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## Litter ant patchiness at the 1-m<sup>2</sup> scale: disturbance dynamics in three Neotropical forests

Received: 23 February 1995 / Accepted: 6 February 1996

**Abstract** Large-scale (>100 m<sup>2</sup>/day) raids by tropical army ants have been linked to litter ant patchiness and diversity. In three Neotropical forests, densities of litter ants vary 10–20 fold at the 1-m<sup>2</sup> scale. A survey of Barro Colorado Island, Panama, revealed that most army ant raids also occur on a 1-m<sup>2</sup> scale with fronts ≤1 m wide. To explore the role that such small scale disturbance may play in creating litter ant patchiness, all litter ant nests were removed from 1-m<sup>2</sup> plots. Control and disturbance plots were resampled 3 months later. In contrast to a previous study of large litter gaps, ant foundresses did not appear to prefer these smaller gaps. Nest densities, species richness, and species composition differed most from controls in a dry hilltop forest in Panama, second most in a wetter ravine forest nearby, and least in a Costa Rican wet forest. Disturbance may not leave a lasting signature in the wetter forests due to higher background levels of disturbance, faster recovery, or both.

**Key words** Litter · Ants · Tropics · Disturbance · Patchiness

### Introduction

Patchiness – heterogeneity in numbers across a landscape – is a basic feature of organisms and a central challenge to ecology. Patchiness arises from at least two processes. First, patchiness results when consumers track patchy resources – resource tracking (MacArthur and Pianka 1966; Harper 1967; Fretwell and Lucas 1970; Tilman 1982). In resource tracking, habitat selection and/or

density dependent mortality yields a match between resource abundance and consumer density.

Patchiness may also arise when there is a lag between disturbance that frees up space (and the resources in it) and recruitment that fills that space. In the disturbance dynamic, high recruitment rates (relative to disturbance) homogenize densities; low recruitment rates allow disturbance signatures to endure (Levin and Paine 1974; Pickett and White 1985). Where disturbance is prevalent it can decrease consumer densities below capacity in some fraction of patches. This in turn obscures the resource-density correlation (Pickett and White 1985). Not surprisingly, sessile organisms that show an appreciable lag between disturbance and recruitment are common subjects in the study of disturbance-based patchiness.

Rainforest trees are a good example of how resource tracking and disturbance dynamics combine to shape patchiness (Holdridge et al. 1971; Clark and Clark 1984; Hubbell and Foster 1986; Hartshorn and Hammel 1994). Variation in soil type (Hubbell and Foster 1983; Lieberman et al. 1985; Hartshorn and Hammel 1994) and light environments (Brokaw 1985) support different species associations and densities. Disturbance, varying in scale from branch falls to hurricanes, creates gaps in these patterns, allowing recruitment of seedlings and immature forms (Hartshorn 1978; Brokaw 1985; Fetcher et al. 1985; Sanford et al. 1986; Denslow 1987). Combined, these processes create a complex mosaic.

### Patch dynamics in tropical litter ant assemblages

Tropical litter ants – colonies of 100 or so workers living in hollow twigs and between leaves – also have patchy distributions, with 0–23 nests/m<sup>2</sup> (Wilson 1959; Levings 1983; Levings and Windsor 1984, 1985; Kaspari 1993a; Byrne 1994; Olson 1994; Kaspari in press). Resource tracking contributes to this patchiness. Studies in three Central American forests show consistent correlations between litter ant density and litter quantity and quality

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(Kaspari in press) but leave over 75% of density variation unaccounted for at the 1-m<sup>2</sup> scale. Patches with the same amount of litter varied tenfold in ant densities (Levings 1983). Below I summarize evidence suggesting that the balance between disturbance and recruitment makes up for part of that 75%.

### Disturbance

A synoptic list of disturbance agents for litter ants has yet to be compiled, but the army ants (Ecitoninae) have been shown to be key, and perhaps keystone predators in the Neotropics (Franks 1980, 1982). Army ants are nomadic raiders that overcome the defenses of their prey through sheer numbers, carrying off brood and adults for consumption (Rettenmeyer 1963; Rettenmeyer et al. 1983; Hölldobler and Wilson 1990). Prey ant colonies are often killed or dislocated (Droual 1981, 1984; La-Mon and Topoff 1981; Otis et al. 1986; Perfecto 1992). *Eciton burchelli* is the best studied tropical army ant. *E. burchelli* cuts swaths up to 15 m wide through the litter, daily opening patches up to 900 m<sup>2</sup> in size. Gaps in prey ant distributions may persist up to 77 days and such gaps have a 50% chance of being hit again in 240 days (Franks and Bossert 1983).

More importantly, *E. burchelli* is but one species among 20 or so army ants found in Central American rain forests (Rettenmeyer et al. 1983). A 6-month trail survey of Barro Colorado Island (BCI), Panama suggests that *E. burchelli* raids (1) are the largest in the forest, and (2) make up only about 19% of the most common species – column raids  $\leq 1$  m wide are 3 times more frequent (Table 1). Not counted were other ant genera like *Gnamptogenys*, *Cerapachys*, and *Leptogenys*, that also raid at the 1-m<sup>2</sup> scale (Wilson 1958; Hölldobler and Wilson 1990). One such species, *G. horni*, is the second most common litter ant in some BCI forests (Kaspari in press). Given the frequency of disturbance at the 1-m<sup>2</sup> scale, little is known about the persistence of these small “ant gaps”.

**Table 1** Small,  $<1$  m wide litter raids are more frequent in the forests of Barro Colorado Island than large swarm raids typical of *Eciton burchelli*. Relative raid frequency was measured from a 6-month, day and night, survey of trails in 1991. Width of each raid column, number of columns per raid, and prey of each species tak-

Army ant species	No. of raids	Column width (m)	No. of Col.	Prey	Source
<i>Eciton hamatum</i>	29	$\leq 1$	1–6	social insects, 13 ant genera	1, 2, 5
<i>Ec. burchelli</i>	13	5–15	1	ca 55% soc. hymenoptera, 11 ant genera	3, 4, 5
<i>Labidus praedator</i>	8	$\leq 4$	1	arthropods including ants	1, 2, 5
<i>Ec. mexicanum</i>	6	$\leq 1$	1	arthropods, 5 ant genera	1, 2, 5
<i>Nomamyrmex esenbecki</i>	5	$\leq 1$	1–5	mostly ant brood	1
<i>Neivamyrmex pilosus</i>	4	$\leq 1$	1–2	mostly ant pupae	1, 5
<i>Ec. vagans</i>	1	$\leq 1$ – $>4$	1–5	mostly ant pupae	1, 5
<i>Ne. iridescens</i>	1	$\leq 1$	1	ant pupae	5
<i>Ec. quadrigulme</i>	1	6	1	social insects	1, 5
<i>La. coecus</i>	1	4	1	arthropods including small ants	1, 5, 6
plus 9 more species					

### Recruitment

When a large colony is killed or dislocated it is replaced in one of three ways. First, a queenright colony may move in. Litter ant colonies may change nest sites every 10–150 days. Second, a polydomous super-colony may move a satellite nest – a group of workers and brood without a queen – into the patch. Polydomous forms represent 1/3 of the species (and more of the nests) in the tropical litter (Kaspari in press). Third, foundresses may colonize a disturbed plot. Foundresses are produced continuously over the wet season on BCI (M. Kaspari and J. Longino, unpublished work).

The mode of colonization shapes patchiness because it helps determine the number of nests that ultimately fill a gap. Queenright and satellite nests may replace colonies in kind. In contrast, foundresses may move in and replace one adult nest with many incipient colonies (Ryti and Case 1988).

A second factor influencing recruitment rates is moisture. In tropical forests litter ant activity increases with humidity (Levings 1983; Kaspari 1993a). Nest relocations may be especially affected by dryness, since ant brood are prone to desiccation. Hence disturbed plots in wet forests may recover more quickly than those in dry forests.

This study explores the impact of artificial 1-m<sup>2</sup> disturbance on litter ant patchiness in three tropical forests arrayed along a moisture gradient. I compare the species richness, composition, and nest density of these plots with controls after 90 days. Three months seemed appropriate, given the 10–120 day turnover in nest sites reported above (Ward 1981; Herbers 1986; Byrne 1994). As it turned out, this 3-month snapshot captured variation in recovery times among the three forests studied.

## Materials and methods

### Study sites

I studied disturbance dynamics at two sites: the Estacion Biológica La Selva, managed by the Organization for Tropical Studies in

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Costa Rica, and Barro Colorado Island (BCI), managed by the Smithsonian Institute of Tropical Studies in Panama. The study took place in the 1991 wet season, in May–August at La Selva, June–September on BCI. At each site, I studied a closed-canopy, undisturbed forest.

La Selva (10° 26' N, 83° 59' W), a lowland tropical wet forest (Holdridge et al. 1971), is on the Caribbean slope of Costa Rica. La Selva has an annual rainfall of 3,991 mm and lacks a true dry season (Hartshorn 1983). The forest studied was along Sendero Sur Oeste, which has a gentle slope on a residual soil. Palms dominated the understory.

BCI (9° 09' N, 79° 51' W) is a 1500-ha island created by the flooding of Lake Gatun in 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 (Croat 1978). I sampled two forests on BCI, both on residual soil. A ravine forest (henceforth Panama-Ra) was in the Allee watershed and had rolling topography. A second hill-top forest (henceforth Panama-Hi) was on a flat, open plateau in the center of the island. Panama-Hi had less canopy and a more open understory than the other two forests. One consequence was increased exposure to drying winds off the lake and more sunshine. Panama-Hi had some of the driest litter on BCI, and Panama-Ra some of the wettest (Levings 1983).

Methods

The basic method at all three forests was to remove litter ant colonies from 1-m<sup>2</sup> plots and replace the litter. Three months later I returned to resample these plots plus control plots located 1 m away in a random direction.

To sample ant nests, I marked out 1-m<sup>2</sup> plots with wire flags and string. I estimated litter depth by gently forcing a wire, marked by 0.5-cm increments, into the litter until it reached the ground. I took eight litter depth estimates, one at each corner of the plot and one each at the corners of the 0.11-m<sup>2</sup> square in the center of the quadrat. In each case I noted the type of litter (leaf, twig, nut, or wood) that the wire first touched.

Sitting on the ground, I picked up each piece of litter and inspected it for ant nests, often by breaking twigs and pulling apart wood (on dark days using a head lamp). The only litter not sampled in this way was large pieces of very hard wood that I could not open with a pocket knife. I placed every nest I found into a plastic bag, recording the location to the 0.11-m<sup>2</sup> quadrat. I returned all litter to the plot.

At the laboratory, I placed each nest into a Fluon-coated tray. I classified each nest to type (twig, wood, leaves, nut/pod). I deposited nest contents (brood, workers, queens and alates) in 70% ethanol. I later identified ants to species or morphospecies (henceforth referred to as species) using keys and reference collections, with vouchers deposited at the Museum of Comparative Zoology, Harvard. Most of the *Pheidole* in this study have been assigned names but await the publication of the monograph (E.O. Wilson personal communication).

I sampled the Costa Rica forest in May and August of 1991. I arranged plots in eight, 10x10 m squares. Each square had plots at each corner and in the center. The squares were in two rows of four. The rows and the plots within each row were 20 m apart. I removed nests from the 40 plots in May. Returning in August, I was able to resample 30 of these plots (plus 30 control plots) in the month allotted.

I sampled the Panama forests in June and September of 1991. Due to thick litter, I was able to sample only nine plots (Panama-Ra) and ten plots (Panama-Hi). These were arranged on a 3x3 grid, and 4x3 grid with each plot 10 m apart. Returning in September, I resampled these plots and their controls. With time remaining in the month, I sampled three extra plots in Panama-Ra, and five extra plots in Panama-Hi (both randomly located as extensions of the original grid). I treat these as additional controls.

The Costa Rica forest was thus sampled more extensively over a larger portion of forest floor (c. 4,000 m<sup>2</sup>) than the two Panama forests (c. 500–800 m<sup>2</sup>). I use conservative Kruskal-Wallis (KW) tests to look for differences between control and treatment plots.

Results

Handling the litter and removing nests may have influenced nest site availability (and hence the opportunity to colonize disturbed plots). To check on this, I measured litter before sampling control and disturbed plots. In the three forests neither litter depth nor the frequency of twigs, leaves, hollow nuts or wood varied significantly between control and disturbed plots (KW test,  $P_s > 0.30$ , Fig. 1). Removing nests three months before did not leave a lasting imprint on these measures of litter quality.

Nest and species density

Each forest responded differently to disturbance. Panama-Hi, the driest forest, yielded 1–12 nests, and 1–9 species in a 1-m<sup>2</sup> plot. Median nest density was 60% lower on disturbed plots (Fig. 2, KW  $X^2_{10,15} = 7.3$ ,  $P = 0.007$ ). Likewise median species richness per disturbed plot was 63% of control (Fig. 2, KW  $X^2_{10,15} = 5.27$ ,  $P = 0.022$ ).

The moist Panama-Ra forest yielded 1–11 nests and 1–7 species in a 1-m<sup>2</sup> plot. Nest density, but not species richness, was lower on disturbed plots. Median nest den-

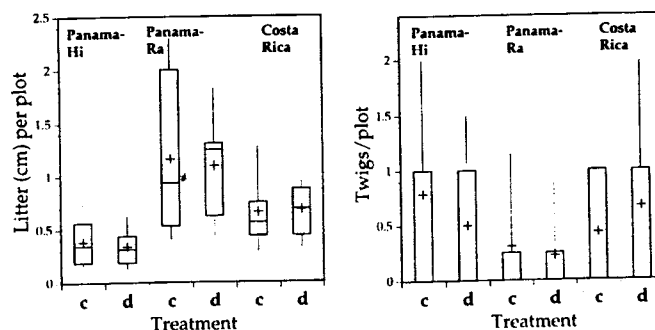


Fig. 1 Two measures of litter quality – litter depth and twig number from 8 sample points – did not differ between control plots (c) and plots disturbed 3 months before (d). Box and whisker icons show the 10th and 90th percentiles (the whiskers), 25th and 75th percentiles (the box), median (horizontal line), and mean (+)

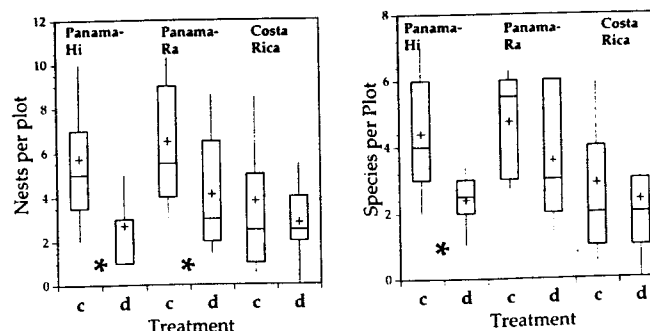


Fig. 2 Comparing the number of nests and species on control (c) vs. disturbed (d) plots in three Neotropical forests. Box and whisker icons as in Fig. 1; \* indicates a significant ( $P < 0.05$ ) difference by a Kruskal-Wallis test

**Table 2** Ant species composition, by number of nests, for three tropical forests. Disturbed plots had all litter nests removed three months before. Morphospecies not italicized

Subfamily/Tribe	Species	Control	Disturbed
La Selva, Costa Rica			
<b>Ponerinae</b>			
Ponerini	<i>Hypoponera</i> 2 <i>Proceratium</i> 1	11	15 1
<b>Myrmicinae</b>			
Myrmicini	<i>Hylomyrma</i> 1	3	2
Pheidolini	<i>Pheidole annectans</i> <i>P. bsh</i> <i>P. c</i> <i>P. cr</i> <i>P. dss</i> <i>P. int</i> <i>P. mgs</i> <i>P. mic</i> <i>P. neb</i> <i>P. ngal</i> <i>P. nigl</i> <i>P. nit</i> <i>P. peb</i> <i>P. pebr</i> <i>P. poc</i>	3 20 2 4 1 2 1 19 2 5 2 1 1	1 17 1 3 2 15 3 2 2 1
Crematogastrini	<i>Crematogaster</i> bb <i>C. ka</i> <i>C. tw</i>	1 1 3	
Solenopsidini	<i>Solenopsis (Diplorhoptrum) dico</i> <i>S. (D.) dicor</i> <i>S. (D.) diga</i> <i>S. (D.) diso</i>	3 6 2	4 6 1 1
Ochetomyrmecini	<i>Wasmannia auropunctata</i>	2	2
Dacetoniini	<i>Strumigenys</i> ljls <i>S. l</i> <i>S. mil</i> <i>S. wk</i>	1 2 1 1	1 1 1
Attini	<i>C. cornutus</i>		1
<b>Pseudomyrmecinae</b>			
Pseudomyrmecini	<i>Pseudomyrmex</i> 1	1	
<b>Formicinae</b>			
Brachymyrmecini	<i>Brachymyrmex</i> am	1	
Lasiini	<i>P. steinheili</i>	10	5
<b>Plots Sampled</b>		30	30
<b>Species Recorded</b>		31	27
<b>Estimated Species Richness</b>		39	39

Subfamily/Tribe	Species	Forest			
		Panama-Ra		Panama-Hi	
		control	disturb	control	disturb
Barro Colorado Island, Panama					
<b>Ponerinae</b>					
Amblyponini	<i>Amblypone</i> b		1		
Ectatommini	<i>Gnamptogenys horni</i>				
Platythyreini	<i>Probolomyrmex boliviensis</i>	2			
Ponerini	<i>Hypoponera</i> b	4	1	6	
<b>Myrmicinae</b>					
Pheidolini	<i>Pheidole</i> cho <i>P. eye</i> <i>P. nigb</i> <i>P. nos</i> <i>P. pebb</i> <i>P. pocb</i>	2 1 3 5	1 1 1 4	7 2 6 1	3 1
Crematogastrini	<i>Crematogaster</i> lo	2		3	

Table 2 (continued)

Subfamily/Tribe	Species	Forest			
		Panama-Ra		Panama-Hi	
		control	disturb	control	disturb
Solenopsidini	<i>Solenopsis (Diplorhoptrum) dior</i>	19	3	11	1
	<i>S. (D.) diss</i>		3	3	3
	<i>S. (D.) ditt</i>		2	4	1
Ochetomyrmicini	<i>Wasmannia auropunctata</i>	9	3	5	
Dacetoniini	<i>Strumigenys st</i>			1	
	<i>S. lj</i>	2	2		
	<i>S. bg</i>	1			
	<i>S. gl</i>	1			
	<i>S. sb</i>	1			
	<i>Neostruma zeteki</i>	3	2	5	
Attini	<i>Apterostigma sq</i>	1		1	1
	<i>A. mi</i>			1	
	<i>Cyphomyrmex costatus</i>	3			
	<i>C. rimosus</i>	8	6	16	9
<b>Dolichoderinae</b>	<i>Sericomyrmex l</i>			1	
Dolichoderini	<i>Dolichoderus imitator</i>	3			
<b>Formicinae</b>					
Lasiini	<i>Paratrechina ha</i>	4	3	6	3
	<i>P. steinheili</i>				3
Camponotini	<i>Camponotus br</i>	1	1		
<b>Species Recorded</b>		23	19	19	11
<b>Plots Sampled</b>		9	12	10	15
<b>Estimated Species Richness</b>		29	36	25	24

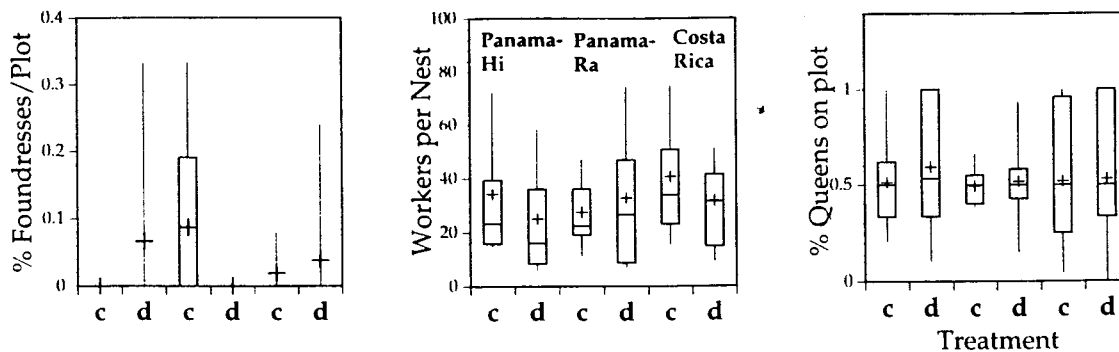


Fig. 3 The percentage of nests with foundresses and average nest size (two indicators of foundress colonization) did not differ between control (c) and disturbed plots (d) in any of the three Neotropical forests tested. Nor did the percentage of nests with queens (a measure of polydomy). Box and whisker icons as in Fig. 1

Mode of colonization

sity on disturbed plots was 55% of control plots (Fig. 2, KW  $X^2_{9,12} = 4.0, P = 0.045$ ); median species richness was 55% of controls, though not significantly different (Fig. 2, KW  $X^2_{9,12} = 2.2, P = 0.14$ ).

The aseasonal wet forest of Costa Rica yielded from 0–18 nests and 0–9 species per 1-m<sup>2</sup> plot. Both nest density and species richness did not differ between control and disturbed treatments (Fig. 2, KW  $X^2_{30,30} < 0.25, P > 0.60$  in both cases). A paired *t*-test, matching each disturbed plot with its own control, gave the same result: (nests:  $T = 1.5, P = 0.14$ ; species:  $T = 1.16, P = 0.25$ ). There was no disturbance effect at La Selva, despite having a greater sample size than the two BCI forests.

Litter ants can colonize open patches of litter in a number of ways: by foundress, by satellite nests of existing colonies, or by mature queenright colonies. Overall, foundresses (nests with queens and brood but no workers) constituted <10% of the nests in the middle of the wet season (Fig. 3). In the Panama-Hi forest foundresses were absent on control plots and made up 7% of the nests on disturbed plots KW  $X^2_{10,15} = 3.1, P = 0.08$ ). In the Panama-Ra forest foundresses made up 9% of the nests on control plots and 0% on the disturbed (KW  $X^2_{9,12} = 3.5, P = 0.06$ ). In Costa Rica foundresses represented 2% of control nests and 4% of disturbed nests, not a significant difference (KW  $X^2_{27,26} = 0.31, P = 0.58$ ). Perhaps in the 3 months of the experiment foundresses raised their first brood to adults. To check for this, I tested for smaller colonies on disturbed plots. The number of workers per nest did not differ between disturbed and control plots in any of the for-

**Table 3** Common species, by percentage of nests, on control and disturbed plots in three forests. Species in **bold** are unique to that forest

Rank	Control		Disturbed	
	%	Species	Species	%
<b>Panama-Hi</b>				
1	18	<i>Cyphomyrmex rimosus</i>	<i>Cyphomyrmex rimosus</i>	32
2	12	<b><i>Solenopsis dior</i></b>	<b><i>Solenopsis diss</i></b>	11
3	11	<i>Gnamptogenys horni</i>	<b><i>Paratrechina steinheili</i></b>	11
4	8	<i>Pheidole cho</i>	<i>Paratrechina ha</i>	11
5	7	<i>Hypoponera b</i>	<i>Pheidole cho</i>	11
6	7	<i>Paratrechina ha</i>	<i>Gnamptogenys horni</i>	7
7	7	<b><i>Pheidole pebb</i></b>		
8	6	<b><i>Wasmannia auropunctata</i></b>		
<b>Panama-Ra</b>				
1	24	<i>Solenopsis dior</i>	<i>Cyphomyrmex rimosus</i>	16
2	11	<b><i>Wasmannia auropunctata</i></b>	<i>Pheidole pocb</i>	11
3	10	<i>Cyphomyrmex rimosus</i>	<i>Solenopsis dior</i>	8
4	6	<i>Pheidole pocb</i>	<b><i>Solenopsis diss</i></b>	8
5	5	<b><i>Hypoponera b</i></b>	<i>Paratrechina ha</i>	8
6	5	<i>Paratrechina ha</i>	<b><i>Wasmannia auropunctata</i></b>	8
7			<b><i>Solenopsis ditt</i></b>	5
8			<b><i>Strumigenys lj</i></b>	5
<b>La Selva</b>				
1	17	<i>Pheidole c</i>	<i>Pheidole c</i>	18
2	16	<i>Pheidole nga1</i>	<i>Hypoponera hypo2</i>	16
3	9	<i>Hypoponera hypo2</i>	<i>Pheidole nga1</i>	16
4	9	<i>Paratrechina steinheili</i>	<i>Solenopsis dicor</i>	6
5	5	<i>Solenopsis dicor</i>	<i>Paratrechina steinheili</i>	5

ests (Fig. 3, Panama-Hi: KW  $X^2_{10,15} = 1.5$ ,  $P = 0.22$ , Panama-Ra: KW  $X^2_{9,12} = 0.0$ ,  $P = 0.86$ ; Costa Rica: KW  $X^2_{27,26} = 1.1$ ,  $P = 0.31$ ). Thus, there was no evidence of increased numbers of foundresses on 1-m<sup>2</sup> disturbances.

Satellite nests of polydomous colonies also did not appear to accumulate on disturbances. A median of 50% of nests had queens in all forest-treatment combinations (Fig. 3, Panama-Hi: KW  $X^2_{10,15} = 0.2$ ,  $P = 0.67$ ; Panama-Ra: KW  $X^2_{9,12} = 0.0$ ,  $P = 0.91$ ; Costa Rica: KW  $X^2_{27,26} = 0.2$ ,  $P = 0.67$ ).

In sum, colony mortality at the m<sup>2</sup> scale did not attract foundresses nor polydomous nests out of proportion to their frequency on control plots.

### Species composition

In all three forests, overall species richness was similar on disturbed and control plots. Using the Chao 1 statistic (Chao 1984; Colwell and Coddington 1994) Panama-Hi yielded similar estimates of total species richness (25 species from control plots, 24 from disturbed, Table 2). Panama-Ra had fewer species on control plots (29 vs. 36), but this was not significant using 95% confidence intervals (Colwell and Coddington 1994). Costa Rica disturbed and control plots yielded the same estimate of 39 species.

Species composition appeared to differ more at sites where treatments diverged in nest densities. In Table 3 I compare the rank of the most common species (those comprising  $\geq 5\%$  of the sampled nests) across the two treatments. In Costa Rica where nest and species richness per plot were most nearly the same, the same five

species dominated both disturbed and control plots. Panama-Ra control plots shared 80% of their common species with the disturbed plots. Panama-Hi, which showed the greatest differences in density and species richness between disturbed and controls, overlapped only 60% in their common species. Different *Solenopsis* species were the second most common species on disturbed and control plots. The majority of species in this study are represented by one or two nests, precluding further statistical analysis.

### Discussion

Ant distributions are of great interest given their critical role in a variety of species interactions (Tilman 1978; Hölldobler and Wilson 1990; Horvitz and Schemske 1990; Cushman and Whitham 1991; Kaspari 1993b; Levey and Byrne 1993). Ant ecologists have focused mainly on the regular spacing of ant colonies, a common pattern among many large, soil-nesting species (Levings and Traniello 1981; Hölldobler and Wilson 1990; but see Rytty and Case 1992). Others have gone farther, showing concrete evidence for density dependent mortality and recruitment as a likely cause of these patterns (Davidson 1985; Rytty and Case 1986; Cushman et al. 1988; Adams and Tschinkel 1995; Wiernasz and Cole 1995). In contrast, surprisingly little study has gone into the question of why so many ant species are patchily distributed (Levings 1983).

Interest in the patch dynamics of ant colonies has grown with the realization that adult colonies may emi-

grate on a weekly, monthly, or annual basis, often in response to predation (Carlson and Gentry 1973; Smallwood 1982a,b; Gordon 1992; Byrne 1994). Besides studies by Franks, numerous other authors have shown how army ants regularly rout ant colonies, forcing nest relocations and occasional colony deaths (Mirenda et al. 1980; Droual and Topoff 1981; LaMon and Topoff 1981; Perfecto 1992). The persistence time of the resulting "ant gaps" varies – some colonies quickly returned to abandoned nests, and others switched to alternate nest sites (Droual and Topoff 1981; LaMon and Topoff 1981; Perfecto 1992). Clearly the dynamics of disturbance may be a relevant, if less studied, aspect of ant distributions.

The present study yielded two results of possible importance. First, small 1-m<sup>2</sup> gaps can leave an enduring density signature over time periods similar to large-scale 100-m<sup>2</sup> gaps left by *E. burchelli*. However, 1-m<sup>2</sup> gaps were colonized in different ways. Compared to controls, 100-m<sup>2</sup> gaps created by *E. burchelli* had both more foundresses of prey species, and more workers of the polydomous genus *Paratrechina* (Franks and Bossert 1983). Small artificial gaps in this study contained the same mix of foundresses, queenright, and satellite nests as control plots.

This is a pattern consistent with other studies of gap size and recruitment. For example, small gaps in intertidal communities tend to be filled by peripheral adults; large gaps are colonized by planktonic larvae (Paine and Levin 1981). Similarly, the prevalence of highly dispersive pioneer tree species increases with gap size on BCI (Brokaw 1985). In ants, winged foundresses and queenless satellite nests may be better able to colonize the interiors of large gaps (Wilson 1971) while adult colonies, although mobile (Herbers 1986; Yamaguchi 1992; Byrne 1994), may take longer to move their queen (a risky proposition for the reproductive future of the colony). Army ants that create gaps of different sizes may thus leave different "life history signatures" in the forest litter.

#### Moisture and the litter disturbance dynamics

A second interesting result was that patch dynamics varied between forests. La Selva, the wettest forest with 4000 mm rain annually, showed no differences in nest density or species richness between control and disturbed plots. The drier two forests on BCI, with about half La Selva's rainfall, had lower nest densities three months post-disturbance. Disturbed plots in BCI's drier hilltop forest lagged farthest behind in species richness and differed most in species composition. Other studies corroborate this result. On BCI, Franks found that *E. burchelli*'s greatest impact on arthropod densities occurred in the island's dry season (Franks 1980). At La Selva, Byrne (1994) using similar methods to this study found no disturbance signature in ant densities after 2 months.

Lowland forests in the Neotropics may receive from 1000 to 6000 mm of rainfall (Holdridge et al. 1971; Gen-

try 1988). This variation in moisture availability may affect both the disturbance and recruitment dynamics in litter assemblages. Although the three forests likely differ in many ways, one working hypothesis links litter patch dynamics to moisture.

First, rainfall could be a source of disturbance in the litter, directly or indirectly. Tropical downpours can flood out ant colonies (Wilson 1971). Branch and tree-falls that destroy fragile litter nests may also occur more often in wetter rainforests (Phillips et al. 1994). Finally, army ants appear to prefer wetter habitats within forests (Rettenmeyer 1963; Levings 1983). Corcovado National Park in Costa Rica, similar in rainfall to La Selva, has almost 4 times as many *E. burchelli* colonies as BCI (M. Swartz, unpublished work). If moisture-based disturbance is higher at La Selva than BCI, then plots – both control and disturbed – may have been re-disturbed during the 3 months of this experiment.

Moisture levels may influence recruitment rates. Even small decreases in humidity can hinder activity in tropical ants (Levings 1983; Levings and Windsor 1984; Kaspari 1993a). Perhaps BCI's drier litter (and the drier litter still on the hilltop vs. ravine forest) hinders nest relocation, retarding recovery from disturbance.

In sum, the failure to find differences between control and disturbed plots at La Selva compared to BCI may reflect increased disturbance rates, recruitment rates, or both. Teasing apart these processes will require ingenuity.

Patchiness emerges from the confluence of many processes (Pickett and White 1985). These processes likely vary geographically (Menge et al. 1994). Although much remains to be discovered, the emerging view is that both resources and disturbance shape litter ant patchiness at the 1-m<sup>2</sup> scale. Further studies of army ants and other sources of disturbance along a rainfall gradient may help sort out the factors regulating litter ant patch dynamics.

**Acknowledgements** I am grateful for discussions with E. Leigh, S. Levings, J. Longino, G. Orians, S. Rand, M. Rosenzweig, W. Sousa, and D. Windsor during the planning and execution of the fieldwork. D. Feener, and J. Munger made many constructive comments on the manuscript. This research was funded by a Smithsonian Fellowship, the Organization for Tropical Studies, a NATO postdoctoral fellowship, and a DOE postdoctoral fellowship. Preparation of the manuscript was performed under the auspices of the U.S. Department of Energy at Lawrence Livermore National Laboratory under contract W-7405-Eng-48. This research was supported in part by an appointment to the Global Change Distinguished Postdoctoral Fellowships sponsored by the U.S. Department of Energy, Office of Health and Environmental Research, and administered by the Oak Ridge Institute for Science and Education.

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