

The Tropical Ant Mosaic in a Primary Bornean Rain Forest

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ABSTRACT

In primary lowland rain forest in Brunei Darussalam, we studied arboreal ant communities to evaluate whether densities and spacing of spatially territorial taxa along 2.9 km of well-studied trails are consistent with existence of a continuous mosaic of dominant ants. A median intercolony distance of 24.5 m, about twice or less distances over which colonies of most included species regularly ranged, suggested a relatively continuous mosaic. Despite relying on nesting sites in preformed plant cavities, carpenter ants contributed > 70 percent of mapped colonies. Most belonged to the *Camponotus* (*Colobopsis*) *cylindricus* (COCY) complex, including SE Asia's 'exploding' ants. Their lack of aggression against certain *Polyrhachis* species was associated with interspecific territory sharing by members of the two groups, and with a dominance-discovery trade-off. Experimental approaches yielded evidence for two putative contributors to positive association. Larger-bodied *Polyrhachis* parasitize food-finding abilities of smaller, more populous *Camponotus* workers, and the two taxa cooperate in territorial defense. Highly territorial and predatory weaver ants (*Oecophylla smaragdina*) were an important component of the ant mosaic in primary forest, second only to codominant COCY and *Polyrhachis* taxa. Members of the genus *Crematogaster* were significantly associated with *Oecophylla* in baiting censuses and regularly monopolized near-nest baits to the exclusion of weaver ants. Litter ant abundances differed between territories of *Oecophylla* and less predatory COCY species, but direction of difference was inconsistent over time. The densely packed mosaic of spatially territorial, and differentially predatory, taxa in Bornean rain forest likely contributes to spatial variation in ant effects on plant and arthropod communities.

Key words: Brunei; *Camponotus*, codominants; *Crematogaster*; dominance-discovery trade-off; information parasitism; *Oecophylla*; *Polyrhachis*; shared territory defense.

MEASURED IN NUMBERS AND BIOMASS IN CANOPY FOGGING SAMPLES, ants (Formicidae) are the numerically dominant arthropods of tropical rain forest canopies (reviewed in Tobin 1991, 1994; Davidson & Patrell-Kim 1996). Functionally, they are also among the most important of arboreal arthropods (Hölldobler & Wilson 1990). Nevertheless, factors regulating ant species diversity and community organization in these complex ecosystems remain poorly elucidated. Early studies, mostly in agroecosystems, documented 'ant mosaics,' *i.e.*, spatial patchworks of territorial 'dominants,' together with positively and negatively associated subordinate ants and other arthropods (Room 1971; Majer 1972, 1976a, b, 1993; Leston 1973, 1978; Jackson 1984). Nevertheless, recent work has challenged both the continuity and existence of such mosaics in primary forests (Majer 1990, 1993; Floren & Linsenmair 2000; for Bornean ants). Possibly contributing to discontinuity is the reliance of most arboreal ants on nests in plant cavities (Dejean *et al.* 1994), together with patchiness of sites where available nest sites and food coincide (Carroll 1979). Exceptionally, territorial weaver ants (*Oecophylla* species) construct their own nests and are important components of many Old World ant mosaics in agroecosystems but are reportedly absent from Bornean primary forests (Floren & Linsenmair 2000). In that same study, replicate fogging samples revealed no difference between actual distributions of positive, negative, and null associations among ant taxa, and those predicted by a neutral model.

Nevertheless, a focus on individual trees, rather than ant territories themselves, could have complicated the search for pattern.

Our study addresses the existence, continuity, and composition of ant mosaics in a primary Bornean rain forest. Rather than choosing specific tree species, or forest patches at random, we investigated positive and negative associations by censusing inside versus outside spatial territories of focal arboreal ant taxa. Elsewhere, negative interspecific associations are enforced by interference competition (*e.g.*, Gibb & Hochuli 2004, Gibb 2005, references above), and we report evidence for such confrontations here. In contrast, mechanisms leading to positive interspecific association remain poorly explored. Preliminary evidence for shared territories therefore led us to test two postulated mechanisms for positive association: information parasitism in food finding (see, *e.g.*, Swain 1980), and shared defense against territorial enemies. In addition to looking for spatial associations among territorial dominants, we also assessed the hypothesis that abundances of subordinate ant taxa (here, leaf litter ants) might also vary with identity of territorial dominant.

Our research took place in lowland dipterocarp rain forest at Kuala Belalong Field Studies Centre (KBFSC), Temburong District, Brunei Darussalam (40°32' N, 115°32' E). Here, a highly species-rich community of medium-to-large-bodied and spatially territorial taxa includes mostly cavity-nesting carpenter ants (genus *Camponotus*). Also represented are *Oecophylla smaragdina* (hereafter *Oecophylla*), species of *Dolichoderus*, *Myrmicaria*, and *Polyrhachis* (informal subgenus *Polyrhachis*), and certain large-bodied *Crematogaster* (informal subgenus *Physocrema*). Commonest among *Camponotus* is a group of at least 16 species from the *Camponotus* (*Colobopsis*) *cylindricus* clade (hereafter COCY taxa; Emery 1925; S. C. Cook *et al.*, pers. comm.). All but the most basal species possess

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hypertrophied mandibular gland reservoirs, extending from the head through the thorax to the gastral tip (Maschwitz & Maschwitz 1974; S. C. Cook & D. W. Davidson, pers. obs.). COCY mandibular glands produce one or more irritant or corrosive irritant compounds, as well as sticky sugars and long-chain aliphatics (Jones *et al.* 2004). More derived members of the group constitute SE Asia's renowned 'exploding' ants and use these products in territorial encounters to cement themselves permanently to conspecific, congeneric, and other enemy ants (Jones *et al.* 2004; S. C. Cook pers. comm.). Strong spatial territoriality is evidenced by consistent deployment of suicidal sacrifice by solitary foragers in one-on-one contests even far from the nest. In contrast to highly predatory and trophobiont-tending *Oecophylla*, COCY species appear to graze microbes and/or their secretions from leaf and stem surfaces, but also feed on extrafloral nectar. Although workers take weak prey (dead mosquitoes) when offered, they rarely retrieve prey under natural circumstances. Thus, *Oecophylla* and COCY may have very different effects on other arthropods and plants. Because both sets of taxa occur terrestrially as well as arboreally, such effects might be apparent on terrestrial ant communities as well as in (more difficult to study) arboreal communities.

At KBFSC, COCY taxa forage regularly and without aggression with *Polyrhachis* (*Polyrhachis*) species (henceforth, *Polyrhachis*), and occasionally also with certain (non-*Physocrema*) *Crematogaster*. Compared to *Polyrhachis* colonies, COCY colonies possess larger numbers of smaller-bodied workers, a trait that should aid in discovering new resources, *i.e.*, in exploitative competition. By contrast, larger *Polyrhachis* workers appear to be superior in interference or encounter competition (*sensu* Schoener 1983), often displacing COCY workers from sugar baits. Together, these observations suggest the sort of dominance/discovery trade-off arguably contributing to point diversity in other tropical and temperate ant communities (Fellers 1987, Savolainen & Vepsäläinen 1989, Morrison 1996, Davidson 1998, Gibb & Hochuli 2004). Tolerance of COCY taxa for *Polyrhachis* species remains curious in view of the abilities of the former ants to kill much larger-bodied workers in contests with one another (S. C. Cook & D. W. Davidson, pers. obs.). However, information parasitism in food finding could help to maintain interspecific sharing of territories. Moreover, preliminary observations of cooperative territorial defense during worker introduction experiments (another study) suggest a second possible contributor to positive association.

Here, we first report on continuity of spatial territories in the ant mosaic at KBFSC. Following this, we present experimental tests for positive association and two putative mechanisms maintaining it. Finally, to assess whether the mosaic of spatial territories affects subordinate members of the ant community, we also analyze the abundance of litter ants across the two most common types of territories.

METHODS

COLONY MAPPING.—Investigators of ant mosaics in agroecosystems have traditionally mapped colonies of dominant ants (or intervening

lacunae) by individual trees, more or less widely spaced in plantation plots. Such an approach is impractical in primary forests, due to the vast areas needed to include numerous territories of dominant ants, foraging over long distances in highly connected and complex vegetation. Instead, we censused ants along transects and, inevitably, with some loss of information (*e.g.*, percentage of unoccupied trees). During > 3000 combined field hours between May 2001 and April 2006, four investigators worked along the 2.5-km long Ashton trail and 400 m of the Enkiang trail at KBFSC. We recorded trail addresses, referenced to permanent markers, for all spatially territorial species ≥ 4 mm body length. (Smaller-bodied taxa may also be spatially territorial [*sensu* Hölldobler & Lumsden 1980] but are not so obvious to observers, and often have more spatially restricted territories.) Colony positions were registered at trail addresses intersected by foragers, defenders, or (rarely) workers taken as prey by predatory weaver ants, presumably at territory boundaries. Where extensive lengths of trail were dominated by the same ant colony (indicated by spatially continuous worker activity), we mapped colonies at midpoints of their ranges. If workers did not cross trails, but nested within 10 m of these curvilinear transects, we mapped colonies at trail addresses directly opposite nests. By following returning workers, we easily found arboreal or terrestrial nests in the understory. However, we frequently failed to locate high canopy nests, and instead mapped trunk trails funneling workers to the canopy. Most COCY colonies were polydomous, with nests located basally (0–3 m) in multiple live tree trunks; a subset of taxa also inhabited dead wood on the forest floor (S. C. Cook & D. W. Davidson, pers. obs.). Polydomous nests usually lay near one another and were considered to represent a single colony unless ≥ 15 m apart or known, from aggression in worker introduction experiments, to house different colonies. *Polyrhachis* species nested terrestrially. Distances between adjacent colonies on the trail map are reported as 'intercolony distances,' and are not equivalent to internest distances, which could be smaller or larger than our measures.

SPECIES ASSOCIATIONS IN BAITING CENSUSES.—In March and April 2006, we assessed COCY–*Polyrhachis* associations by systematically censusing ant visitation to sugar baits (cotton wool soaked in 20% aqueous sucrose solution) near eight COCY nests and including one colony per COCY species. Each such census was paired with one (a control) at a nearby (if possible) trail location midway between, and ≥ 25 m from, mapped COCY colonies. Beginning between 0850 h and 0930 h, we monitored ant activity continuously for 4 h at 12 understory baits, 0.5–1.5 m high in vegetation, and distributed over 12–15 m along trails. An investigator recorded arrival times by species at each bait. Rather than placing baits at equal intervals, we positioned them relatively evenly but in sites not obviously and directly connected by vines and other vegetation. Baits were renewed when declining worker activity began to indicate resource depletion.

In a contingency test, we analyzed presence versus absence of *Polyrhachis* spp. in COCY and control areas. Across all sites where both taxa were represented, we also tested whether presence of *Polyrhachis* at individual baits was independent of that of the COCY species. *Polyrhachis* in these and other COCY territories were

identified to species, in order to assess specificity of relationships. Finally, we evaluated spatial overlap between territories of COCY species and *Oecophylla*, the two most common spatially territorial taxa (below), and determined whether (non-*Physocrema*) *Crematogaster*, frequent visitors to census baits overall, differed in representation across the two types of territories and intervening space.

TESTS FOR SHARED TERRITORIAL DEFENSE.—During March–April 2006, we located six COCY colonies (one per species) with relatively high numbers of *Polyrhachis* in their trunk trails along fallen logs. An investigator then visited each colony once on each of seven days, each time recording the interval (± 30 sec) between his arrival and arrival of the first *Polyrhachis* worker at a specific point on the shared trail. An *Oecophylla* worker was then held by forceps and introduced to each of ten COCY workers without physically contacting them or the substrate. Time to first-arriving *Polyrhachis* was again recorded. No more than one trial per colony was performed per day. Mean arrival times under control and experimental treatments were calculated by colony, and compared in a one-tailed paired *t*-test against the prediction that *Polyrhachis* arrive more quickly after confronting COCY workers with territorial enemies.

Polyrhachis behavior was scored on the following ordinal scale: 0 = walk past introduction point without stopping, and/or antennate local COCY species; 1 = stop, investigate and ‘guard’ point of introduction; 2 = circle introduction point; 3 = run frenetically, bumping COCY workers, mark substrate, shudder (vibrate gaster against substrate). Multiple scores were possible for individual workers, represented in analyses by mean responses.

Finally, to determine whether COCY might also contribute to defense of shared territories, we compared responses of the most common COCY species (*Camponotus saundersi*) to introduced workers of ‘local’ *Polyrhachis* (from the same territory), versus those introduced from colonies at least 100 m distant. *Polyrhachis* were collected from colonies foraging with one of three *C. saundersi* colonies, and were isolated in aerated plastic tubs for at least 2 h before introduction experiments. *Polyrhachis* were then introduced to one of four *saundersi* colonies, including the (control) colony with which it shared a territory. Responses (one per worker) of the first *saundersi* worker to encounter each introduced *Polyrhachis* were categorized on an ordinal scale as: 0 = neutral (ignore, avoid), 1 = investigative (antennate), 2 = submissive (back up abruptly and run, avoid and run, avoid, raise gaster and run), and 3 = aggressive (bite, spray formic acid, explode suicidally, charge, raise gaster, back up, spin around frenetically, chase away). *Camponotus saundersi* behaviors were then tested to determine whether they differed in response to introduction of *Polyrhachis* from local versus distant colonies. With unique pairings of colonies considered to be independent data points, there were six experiments with *Polyrhachis* from distant colonies and four with workers from local colonies.

SAMPLING OF LITTER ANTS.—The disparate diets of the two most widespread territorial taxa (COCY and *Oecophylla*, above and below) led us to investigate abundances of subordinate ants in the two types of territories. Within protected forests surrounding KBFSC, comparisons by canopy fogging would have been prohibitively de-

structive, and focal taxa were rare or missing in more disturbed forests. Instead, we compared abundances of litter ants extracted by Winkler sampling (see *e.g.*, Besuchet *et al.* 1987, Olson 1991, Longino *et al.* 2002). Litter from paired COCY and *Oecophylla* colonies (nearby, where possible) was sampled on the same day. A single bulked sample from four adjacent 0.25 m \times 0.25 m samples was taken per colony per year, except that due to rarity of *Oecophylla*, we occasionally sampled two distant ends of the same (extensive) colony. (When sampling at the same colonies in different years, we also used different locations within those territories.) Otherwise haphazardly positioned sampling quadrats were placed at sites lacking trees and saplings, and with high terrestrial activity of *Camponotus* or *Oecophylla*. Winkler sacks were suspended outside the KBFSC lab in partial sun during the day, and moved inside at night to a room heated by several incandescent bulbs. When thoroughly dry, litter was removed and weighed on a 600-g Pesola scale. Ants were sorted from other arthropods, counted beneath a Leica MZ8 stereoscope, and their abundance (including rare reproductives) expressed both per m² and per gram of litter. In all, we sampled 22 and 26 locations within *Oecophylla* and COCY territories, respectively, 12 and 16 during October–November 2004, and ten per taxon during May–June 2005. *Camponotus saundersi* accounted for seven of the COCY samples in 2004 and five in 2005.

All analyses were performed using JMP v.4.0 (SAS Institute, 2001). Only two COCY taxa could be identified to species; others are referenced by numbers and descriptive names (Table 1). Voucher specimens of all species reside in the entomology collections of the Natural History Museum of Los Angeles County.

RESULTS

COLONY MAPPING.—Omitting *Polyrhachis* (*Polyrhachis*) species, which shared territories with COCY taxa (below) and were not found alone, we mapped 96 points where spatially territorial species either intersected censused trails or possessed nests or trunk trails near the trails. Along the 2.9-km transect, this equates to approximately one colony every 33 m. With trail intersection lengths scored at their midpoints, Fig. 1 graphs the distribution of intercolony distances (median = 24.5 m, mean = 28.5 m).

Cavity-nesting *Camponotus*, and COCY species alone, accounted for 72.2 percent and 69.1 percent of mapped colonies, respectively. Next most abundant was *Oecophylla*, contributing 17.5 percent of colonies and trail coverage disproportionate to colony numbers. *Crematogaster* (*Physocrema*), *Myrmecaria* and *Dolichoderus* comprised 4.1 percent, 4.1 percent, and 2.1 percent of colonies, respectively. Territorial combat was observed frequently during worker introduction experiments (S. C. Cook, pers. comm.), as well as occasionally under natural conditions.

SPECIES ASSOCIATIONS IN BAITING CENSUSES.—*Polyrhachis* species visited baits in all eight COCY areas but in no (control) area lacking COCY ($\chi^2 = 22.2$, $P < 0.0001$, in a contingency test). The median number of baits visited per census by COCY exceeded that for *Polyrhachis* (5.5 vs. 3.0), but this inequity was not significant ($P >$

TABLE 1. Associations between particular *Polyrhachis* (*Polyrhachis*) and *COCY* species; entries are numbers of species cooccurrences. The survey is not comprehensive. Just four names are available for *COCY* in all of Borneo, and nine for the group as a whole (Emery 1925). Except where names can be assigned with confidence, taxa are identified by descriptive names. Observations are limited to one colony each for species (1), (2), and (12). Additional *COCY* taxa exist near KBFSC but have not been registered on the trails censused for this study.

	<i>Polyrhachis</i> (<i>Polyrhachis</i>) sp.			No. colonies with no <i>Polyrhachis</i>
	<i>bihamata</i>	<i>olybria</i>	<i>ypsilon</i> sp. 1	
(1) Small all black				1
(2) Crimson head				1
(3) All black			1	1
(4) Barbecue	4			
(5) Red head yellow goo	2			
(6) Yellow goo	1		1	
(7) Large 'cylindricus'				1
(8) Intermediate 'cylindricus'	2			
(9) Red head orange goo	2	1		
(10) All red	3	2		
(11) Near <i>saundersi</i>	1			
(12) Small <i>cylindricus</i>				1
(13) <i>saundersi</i>	5	1		
(14) <i>clerodendri</i>	3		1	

0.05 in Wilcoxon test). Perhaps because we baited intentionally near *COCY* colonies, the total number of species-baits (novel species per bait) was significantly greater in *COCY* than in control censuses ($P = 0.01$, in Wilcoxon test), and the number of undiscovered baits, marginally lower at *COCY* sites (medians of 2.5 vs. 5.0, $P = 0.07$). Calculated over all species-baits per census, neither mean

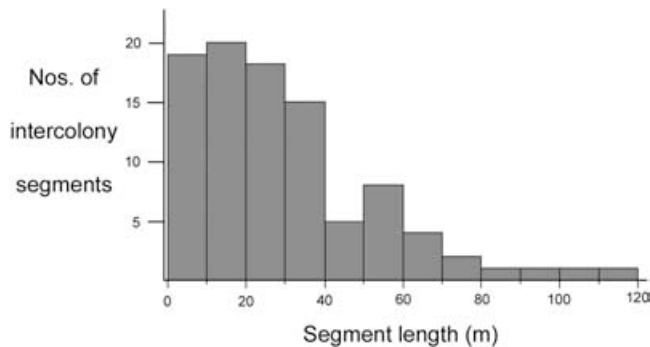


FIGURE 1. Distribution of linear distances separating adjacent colonies of relatively large-bodied and spatially territorial arboreal ant species along the 2.5-km Ashton trail, and proximal 400 m of the Enkiang trail, at KBFSC. Colonies were identified over a 5-yr period, and most were evident repeatedly, if not constantly, subsequent to their discovery. Also included are two colonies where overzealous harvesting may have contributed to colony demise.

nor median time to discovery differed between *COCY* and control censuses ($P > 0.05$).

Polyrhachis tended to arrive late in census periods (mean/median = 134/149 min, vs. 48/33.5, for *COCY* spp.) and was overrepresented on baits previously discovered by *COCY* workers (Likelihood Ratio $\chi^2 = 11.21$, $P = 0.0008$, in contingency test). Of 26 baits visited by *Polyrhachis* across all censuses, 19 (73%) had previously been visited by *COCY*, this despite occurrence of *COCY* on just 46 percent of baits. For baits shared with *Polyrhachis*, *COCY* workers arrived first at 100 percent of baits in six censuses, 67 percent in one census, and zero percent in a final census. In this last case, nestbound *Polyrhachis* workers were traced to a location relatively far from the focal *COCY* colony, and closer to a *COCY* colony of a different species. Recruiting heavily to the first bait(s) at which they arrived, *Polyrhachis* discovered comparatively few baits overall (range = 2–5, median = 2, vs. range of 1–8, median = 5.5 for *COCY*). At 61.1 percent of baits shared with earlier arriving *COCY*, *Polyrhachis* eventually usurped control of the resource. (In no case did *COCY* taxa usurp a bait from *Polyrhachis*.) In other cases, either massive recruitment by *COCY* species prevented takeover by *Polyrhachis*, or late-arriving *Polyrhachis* failed to recruit sufficiently before the end of the census.

Only *P. bihamata* (Drury) and *P. ypsilon* (Emery) were associated with *COCY* spp. in this census. A larger but not comprehensive survey included two other associates: *P. (Polyrhachis) olybria* Forel, and an unidentified species from the same subgenus. Table 1 documents lack of species-specificity in relationships between *COCY* and *Polyrhachis* species.

Oecophylla occurred in three control censuses and at one end of a line of baits in a *COCY* territory, where the latter colony discovered just a single bait. Most abundant of the nonfocal ant taxa by species-bait were (non-*Physocrema*) *Crematogaster* (23.9% of such colonies), often represented within censuses by multiple species. Despite small sample sizes for *Oecophylla* territories, *Crematogaster* were significantly more common by species-bait in censuses within *Oecophylla* territories (mean/median = 3.0/2.5) than in *COCY* territories (1.0/1.0) or in control areas lacking *Oecophylla* (1.0/1.0) ($\chi^2_{[2]} = 6.28$, $P < 0.05$, in a Wilcoxon test). They also accounted for a significantly larger fraction of nonfocal species in *Oecophylla* territories: 47.6 percent of 21 species, vs. 12.2 percent of 41 species in *COCY* territories, and 19.2 percent of 26 species in control areas lacking *Oecophylla* (LR $\chi^2_{[2]} = 9.40$, $P = 0.0091$, in contingency test). In both analyses, data were included twice for the census in which both *Oecophylla* and the *COCY* species visited baits: once for territories of each species. Of 20 baits occupied by one or the other of the two taxa, 75 percent were visited by only one species. Considering just shared baits, *Crematogaster* usurped a single bait from *Oecophylla*, and the reverse took place twice. All three takeovers were on baits at which first-arriving species were represented by few workers. Other shared baits were controlled by first-arriving taxa.

TESTS FOR MUTUAL TERRITORIAL DEFENSE.—*Polyrhachis* workers arrived more quickly after introduction of *Oecophylla* to territory-sharing *COCY* species (3.25 min vs. 5.49 min without introduction; $t = -3.00$, $df = 5$, $P = 0.0151$). They also displayed more aggressive

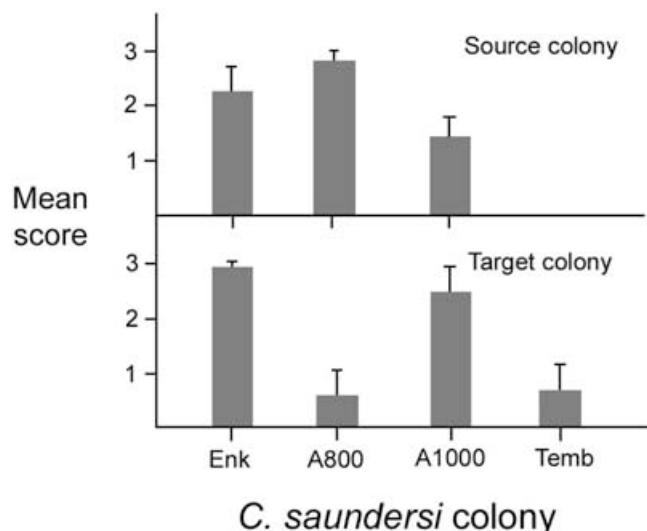


FIGURE 2. Mean behavioral scores (3 = maximum aggressive response) for the first *C. saundersi* workers (per experiment) responding to introduced *Polyrhachis* workers from distant colonies. 'Source' and 'target' colonies both refer to *Polyrhachis*. (All introductions from colony A800 were to Enk.) See text for details.

behaviors upon arrival than did workers in the initial observation period (1.19 vs. 0.05, $t = 15.14$, $df = 5$, $P < 0.0001$).

Camponotus saundersi responses to introduced *Polyrhachis* workers were significantly stronger toward distant than toward local *Polyrhachis* (1.77 vs. 0.00; $\chi^2_{[1]} = 5.17$, $P = 0.025$ in a one-tailed test). For each of 17 individual reintroductions of local *Polyrhachis* workers, behavioral scores of *C. saundersi* were zero, signaling lack of aggression. Mean scores were nonzero for five of six introduction experiments involving foreign *Polyrhachis*, and varied with both source and target colony (Fig. 2). They were greatest for interactions involving colony 'Enk' (Enkiang trail), which had a distinctive species of *Polyrhachis*, *P. ypsilon* as opposed to *P. biamata* in the remaining colonies. Overall, our results suggest that *C. saundersi* respond aggressively toward workers of foreign *Polyrhachis* colonies, both conspecific and heterospecific with those sharing their territories.

LITTER SAMPLING.—In 2004, and in accord with our prediction, litter ant abundance per gram of litter was significantly greater in COCY territories than in *Oecophylla* territories (medians = 0.7/g vs. 0.3/g; $\chi^2_{[1]} = 5.84$, $P < 0.02$). Most of this difference was accounted for by *C. saundersi* ($\chi^2_{[1]} = 8.1$, $P < 0.005$, compared with *Oecophylla*), whose territories held significantly more litter ants than did those of a mix of other COCY species (medians = 0.9/g vs. 0.5/g; $\chi^2_{[1]} = 4.84$, $P = 0.028$). Abundance did not differ between territories of the latter species alone and those of *Oecophylla* ($P > 0.05$). Expressed per m^2 of surface sampled, trends for greater ant densities in COCY and *C. saundersi* territories were not significant ($P = 0.09$ in both comparisons).

In 2005, low sample size prevented treatment of *C. saundersi* separately from other COCY taxa. Contrary to expectation, ant

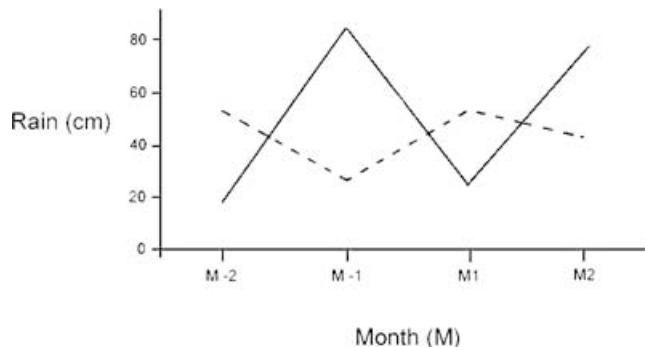


FIGURE 3. Total rainfall (cm) during the first and second months of litter sampling, and for the two months immediately prior to sampling (solid line = 2004; broken line = 2005).

abundance per gram of litter was significantly lower in COCY territories than in *Oecophylla* territories (medians = 0.7/g vs. 0.9/g; $\chi^2_{[1]} = 3.84$, $P = 0.05$). Related to this reversal in pattern, 2005 litter ant abundances exceeded 2004 abundances in *Oecophylla* territories ($\chi^2_{[1]} = 10.44$, $P = 0.0012$) but not in COCY territories ($P \gg 0.05$). The former trend was also significant with abundances expressed per m^2 ($\chi^2_{[1]} = 5.63$, $P = 0.0176$). Differences in abundance between sampling periods prevented combination of 2004 and 2005 data.

Although the climate is not strongly seasonal at KBFSC, weather conditions differed between the two sampling periods (Fig. 3). Conditions were drying out during the month prior to 2004 sampling, but becoming wetter in the month preceding sampling in 2005.

DISCUSSION

We first consider continuity in the mosaic of spatially territorial ants at KBFSC and then discuss interspecific associations between these taxa and other ants.

CONTINUITY OF THE ANT MOSAIC.—The arboreal ant mosaic at KBFSC is surprisingly continuous given that cavity-nesting *Camponotus* account for > 70 percent of mapped colonies (Fig. 1). Although trunk trails can funnel workers of adjacent colonies in opposite directions, it remains impressive that the median intercolony distance along our curvilinear transects (trails) was less than twice the horizontal distances (10–15 m) traveled in the subcanopy by workers of the least wide-ranging territorial taxa. Integration of workers from different colonies is likely greater still in the canopy, where workers fan out to forage solitarily (authors' pers. obs. of COCY taxa from three canopy walkways). This suggestion is bolstered by observations of fighting pairs of workers falling from the canopy at considerable distances from their respective mapped colonies.

Most of the mapped colonies are known to have existed for at least 4 yr, and some (first noticed during other studies) for as

long as 6 yr. Given low overall mortality (two COCY and two *Physocrema* colonies disappearing naturally over 4 yr), they are likely much older. Even disappearing colonies may have been present just transiently in the understory when treefall events temporarily interrupted canopy life. Possibly contributing to long colony life spans, many COCY species inhabit long-lived nests in cavities of live trees. Lack of species-specificity in ant-host relationships (S. C. Cook, pers. comm.) likely promotes continuity in the territorial mosaic.

Essential to discovering relative continuity in the ant mosaic of this forest was the tendency for many territorial taxa to nest, and sometimes forage, in the understory. Also crucial were the many hours spent along focal trails while conducting other studies. Although COCY workers are conspicuous in trunk trails, this is not so for either solitary foragers or stationary workers guarding routes on stems and trunks. Infrequent tree falls, and added time spent baiting in putative 'lacunae' between COCY colonies, contributed previously undiscovered colonies through even the last week of field studies. Undoubtedly future work will continue to add colonies. Nonetheless, a limitation of our survey is that sampled trails mainly followed ridge lines, where magnified effects of periodic droughts could have weakened trees to infection by root- and butt-rot fungi that then enhanced available nest cavity space.

POSITIVE SPECIES ASSOCIATIONS.—Territories of *Polyrhachis* (*Polyrhachis*) species are strongly associated with those of COCY taxa. Indeed, we have no evidence that these *Polyrhachis* occur independently of COCY. Nevertheless, intimacy of these relationships in the understory varies through time (authors' observations). Associations between the two taxa are not species-specific (Table 1), and in one case, a single *Polyrhachis* species even 'adopted' a neighboring colony of COCY species (6), when its former colony (species 10) disappeared. The capacity to nest terrestrially could be integral to the ability of *Polyrhachis* to overlap spatially with cavity-nesting ants, for which suitable nest sites are potentially more limited and/or patchily distributed.

Our studies document two likely contributors to the formation and persistence of COCY-*Polyrhachis* associations: parasitism of resource-finding abilities, and cooperation in defense of shared territories. First, and consistent with preliminary observations, *Polyrhachis* followed COCY to food, then quickly recruited nestmates and often usurped resources. Intriguingly, COCY workers seldom aggressed against the intruders, perhaps because their unique defenses are ineffective against such large and armored opponents (with elevated thorax and hypertrophied pronotal, mesonotal, and petiolar spines; S. C. Cook, pers. comm.). Utilizing epiphytic microbes and/or their minute (and perhaps ephemeral) secretions on plant surfaces, COCY species may also have exclusive resources for which *Polyrhachis* do not compete.

Despite *Polyrhachis* arriving more dependably at baits already exploited by COCY taxa, their arrival was not rapid (mean/median = 88/80 min after *Camponotus* arrived). This substantial delay may reflect the implementation of our experiments during a time of noticeably low *Polyrhachis* activity in the understory. Information on food finds may also propagate slowly because colonies of

both species are spread over large areas of the canopy. Although the nature of the parasitized signal remains unidentified, COCY species may (as do other formicines; Hölldobler & Wilson 1990) mark trails to significant food finds with hindgut secretions that could be detected by *Polyrhachis* workers. Importantly, however, we have often witnessed *Polyrhachis* workers stationed at COCY nest entrances and examining mandibles of outgoing workers. If information parasitism depends on this activity, arrival of *Polyrhachis* at the food source would be delayed until a *Polyrhachis* worker had first located near a COCY nest entrance and then discovered and followed an outgoing *Camponotus* worker that was revisiting a significant (possibly distant) resource. As a consequence of delayed arrival, information parasitism may benefit *Polyrhachis* most for long-lasting resources. Such resources may include, e.g., extrafloral nectar (EFN). Whatever the proximate mechanism of information parasitism, our observations support the so-called 'dominance-discovery' trade-off, first proposed by Fellers (1987) to mediate coexistence in temperate ant communities.

Second, in staged confrontations, both *Polyrhachis* and COCY workers defended against one another's territorial enemies: *Polyrhachis* against *Oecophylla*, an enemy of both species, and COCY against *Oecophylla* and both conspecific and heterospecific *Polyrhachis* from distant colonies. We can only speculate that defense against such 'foreign' *Polyrhachis* may favor a COCY colony by reducing conflict between *Polyrhachis* colonies (or species) inside the COCY territory, but other explanations are possible. COCY species also aggress against *Oecophylla* (above). Shared territories of COCY and *Polyrhachis* species abutted on, but did not overlap, those of weaver ants. However, one territorial boundary was included in a baiting census, and at several others, we found *Oecophylla* workers with dead COCY workers glued to their heads. In one-on-one contests between *Polyrhachis* and *Oecophylla* workers, *Polyrhachis* prevailed by breaking or severing petioles of weaver ants.

Although sharing of territories has been described for ants of other tropical forests, these relationships have involved nondominant ants sharing trails with dominants (e.g., Dejean *et al.* 2000). Because both COCY and *Polyrhachis* species aggressively defend space *per se* against other ant taxa, they are recognized here as 'codominant' territorial species, a type of association not previously proposed for taxa in the tropical ant mosaic, but one which could prove to be more common upon closer study (see, e.g., Swain 1980, Davidson 1988). Together, these taxa dominate shared territories not only numerically, but also behaviorally, thus qualifying them as ecological dominants (Davidson 1998). Large body size enables *Polyrhachis* to win aggressive encounters with other taxa by brute force, and COCY species either recruit powerful major workers (larger-bodied taxa basal in the clade) or employ extraordinary fighting techniques (voluntary self-sacrifice in smaller, more derived species; Jones *et al.* 2004; S. C. Cook pers. comm.).

Surprisingly, in view of early observations, our data suggest that (non-*Physocrema*) *Crematogaster* species are more common within *Oecophylla* territories than elsewhere, though further study is warranted. *Oecophylla* can remove small numbers of *Crematogaster* by grasping them at the petiole (waist) from the anterior end, but if arriving first, small-bodied *Crematogaster* can also exclude *Oecophylla*

by recruiting massive numbers of workers that surround food finds with raised gasters ready to apply potent chemical defenses (e.g., Leclercq *et al.* 2000). It is less clear why *Crematogaster* were not more common within COCY territories and in control areas lacking *Oecophylla*. An answer may be provided by future studies including certain *Crematogaster* species living in close association with COCY colonies but not seen elsewhere (authors' observations).

LITTER ANTS.—We hypothesized that the abundance of litter ants in shared territories of weakly predatory COCY and *Polyrhachis* taxa should exceed that in territories of highly predatory *Oecophylla*. Early sampling of litter ants, under desiccating conditions, supported this hypothesis. During a wetter period, however, litter ants were more abundant in *Oecophylla* territories than in COCY-*Polyrhachis* territories due to increased densities in the former territories only. Temporal differences in *Oecophylla* behavior may account for the discrepancy in results. In addition to preying on litter arthropods, *Oecophylla* workers tend trophobionts in the arboreal zone (Blüthgen *et al.* 2004). The balance of these activities might change depending on rainfall, and indeed, we have noted (but not quantified) marked temporal variation in the terrestrial activity of colonies. If increasingly mesic conditions led to greater trophobiont-tending by *Oecophylla* in 2005, such conditions could also have allowed litter ants to recover rapidly from depredations of *Oecophylla* (see, e.g., Levings 1983), and even to exceed those in areas with frequent terrestrial traffic by COCY workers. Overall, variation in our data suggests the need for further study, stratified to include temporal variation in terrestrial activity of weaver ants.

In summary, a focus on the ant territory, rather than on random points (or trees) in the primary forest, promises to enhance our understanding of tropical ant communities and their possible effects on other species in primary forest. We have identified a relatively dense mosaic of spatial territories of mainly cavity-nesting *Camponotus* and codominant *Polyrhachis*, both of which forage high in the canopy despite nesting principally near (*Camponotus*) or in (*Polyrhachis*) the ground. So far as we can determine from observations in the understory, and from three canopy walkways, the predominant spatially territorial taxa here (COCY species) do not depend substantially on trophobiont-tending, as do taxa in tropical ant mosaics elsewhere (e.g., Dejean *et al.* 2000, Blüthgen *et al.* 2004). Substantial reliance of these taxa on phylloplane microbes and/or their secretions, rather than on prey, could potentially influence distributions of not only subordinate arboreal and litter ants, but also of terrestrial and arboreal nonant arthropods and even plants. Interestingly, COCY species were poorly represented (rare colonies of just 2–3 species), and *Oecophylla* absent, in two disturbed forests surveyed in Brunei. Underrepresentation of such key taxa begs for both explanation and an in-depth analysis of consequences.

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