources by establishing extensive aggressively defended territories (*e.g.*, Adams 1994). Tropical arboreal ants, particularly those that are numerically or behaviorally dominant, not only commonly forage for carbohydrate-rich homopteran honeydew and plant exudates (Tobin 1997, Davidson *et al.* 2003, Blüthgen *et al.* 2004), but also require substantial amounts of nitrogen-rich protein sources to promote colony growth and development. Until recently, a better understanding of competition and coexistence in tropical canopy ant communities was limited by a lack of understanding of the diets of canopy ants. Davidson and colleagues, using stable isotope analyses and foraging observations (Davidson & Kim 1996, Davidson *et al.* 2003), were able to identify the predominant foraging modes of the arboreal ants in two diverse assemblages in Peru and Brunei. By examining the ratio of ¹⁵N/¹⁴N, ants can be reliably classified into trophic guilds ranging from strict herbivores to scavengers and predators (Blüthgen *et al.* 2003, 2004). To date, the study of ¹⁵N/¹⁴N isotope ratios of tropical canopy ants and the study of ant mosaics have not been well integrated (but see Blüthgen *et al.* 2003, 2004) but integration of available information on isotopic ratios and trophic

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guilds in canopy ants can greatly increase our understanding of ant mosaics and the structure of arboreal ant assemblages.

Here, we take advantage of the increased understanding of resource use and foraging modes of arboreal ants to reconsider an arboreal ant mosaic from a cocoa farm in Brazil (Majer *et al.* 1994). The issues we address in this paper are much larger than just a re-examination of a particular ant mosaic in Brazil. Considerable research in ecology over the past 30 yr has examined whether interspecific competition structures ecological communities (Diamond 1975, Gotelli & Graves 1996, Weiher & Keddy 1999). The most contentious, but perhaps best-cited, evidence comes from examining static patterns of co-occurrence among assemblages and testing whether those patterns differ from patterns generated in the absence of competition (Gotelli & Graves 1996). Ant mosaics remain a classic example of what are thought to be nonrandom patterns of co-occurrence, but remain poorly explored in the context of our new understanding of the diets of tropical ants. In this paper, we use null model analyses to examine the spatial structure of arboreal ant assemblages. Specifically, we ask four interrelated questions:

1. Does the entire assemblage (*i.e.*, all ant species, regardless of dominance status) show evidence of nonrandom co-occurrence?
2. Do dominant species co-occur with one another less than expected by chance?
3. Do particular trophic guilds show stronger evidence of competition than other guilds?
4. What are the effects of dominant species on co-occurrence patterns in the rest of the ant assemblage?

METHODS

SPECIES DATA AND TROPHIC GUILDS.—We chose to analyze data from tropical arboreal ant assemblages studied by Majer *et al.* (1994) because two of us (Majer and Delabie) are personally familiar with the ant mosaic therein, the data set is among the richest to date for arboreal ants in terms of the number of trees sampled (1100) and the species are, for the most part, studied with sufficient detail to identify trophic guild, either based on behavioral observations or isotopic analysis from the literature.

The arboreal ant distributions were generated during a study conducted on the experimental plantations at the Centre for Cocoa Research (14°45' S, 39°13' W) at Ilhéus, Bahia, Brazil (Majer *et al.* 1994). Ant species were surveyed on 1100 randomly selected trees (exclusively cocoa trees, *Theobroma cacao* Sterculiaceae) by visually scanning each tree for 5 min and collecting any workers, followed by beating the canopy onto a 2 × 2 m sheet. Each sampled tree was at least 15 m from the nearest other sampled tree. In total, 91 ant species were detected. Though there are many ways to quantify species dominance (*e.g.*, LeBrun 2005), to make analyses here directly comparable to those in Majer *et al.* (1994), we used their definition of dominance. Five ant species were classified by Majer *et al.* (1994) as dominant based on the following criteria: overall abundance, the occupation of large blocks of trees, relative worker biomass compared to other ants, and the number

of positive or negative associations with other ants. These species include *Crematogaster limata* Fr. Smith, *Wasmannia auropunctata* (Roger), *Ectatomma tuberculatum* (Olivier), *Azteca muelleri* Emery, and *A. chartifex spiriti* Forel. For additional details of the sampling and figures of the plots, see Majer *et al.* (1994).

We examined the effect of competition by dominant species on the structure of arboreal ant assemblages, and we also considered whether the effect varied among trophic guilds. We used Davidson *et al.*'s (2003) paper to categorize species into five trophic guilds: plant tenders, homopteran tenders, omnivores, predators, and specialist predators (see Davidson *et al.* 2003 for a discussion of each of these groupings and the isotope ratios to which they correspond). For species that did not occur in the Davidson *et al.*'s paper, we assigned them to a trophic guild based on what is known about their natural history, using our own observations and relevant literature sources (*e.g.*, www.evergreen.edu/ants/AntsofCostaRica.html, Brown 2000). Twenty-four of the species fell into this category.

ANALYSES.—To address the four questions outlined in the Introduction, we arranged the mosaic data into presence–absence matrices, with a “1” indicating presence and a “0” indicating absence at the individual tree-level. In each matrix, species were rows, and individual trees were columns. To test whether the entire assemblage showed nonrandom patterns of species co-occurrence, we constructed a 91 × 1100 matrix, with all 91 species detected in the surveys as rows, and individual trees as columns. To test whether dominant species co-occur less than expected by chance, we constructed a 5 × 1100 submatrix with the five dominant species as rows and the trees as columns. To examine whether the evidence for intraguild competition was stronger than the evidence for interguild competition, we constructed a submatrix for each of the guilds (plant tenders, homopteran tenders, omnivores, predators, and specialist predators) that consisted of just the trees on which at least one species from the guild occurred. For this analysis, we ignored the effect of dominant ants (*i.e.*, they were treated the same as all other ants).

We assessed the effect of each dominant species on the rest of the ant assemblage by constructing five submatrices. A submatrix consisted of those trees on which a particular dominant ant was found. There was one submatrix associated with each dominant ant species. Each submatrix consisted of only the trees on which a dominant species was detected and the other species that occurred on the trees (*i.e.*, the dominant species were not included in the analyses because we were assessing their effect on the rest of the ant community).

We used the C-score of Stone and Roberts (1990) as a measure of co-occurrence. The index quantifies the number of “checkerboard units” that can be found for each species pair, where the number of checkerboard units is $(R_i - S)(R_j - S)$, R_i is the number of occurrences (equal to the row total) for species i , R_j is the number of occurrences for species j , and S is the number of sample plots in which both species occur. The C-score is the average number of checkerboard units for each unique species pair. If this index is unusually large compared with a null distribution, there is less pairwise species co-occurrence (segregation) than expected by chance. If the index is unusually small, there is more species co-occurrence

(aggregation) than expected by chance. We used EcoSim Version 7.0 (Gotelli & Entsminger 2005) to compare the observed C-score to the average C-score generated from 5000 randomly constructed assemblages. We used the most conservative null model, a fixed-fixed model, to generate randomly constructed assemblages. In this null model, row sums are fixed, so that each species occurs with the same frequency in the randomly constructed assemblages as in the observed assemblages. Column totals are also fixed, so each tree has the same number of species in the null assemblages and in the observed assemblages, as would be the case were some trees to provide better habitats than do others. *P*-values are calculated directly from comparing the observed C-score to the histogram of C-scores from the 5000 randomly constructed assemblages. For example, a *P*-value of 0.05 indicates that the observed C-score was larger than the C-scores of 95 percent of the randomly constructed assemblages.

Our last goal was to examine whether trophic guilds differed in their co-occurrence patterns. The null model that we used to examine whether co-occurrence patterns differed among trophic guilds differs slightly from the other null model analyses. In this model, the data are arranged in a single tree \times species matrix, and each species is assigned a label that corresponds to its trophic guild. Then, the labels are reshuffled, but the underlying presence-absence matrix remains intact. After 5000 reshuffles of the guild identities, a C-score and variance are calculated for each of the trophic guilds separately. If the observed variance in C-scores among trophic guilds is significantly larger than expected by chance, then the co-occurrence patterns among trophic guilds differ significantly from one another. In other words, some trophic guilds have relatively large C-scores and some have relatively small C-scores, relative to a random assignment of samples.

RESULTS

Overall, the ants in the tropical canopy assemblage studied (*i.e.*, all ant species, regardless of dominant status) co-occur much less than expected by chance (segregation; Fig. 1). In contrast to much of mosaic theory, the five dominant ant species, when considered together, apparently co-occur randomly with respect to one another (Fig. 2). Table 1 shows the within guild C-scores, none of which indicate that co-occurrence patterns within guilds differ from random. Moreover, C-scores did not differ from one another among guilds ($P = 0.25$). In the presence of dominant ant species, co-occurrence patterns of the rest of the species in these assemblages were random, but in the absence of dominant ant species, they were highly segregated (Table 2).

DISCUSSION

Across all ant species, we found evidence that species co-occurrence is much less than expected by chance. In studies that compare observed patterns of spatial distribution to null models, nonrandom

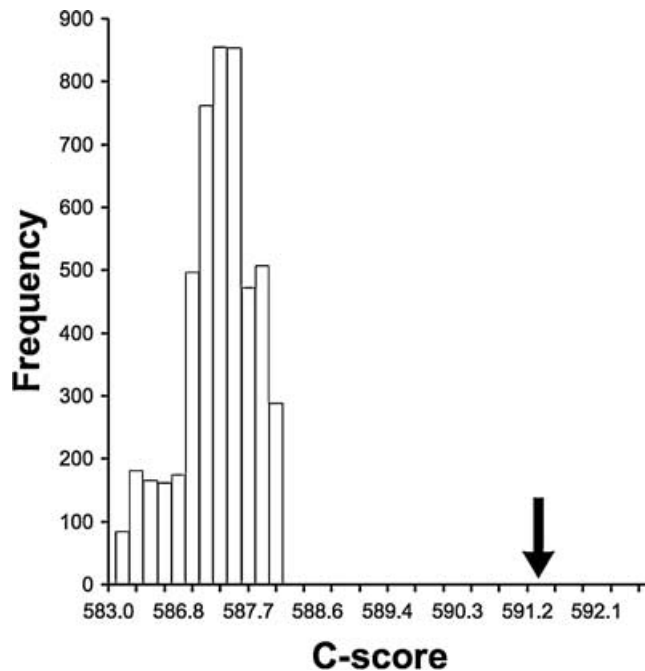


FIGURE 1. Co-occurrence pattern for all ants. The histogram shows the frequency of the simulated C-scores, and the arrow indicates the location of the observed C-score. Larger than expected C-scores are evidence of species segregation.

co-occurrence seems to be common, especially in ant assemblages. For instance, Gotelli and McCabe (2002) examined co-occurrence patterns in six ant assemblages and found that species tended to co-occur less than expected by chance. Several more recent studies have also found evidence that ant species in a variety of systems co-occur less than expected by chance (*e.g.*, Sanders *et al.* 2003, Badano *et al.* 2005). Blüthgen *et al.* (2004) documented both behavioral and spatial evidence for nonrandom co-occurrence of two dominant ant species. A recent synthesis of 14 ant mosaic studies, not all from tropical arboreal assemblages, showed that in seven studies species co-occurred less than expected by chance (Ribas & Schoereder 2002).

One reason for nonrandom co-occurrence of canopy ant species, and perhaps the most often cited explanation, is that dominant ant species do not co-occur because of competitive exclusion (*e.g.*, Leston 1978, Adams 1994, Blüthgen *et al.* 2004). However, the suite of five dominant species in this system showed random co-occurrence patterns, suggesting that interspecific competition may not shape their distribution among cocoa trees (Fig. 2), or that such an effect is weak and statistically undetectable. As an example of the degree of co-occurrence of dominant species, even the two dominant *Azteca* species (*A. chartifex spiritii* and *A. instabilis*), co-occurred with one another reasonably frequently. Six percent of the trees with *A. chartifex spiritii* also had *A. instabilis*. Importantly, *A. chartifex spiritii* is closely related to the species of *Azteca* that has been shown elsewhere (Adams 1994) to form mosaics with other dominant ants. In light of the recent analysis by Ribas and

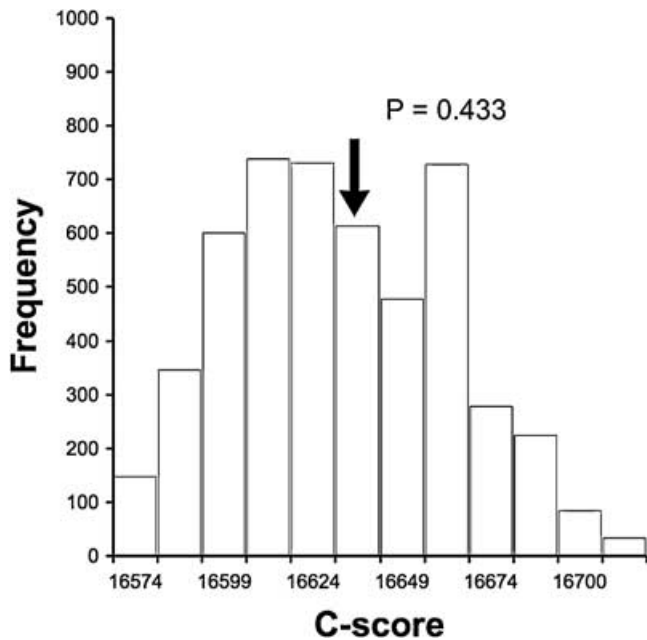


FIGURE 2. Co-occurrence pattern for the five dominant ant species. The histogram shows the frequency of the simulated C-scores, and the arrow indicates the location of the observed C-score. Larger than expected C-scores are evidence of species segregation.

Schoereder (2002), however, who found that in only two of eight instances did “dominant” ant species co-occur less than expected by chance, these results may not be so surprising. Our re-analysis of this ant mosaic, along with the review by Ribas and Schoereder (2002), suggests that perhaps true spatial mosaics among dominant species are the exception rather than the rule, especially when observed patterns are compared to patterns generated by null models that assume no interactions among species.

There are at least two reasons why not all arboreal ant mosaics actually reflect the outcome of competition when compared to a rigorous null model. First, though competition might be the “hallmark of ant ecology” (Hölldobler & Wilson 1990), perhaps its importance, relative to other interactions (Gotelli 1996, Feener

TABLE 1. Within trophic group co-occurrence analyses. Shown are the observed C-scores for the trophic guilds and the mean C-scores from 5000 randomly generated matrices. The P-values indicate the probability that the observed index is larger than expected on the basis of indices from the randomly generated matrices.

Trophic guild	Observed C-score	Mean of simulated C-scores	P (observed > expected)
Plant tenders	1392	1391	0.50
Omnivores	250.4	251.9	0.88
Homopteran tenders	93.04	93.52	0.76
Predators	350.5	349.8	0.26

TABLE 2. The effect of dominant ant species on the rest of the arboreal ant community. Shown are the observed C-scores for the entire assemblage minus the dominant species and the mean C-scores from 5000 randomly generated matrices. The P-values indicate the probability that the observed index is larger than expected on the basis of indices from the randomly generated matrices.

Dominant species	Observed C-score	Mean of simulated C-scores	P (observed > expected)
<i>Azteca muelleri</i>	2.82	2.82	0.56
<i>Azteca chartifex</i>	6.88	6.93	0.76
<i>Creumatogaster (orthocrema) limata</i>	9.17	9.14	0.26
<i>Ectatomma tuberculatum</i>	5.75	5.74	0.49
<i>Wasmannia auropunctata</i>	12.40	12.43	0.70
No dominant ant species present	183.1	182.1	< 0.0001

2000) or factors such as variation in the abiotic environment, microclimate, or disturbance (Majer & Nichols 1998), is minimal or conditional. Few mosaic studies have considered the importance of noncompetitive interactions such as nest site limitation, even though these factors can be critically important in ant assemblages (e.g., Majer 1976a, b, c; Philpott & Foster 2005). Second, and the explanation some of us favor, species that are ecologically or numerically dominant may differ sufficiently in their natural histories, foraging modes, and resource use, such that they might not directly compete for resources (Fellers 1987, Davidson 1998), except under very specific circumstances.

Even if niche differentiation precluded the formation of a mosaic among dominants, we might still expect to find species segregation when we focus on only those species with similar diets. Blüthgen *et al.* (2004) make the more specific suggestion that trophobionts should show evidence of nonrandom co-occurrence more so than other trophic guilds. However, when we examined co-occurrence patterns of species within trophic guilds, we found no evidence of nonrandom co-occurrence patterns, whether for trophobionts or for other trophic guilds (Table 1). There was also no evidence that particular guilds differed from one another in their co-occurrence patterns ($P = 0.25$). Even the dominant trophobionts, which have been predicted to be the group of species most likely to show nonrandom co-occurrence (Blüthgen *et al.* 2004), were often found occurring in the same tree.

Why did we find less species co-occurrence than expected by chance when all species were considered, but not within trophic guilds or among dominant ant species? One candidate explanation might be that, within a guild, coexistence is promoted by temporal, spatial, or even resource niche differentiations that are more subtle than our groupings (Albrecht & Gotelli 2001, Blüthgen *et al.* 2004). Nonetheless, when all ants, regardless of their trophic classification, are considered, we did detect nonrandom co-occurrence patterns (species segregation). The most likely explanation for these patterns seems to be that species (regardless of dominance or trophic guild) are nonrandomly distributed across trees with respect to some factor

associated with those trees. Although mosaic studies implicitly treat trees as identical, even in orchards they are not and the differences among trees may be more important than pairwise interactions among species in structuring many canopy ant assemblages.

Regardless of the mechanism underlying the nonrandom distribution of ants overall, this pattern was influenced by dominant ants, just not in the way long hypothesized in the tropical ant literature. Tropical ant studies have long suggested (e.g., Leston 1978) that suites of “subordinate” ants tend to be associated with particular dominant ants. Adams (1990) has shown, for example, that the ant species *Cephalotes* (= *Zacryptocerus*) *maculatus* is associated with the dominant ants of the genus *Azteca*, but not with ants of other genera. *Cephalotes maculatus* actually follows *Azteca* spp. foraging trails to food (Adams 1990; *C. maculatus* occurred in the plots, but was only collected once). In contrast to the predictions of Leston (1978) and studies of individual species pairs, dominant ants appeared to increase the randomness of the rest of the ant community. For trees on which any of the dominant species occurred, co-occurrence patterns of nondominant ants did not differ statistically from random (Table 2). However, for the trees on which no dominant species occurred, species co-occurred much less than expected by chance (Table 2). This suggests that, in the absence of dominant ant species, these tropical arboreal ant communities are structured by competition, but the dominant ants “disassemble” these communities. Such a disassembling effect by dominant competitors might be common. Two recent studies (Gotelli & Arnett 2000, Sanders *et al.* 2003) showed that communities of native ants show highly nonrandom patterns of co-occurrence, but in the presence of dominant invasive ant species, co-occurrence patterns of the native community are indistinguishable from random. These two studies are from temperate environments, but the study reported here is the first study to our knowledge that shows community disassembly in a tropical ant assemblage.

The best explanation for the randomness of the species that occur with dominant ants is that dominant ants reduce the abundance of other ant species, but that that effect does not depend on species identity (e.g., *Azteca* spp. favor the presence of *C. maculatus* and disfavor species *X*), but rather on broad groups of traits. For example, Majer *et al.* (1994) were able to show that in the same ant community we considered, the large dominant ant (*Ectatomma tuberculatum*) excluded other large species, whereas the smaller dominant ants (*Creumatogaster erecta*, *A. chartifex spiritii*) excluded smaller ants of their approximate size. If these effects were specific with respect to body size, but did not favor any particular species (e.g., all small bodied species had similar probabilities of establishment with *E. tuberculatum*), it would produce the observed pattern. Related to this hypothesis, it is possible that the effect of the dominant ants on other ants is simply to reduce their number such that the probability of detecting nonrandom patterns of distributions is reduced.

If, as we suggest, community disassembly occurs on the trees with dominants, it complicates our understanding of tropical ant mosaics. It suggests that, at least in the ant community studied here, when dominant ants are present, the other ants present with them are a random subset of the overall community, with their

occurrence perhaps governed by a mix of trait effects (e.g., a certain body size is favored) and the stochastic aspects of colonization and extinction. In contrast, where dominant ants are absent, species are nonrandomly distributed across trees, perhaps due to differences in those trees or the surrounding environment or to the structuring effects of competition. These results suggest obvious experiments that manipulate the presence of dominant species, habitat structure, or the abiotic environment to elucidate the underlying mechanisms driving arboreal ant distributions (Adams 1994, Palmer *et al.* 2002, Gibb & Hochuli 2004). Both observational and experimental work of ant behavior and distribution within treecrowns, while often logistically difficult, would be useful in understanding how ants might spatially or temporally partition individual trees and would add greatly to the future direction of ant mosaic research and tropical arboreal ant ecology.

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