An Ant Mosaic in the Colombian Rain Forest of Chocó (Hymenoptera: Formicidae)

by

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ABSTRACT

We investigated the ant (Hymenoptera:Formicidae) distribution in a primary rain forest located in the central coast of the Colombian Choco. We sampled ants on 45 trees located in three 20mx45m plots, by means of visual search, tuna baits, and foliage shaking, once a month, for ten consecutive months. A chemical knockdown was done at the fifth month on three trees and the arthropod biomass was recorded. We found a total of 117 ant morphospecies from which three were catalogued as dominant and ten as subdominant. The most remarkable dominant species *Azteca instabilis* and *Crematogaster carinata* complex showed a clear exclusion pattern both in space and time throughout the ten months. The population fluctuation of these two ant groups in the border of their territory suggests pulses in the dominance of either of the groups of ants in time and possibly in space. Another dominant ant species, *Wasmannia auropunctata* was apparently excluded from one plot by *Dolichoderus bispinosus* and *Azteca* sp. The knockdown technique revealed an ant biomass of 576 mg, which represented between 4% and 25% of all arthropod biomass. Two dominant ants, *C. carinata* and *A. instabilis,* and to a less extent *Dolichoderus bispinosus* contributed the majority of ant biomass in the samples. This is the first time that the ant mosaic is registered for Colombia and the relative importance of dominant ants is shown both spatially and temporally.

Key words: ant mosaic, tropical rain forest, Choco, Colombia, ant temporal distribution, ant spatial distribution.

INTRODUCTION

The "ant mosaic" hypothesis, (Leston 1978), states that in the humid tropics, where the vegetation is more or less stable, a limited number of dominant ants are distributed in a tridimensional mosaic fashion. The dominant ants are those species which display high populations, are mutually exclusive in their distribution and tend to occupy large territories of forest or tree crop canopies (Room 1971, Leston 1978,

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Majer *et al.* 1994). Associated with this mosaic are the subdominant ants, which are also numerous and reach high population densities only under exceptional circumstances, usually coexisting with dominant ants (Majer 1993). Each dominant ant may have a group of subdominant ants commonly associated with it (i.e. cocoa farms: Room 1971). The non-dominant ants, which constitute the majority of the species in the system, occur in or between the territories of the dominant species (Majer *et al.* 1994).

Dominant ant species, which are usually broad-spectrum predators and polydomous (i.e. they have colonies made up of several nests) (Leston 1973) may be playing a major role in structuring with other components of the arthropod community (Room 1971, 1975, Majer 1993). Understanding how the ant mosaic operates can be very important to design pest control programs on relatively stable crops such as cocoa, mango (Leston 1973, Majer 1976 a, 1976b, Delabie 1990, Majer & Camer-Pesci 1991, Way & Koo 1992, Majer *et al.* 1994, Medeiro *et al.* 1995), possibly coffee (Majer & Queiroz 1993) and pear orchard (Paulson & Akre 1991).

In Neotropical forests the ant mosaic has been regarded as one of the major biotic organizational features determining the composition and diversity of biota (Gilbert 1980). Dominant ants within the mosaic have a detectable impact on the composition of other invertebrates which occur on the trees, and this can be explained by several reasons: the existence of species-specific ant-homopteran associations (Majer 1993, Dejean & Gibernau 2000, Dejean *et al.* 2000), the preference of particular dominant ant species for particular prey types of prey size ranges within its territory (Majer 1993), the possession of certain feeding regimes by the dominant ant species (Majer 1993), the association of dominant ants with sub-dominant ants (Room 1971) and the association of different elements of the ant mosaic with plants that have extrafloral nectaries (Dejean *et al.* 2000).

On the one hand, it is believed that the main mechanism which generates the ant mosaic is interespecific competition (Majer 1976 a, 1976b, Cole 1983, Adams 1994, Savolainen 1988, 1989), a phenomenon which is manifested through interspecific aggression in the border of territories (Adams 1994) and in the overdispersion of nests and territoriality (Levings & Trianello 1981, Levings & Franks 1982). On the other hand, the ant mosaic may enhance associated ant biodiversity through a different mechanism. This mechanism is the coexistence of submissive and dominant ant species by niche differentiation and behavioral responses when the top dominants are present (Savolainen & Vepsalainen 1988, 1989).

Colombia is considered one of the world's megadiverse countries (Brown 1991), also possessing several endemic centers (Terborgh & Winter 1983). Although the Chocoan biogeographic region in Colombia was once considered to be the richest in plant species (Gentry 1986), it has received very little attention from the scientific community. This region is also highly vulnerable to environmental destruction (Jimeno *et al.* 1995, Armbrecht & Armbrecht in press).

The aim of this study is to describe the ant community in a rain forest located in the Colombian Choco and to determine if the community fits the ant mosaic pattern. It is also a goal of this research to examine the spatial and temporal fluctuations of dominant ants and to determine the relative importance of these species with respect to other elements of the arthropod community.

MATERIALS AND METHODS

Study site

The study was carried out at the region of Cabo Corrientes, Pacific coast of the Chocoan Department of Colombia, Municipality of Nuquí, district of Arusí (77º30W; 5º30 N). The life zone corresponds to the very humid tropical forest according to the Holdridge system of classification (Espinal 1967), with an annual average precipitation of 5000mm, distributed between a rainy season that extends from August to November, and a "dry" (less rainy) season from January to March. The area has a rugged topography with numerous creeks and is covered by dense primary forest, although some precious wooded trees have been selectively extracted (Galeano *et al.* 1993, Pardo & Cediel 1994).

The fieldwork consisted of ten consecutive monthly sampling sessions between November 1998 and September 1999, and a chemical knockdown for arthropods on three individual trees. Three 45m x 20 m plots named "Natalie", "Librado" and "Fundación" separated by at least 300m from each other were established. The total area of forest covered by the three plots was 2700 m².

Inside each plot, fifteen relatively equidistant trees (approximately 10-15m) were selected and spatially located through a coordinate system of sequential letters and numbers assigned for Y and X axis respectively every five meters. Tree species were identified to the least level possible and voucher specimens were deposited in the Herbarium of the Universidad del Valle, Cali, Colombia. Monthly precipitation data were obtained from the "Fundación Inguede" meteorological station located at the study-site.

Table 1. Tree identity, dominant ants present, and number of ant species found on each tree after ten months of sampling. N/A: identification not available.

Tree code	Family, scientific name (if available)	Dominant ant species	N° of ant species
	NATALIE PLOT		
NA1	Violaceae (*Rinorea sp*)		26
NA3	Rubiaceae (*Palicurea* sp)	*C. carinata*	14
NA5	Sapotaceae (*Chrysophyllum* sp.)	*C. carinata*	23
NA7	Clusiaceae (*Clusia* sp2)	*C. carinata*	23
NA9	Euphorbiaceae sp	*C. carinata*	17
NC1	Lauraceae sp		18
NC3	Violaceae (*Rinorea* sp)		16
NC5	Sapotaceae(*Chrysophyllum* sp.)	*A. instabilis*	13
NC7	Euphorbiaceae sp	*A. instabilis*	19
NC9	Chlorantaceae (*Hedyosmun scaberrimun*)	*W.auropunctata*	13
NE1	Chysobalanaceae (*Hirtella* sp)	*A. instabilis*	14
NE3	Violaceae (*Rinorea* sp)		24
NE5	Palmaceae (*Welfia regia*)	*W.auropunctata*	22
NE7	Moraceae (*Brosimun utile*)	*C. carinata*	17
NE9	Clusiaceae (*Clusia* sp)	*C. carinata*	23
	LIBRADO PLOT		
LA1	Moraceae (*Brosimun utile*)		18
LA3	Clusaceae(clusia sp1)	*C. carinata*	20
LA5	N/A	*C. carinata*	21
LA7	Myristicaceae (*Virola* sp)		24
LA9	Bombacaceae (*Maticia* sp)		16
LC1	Fabaceae sp. 1	*A. instabilis*	13
LC3	Fabaceae (*Bagata* sp)		16
LC5	Melastomataceae (*Miconia* sp)	*C. carinata*	18
LC7	Chrysobalanaceae (*Hirtella* sp)	*W.auropunctata*	18
LC9	Palmaceae (*Welfia regia*)	*W.auropunctata*	21
LE1	Caesalpinaceae sp 1	*A. instabilis*	9
LE3	Melastomataceae (*Miconia* sp)		13
LE5	Myristicaceae (*Otoba* sp)	*C. carinata*	15
LE7	Myrtaceae (*Psidium* sp)	*W.auropunctata*	14
LE9	Myristicaceae (*Virola* sp)	*W.auropunctata*	25
	FUNDACION PLOT		
FA1	Palmaceae (*Wettinia radiata*)		18
FA3	Mimosaceae (*Inga* sp1)		20
FA5	Rubiaceae (*Palicurea* sp)		17
FA7	Annonaceae	*A. instabilis*	19
FA9	Melastomataceae (*Miconia* sp)	*C. carinata*	22
FC1	Palmaceae (*Wettinia radiata*)		15
FC3	Casesalpinaceae (*Brownea rosademonte*)	*C. carinata*	24
FC5	Araliaceae (*Dendropamax* sp)	*C. carinata*	18
FC7	Mimosaceae (*Inga* sp1)		27
FC9	Rubiaceae (*Palicurea* sp)		25
FE1	N/A	*C. carinata*	35
FE3	N/A		26
FE5	Lecitidaceae (*Lecitis* sp)		26
FE7	Melastomataceae (*Miconia* sp)	*A. instabilis*	19
FE9	Casesalpinaceae (*Brownea rosademonte*)	*A. instabilis*	17

Ant sampling

Each tree was sampled once a month using the following four sampling methods: 1) Five minutes of visual registration and manual capturing according to abundance criteria established by Majer *et al.* (1994). The visual technique is one of the most important and frequently used method for ant mosaic studies (i.e. Adams 1994, Majer *et al.* 1994, Dejean & Gibernay 2000). 2) Vegetation shaking: both, the tree trunk and foliage were hit and shaken using a long rod or palm leaves. The falling ants were collected on a 3mx3m white screen previously placed under the tree. 3) Arboreal tuna bait: approximately 3g of tuna-in-oil were hung at 1.7m on the tree trunk. 4) Ground tuna bait: it was placed at the base of the tree trunk previously isolated from the arboreal tuna bait by a surrounding 10cm wide tape smeared with Vaseline. The attracted ants were collected from both arboreal and ground baits after one hour.

All samples were transported in 70% ethanol to the laboratory at the Universidad del Valle, Cali, where they were identified to genera level according to keys from Holldobler & Wilson (1990), Jaffee *et al.* (1993), Bolton (1994) and Mackay & Vinson (1989) and those keys adapted by Baena (1992) for the Colombian Pacific coast. The species were identified using the reference collection from the Entomological Museum of the Universidad del Valle. Voucher specimens were deposited in the Entomology Museum of this same University.

Criteria to define the ant dominance

According to Majer *et al.* (1994), ants were considered dominant if recruited massively (at least 100 individuals), occupied contiguous tree blocks excluding other ant species, and showed a relatively high biomass. Following Majer's quantitative method (1994), we calculated the association between each possible pair of the most abundant ant species using Yates' corrected X^2 (using Systat 7.0 ® program for Windows). The Dominance Index was calculated for each of these species using the formula:

ID= N-P/N+P

where N= Number of negative associations, and P= number of positive associations.

A positive association occurs if two given species are present in the same places more than by random, while a negative association occurs when two given species tend to be mutually exclusive (Ludwig & Reynolds 1988).

Chemical knockdown

In April 1999, three randomly chosen trees (excluding the study

Natalie plot
N=80

Librado plot
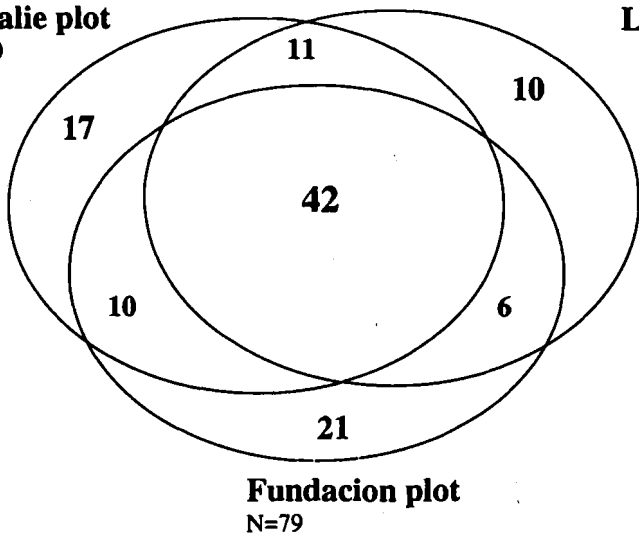N=69

11

10

17

42

10

6

21

Fundacion plot
N=79

Fig. 1. Number of shared and exclusive ant morphospecies found in three plots from a Chocoan rain-forest. Each circle represents the corresponding labeled plot and the numbers represent ant morphospecies.

trees) inside the plots were fogged up to 10m, with a diluted solution (0.25 g/l) of K-Otrine (a Cialotrine). One day before, the floor under each tree was cleared and a 5x5 white screen was extended across it. One hour after fogging, each tree was strongly shaken and the fallen
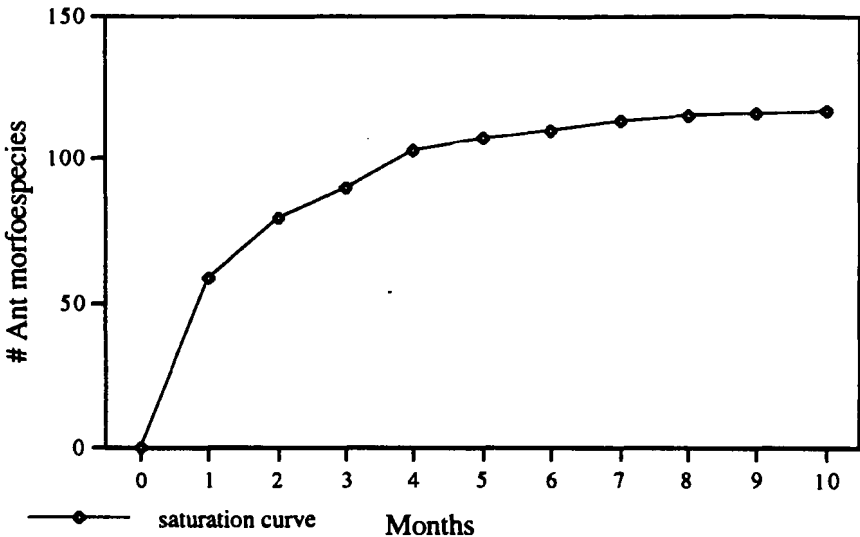
Fig. 2. Saturation curve for the ant morphospecies in all plots during ten sampling months.

Arthropods were collected. Once in the laboratory, the arthropods were separated from the ants, sorted by class and order (only insects) and filtered for 14 hours, after which they were weighted with an analytical balance. The weight of these samples was considered to be an estimate of the live weight of arthropods in the 0-10m stratum of the trees.
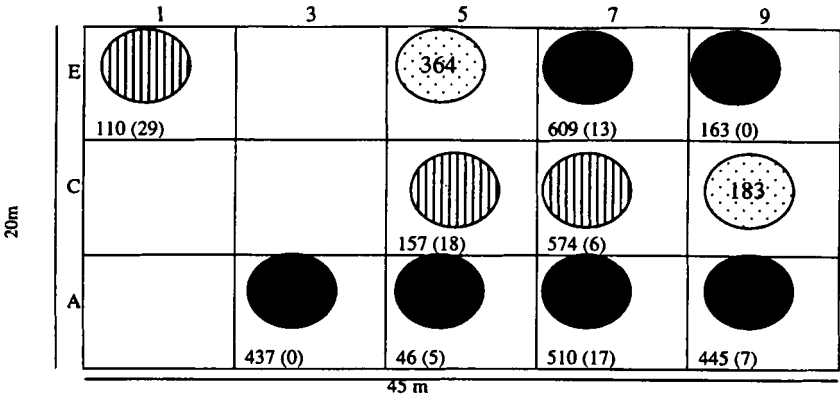
RESULTS

A total of 33,527 ants grouped in 117 morphospecies were observed/ collected during the 2,248 capture events. The total number of captures per species were significantly related to the number of individuals captured/observed (R^2=0.93; F = 752.25; df = 1, 115; P <0.001), thus both measures can be confidentially used as estimates of abundance. The three plots exhibited similar numbers of morphospecies with high overlap among them (Fig. 1). The frequency of appearance of new ant morphospecies stabilized before the eighth month as seen in the species saturation curve (Fig. 2).

Although each of the sampled trees showed high numbers of ants morphospecies, 62% were numerically dominated by either one of the three most important ant species groups: *Azteca instabilis*, *Crematogaster carinata** and *Wasmannia auropunctata* (Table 1). Moreover, 100% of the trees registered the presence of any of these ants at least once.
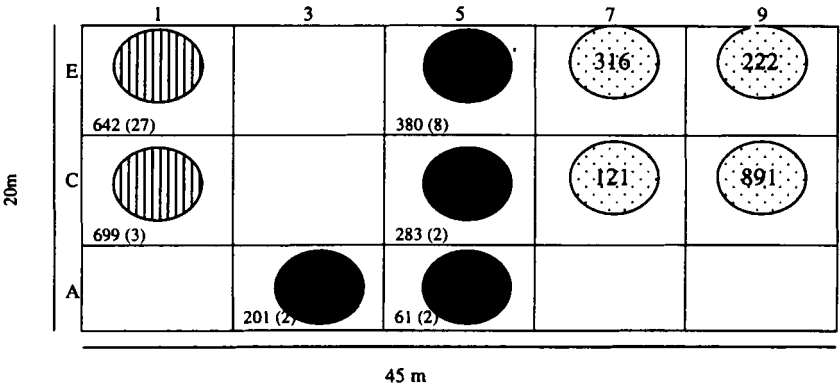
The majority of the trees in two plots (Natalie and Librado) and near a half in the third plot were part of the territories of one of three dominant species (Fig. 3). The number of associated ant species present within the dominant ant's territories fluctuated between 8 and 34, averaging 14, 18 and 20 for *A. instabilis*, *W. auropunctata* and *C. carinata*'s territories respectively. The average ant richness in the remaining "non-dominated" trees, i.e. those in which none of the former ants are clearly established, was 19 in average. No differences were detected among the number of associated ants in the four groups of territories described above (F = 2.512, df = 3, 41; P > 0.05), although it was noted a tendency toward lower numbers of associated ants in *A. instabilis* territories.

*Where the word *carinata* occurs in the text, the reader should understand this to mean *carinata* complex. The *Crematogaster carinata* complex will be considered as an ecological unit for the purpose of the questions addressed in this study. This complex is composed of three ant species which are indistiguishable (morphologically) in the field, share their foraging territories and nest in trees, their dead stems, or their epiphytes. These ant species are: *C. carinata* [including *C. limata (sic) parabiotica* which are considered the same species by J. Longino (pers. com)], *C. brasiliensis* and *C. longispina tenuicula*. Their approximate proportions in the populations studied were 61%, 26% and 13% repectively. This complex was discovered soon before the publication of this article.
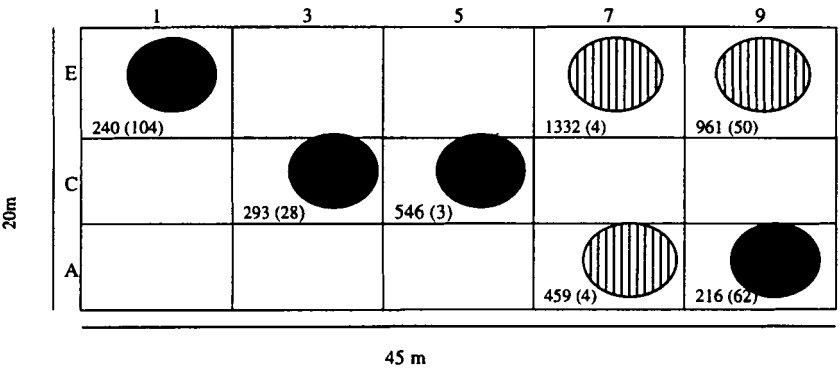
NATALIE PLOT

LIBRADO PLOT

FUNDACION PLOT

Description of the ant mosaic

The seventeen most abundant ant species were pairly tested using Yates corrected Chi-square, for interspecific association (Ludwig & Reynolds 1988). Twentyone of such tests resulted in significant asso-

Fig. 4. Positive (solid lines) and negative (broken lines) associations between the various ant species in a rain forest of the Colombian Choco. Dominant ants are shown in Bold. Thick line: $p=0.001$, thin lines: $p<0.05$ using Yates corrected Chi square analysis.

Fig. 3. Territories of the three most important ant species during the study, *A. instabilis* (vertical lines), *C. carinata* (black) and *W. auropunctata* (dots). The total number of individuals from the dominant ant is written first at the lower left corner (except *W. auropunctata*). In parenthesis the number of individuals either of *A. instabilis* or *C. carinata* complex depending on the territorial domain.

Note the decision to assign a territory to a specific ant was based upon information about both abundance (in terms of number of captures and individuals) and stability in time (number of months present).

Table 2. Dominance status and dominance indexes for each one of the seventeen ant species tested for interespecific associations. Status: D=dominant, SD =subdominant and ND=non-dominant.

Ant species	Status	% trees present	Dominance Index	TotaN° captures	Total N° individuals
Crematogaster carinata	D	100	0.6	403	7638
Azteca instabilis	D	96	1	298	6649
Wasmannia auropunctata	D	69	1	157	3415
Atta cephalotes	SD	82	1	119	317
Pheidole (M13)	SD	69	1	91	1553
Solenopsis (M08)	SD	64	1	59	446
Dolichoderus bispinosus*	SD	20	1	55	786
Azteca (D05) *	SD	22	1	37	1347
Azteca (D13) *	SD	13	0	29	2358
Odontomachus bauri	SD	51	1	58	108
Camponotus sericeiventris	SD	31	0	95	820
Paratrechina (F02)	SD	11	0	41	456
Tapinoma melanocephalum	SD	38	0	36	373
Brachymyrmex heeri	ND	44	-1/3	62	683
Pheidole (M01)	ND	47	-1	69	1099
Megalomyrmex (M04)	ND	49	-1	59	1425
Anochetus emarginatus	ND	20	-1	43	660

* abundant ants species restricted to only one plot

ciations ($P < 0.05$), although seven of them were discarded for their low numbers of expected frequencies. The high importance of the three dominant species in the Chocoan ant mosaic is evidenced from the diagram of negative and positive associations (Fig. 4).

Based upon the following three criteria: the dominance indexes (o.8 or more) (Majer 1994); the ant species abundance (ten times more number of individuals than the total average per species, i.e. 286.5, a criterion established by us); and permanence in well defined territories, that is, species occupying extensive contiguous blocks of trees in the absence of other such species (Majer et al. 1994), we classified three ant species (Azteca instabilis, Crematogaster carinata complex and Wasmannia auropunctata) as dominant, ten as subdominant and the 104 remaining ones as non-dominant (Table 2).

The antagonic relations of Azteca instabilis and Crematogaster carinata complex

The two most abundant species groups in the study, A. instabilis and C. carinata complex also exhibited the highest significance in the Chi square analysis (P=0.001). The spatial and temporal scales in this study permitted us to detect a clear exclusion pattern between these two ant
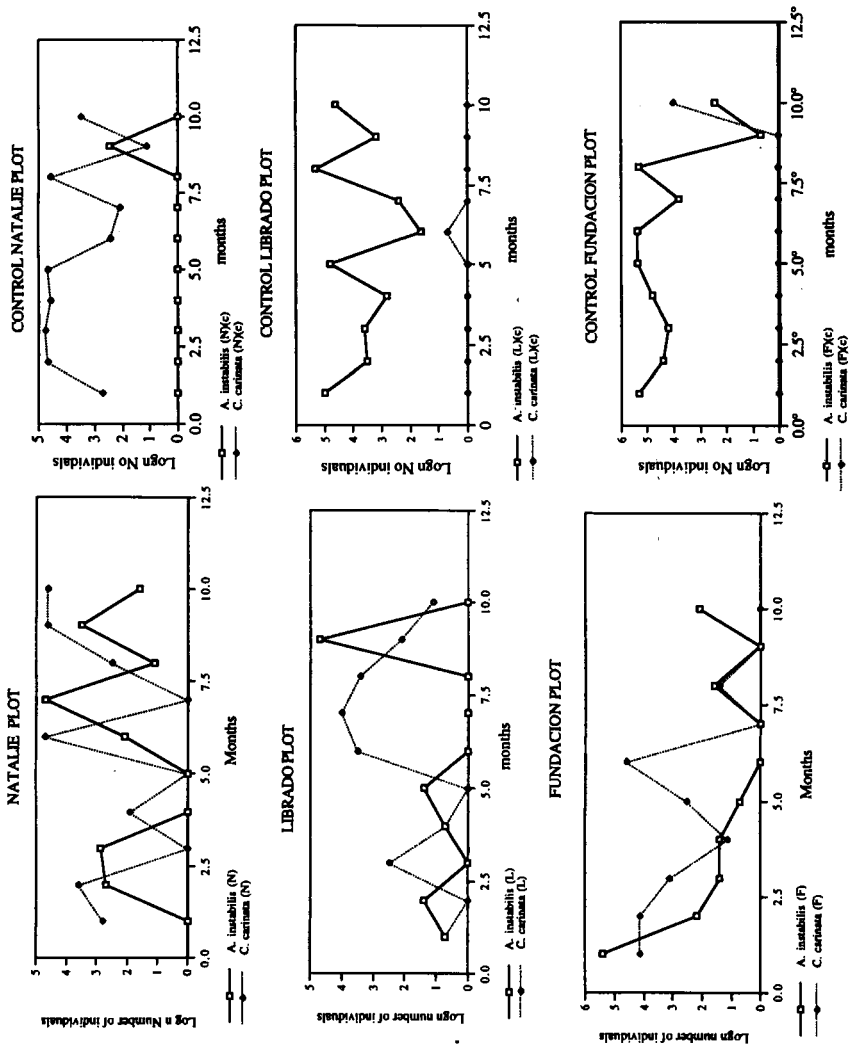
Fig. 5. Antagonic population fluctuation in territory borders and in controls (well-defined territories).
A. Fluctuation in the boundaries of *A. instabilis* and *C. carinata* territories. Data correspond to trees
encoded A1, C1, C3 & E5 in the "Natalie"plot; C3 & E3 in the "Librado" plot; E5, C7, C9 & A5 in
the "Fundacion" plot (see Fig. 3 for location codes). B. Controls for Fig. 5A, the territory of a
randomly chosen tree belonging to either of the two ant species in each of the plot studied. The
control trees correspond to E7 in "Natalie", C1 & E7 in "Librado" and "Fundacion" plots respectively.

Table 3. Arthropod biomass detached from three randomly chosen trees after a chemical "Knockdown" in a primary rainy forest of the Colombian Choco. The approximate location of each tree (see Fig. 5 for coordinates) is: *W. quinaria*: Palmae FC5; *Rinorea* sp.:Violaceae: FC7; and *Chrysophyllum* sp.:Sapotaceae NA5.

Wettinia quinaria			*Rinorea* sp.			*Chrysophyllum* sp.		
Taxa	Weight (mg)	%	Taxa	Weight (mg)	%	Taxa	Weight (mg)	%
Heteroptera	10.1	2.0	Heteroptera	43.1	2.4	Heteroptera	17.1	0.6
Homoptera	15.4	3.1	Orthoptera	738.1	40.5	Orthoptera	786.1	27.3
Orthoptera	216.6	43.4	Arachnida	375.2	20.6	Arachnida	538.0	18.7
Arachnida	36.5	7.3	Crustacea	91.9	5.0	Crustacea	228.6	8.0
Crustacea	22.5	4.5	Microcoryphia	28.9	1.6	Microcoryphia	139.5	4.8
Microcoryphia	2.7	0.5	Coleoptera	260.4	14.3	Coleoptera	693.5	24.1
Coleoptera	50.1	10.0	Lepidoptera	152.8	8.4	Lepidoptera	16.8	0.6
Lepidoptera	18.4	3.7	Blattodea	28.1	1.5	Blattodea	2.2	0.07
Formicidae	**126.7**	**25.4**	Diptera	17.2	0.9	Diptera	3.8	0.13
			Hymenoptera	15.7	0.9	Hymenoptera	42.2	1.6
			Thysanoptera	0.1	0.005	Thysanoptera	0.2	0.01
			Formicidae	**68.5**	**3.8**	Isoptera	26.7	0.9
						Formicidae	**380.7**	**13.2**
Total	499.0	100	Total	1820.0	100	Total	2875.3	100

species groups through time by comparing their abundance at the border of their territory in each of the three plots (Fig. 5). For purposes of comparison, we used a randomly chosen tree belonging to either of the ant species territory as control (Fig. 5).

Arthropod biomass

The results from the chemical knockdown demonstrate the importance of the ant biomass, which averaged 11.1% with respect to that of other arthropods (Table 3), some of them with heavy bodies, and such as crickets, beetles, crabs and scorpions. 25.4 percent of the arthropod biomass in *Wettinia quinaria* was due to three ant species: *C. carinata* (47.6 mg), *D. bispinosus* (53.0 mg) and *Paratrechina* sp. (F06) (22.5 mg). This palm was located close to a *C. carinata* complex territory in the Fundación plot. Contrasting with this result is the 3.8% ant biomass found in *Rinorea* sp., an almost neighboring tree, which was located in a "neutral" territory. In this case most of the ants were *A. instabilis* (51.4 mg), although *Odontomachus bauri* (7.5 mg) and *Dolichoderus bispinosus* (9.5 mg) were also present. A remarkable fact in Fundación plot was the near disappearance of *W. auropunctata* and the massive presence of two ant species not detected in the other two plots: *Azteca* (D13) and *Dolichoderus bispinosus* (see Table 2 for abundance). Note that the *C.*

carinata complex was negatively associated with *W. auropunctata* but positively associated with *D. bispinosus* (Fig. 4). The 13.2% ant biomass in *Chrysophyllum* sp., which exhibited the densest canopy (pers. obs.), belonged entirely to *C. carinata complex.*

Relation between precipitation and ant abundance

A total amount of 6581 mm were registered during the ten study months, which were distributed in two seasons, a dry season between February and April 1999 and a humid one the rest of the time. Although climate and microclimate have been reported to affect the foraging activity of ants in other studies (Torres 1984, Perfecto *et al.* 1996, Perfecto *et al.* 1997), we found no relationship between monthly precipitation and foraging activity of neither *C. carinata* (R^2 = 0.004, P = 0.87, N = 10), *A. instabilis* (R^2 = 0.07, P = 0.48, N = 10), nor *Wasmannia auropunctata* (R^2 = 0.35, P = 0.09, N = 10) (Fig. 6).

DISCUSSION

The evidence gathered in this study strongly indicates that there is a well-defined ant mosaic in this rain forest of the Colombian Choco. This study constitutes the first report of the ant mosaic in Colombia and it is also the first one reporting on the temporal changes of the mosaic. Only one previously known Colombian study, which was done in a cloud
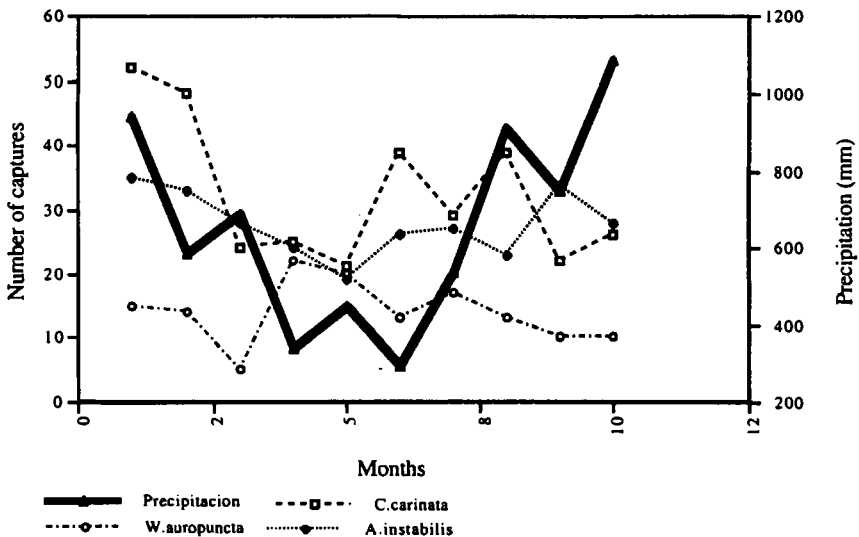

Fig. 6. Monthly precipitation and abundance of the three main dominant ant species in a rain forest of Colombian Choco. Data from November 1998 through August 1999.

forest from the Andean region, did not find evidence to support the existence of the ant mosaic in such natural forest ecosystem (Usma *et al.* 1997). The mosaic-fashion distribution of the dominant ant species in this study, in addition to their highly significant negative associations, their high abundance and stability in time, allows us to support the existence of the ant mosaic that we are reporting here. Moreover, the ant mosaic in this study resembles other South Americanant mosaics found in Brazilian cocoa farms (Majer 1993, Majer *et al.* 1994, Medeiro *et al.* 1995) and in a French Guiana rain forest (Dejean *et al.* 1999) in that they display dominant species from the genera *Azteca* (i.e. *A. instabilis* as in Majer *et al.* 1994 and Dejean *et al.* 1999) *Crematogaster* spp. and *Wasmannia* (*W. auropunctata* as in Majer 1993, Majer *et al.* 1994 and Medeiro *et al.* 1995). The coincidence in the presence of similar dominant ants all throughout this extensive region is an interesting fact that should be studied further from an evolutionary and biogeographic perspective. We propose here that the extremely similar *Crematogaster* species discovered in the *carinata* complex are behaving as a supraspecific entity in terms of their ecological function, transcending the rigid limits of each species definition. This complex clearly excludes other dominant ant species while it tolerates the non-dominant ants, thus exhibiting high ant species richness in their territorial trees. Whether a facilitation occurs among these *Crematogaster* species, how they interact in this forest, and how they might have evolved sympatrically are questions to be addressed by future studies.

Dominant ants and the associated ant biodiversity

One of the most remarkable findings in this study is the temporal antagonic behavior between *A. instabilis* and *C. carinata* complex inside their territories and within their territorial borders. *A. instabilis* showed a more focalized distribution, with very high numbers of individuals within its territories and around its carton nests. Savolainen & Vepsalainen (1988) discussed that ant species can be catalogued in a competitive hierarchical rank according to differences in social organization and behavior ranges. The three hierarchical levels proposed by them are: 1) the "territorials", which defend their foraging areas, and correspond to the dominant species in this study, *A. instabilis, C. carinata* and *W. auropunctata*; 2) the "encounterers", which defend food resources, and which correspond to the subdominant ants in this study (Table 2); and 3) the "submissives", which defend only their nests, and which correspond to the 104 remaining non-dominant ants in this study. The behavior at a small scale would be determining the patterns of distribution at a larger scale processes (Savolainen & Vepsalainen

1988), and thus the mosaic structure, implying the possibility that this mosaic enhances biodiversity. In this study, it was noticeable that many of the subdominant ants also displayed focalized distributions (i.e. *Anochetus emarginatus, Azteca* spp. *Dolichoderus bispinosus* and *Pheidole* (M13), and negative associations with some dominant species, as occurs with *Pheidole* (M13), *Azteca* (D13), *Azteca* (D05), *Camponotus sericeiventris* and *Brachymyrmex heeri* (fig. 4). Patterns as this, may be the manifestation of compartments inside the mosaic at different scales, which, viewed at a higher scale will result in a higher cumulative biodiversity.

The presence of energetic resources as extrafloral nectaries and associations with homopterans may allow the high abundance and stability (Fig. 6) of the dominant species in the mosaic (Dejean et al 2000) and perhaps the coexistence of other associated ants. In this study, a total average of 19.7 ant morphospecies were found per tree, which is a high number compared to the maximum of 8.8 found in Cacao crops in Brazil (Majer *et al.* 1994). Room (1975) demonstrated that the species positively associated with one dominant ant species were different from those associated with another dominant, in cocoa plantations from New Guinea. We found cumulative numbers of 79, 52 and 54 ant species present in *C. carinata, A. instabilis* and *W. auropunctata* territories respectively from which only 20 were shared all among of them. Our data thus demonstrate that mutually exclusive dominant species can coexist with many other ant species. Some of these less abundant ant species inside the territories of dominant ants were found on epiphytic plants, ant gardens (i.e. *Anochetus emarginatus*), foliage or accumulated litter on the tree trunks and branches.

The border conflict

Part of the operating mechanism of the ant mosaic has been uncovered for *Azteca trigona* in Panama's mangroves, in which various *Azteca* species (including *A. instabilis*) occupy mutually exclusive territories (Adams 1994). *A. trigona* displays a vigorous defense in its territorial borders, where it recruits a higher proportion of majors, using also different kinds of pheromones from various glands as part of their strategy. The territories reported by Adams (1994) for *A. instabilis* and *Crematogaster* sp. have spatial scales similar to the dimensions found in the present study (Fig. 5). The pattern of alternation of dominance observed between *A. instabilis* and *Crematogaster* sp. in the border of their territories (Fig. 5A) suggest that the territories do not have sharp borders, and that these borders are constantly being contested. It is possible to expect that these population fluctuations

correspond to periodical pulses in the area of the territories, with the consequent shortening or enlarging of the corresponding territories. However, the scale at which this study was conducted does not allow us to test this hypothesis.

The Influence of other key ants: the Fundacion plot case

Wasmannia auropunctata, a tramp ant (Passera 1994) which has been repeatedly labeled as a dominant in several Neotropical habitats (Majer 1993, Majer et al. 1994, Ulloa-Chacon & Cherix 1994, Armbrecht & Ulloa-Chacon 1999) almost disappeared in Fundacion plot, where we got only eight scattered captures of it. Instead, we registered the massive presence of two species, *Dolichoderus bispinosus* and *Azteca* sp. (D05) which were not recorded in the other two plots and which were negatively associated with *W. auropunctata*. At the same time we noted a slightly different behavior from *A. instabilis* and *C. carinata* populations in this same plot (Fig. 5A). Although we did not have replicates for this phenomenon in an entire plot, it is likely that the incorporation of certain influencing ant species (i.e. *D. bispinosus*, *Azteca* spp. *Camponotus sericeiventris*, *Atta cephalotes*) at a local spatial scale may influence the mosaic structure and the abundance behavior of dominant ants.

The data reported in this study once more shows the importance of the ants in the community structure of arboreal arthropods. This study: 1) demonstrates the existence of a well defined ant mosaic in the rain forest of the Colombian Chocó; 2) Demonstrates that the presence of mutually exclusive dominant ants do not reduce the associated ant species diversity in the trees within their territories; 3) Strongly suggests that the territories of the dominant ants, although fairly stable through time (ten months of the duration of this study), fluctuate spatially. In other words, the boundaries of the territories are not sharp and stable and appear to be contested by other neighboring dominants. 4) Reports an ant biomass representing 11% of the arthropods in the canopy of trees.

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REFERENCES

Adams, E.S. 1994. Territory defense by the ant *Azteca trigona*: the maintenance of an arboreal ant mosaic. Oecologia 97:202-208

Armbrecht, I. & H. Armbrecht. Observaciones sobre la variación espacial y temporal de hormigas en el bosque lluvioso del Chocó Colombiano. En prensa. Boletín del Museo de Entomología de la Universidad del Valle.

Armbrecht, I. & P. Ulloa-Chacón. 1999. Rareza y diversidad de hormigas en fragmentos de bosque seco colombianos y sus matrices. Biotropica 31:646-653.

Baena, M. 1992. Relaciones biogeográficas de las hormigas de la isla Gorgona. Tesis de Grado. Universidad del Valle. Departamento de Biología. Cali, Colombia.

Bolton, B. 1994. Identification guide to the ant genera of the world. Harvard University Press. Cambridge, Massachusetts.

Brown, K. Jr. 1991. The conservation of Neotropical environments. Insects as indicators. Pages 349-404 *in*. N.M Collins and J.A. Thomas, Editors. The conservation of insects and their environments. Academic Press. London.

Cole, B. J. 1983. Assembly of mangrove ant communities: patterns of geographical distribution. Journal of Animal Ecology 52:339-347.

Dejean, A., B. Corbara & J. Orivel. 1999. The arboreal ant mosaic in two Atlantic rain forests. Selbyiana 20:133-145.

Dejean, A. & M. Gibernau. 2000. A rainforest ant mosaic: the edge effect (Hymenoptera: Formicidae). Sociobiology 35:385-401.

Dejean, A, D. McKey, M. Gibernau & M. Belin. 2000. A rainforest ant mosaic: the edge effect (Hymenoptera: Formicidae). Sociobiology 35:403-423.

Delabie, J.H. C. 1990. The ant problems of cocoa farms in Brasil. Pages 555-569 *in*. R.K. Vandermeer, K. Jaffee and A. Cedeno, Editors. Applied Myrmecology: a world perspective. Westview, Boulder.

Espinal, L.S. 1967. Apuntes sobre Ecología Colombiana. Universidad del Valle, Cali, Colombia.

Galeano, G., J. Cediel, M. Pardo & C. Hernández. 1993. Composición y diversidad de los bosques de la región del Cabo Corrientes, costa Pacífica del Chocó. Informe final-primera fase. Instituto de Ciencias Naturales, Universidad Nacional. Bogotá, Colombia.

Gilbert, L.E. 1980. Food web organization and the conservation of Neotropical diversity. Pages 11-33 *in* M.E. Soulé and B.A. Wilcox, Editors. Conservation biology: an evolutionary-ecological perspective. Sinawer, Massachusetts. USA:

Hölldobler, B. & E.O. Wilson. 1990. The Ants. Harvard University Press. Springer-Verlag. Berlin, Heidelberg.

Gentry, A. 1986. Species richness and floristic composition of Choco region plant communities. Caldasia 15:71-91.

Jaffee, K., E. Pérez & J. Lattke. 1993. El Mundo de las hormigas. Equinoccio

Ediciones. Universidad Simón Bolivar, Venezuela.

Jimeno, S., M.L. Sotomayor & L. Valderrama. 1995. Choco, diversidad cultural y medio ambiente, Fondo FEN de Colombia. Bogotá.

Leston, D. 1973. The ant mosaic-tropical tree crops and the limiting of pest and diseases. PANS 19:311-340.

Leston, D. 1978. A Neotropical ant mosaic. Annals of the Entomological Society of America 71:649-653.

Levings S.C. & J.F.A. Traniello. 1981. Territoriality, nest dispersion, and community structure in ants. Psyche 88:265-316.

Levings, S.C. & N.R. Franks. 1982. Patterns of nest dispersion in a tropical ground ant community. Ecology 63:338-344.

Ludwig, J.A. & J. Reynolds. 1988. Statistical ecology: a primer on methods and computing. Wiley, New York.

Mackay, W.P. & S.B. Vinson. 1989. A guide to the species identifications of the New World ants. Sociobiology 16(1): 3-47.

Majer, J.D. 1976a. The maintenance of the ant mosaic in Ghana cocoa farms. Journal of Applied Ecology 13:123-144.

Majer, J.D. 1976b. The influence of ants and ant manipulation on the cocoa farm fauna. Journal of Applied Ecology 13:157-175.

Majer, J.D. 1983. Ants: bio-indicators of minesite rehabilitation, land use and land conservation. Environmental Management 7: 375-383.

Majer, J.D. 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia -its structure and influence on arthropod diversity. Pages 115-141 in J. LaSalle and I.D. Gauld, Editors. Hymenoptera and Biodiversity, CAB International. Wallingford, United Kingdom.

Majer, J.D. & P. Camer-Pesci. 1991. Ant species in tropical australian tree crops and native ecosystems- is there a mosaic? Biotropica 23:173-181.

Majer, J.D., J.H.C. Delabie, & M.R.B. Smith. 1994. Arboreal ant community patterns in brazilian cocoa farms. Biotropica 26:73-83

Majer, J.D. & M.V.B. Queiroz. 1993. Distribution and abundance of ants in a Brazilian subtropical coffee plantation. Papua New Guinea Journal of Agriculture, Forestry and Fisheries 36:29-35.

Medeiro, M.A.D., H.G. Fowler, & J.H. Delabie. 1995. The ant mosaic (Hymenoptera: Formicidae) of cocoa plantations in southern Bahia. Cientifica (Tacoticabal) 23:291-300.

Pardo, M. & J. Cediel. 1994. Composición y diversidad florística de los bosques de Cabo Corrientes, Costa Pacífica del Chocó. Pages 85-91 in Primer Congreso Nacional sobre Biodiversidad, Resúmenes. Cali, Colombia.

Passera, L. 1994. Characteristics of tramp species. Pages 23-43 in D.F. Williams, Editor. Exotic Ants. Westview Press, Boulder, Colorado, USA.

Paulson, G.S. & R.D. Akre. 1991. Behavioral interactions among formicid species in the ant mosaic of an organic pear orchard. Pan-Pacific Entomologist 67:288-297.

Perfecto, I., R.A. Rice, R. Greenberg & M.E. Van Der Voort. 1996. Shade coffee: a disappearing refuge for biodiversity. Bioscience 46:598-608.

Perfecto, I., J. Vandermeer, P. Hanson & V. Cartin. 1997. Arthropod biodiversity

loss and the transformation of a tropical agroecosystem. Biodiversity Conservation 6:935-945.

Room, P.M. 1971 The relative distribution of ant species in Ghana's cocoa farms. Journal of Animal Ecology. 40:735-751.

Room, P.M. 1975. Relative distributions of ant species in cocoa plantation in Papua New Guinea. Journal of Applied Ecology. 12:47-62.

Savolainen, R. & K. Vepsalainen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51:135-155.

Savolainen, R. & K. Vepsalainen. 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos 56:3-16.

Terborgh, J., & B. Winter. 1983. A method for sitting parks and reserves with special reference to Colombia and Ecuador. Biological Conservation. 27:45-58.

Torres, J.A. 1984. Diversity and distribution of ant communities in PuertoRico. Biotropica 16:296-303.

Ulloa-Chacon, P. & D. Cherix. 1994. Perspectives on control of the little fire ant (*Wasmannia auropunctata*) on the Galapagos Islands. Pages 63-72 *in* D. F. Williams, Editor. Exotic Ants. Westview Press, boulder, Colorado, USA.

Usma, S., R. Aldana & G.H. Kattán. 1997. Patrones de distribución espacial y temporal y el modelo del mosaico de hormigas en un bosque de niebla andino. Page. 4 *in* G.H. Kattán and C. Murcia Editors. Primer Congreso Nacional de Biología de la Conservación: Programa y Resúmenes. Universidad del Valle, Cali, Colombia.

Way, M.J. & K.C. Khoo. 1992. Role of ants in pest management. Annual Review of Entomology 37:479-503.