

## Testing resource-based models of patchiness in four Neotropical litter ant assemblages

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In four Neotropical forests I studied how resource availability affected patchiness in litter ants, colonies of about 100 workers living in hollow twigs. At the regional scale, and contrary to Species Energy Theory, Costa Rica and Panama forests had similar species richness, despite the former being more productive. At the m<sup>2</sup> scale, nest densities varied 10-fold, often exceeding 10 nests/plot. I tested four predictions linking this patchiness to resource limitation and depletion. First, nest densities increased weakly with estimates of litter quantity and quality. Second, nest addition experiments doubled colony densities after four months in the two Panama assemblages. Third, colonies of most common species appeared to grow as fast when they were small as when they were large. Fourth, there was no suggestion of self-thinning among colonies: plots with large colonies did not have fewer colonies after removing the effects of litter. Combined, these results suggest that resources in the litter, most notably nest sites, may limit local patchiness, but that there is little evidence for food depletion. The unstable litter environment may preclude tropical litter ant colonies from growing large or populous enough to saturate their environment.

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At both the local and regional scales, resource gradients may shape the distribution and abundance of animals (MacArthur 1972, Ricklefs and Schluter 1993, Rosenzweig 1995). In the developing field of Species Energy Theory, regional gradients in productivity have been correlated with species richness for a variety of animals, mainly vertebrates (Currie 1991, Wright et al. 1993, Rosenzweig 1995). At the local scale, resource regulation of species richness is complicated by the effects of predation, disturbance, and abiotic gradients (Andrewartha and Birch 1954, Hairston et al. 1960, Brown 1981, Yodzis 1986, Currie 1991, Ricklefs and Schluter 1993, Tilman and Pacala 1993) whose strength may vary along regional productivity gradients (MacArthur 1972, Fretwell 1977, Power 1992).

The role of resources in shaping the distribution of ant diversity is unresolved despite much interest in ant

ecology (Brown 1973, Hölldobler and Wilson 1990). At the regional scale, Species Energy Theory appears to hold in at least some deserts (Davidson 1977, Morton and Davidson 1988) but the link between diversity and productivity in richer ecosystems is unknown. At the local scale, competition is seen as the main factor regulating ant populations (Jeanne and Davidson 1984, Hölldobler and Wilson 1990, Andersen 1991) but evidence for resource limitation and depletion among ant colonies is still thin (see review in Deslippe and Savolainen 1994). For example, studies of patchiness along resource gradients are rare (e.g., Savolainen and Vepsäläinen 1988, Deslippe and Savolainen 1994) relative to nest dispersion studies targeted at uniform resource gradients (Levings and Traniello 1981, Cushman et al. 1988, Rytty and Case 1992, Deslippe and Savolainen 1994). Studies of distributions along re-

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source gradients, however, have much to offer. They allow one to examine both requisites of exploitative competition (Martin 1987): resource limitation (increases in population densities or colony fitness with added resources) and resource depletion (the denial of that resource to other individuals).

Litter ant species which nest in twigs and nuts on the forest floor are a conspicuous part of the tropical fauna (Wilson 1959). Both the tropical litter and tropical litter ants are notoriously patchy, varying ten-fold in density at the m<sup>2</sup> scale (Wilson 1959, Levings 1983, Kaspari 1993, Byrne 1994). The former may drive the latter, since litter provides nest sites and food to litter ant colonies. But to date studies have linked litter depth to the number of individual ants (Levings 1983). A better test would correlate the density of colonies, which may vary in size, to the amount of litter resource. Here I test four predictions arising from the hypothesis that litter resources limit ant populations, and that their depletion constrains colony size and density. I outline these 4 predictions below.

*Prediction 1: Nest densities track changes in litter quantity and quality*

Tropical litter varies in depth and nutrient value over the year. During the dry season litter accumulates. At the onset of the wet season, rains release a pulse of nutrients from the litter that quickly ebbs (Cornejo et al. 1994). Concurrently, there is a pulse of microflora and fauna (Frankie et al. 1974, Levings and Windsor 1982, Levings and Windsor 1984, Cornejo et al. 1994). Thus as the wet season progresses, both food and nest site availability should decline. If food and nest sites limit litter ant densities, I predict that 1) litter ant densities should correlate with litter volume, and 2) the same volume of litter will support fewer nests later in the wet season.

*Prediction 2: Adding nests increases colony densities*

Litter nests are continually rotting from around their occupants (Byrne 1994). If the supply rate of new twigs is low, then fresh nest sites may be at a premium. Adding small pieces of bamboo to the litter should increase the availability of twigs without changing litter microclimate or food supply. If population densities increase on supplemented plots, this would be strong evidence for nest site limitation in litter ants (Herbers 1986) and a mechanism for a litter depth-nest density correlation.

*Prediction 3: Growth rates decline with colony size*

A colony allowed to grow uninterrupted must eventually deplete the food around the nest (Wilson 1971). This should cause colony size to stabilize as per-capita growth rate declines. Since each nest includes a colony's present and future work force (Michener 1964) the growth rate of the colony can be inferred from a plot of

worker pupae against worker number. If a colony depletes resources as it grows, the pupae-worker curve should plateau as less and less food is harvested per worker. If pupae-worker curves are linear or accelerate then some factor other than food supply (like disturbance) may limit colony size (Cole 1984, Kaspari and Byrne 1995).

*Prediction 4: Colonies are self-thinning*

Assume food limits colony growth and colonies deplete food locally. If so, as colonies on a plot grow, the number of colonies on that plot must decrease. Plant ecologists call this progressive winnowing "self-thinning" (Harper 1977). Self-thinning in ant assemblages may occur through mortality of incipient colonies (Ryti and Case 1986, Cushman et al. 1988) or habitat selection by foundresses or adult colonies (Fretwell and Lucas 1970, Kaspari and Vargo 1994). Regardless of the mechanism, self-thinning should produce an inverse correlation between average colony size and colony density. Failure to find self-thinning would argue that resource depletion is not a major factor shaping the distribution of ants in the litter.

## Study sites

I studied four Neotropical rainforest assemblages in the wet season, a period of high ant activity and reproduction (Wilson 1959, Levings 1983, Kaspari 1993, Byrne 1994, Kaspari and Byrne 1995). I began this study in July 1990; the bulk was conducted from May through November 1991. It took place at two sites: the Estacion Biológica La Selva (10° 26' N, 83° 59' W), managed by the Organization for Tropical Studies in Costa Rica, and Barro Colorado Island (9° 09' N, 79° 51' W) managed by the Smithsonian Institute of Tropical Studies in Panama. At each site I studied one closed canopy forest and one more open forest with litter stressed by periodic flooding or drying winds.

La Selva is a lowland tropical wet forest (Holdridge et al. 1971) on the Caribbean slope of Costa Rica. It has an annual rainfall of 3991 mm, a 1-month dry season, and an estimated net primary productivity (NPP) of 1200 g carbon m<sup>2</sup> yr (unpublished data, Kercher et al. 1992, Sanford et al. 1994). I sampled two forests. La Selva-1 had a high, closed canopy. The soil was residual with a gentle slope far from permanent water. Palms dominated the understory. I sampled La Selva-1 in May and August of 1991. I arranged plots in 8, 10 × 10 meter squares. Each square had plots at each corner and in the center. The squares were in two rows of four. The rows, and the squares within each row, were 20 m apart.

La Selva-2 had a relatively open canopy and was once a pasture, abandoned 15 yr before this study. It

floods often during the wet season (pers. obs. over 3 wet seasons) by a stream that cuts through gently rolling hills. The soil is alluvial with an understory of palms. I sampled La Selva-2 along a transect, with 28 plots separated by 10 m in July 1990.

BCI is a 1500-ha hill in Lake Gatun, created by the construction of the Panama canal. BCI is a lowland tropical moist forest (Holdridge et al. 1971) averaging 2600 mm rainfall yearly, with 90% of the rain coming during the May-December wet season and an estimated NPP of 1100 g carbon/m<sup>2</sup>/yr. less than La Selva (unpublished data, Croat 1978, Dietrich et al. 1985, Kercher et al. 1992). BCI-1 was primary forest on a residual soil in a sheltered ravine. BCI-2 was on a flat, open hilltop with less canopy and understory than BCI-1. BCI-2 had the driest litter of any lowland sites on BCI (Levings 1983). I sampled both BCI forests in June-July, and September-November, 1992. I used parallel transects oriented East West, producing a grid with each plot 10 m apart.

The timetable of this study is presented in Table 1. I sampled La Selva and BCI at the beginning and middle of the wet season. The aim was to sample the litter during and after the litter nutrient pulse. Deep litter constrained the number of sample plots on BCI early in the wet season.

## Methods

To sample ant nests, I marked out m<sup>2</sup> plots with wire flags and string, then split them into 9 0.11-m<sup>2</sup> quadrats. I estimated litter depth by gently forcing a wire, marked in 0.5-cm increments, into the litter until it reached the soil. I measured depth at each corner of the plot, and the corners of the central 0.11-m<sup>2</sup> square. The mean of the eight measures was the estimate of overall litter depth.

Sitting on the ground, I inspected each piece of litter for ant nests, using a head lamp on dark days. The only litter not sampled were large pieces of very hard wood that I could not open with a pocket knife. I placed each nest (defined as workers with brood) into a plastic bag. I returned all litter to the plot.

At the laboratory I classified nests to type (twig, wood, between leaves, hollow nut or pod) and stored

Table 1. Number of plots sampled at each site for this study. La Selva-2 was sampled in 1990, all other forests were sampled in 1991.

Forest	Early wet season			Late wet season		
	May	June	July	August	Sept.	Oct.
La Selva-1	40			30		
La Selva-2			28			
BCI-1		11	11		13	15
BCI-2		12	12		15	15

nest contents (brood, workers, queens and alates) in 70% ethanol. I later identified ants to species or morphospecies (henceforth referred to as species, but identified by a 4-letter species code) using keys and reference collections, with vouchers deposited at the Museum of Comparative Zoology, Harvard Univ. A complete list of species is available from the author.

I used the Chao 2 statistic (Chao 1984, Colwell and Coddington 1994) to estimate species richness from a sample. The Chao 2 statistic is nonparametric, works well when most species are rare, and is accurate at sample sizes of 25 plots and over (Colwell and Coddington 1994). I tested for patterns of species association among m<sup>2</sup> plots within forests using Spearman rank correlation matrices for species represented by at least 10 nests.

### *Prediction 1: Nest densities track changes in litter quantity and quality*

I used Analysis of covariance to explore the effects of litter quantity (measured by depth) and declining quality (early vs mid-wet season) on log<sub>10</sub> nest density and species richness. I used forest site as an additional class variable to look for consistency of effects.

### *Prediction 2: Adding nests increases colony densities*

I evaluated relative nest site limitation at the 4 forests by placing out 5 artificial nests on transects of fifty 1-m<sup>2</sup> plots, 10 m apart. The nests were small (ca 15 cm) bamboo internodes with one end open. I placed out and collected bamboo in each of two 45-d periods, corresponding to early and mid-wet season (in Panama and La Selva-1) and one 45-d period in the early wet season (at La Selva-2). Differences in the proportion of nests colonized would, I posited, reflect differences in the rarity of nest sites.

I measured nest site limitation directly in the two Panama forests. In July 1991 I set up transects of fifty 0.11-m<sup>2</sup> plots, separated by 5 m. Two wire flags marked the plot's location. Alternate plots were supplemented with 4 pieces of bamboo: the other plots served as controls. After four months, I harvested all nests on the plots.

### *Prediction 3: Growth rates decline with size*

Each harvested nest (save for foundress nests) yielded pupae and workers. Originally, tests for decreasing production efficiency in social insects ("reproductivity", Michener 1964) plotted pupae-worker ratios against worker number. I instead regressed pupae number on worker number using stepwise regression (with linear and quadratic worker terms) to test for saturation in pupae production. This avoids using worker number both as the dependent and independent variable. I focused on species that occupy a single nest represented by 15 colonies or more. Seven species (9 populations) met this criteria. In a separate paper, pupae-worker

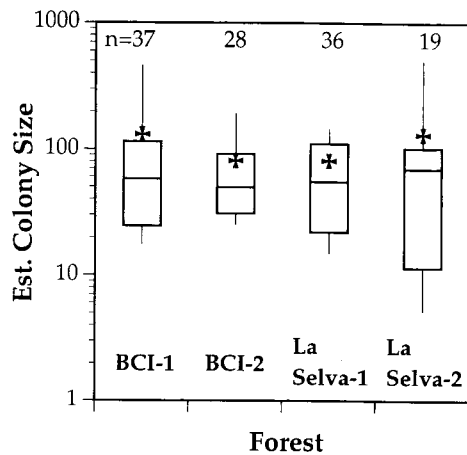


Fig. 1. The average estimated colony sizes of litter ant species from four Neotropical forests. Crosses are the arithmetic mean. Box and whisker plots represent, top to bottom, 90th percentile, 75th percentile, median, 25th percentile, and 10th percentile. "n" is the sample size for each assemblage.

curves have been analyzed for 4 species (5 populations) of *Pheidole* from the forests in this study (Kaspari and Byrne 1995).

#### Prediction 4: Nests are self-thinning

I tested for self-thinning by regressing the nest density of plots against litter depth, and then the mean colony size on that plot. All three variables were  $\log_{10}$  transformed to improve normality.

## Results

### Natural history of the four litter ant assemblages

Assemblages were diverse, 1/4 to 2.5 of collected species were represented by a single nest. Species were deemed monodomous (= every nest queened) if over half the nests yielded queens (queens are often the first to abandon a litter nest during collection, so this likely underestimates the frequency of monodomy). By this criterion monodomous species represented about 2 of 3 litter ant species (BCI-2: 61%, BCI-1: 68%, LS-2: 63%, LS-1: 64%). Average colony size (the number of workers per queened nest) varied between 84 and 135 workers (Fig. 1). The volume of a litter ant colony (workers, queen and pupae) rarely exceeded 0.2 ml (unpubl.).

In each assemblage, the subfamily Myrmicinae represented 67–76% of the species, followed by the Ponerinae (14–25%), Formicinae (6–11%), and the Dolichoderinae and Pseudomyrmecinae (0–2%). At the genus level, *Pheidole*, *Solenopsis* and *Strumigenys* were species rich in all four forests. Refuse piles typically

included dead insects and seeds, suggesting that omnivory was common. The Attini, which culture fungus on detritus, were common on BCI and rare at La Selva. Predators, both generalist (e.g., *Hypoconera*, *Pachycondyla*) and specialist (e.g., *Thaumatomyrmex*, *Strumigenys*, *Neotruma*) round out the list (Hölldobler and Wilson 1990).

### Patterns of species richness at regional and local scales

At the regional scale we can compare estimated species richness of the forests using the Chao II statistic ( $\pm$  95% confidence limits). The pristine forests had similar species richness. BCI-1 yielded an estimated 71 ( $\pm$  2.4) species from 54 species collected on 51 plots. La Selva-1 had an estimated 74 ( $\pm$  3.4) species from 44 species collected on 70 plots. Forests with stressed litter had similar numbers of species but fewer than pristine forests. BCI-2, with dry litter, had an estimated 43 ( $\pm$  1.2) species from 36 sampled species on 54 plots. La Selva-2, exposed to periodic flooding, had an estimated 37 ( $\pm$  2.1) species from 28 collected on 28 plots and was likely more species-rich given the low sampling effort.

At the  $m^2$  scale, plots yielded 0–23 nests and 0–14 species. There was little evidence of species assortment. Across the 4 forests 5–10 species were common enough ( $n \geq 10$ ) to enter the association analysis. No species associations were found in the two Costa Rican forests (15 and 9 Spearman rank correlations, all  $p > 0.05$ ). At BCI-1 associations occurred no more than predicted by the  $p < 0.05$  threshold (2 of 36, 6%). In BCI-2 15% (7 of 45) of possible comparisons were significant. Half of BCI-2's associations were due to one species (*Solenopsis* spp.) co-occurring with *Paratrechina* paha and *Cyphomyrmex costatus* (Mann), and avoiding the congener *Solenopsis* dior.

To summarize, the litter ant assemblages included a variety of taxa, life histories, and diets. The typical litter ant species from these forests had about 100 workers in a single queened nest, lived in a twig, and was omnivorous. Pristine and stressed forests from both sites had similar species richness. At the  $m^2$  scale, species associations were rare.

### Nest patchiness and resource limitation

Litter depth was patchy, varying five to ten-fold across  $m^2$  plots in the same time block. Litter depth (measured in all forests but La Selva-2) varied across forests (ANCOVA:  $F_{2,172} = 9.5$ ,  $p < 0.0001$ ) and was deepest at BCI-1 (Fig. 2). Litter depth declined uniformly in all forests as the wet season progressed ( $F_{1,172} = 16.6$ ,  $p < 0.0001$ , interaction NS).

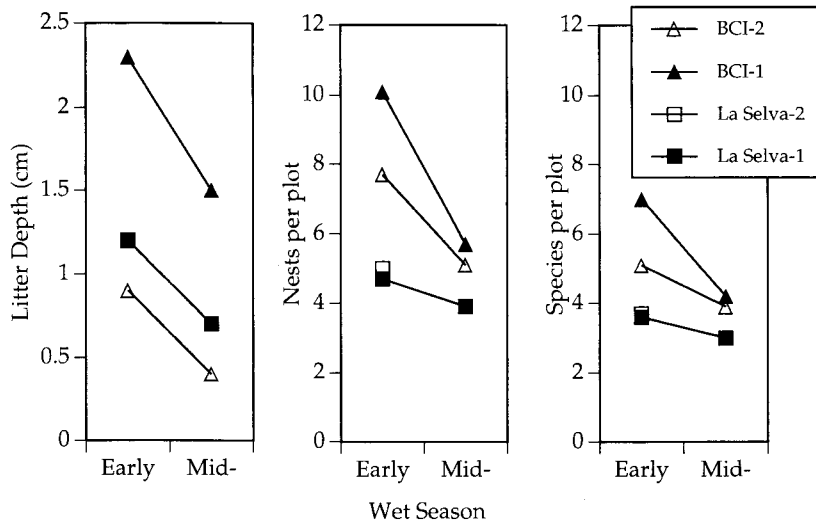


Fig. 2. Litter depth, nest density and species per  $m^2$  decreases from early to mid-wet season in three forests. Only litter depth differs significantly between sites (Table 2). The forest La Selva-2 was sampled once and litter depth was not measured.

Nest densities and species richness per plot also declined over the wet season and varied between sites (Fig. 2). Nest density and species richness on a plot were highly correlated in all four forests (Fig. 3), slopes of 0.73 to 0.80 suggest that about 1/4 of the nests in any plot are multiple samples of the same species. Since density accurately predicts diversity, I focus only

on patchiness in nest density for the rest of the analyses.

*Prediction 1: Nest densities track changes in litter quantity and quality*

As predicted, nest densities increased with litter depth (Fig. 4, Table 2,  $p < 0.04$ , interactions NS) and the same litter depth supported fewer species later in the wet season ( $p < 0.04$ , interactions NS, Fig. 4). Both trends were consistent across the three forests (interactions,  $p > 0.20$ ). This ANCOVA accounted for 25% of the variation in litter ant density across the three forests sampled.

The litter depth–nest density correlation may be weakened if ant species prefer plots with differing amounts of litter. This would erode the correlation by causing species turnover, not accumulation, as litter depth increased. I looked for between-species differences in  $\log_{10}$  depth using species with  $\geq 10$  nests. Some nest depth differences existed among species at BCI-2 (Fig. 5,  $F_{7,236} = 3.6$   $p = 0.009$ ,  $r^2 = 0.10$ ). Both pristine forests, however, failed to show litter depth differences between species (BCI-1:  $F_{8,258} = 1.8$   $p = 0.08$ ,  $r^2 = 0.05$ ; La Selva-1:  $F_{5,176} = 1.9$   $p = 0.10$ ,  $r^2 = 0.05$ ). In all cases species accounted for less than 11% of variation in litter depth.

*Prediction 2: Adding nests increases colony densities*

Litter ants in this study nested between leaves, in chunks of rotten wood, and in hollowed seeds. Twigs were the core nest type for most of the common ( $n \geq 10$ ) species in Panama (BCI-1: 24–100% BCI-2: 51–90%) and Costa Rica (La Selva-1: 30–100%, La Selva-2: 50–100%). Many of these twig nests were decayed and broke easily in the hand. The recovered

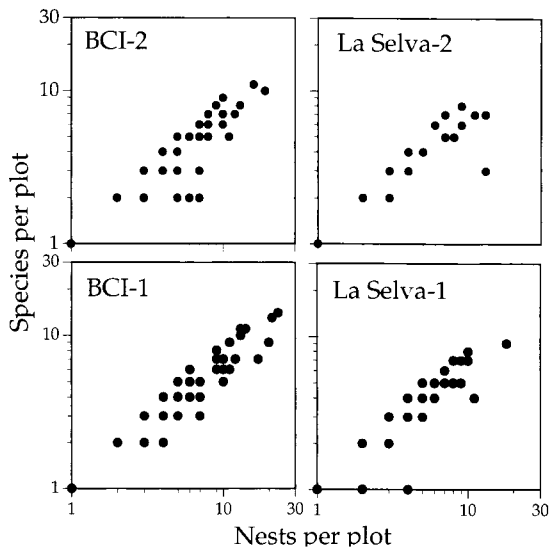


Fig. 3. The number of species in a  $m^2$  plot increases with nest density in a similar fashion in the four forests studied. An ANCOVA with species richness as the dependent variable yields a significant effect of nest density (Type III SS = 9.0,  $F = 702.98$ ,  $p = 0.0001$ ) but not forest type or interaction ( $F < 0.6$ ,  $p > 0.65$ ). Best fit regressions: (BCI-1) Species = Nests<sup>0.77</sup>,  $r^2 = 0.84$ ; (BCI-2) Species = Nests<sup>0.78</sup>,  $r^2 = 0.76$ ; (La Selva-1) Species = Nests<sup>0.80</sup>,  $r^2 = 0.80$ ; (La Selva-2) Species = Nests<sup>0.73</sup>,  $r^2 = 0.83$ .

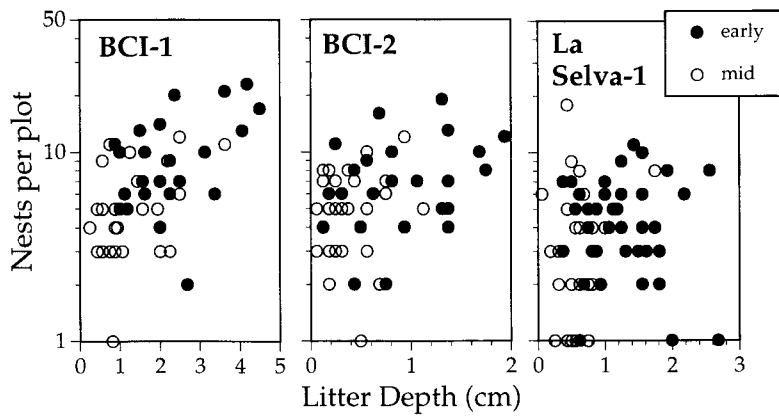


Fig. 4. Nest density increases weakly with litter depth on  $m^2$  plots in three Neotropical forests, and decreases from early to mid-wet season (see Table 2).

bamboo nests used in this experiment were weathered but firm.

To compare relative nest limitation, bamboo twigs were put out, 5 per  $m^2$  plot, and collected 45 d later. Less than 1 bamboo twig in five on each plot was used by ants. However, colonization in Costa Rica (La Selva-1 13.2%, La Selva-2 16.5%) was double that in Panama (BCI-1 5%, BCI-2 7.4%,  $\chi^2_3 = 23.2$ ,  $p < 0.0001$ ).

To directly test for nest site limitation, 4 bamboo internodes were added to  $0.11\text{-}m^2$  plots in the 2 Panama forests. Four months later, litter and bamboo were collected. Nest densities doubled on bamboo plots compared to controls (BCI-1: Kruskal Wallis  $\chi^2_{2,50} = 5.0$ ,  $p < 0.026$ ; BCI-2: KW  $\chi^2_{2,50} = 9.6$ ,  $p < 0.002$ ; Fig. 6). On average, one twig nest and one bamboo nest was occupied in each bamboo plot.

In sum, artificial nest sites were used more than twice as frequently in Costa Rica as in Panama. In Panama, adding extra nest sites to  $0.11\text{-}m^2$  plots increased local nest density in both forests. In all cases, however, most of the supplemented nests remained unused.

Table 2. Nest density on  $m^2$  plots varies with litter quality (which decreases from early to mid-wet season) and litter quantity. Lack of significant interactions suggests these effects are consistent across three tropical forests (see Fig. 2).

Main effects	Degrees of freedom	Sum of squares (Type III)	F	p-value
Season	1	0.30	4.3	0.04
Forest	2	0.16	1.1	0.33
Litter depth	1	0.31	4.5	0.04
Forest $\times$ Season	2	0.11	0.79	0.46
Litter $\times$ Forest	2	0.02	0.11	0.90
Litter $\times$ Season	1	0.04	0.56	0.46
Litter $\times$ Forest $\times$ Season	2	0.17	1.17	0.31
Error	156	11.0		

#### Prediction 3: Growth rates decline with size

Pupae-worker curves varied greatly in the tightness of the correlation (Fig. 7, significant  $r^2$ 's = 0.35–0.60) and yielded a variety of shapes. A saturating curve showed up statistically only once (*Pheidole* pint), and was driven by an outlier (Fig. 7). Accelerating curves were most common (3 spp). Linear pupae-worker curves were found in two populations of the attine *Cyphomyrmex rimosus*. Two species (representing three populations) showed no significant pupae-worker curve at all.

Adding these results to those of 4 *Pheidole* species (5 populations) from these sites (Kaspari and Byrne 1995). 7 of 11 species (7 of 13 populations) tested had colonies growing at least as fast when small as when large. Only 2 of 11 species showed the saturating pupae-worker curve consistent with resource depletion.

#### Prediction 4: Nests are self-thinning

If resources are limiting and resource depletion increases with colony size, then plots with larger colonies should have fewer colonies. Plots of nest density against mean colony size showed considerable scatter in all four forests (Fig. 8).

In none of the forests was there evidence of self-thinning. Once litter depth effects were removed, plots with larger mean colony sizes failed to have fewer colonies (Table 3). At BCI-1, density actually increased with colony size. La Selva-2, which lacks litter data, also failed to show any relationship between colony size and nest density.

The bamboo experiment provides a second test for self-thinning. Even as densities doubled on bamboo plots, mean nest size did not differ from controls in either BCI-1 (control = 32.9 workers nest, bamboo = 39, Kruskal Wallis  $\chi^2_{22,29} = 0.5$ ,  $p < 0.49$ ) or BCI-2 (control = 39.7, bamboo = 29.8. KW  $\chi^2_{2,27} = 0.0$ ,  $p < 0.98$ ).

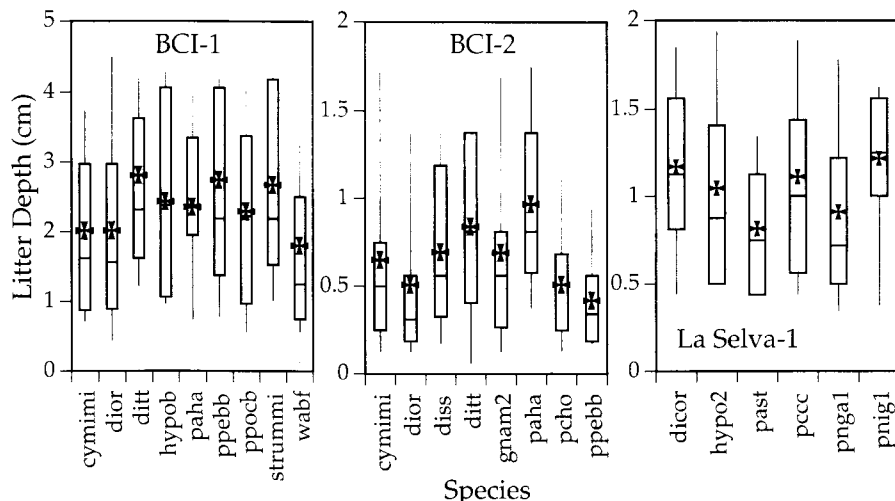


Fig. 5. Common ant species at three sites overlap broadly in the depth of litter in which they are found. One forest, BCI-2, shows significant species differences. Box whisker plots as described in Fig. 1. Key to species names: cymimi = *Cyphomyrmex rimosus* (Spinola), dicor = *Solenopsis dicor*, dior = *Solenopsis dior*, diss = *Solenopsis diss*, ditt = *Solenopsis ditt*, gnam2 = *Gnamptogenys horni* (Santschi), hypo2 = *Hypoponera* 2, hypob = *Hypoponera* b, paha = *Paratrechina ha*, past = *Paratrechina steinheili*, pccc = *Pheidole ccc*, pcho = *Pheidole cho*, pngal = *Pheidole nga1*, pnigl = *Pheidole nig1*, ppebb = *Pheidole pebb*, ppocb = *Pheidole pocb*, strummi = *Neotruma zeteki* (Brown), wabf = *Wasmannia auropunctata* (Roger).

## Discussion

Ecology strives to understand the causes of species, population, and individual patchiness at different spatial scales. In this study, resource availability helped predict tropical litter ant patchiness at the local but not the regional scale. However, even with resource limitation, ant populations rarely appeared to achieve densities where they deplete local resources.

Tropical litter ants comprise a large fraction of the earth's ant species (Wilson 1959) but we know little of their basic ecology. It is encouraging, at least, that the four assemblages in this study shared many features. The mean colony size and fraction of polydomous colonies varied little (Fig. 1). Common species were found in plots with similar amounts of litter (Fig. 2).

Nest densities and species richness were patchy at the  $m^2$  scale and responded similarly to changes in litter quantity and quality (Fig. 4). These broad similarities, linked with those of other studies (Levings 1983, Byrne 1994), give hope that a robust theory of tropical litter ant ecology may evolve.

### Patterns of local and regional species richness

Species Energy Theory predicts a correlation between a site's productivity and its species richness (Wright 1983, Wright et al. 1993). Ant assemblages so far have shown mixed support for this theory. Where productivity is low, the species richness of harvester ant assemblages increases with rainfall in North America but not Australia (Davidson 1977, Morton and Davidson 1988, Kaspari 1993). At the high end of the productivity gradient, the forests of BCI with less estimated NPP than La Selva, had similar species richness after controlling for litter stress. If supported by more surveys, this may represent a diversity plateau in rich habitats like that reported for tropical trees (Gentry 1988).

Within the four forests, there was little evidence of species associations at the  $m^2$  scale. In all but one forest, BCI-2, common species showed no regular pattern of assortment. "Ant mosaics" conspicuous in many tropical trees (Leston 1973, Majer 1976, Adams 1994) are not evident on the forest floor (Jackson 1985). Instead, like tropical trees, a litter ant colony likely may encounter a wide and unpredictable range of species in its lifetime (Hubbell and Foster 1986).

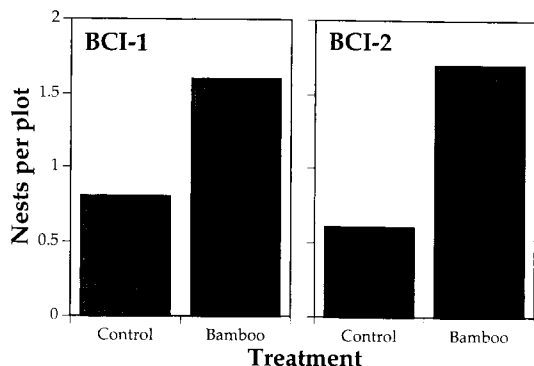


Fig. 6. Four months after four bamboo twigs are added to  $0.11\text{-m}^2$  plots, nest densities are double those of control plots.

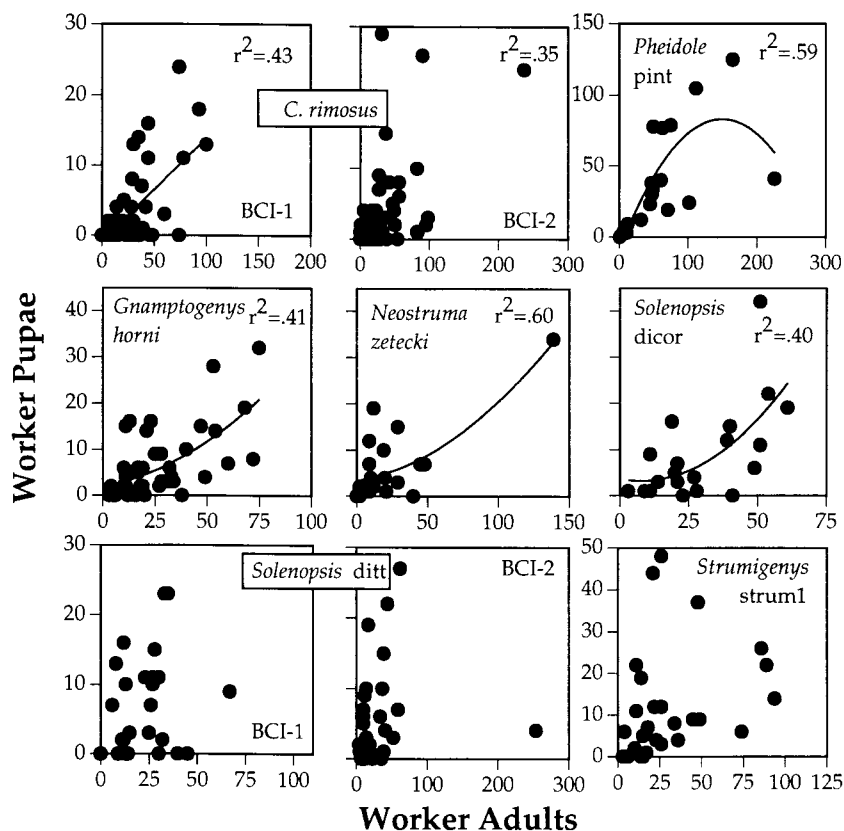


Fig. 7. Tests of declining pupae-worker ratios with increasing colony size for 7 ant species (2 species found in 2 forests). Each point represents a sampled colony. The number of pupae per-worker is constant or accelerates in the majority of litter ant species sampled. Using polynomial regression, 1 species (2 populations) has a linear growth curve, 3 species accelerate, 2 species (3 populations) show no relationship and 1 species shows a decelerating growth rate driven by an outlier. Curves as follows: (Top row): *C. rimosus*: Pupae =  $0.8 + 0.15\text{Workers}$ , *C. rimosus*:  $P = 0.1W$ , *P. pint*  $P = 1.2W - 0.004W^2$ ; (Middle row): *G. horni*  $P = 3.0 + 0.000W^2$ , *N. zetecki*  $P = 4.1 + 0.002W^2$ , *S. dicor*  $P = 0.006W^2$ , (Bottom row): NS.

### Resource tracking as a cause of nest patchiness at the $m^2$ scale

Although ant ecology has often focused on why nests are so hyper-dispersed (Levings and Traniello 1981) the tropical litter – with from 2 to 23 nests and 1 to 16 species in nearby plots – inspires the opposite question: why are nests so patchy (Levings 1983)? To some degree ant patchiness at the  $m^2$  scale tracks litter patchiness – differences in nest densities between forests (Fig. 2) were accounted for by equivalent, if weak, responses to litter depth and time of year (Table 2). Particularly intriguing is the decline in densities over the wet season beyond that predicted by concurrent litter declines (Fig. 4, Table 2). Fewer nutrients supporting fewer ant colonies is one explanation (Facelli and Pickett 1991, Cornejo et al. 1994). Increased exposure to harsh weather or predators appear to be equally valid explanations at this point and merit further study.

Nest site limitation is likely one cause of the correlation between litter depth and nest density. The litter that falls and rots on the forest floor has long been sus-

pected to limit ant populations (Wilson 1959). Nest site limitation is shown here for two Panama forests. It may be more significant in the wet forests of eastern Costa Rica which had twice Panama's nest site colonization rate after 1.5 months (see also Herbers 1986).

As different tree species shed litter over the year (Frankie et al. 1974, Croat 1978, Denslow 1987) litter ant distributions may form a fluid mosaic, tracking the shifting access to nest sites.

However, even with resource limitation, three lines of evidence suggest little sign of resource depletion – use of the resource often did not seem to deny it to others. First, from 75–85% of bamboo nest sites were unoccupied after 1.5 to 4 months in this study. Common litter ants may relocate nests every 34–140 d (Herbers 1986, Byrne 1994) even when nests remain in good condition.

Second, there was no evidence of self-thinning in the four forests. When litter quantity is removed as a factor, there was no negative relationship between average nest size and nest density (BCI-1 showed a positive relationship). Many temperate assemblages, in contrast, show self-thinning as high densities of foundress nests



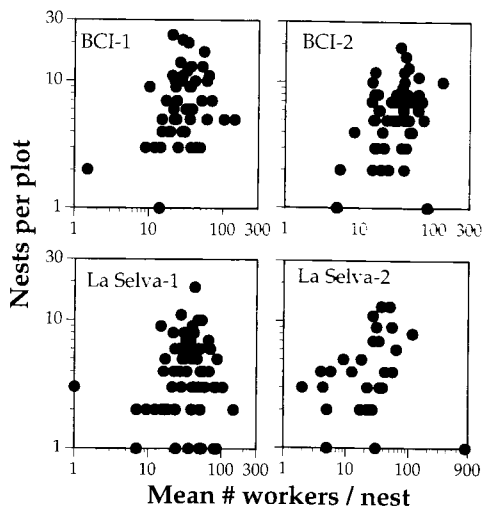


Fig. 8. Self-thinning predicts a negative slope between colony density and mean colony size. Once the effect of litter depth is removed, only BCI-1 shows a significant slope, and it is positive (see Table 3).

give way to fewer, larger adult colonies (Cushman et al. 1988, Ryti and Case 1988a, Adams and Tschinkel 1995, see also Savolainen 1990).

Third, in this and a second study (Kaspari and Byrne 1995) only two of 11 species showed evidence of saturating pupae-worker curves. Instead, linear or accelerating curves were most common suggesting that colonies are disappearing before they reach a size where foraging efficiency decreases. Many of these species show reproductive optima well beyond the observed colony sizes (Kaspari and Byrne 1995). One intriguing possibility is that colonies of some species split before resources can be locally depleted. I currently have no data for or against this hypothesis. A second possibility is that something is killing or cropping colonies before they can achieve that optimum size.

### Alternatives to bottom-up control

The litter is a precarious place for an ant colony of 100 tiny workers. A tropical downpour can flood out the nest or wash away recruitment trails: falling debris can break open nests; army ants – up to 20 species occupy

a Neotropical forest (Rettenmeyer et al. 1983) – may periodically raid colonies (Franks and Bossert 1983, Perfecto 1992). If any of these factors regularly kill or force risky emigrations, then ant colonies may never reach densities high enough to occupy all the nest sites or deplete food resources. In this way, predation may disrupt density-resource correlations (Schoener 1986) and help explain why some  $m^2$  plots with the same amount of litter can vary ten-fold in nest density (Fig. 4).

The relative importance of resource driven (bottom-up) vs disturbance-driven (top-down) population regulation is a subject of keen interest in ecology (see excellent review in Power 1992). This is particularly true in tropical forests, where evidence for seasonal shifts in resource abundance – much of it done on Barro Colorado Island (Leigh et al. 1982, Wright et al. 1994) – is weighed against the importance of top predators in regulating tropical populations (Terborgh 1988). On BCI, with its four-month dry season, both processes likely shape the litter ant assemblages. Harsh dry seasons knock down ant populations (Levings 1983) while in the wet season army ants and downpours are common (Franks and Bossert 1983). In the wet season resources, while still important, may play a secondary role in regulating litter ant populations. Predator exclosure and food addition experiments in tropical wet and dry seasons may help clarify this interaction.

In sum, data from four neotropical forests suggest that the availability of fresh nests may increase local ant densities. However, disturbance or other factor(s) may not allow ant populations to increase to a size that depletion of food resources becomes commonplace.

### Caveats

These conclusions constitute new working hypotheses. A number of other alternatives should be considered.

#### *Litter is complex*

The weak litter depth–nest density correlation may mean that litter depth is an incomplete measure of resource availability to litter ants. Forest litter is a complex organic matrix from many species of trees, in

Table 3. Testing for self-thinning among litter ant colonies on  $m^2$  plots. Regressions of nest density against mean colony size after first removing the effects of litter depth (no litter data available for La Selva-2). Values are  $\log_{10}$  parameter estimates. In none of the four forests is mean colony size a negative function of density. \*  $p < 0.05$ . \*\*  $p < 0.01$ .

Terms	BCI-1	BCI-2	Forest	La Selva-1	La Selva-2
Intercept	0.31 NS	0.48*		0.42*	0.49**
Litter	0.38**	0.19*		0.15 NS	–
Colony size	0.30*	0.21 NS		0.09 NS	0.08 NS
Model $F$	$F_{2,47} = 9.6$	$F_{2,35} = 3.6$		$F_{2,63} = 0.8$	$F_{2,26} = .43$

different stages of decomposition, and with a diverse and patchy biota (Uetz 1975, Stanton 1979, Day 1983, Levings and Windsor 1985). Different tree species may vary widely in litter fall timing, chemical content, and palatability to arthropods (Croat 1978, Dudgeon et al. 1990). Moisture, nutrient content and decomposition rate may be non-linear functions of time and litter depth (David et al. 1991, Cornejo et al. 1994). Comparisons of litter fauna under different tree species begin to address these issues.

#### *Species are different and resist lumping*

In this study, the variable "nest density" subsumes all the ant species that nest in the litter. This is a necessary simplification brought on by the abundance of rare tropical species. It assumes that the species respond similarly to resource gradients. Species-level differences in diets, body size, and other factors likely invalidate this assumption to some extent. However, three lines of evidence suggest that this is a good first guess. Most species overlap broadly in colony size (Fig. 1). They also tend to overlap broadly in litter depth (Fig. 5). Finally, strongly interacting species pairs would likely show up as associations, positive or negative, and these were relatively rare (9 of 107 possible correlations) and concentrated at one site (7 at BCI-2).

#### *Soil-nesting ants may shape litter ant distributions*

Some aggressive ant species (e.g., *Pheidole biconstricta*-group) have large colonies that nest in the soil. These ants may compete with or prey upon the litter ant assemblage. If so, the patchiness of soil-nesting species may ramify (invisibly in this study) through the subordinate litter ant assemblage (e.g., Savolainen and Vepsäläinen 1988). This question is currently under study.

#### *Food limitation may express itself as a reproductive response, not numerical response*

If moving a nest is sufficiently risky, colonies should stay put rather than track shifting litter resources. If so, then changes in litter may be reflected, not in colony densities, but in colony growth and reproduction. There are two arguments against this hypothesis. First, the litter ants in these assemblages do move, often monthly (Byrne 1994, Kaspari unpubl.). Second there is little evidence for reproductive response in this data set. Reproductive output in ants is typically linked to colony size in these ants (unpubl., Kaspari and Byrne 1995), yet average colony size did not increase with litter quantity in any of the 3 forests where it was measured (BCI-1  $r_s = 0.12$ ; BCI-2  $r_s = 0.00$ ; La Selva-1  $r_s = -0.15$ ,  $p$ 's  $> 0.20$ ). While richer habitats in some studies produce colonies with more reproductives (Brian et al. 1967, Brian 1979, Herbers 1990, Backus and Herbers 1992) these studies did not tease apart numerical from reproductive responses.

## Conclusions and prospectus

Litter nesting species are a diverse and conspicuous part of temperate and tropical ant faunas (Talbot 1957, Wilson 1959, Levings 1983, Herbers 1986, Byrne 1994). Yet much of what we know about the population and community ecology of ants comes from large, soil-nesting species from the temperate zone. For example, the importance of competition is a recurring theme in most reviews of ant ecology (Jeanne and Davidson 1984, Hölldobler and Wilson 1990, Andersen 1991). Large-colony species in the field often show 1) saturating growth (Michener 1964, Wilson 1971, Tschinkel 1988), 2) self-thinning (Cushman et al. 1988, Savolainen and Vepsäläinen 1988, Ryti and Case 1992), 3) interspecific territoriality (Leston 1973, Hölldobler 1976, Majer 1976, Adams 1994) and 4) density dependent recruitment (Brown et al. 1979, Davidson 1985, Ryti and Case 1988b). Even the North temperate litter ant communities may be regulated in part through food and nest site limitation (Herbers 1990, Backus and Herbers 1992).

In the tropics, where army ants are more common (Watkins 1976) and colony sizes are smaller (Kaspari and Vargo 1995), a new picture is emerging. At La Selva and BCI, most litter species from four forests 1) had linear or accelerating pupae-worker curves, 2) failed to show self-thinning, and 3) showed little interspecific sorting. Tropical litter species are beginning to suggest a picture of tiny, mobile, nest site limited colonies that die before they grow large enough to deplete resources. Litter ants, in contrast to larger soil-nesting species, may experience only weak "bottom-up" control (Power 1992, Byrne 1994, Kaspari and Byrne 1995). The main determinants of their patchiness in time and space await further study.

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