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Community structure and the habitat templet: ants in the tropical forest canopy and litter

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The tropical forest canopy and litter differ in physical structure, resource availability, and abiotic conditions. We used standardized bait experiments in the canopy and litter of four neotropical tree species to explore how these differences shape the behavior, morphology, and diversity of ant assemblages. Ant activity (biomass at a bait after 32 min) was higher in the canopy, and higher on protein baits than carbohydrate baits. Aggressive bait defense occurred more frequently in the canopy (60%) than in the litter (32%), but was not associated with tree species or bait type in either habitat. The median size of workers of species in the canopy and litter was nearly identical, but body size distribution was unimodal in the canopy and bimodal in the litter. The colony size of the most aggressive species was an order of magnitude larger in the canopy. Species richness at a bait was relatively uniform across tree species and habitats. Litter and canopy shared no species, but overlap among tree species was three times higher in the litter assemblages. Litter assemblages showed less activity, less interference, less differentiation across the landscape, and different size distributions than canopy assemblages. The canopy and litter templets subsume a number of environmental gradients that combine to shape ant community structure.

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Community structure arises when taxa interact with the abiotic and biotic features that comprise the habitat templet (Southwood 1988). Here we focus on the way that ant community structure (diversity, behavior and morphology) differs systematically between the canopy of a tropical forest and the litter below.

Ants (Hymenoptera: Formicidae) are useful taxa for canopy-litter comparisons. They are common and diverse in both habitats, constituting 17–50% of arthropod biomass reported from canopy studies (Tobin 1991, 1995, Davidson 1997, Stork and Hammond 1997). Ants play key ecological roles as herbivores, predators, and mutualists (Hölldobler and Wilson 1990a) and are taxonomically better resolved at the species level than many other invertebrate groups (e.g., Bolton 1995).

The canopy and litter of tropical forests form distinct habitat templets for ants occurring in each. Some of the principal differences between these templets include:

Resource quality. Most of the net primary production (NPP) of tropical forests occurs in the canopy. Canopy food webs are generally based on living vegetation, which yields carbon:nitrogen ratios of 40:1 or more. Litter communities are founded on detritus, with decomposers like bacteria and fungi yielding C:N ratios of around 10:1 (Swift et al. 1979, Begon et al. 1996).

Resource predictability. Arboreal ants commonly harvest plant exudates (e.g., homopteran excreta and extrafloral nectar; Tobin 1991, Davidson 1997) that are dependable in space and time (Beattie 1985). Litter ant food webs, in contrast, start with feces and decaying

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vegetation, and the decomposers that harvest them. These resources, patchy in both space and time, are less predictable than the exudates above (Swift et al. 1979, Coleman and Crossley 1996, Kaspari 1996a, b).

Large-scale heterogeneity. On a scale of hectares, tree crowns represent islands to nonvolant organisms (Hölldobler and Lumsden 1980, Davidson 1998). Tree species differ in crown structure (e.g., Hallé et al. 1978), bark morphology (Whitmore 1962), and chemical resistance to herbivory (Coley and Barone 1996). In contrast, the forest litter is a more or less continuous landscape, and decomposition processes tend to homogenize the chemical and physical structure of its components (Swift et al. 1979, Begon et al. 1996).

Physical complexity. From the perspective of a small arthropod, the canopy is an interlaced collection of linear runways (i.e., branches and lianas). The litter is covered with leaves, twigs and other obstacles, forming a complex, two-dimensional environment (Kaspari and Weiser 1999).

Microclimate. The canopy is generally drier, windier, and receives more sunlight than the litter (e.g., Nadkarni 1994, Parker 1995).

These differences between canopy and litter templets potentially shape many facets of ant community structure. We hypothesized that such habitat differences would be reflected in the behavior, size, and diversity of ants occupying them.

Ant behavior – greater activity, resource defense, and nitrogen limitation in the canopy

Interference competition has long been associated with both terrestrial and arboreal ant communities (Savolainen and Vepsäläinen 1988, Hölldobler and Wilson 1990a, Majer et al. 1994, Andersen 1997). Davidson (1997, 1998) argued that the abundance of carbohydrates (CHOs) in the canopy should fuel high activity (or "tempo" sensu Oster and Wilson 1978) and aggression in canopy ants. At least two other factors may promote greater aggression in the canopy than in the litter: 1) plant exudates are predictable resources with restricted defensible access points; and 2) branches form convenient runways to and from the nest (Carpenter and MacMillen 1976, Hölldobler and Lumsden 1980, Davidson 1997, 1998). In contrast, several lines of evidence suggest that disturbance, not competition, is a major force structuring tropical litter ant assemblages (Franks 1982, Byrne 1994, Kaspari 1996a, b).

The litter habitat offers a high relative abundance of N, especially for omnivorous, predaceous, and fungivorous ant species (Byrne 1994, Tobin 1994). In the canopy, more ant biomass is supported on proportionately less protein (N). Canopy assemblages should thus be more N-limited.

Ant size – larger ants and larger colonies in the canopy

The energy available to consumers as photosynthate is, by definition, higher in the canopy than in the litter below. If colony mass is constrained by energy availability, then the canopy should allow the growth of larger colonies and larger workers than in the litter. In addition, the more dependable, defensible resources in the canopy should favor the existence of large, aggressive colonies (Hölldobler and Lumsden 1980, Davidson 1997).

Environmental conditions should also favor larger worker size in the canopy. Desiccation stress can be significant to small terrestrial invertebrates, and arboreal ants experience a drier microclimate than litter ants. Gradients of decreasing moisture can select for larger ant workers (Kaspari 1993) or thicker waxy cuticles (Hood and Tschinkel 1990) to prevent desiccation.

Ant diversity – low species overlap between canopy assemblages

Differences in physiognomy between tree species create large-scale structural heterogeneity within the forest canopy. Likewise, the distribution of palatable plant exudates (and perhaps species of mutualistic Homoptera) is a function of the distribution of tree species, which differ in defensive chemistry. If such spatial variability promotes specialization, then canopy ant taxa should differ across tree species, thus contributing to high regional diversity (cf., Erwin 1982). In contrast, the relative structural and chemical uniformity of the litter from different tree species provide few obvious gradients allowing ant specialization. Although tropical ant species distributions are patchy in both the canopy (Majer 1972, Adams 1994) and litter (Kaspari 1996a), there are few studies explicitly linking ant species to particular tree species in the tropics (but see Hölldobler and Wilson 1990b).

The comparative ecology of the tropical canopy and litter is poorly developed, in part for lack of standardized sampling protocols suitable for use in both habitats. Area-based sampling (e.g., quadrats) works well in the litter, but is difficult to implement (and interpret) in the canopy. Likewise, volumetric sampling (e.g., fogging) is less thorough (Adis 1990, Stork and Hammond 1997) and difficult to compare directly with area-based litter samples. Bait studies are often used in ant research (Culver 1974, Fellers 1987, Savolainen and Vepsäläinen 1988, Andersen 1992), and offer a viable alternative to area- or volume-based sampling. Although bait studies include some biases (e.g., baits are unlikely to attract specialized predators), baiting is logistically simple and readily employed in both canopy

and litter environments, and thus an effective tool in contrasting the two ant assemblages. We used standardized bait experiments to show that canopy and litter ant assemblages differ with respect to activity, aggression, and size distribution.

Materials and methods

This study was conducted in the lowland, seasonally wet forest of Barro Colorado Island (BCI), Panama (see Leigh et al. 1996 for a site description). All data were gathered during the early dry season (November through December) of 1997.

Bait experiments

We used mature canopy or emergent individuals of four tree species in the study: *Pseudobombax septenatum* (Bombacaceae), *Ceiba pentandra* (Bombacaceae), *Dipteryx panamensis* (Fabaceae), and *Anacardium excelsum* (Anacardiaceae). We selected these species because they are relatively common in the BCI forest (Croat 1978). In addition, they differ markedly in bark roughness (high in *Anacardium* and *Ceiba*, low in *Pseudobombax* and *Dipteryx*), which may influence ant and other invertebrate diversity through microhabitat availability (e.g., Nicolai 1986) and epiphyte assemblage structure (e.g., Dejean et al. 1995). The trees were distributed over ca 300 ha and separated by >50 m. All data were collected between 09:00 and 15:00 in fair to sunny weather.

We recorded ant recruitment to baits in the crowns and understory litter of five individuals of each tree species. Two types of bait were used: cotton soaked in saturated sucrose solution (hereafter, "CHO bait"), and meat (cooked turkey or canned tuna; hereafter, "N bait"). A third bait, cotton soaked in distilled water, was also used as an inert control to measure baseline ant activity. Water baits were rarely visited and never provoked aggression; we ignore them for the remainder of this paper. Each bait was ca 4 ml in volume, had an exposed area of 7–9 cm^2 and circumference of 7–10 cm. One set of baits (N, CHO, and water) was used in the crown of each tree. Canopy baits were placed directly on bare upper surfaces of branches near the main fork of each tree crown, which was between 17 and 35 m above the ground, depending on tree morphology. Individual baits were located 0.2–1.0 m apart to facilitate censusing and to allow foraging ants approximately equal access to all baits within the experimental time span. Trees were climbed using the single-rope technique (Perry 1978).

We observed baits continuously, and recorded the abundance of each (morpho)species present at 1, 2, 4, 8, 16, and 32 min after bait placement. The nature and outcome of aggressive interactions among species were noted during the observation period. We collected vouchers for species determinations at the conclusion of the observations, then repeated the procedure in the litter immediately beneath each tree. Litter baits were placed on the upper surfaces of intact leaves so that all foraging ants were clearly visible.

Species were identified in the laboratory, mounted on pins, and head length (mm) was measured to the nearest 0.1 mm using an ocular micrometer and dissecting scope. We estimated the biomass (mg) of workers for each species using subfamily-specific equations linking head length to mass (Kaspari and Weiser 1999). At least five workers of each species were measured when possible; some rare species offered fewer individuals. Vouchers of all species and morphospecies were deposited at the Univ. of Oklahoma; the Museum of Comparative Zoology, Harvard Univ.; the Smithsonian Tropical Research Institute, Panama; and the Univ. of Panama, Panama City.

Ant behavior – greater activity, resource defense, and nitrogen limitation in the canopy

To compare ant activity, we calculated the biomass of ants at baits after 32 min by multiplying the abundance of each species by its worker mass. We used a two-way ANOVA (log-transformed data) to analyze the effects of bait type (N vs CHO) and location (canopy vs litter) on biomass.

To test for heightened aggression in the canopy, we tallied the number of baits at which behavioral dominance occurred in the litter (out of a possible 40) and canopy (out of a possible 37; three baits were never visited). We defined a behaviorally dominant species as one that increased in abundance over the course of observations at a bait and had some direct effect on the presence or abundance of one or more submissive species at a bait. We restricted this definition by excluding monopolization of a bait by a single species with no aggressive interspecific interactions. We defined submissive species as those that: 1) decreased in abundance while a dominant species increased, 2) were denied access to the bait by a dominant species already present, or 3) were able to access the bait, but only for very short time periods prior to being swarmed and subsequently ousted by an aggressive species.

Using observations of aggressive interactions at baits, we assigned ant genera to a competitive hierarchy following standard terminology (Savolainen and Vepsäläinen 1988, Davidson 1998): *encounter* species defend food finds against competitors; *submissive* species are behaviorally subordinant. Within encounter species, we distinguished between *obligate encounter* taxa that defended baits against all other genera, and *facultative encounter* taxa that defended baits in the absence of obligate encounter species.

Ant size – larger ants and larger colonies in the canopy

We used worker mass (mg) and colony size estimates to compare the size distribution of species between the canopy and litter. Worker mass data were obtained from collected vouchers as described above. Colony size data are unavailable for most ant species (Kaspari and Vargo 1995), so we relied on published estimates to make comparisons within a behavioral subset – the obligate encounter species.

Ant diversity – low species overlap between canopy assemblages

We constructed a cumulative species list for the canopy and litter ant assemblages of each tree species. The occurrence of a species was quantified as the number of trees in which it was found (e.g., the maximum value in each case was five, indicating a species found in all five individuals of a tree species). We estimated overall species richness, assuming bait sampling had continued until all species were collected, using the Chao II statistic (Colwell and Coddington 1994, Colwell 1999). We used the Morisita-Horn index (Brower et al. 1990) to calculate species overlap among assemblages (ranging from 0 to 1, with 1 representing complete overlap). SAS programs were used for all other statistical tests (SAS Institute 1989).

Results

Baits were quickly discovered by ants in both habitats; the median time to first discovery of all three baits in the canopy and the litter was 2 min. All of the sugar (CHO) and meat (N) baits in the litter were used (40 of 40), while 37 of 40 canopy baits were visited during the 32-min observation periods.

Ant behavior – greater activity, resource defense, and nitrogen limitation in the canopy

Ant activity (biomass at 32 min) at N baits was higher than at CHO baits, and activity in the canopy was greater than in the litter (Fig. 1, Table 1). The number of species per bait did not differ between canopy and litter (range 1–3, Kruskal-Wallis $\chi^2 = 1.43$, $P > 0.32$), but was significantly greater on CHO baits than N baits (medians = 2 and 1, respectively; Kruskal-Wallis $\chi^2 = 4.56$, $P < 0.033$).

Behavioral dominance occurred at 62% of canopy baits and 30% of litter baits ($\chi^2 = 5.23$, df = 1, $P < 0.03$). The frequency of dominance was not associated with bait type or tree species in the canopy or litter

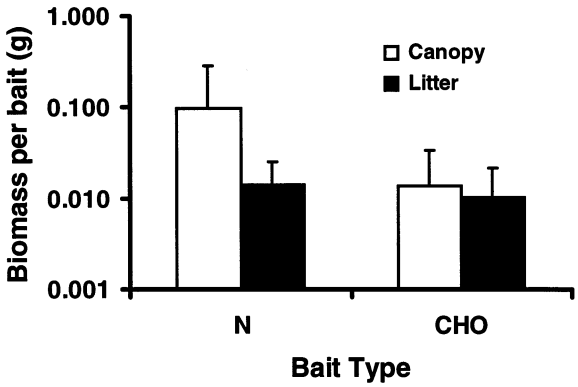

Fig. 1. Average mass (+ 1 SD) of ant workers present at meat (N) and sugar (CHO) baits in the canopy and litter after 32 min. ANOVA results are shown in Table 1.

(Fisher's exact tests: df = 1; canopy $P > 0.9$; litter $P > 0.9$).

Based on aggressive interactions observed at baits, two taxa in each habitat were obligate encounter genera: *Ectatomma* and *Wasmannia* in the litter; and *Azteca* (four species) and *Crematogaster* (three species) in the canopy. Species of *Cyphomyrmex* and *Trachymyrmex* were submissive in the litter, whereas species from four genera, *Pachycondyla*, *Odontomachus*, *Pseudomyrmex*, and *Cephalotes* (subgenus *Zacryptocerus*) were submissive in the canopy. Although species of *Pachycondyla* often behaved aggressively (as insinuators, sensu Wilson 1971) and some *Cephalotes* (*Z.*) species were trail parasites of *Azteca* (Adams 1990), these genera consistently acted as subordinates to facultative and obligate encounter species in the canopy. Within litter and canopy habitats, all remaining taxa listed in Table 2 were facultative encounter species.

Ant size – larger ants and larger colonies in the canopy

The distribution of average worker size was strongly bimodal in the litter and unimodal in the canopy (Fig. 2). This difference was reflected by comparisons of the average body size of obligate encounter genera in both habitats (Table 3): the mean size of *Azteca* and *Crematogaster* workers was similar, whereas the mean size of *Ectatomma* and *Wasmannia* workers diverged by two

Table 1. The effects of bait type (meat vs sugar) and location (canopy vs litter) on biomass of ants present after 32 min.

Effect	df	Type III SS	*F*	*P*
Bait type	1	4.55	10.38	0.0019
Location	1	2.31	5.28	0.0246
Bait × location	1	0.83	1.89	0.1741
Error	70	30.67		

Table 2. Composition and occurrence of ant species in canopy and litter assemblages. Species lacking an authority are morphospecies. Values are the number of individual trees of a given species (max = 5) in which an ant species was found. Ana = *Anacardium*, Cei = *Ceiba*, Dip = *Dipteryx*, Pseu = *Pseudobombax*.

Canopy	Ana	Cei	Dip	Pseu
Azteca forelii Emery	–	–	–	3
A. instabilis F Smith	–	2	–	2
A. nigricans Forel	–	–	1	–
A. cf. *trigona/chartifex*	2	–	–	–
Camponotus cf. *auricomas*	–	–	2	2
C. christopherseni Forel	–	1	–	–
C. novogranadensis Emery	1	1	–	1
C. senex F Smith	–	2	3	1
C. sericeiventris Guerin-Meneville	–	1	–	–
Cephalotes atratus L.	–	–	2	2
C. (*Zacryptocerus*) *grandinosus* F Smith	–	–	–	1
C. (*Z.*) *multispinus* Emery	–	–	1	–
C. (*Z.*) *umbraculatus* Fab.	–	–	–	1
Crematogaster brevispinosus Mayr	–	–	–	1
C. crinosa Mayr	–	–	1	–
C. distans Mayr	–	–	1	–
Dolichoderus bispinosus Olivier	–	1	–	–
D. curvilobus Lattke	1	–	–	–
Odontomachus meinerti Forel	1	1	–	–
Pachycondyla foetida L.	–	1	1	–
Paratrechina spp.	1	1	–	–
Pheidole brn	–	1	–	1
P. orng	3	–	–	–
Pseudomyrmex cubaensis Forel	–	–	1	2
P. gracilis Fab.	–	–	–	1
P. oculatus Smith	–	–	2	1
P. simplex Smith	–	–	–	1
P. tenuissimus Emery	–	1	–	–
P. viduus Smith	–	1	–	–
Solenopsis can1	–	2	–	–
S. can2	1	–	–	–
Wasmannia rochai Forel	–	1	–	–
Litter	Ana	Cei	Dip	Pseu
Cyphomyrmex major Forel	1	–	–	–
C. rim1	–	1	–	–
Ectatomma ruidum Roger	4	1	5	5
Odontomachus bauri Emery	2	4	–	–
O. hastatus Fab.	–	–	1	–
Pachycondyla harpax Fab.	–	1	–	–
P. impressa Roger	1	–	–	–
P. obscuricornis Emery	–	2	–	–
Pheidole multispina Wilson and Brown MS	2	3	1	3
P. nov3	1	–	–	–
P. nov10	1	–	1	–
P. rugiceps Wilson and Brown MS	–	–	1	–
P. skd	–	1	–	–
Solenopsis cl1	–	1	–	2
Trachymyrmex cornetzi Forel	1	3	2	1
Wasmannia auropunctata Roger	1	2	4	2

orders of magnitude. Although both canopy and litter assemblages had ants from < 0.01 mg to > 10 mg, the modal size class of the canopy was entirely absent from the litter. There was no difference in the median size of workers between habitats (Kruskal-Wallis $\chi^2 = 1.20$, $P > 0.27$). Colony size estimates obtained from the literature suggest that canopy dominants also had larger colonies (Table 3).

Ant diversity – low species overlap between canopy assemblages

We recorded twice as many species visiting baits in the canopy (32) than in the litter (16). The litter and canopy shared no species at baits (Table 2). Based on the Chao II statistic, the estimated number ($\pm$ SD) of species (had sampling gone to completion) was 56

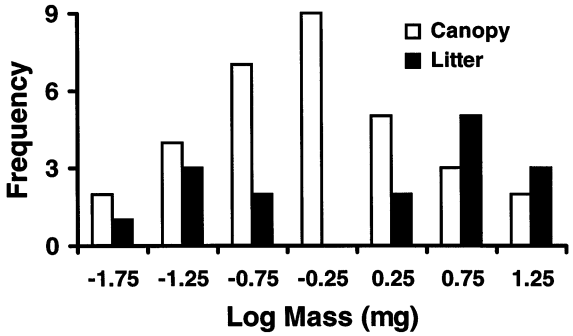

Fig. 2. Size distribution of ant species using baits in the canopy and litter. Frequency = number of species within a size class. Size class " − 1.75" includes species with $\log_{10}$ worker mass ≤ -1.75, class " − 1.25" includes species with worker mass > -1.75 and ≤ -1.25, etc.

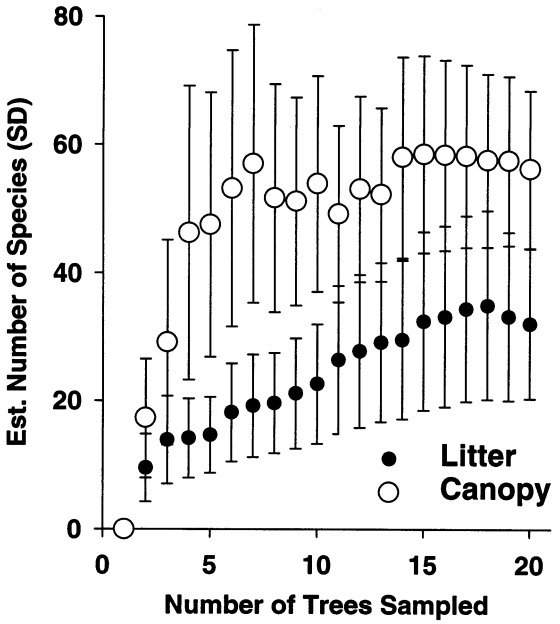

Fig. 3. Accumulation curves relating the estimated species richness of both habitats to the number of trees sampled. Points represent the means (± SD) of 50 random permutations of the data.

(± 12.25) in the canopy and 32 (± 11.75) in the litter. A plot of sampling effort against estimated species richness (drawn from 50 random permutations of the data; Colwell 1999) suggests that these estimates stabilized after the accumulation of 20 samples (Fig. 3).

Ant species composition varied with tree species within the two habitats (Tables 2 and 4), and the canopy assemblages were less similar between tree species than the litter assemblages. The average Morisita-Horn index of overlap was 0.21 for the canopy and 0.65 for the litter (Kruskal-Wallis $\chi^2 = 6.6$, $P < 0.02$). This pattern was best illustrated by *Anacardium* and *Dipteryx* trees, which shared no canopy species; whereas five of seven ant species found beneath *Dipteryx* were also found at *Anacardium* litter baits.

Discussion

The potential importance of CHOs in maintaining aggressive, high-tempo, high-biomass ant assemblages in tropical forest canopies was hypothesized by Tobin (1991) and Davidson (1997). Ours is the first study to directly test their hypotheses by comparing ant activity and resource defense between the forest canopy and litter. The canopy and litter differ in a variety of ways, including insolation, travel costs, and food quality and quantity. As such, they constitute two habitat templets (sensu Southwood 1988) only 20 m apart and available to a diverse ant fauna. We argue that these differing templets select for distinct ant assemblages.

Our results support the hypotheses of Davidson and Tobin by showing that behavioral dominance is more common and ant activity is greater in the forest canopy than in the litter. Species of the canopy specialist *Azteca* (a "dominant dolichoderine" sensu Andersen 1995) and the myrmecine genus *Crematogaster* likely contributed much to this pattern. Both genera are common on BCI (Table 2), and have relatively large, often polydomous colonies. Although the frequency of behavioral dominance was not associated with bait type in either habitat, N-baits, especially in the canopy, recruited more ant biomass concentrated among fewer species. This suggests that canopy ants are N-limited to a greater extent than litter ant assemblages.

The difference in aggression we observed between canopy and litter ants arose because canopy species recruited larger numbers of workers and defended baits in different ways. Dominant litter ants used stings and

Table 3. Characteristics of obligate encounter genera (sensu Davidson 1998) in the canopy and the litter. Worker size is average dry weight. Ranges in parentheses.

Canopy	No. of trees	Worker size (mg)	Colony size (workers only)	Citation
Azteca	10	0.39 (0.24–0.57)	50 000–100 000	J T Longino pers. comm.
Crematogaster	3	0.26 (0.09–0.53)	1085–5000?	Van Pelt 1958
Litter				
Ectatomma	15	2.08	105	Breed et al. 1990
Wasmannia	9	0.04	839	Kaspari and Vargo 1995

mandibles to defend baits – mechanisms requiring close contact to be effective (i.e., after an invader encountered the bait). Dominant canopy ants primarily used chemical defenses, which acted at a larger spatial scale and may have prevented submissive species from contacting the baits. Consequently, the chance that fragments of bait could be successfully stolen by a vigilant invasive species was far lower in the canopy (SPY, pers. obs.).

Contrary to our hypothesis, diurnally active canopy ants were not larger than litter ants. Our baits, however, did not attract the largest ant in the forest (the arboreal forager *Paraponera clavata*), nor did they attract many small species of the litter (e.g., the tribes Dacetini and Basicerotini, the genus *Hypoponera*, and other specialized predators). So it is possible that the failure to find differences was a sampling artifact. A more intriguing result was the difference in body size *distribution* between habitat templets, which may be related to differing constraints on locomotion. In the network of branches of the canopy, movement occurs primarily over a linear environment with a low frequency of obstacles. In contrast, the litter is two-dimensional; large ants can step over gaps between leaves, and small ants can walk through the litter interstices (Kaspari and Weiser 1999). Intermediate ant sizes are comparatively ineffective at either function. Thus, the litter environment may be more likely to favor divergent body sizes.

The lower frequency of aggressive bait defense in the litter may also be related to the effects of physical complexity on body size. The two obligate encounter species in the litter differed in size by two orders of magnitude (Table 3). Larger species in the litter generally recruited to baits by traveling on the exposed upper surfaces of litter, while smaller species recruited through the litter and accessed baits at their margins or from below (SPY, pers. obs.). This difference in access appeared to promote spatial partitioning of the bait among recruiting species in the litter. In contrast, the simpler canopy environment offered only one access route to the bait. The physical complexity of the litter may be another mechanism reducing the frequency and intensity of interspecific interactions relative to the canopy.

Table 4. Morisita-Horn index of ant species similarity among assemblages in the crowns and litter of the focal tree species.

Canopy	*Ceiba*	*Dipteryx*	*Pseudobombax*
Anacardium	0.14	0.0	0.04
Ceiba	–	0.28	0.29
Dipteryx	–	–	0.49
Litter	*Ceiba*	*Dipteryx*	*Pseudobombax*
Anacardium	0.61	0.74	0.78
Ceiba	–	0.44	0.48
Dipteryx	–	–	0.83

These results, along with those of Andersen (1995, 1997), constitute continuing steps toward the development and field-testing of a templet-based model of ant community organization. One key result supports the growing view that competition between ant colonies is diminished in the tropical forest litter relative to the canopy. However, few studies have thus far quantitatively compared the two assemblages. Furthermore, the relative contribution of gradients in CHO abundance (Davidson 1998), temperature (Andersen 1995), predation and disturbance (Kaspari 1996a, b), and habitat complexity to this pattern have yet to be worked out. Many, if not most, of these gradients are subject to experimental manipulation and covary to different degrees across other habitat templets (Kaspari et al. 2000).

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