

## Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy

Sérvio P. RIBEIRO, Nádia B. ESPÍRITO SANTO, Jacques H.C. DELABIE & Jonathan D. MAJER



### Abstract

A canopy crane was used to assess ant defensive behaviour and recruitment at baits in the Parque Natural Metropolitano, Panama. Sardine-honey baits were set within a grid of 25 paired upper and lower canopy points, for which coordinates and height were recorded. We tested the hypothesis that interactions in the ant mosaic become stronger as one moves from the lower to the upper canopy.

We sampled 23 ant species, with *Azteca* (*A. trigona*, *A. velox*, *Azteca* nr. *chartifex*, and *A. snellingi*) being by far the most abundant genus, recruiting to 63% of baits and excluding all other ant genera. *Camponotus* (*Myrmobrachys*) sp. 1 also showed a statistically significant exclusion of other ant species over 95% of its occurrence. *Cephalotes umbraculatus* and *Dolichoderus bispinosus* had exclusive occurrences in smaller areas. Exclusion between dominant or sub-dominant species was more frequent in the upper than lower canopy. Permeable borders and territory-free spaces are important for ant species diversity, and were more frequent in the lower canopy. Here, a combination of more costly patrolling conditions and less profitable resources, such as extra-floral nectaries and trophobionts, may be the most likely cause of this pattern. The findings presented here could account for the viewpoint of some that ant mosaics exist in plantations but not necessarily in tropical forest canopies.

**Key words:** Animal territory, assemblage structure, competition, Panama, semi-deciduous tropical forest, Formicidae.

Myrmecol. News 18: 113-120

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 26 June 2012; revision received 18 January 2013; accepted 31 January 2013

Subject Editor: Jens Dauber

*Sérvio P. Ribeiro (contact author), Laboratório Ecologia Evolutiva de Insetos de Dossel e Sucessão Natural, Departamento de Biodiversidade, Evolução e Meio Ambiente / ICEB, Universidade Federal de Ouro Preto, Ouro Preto 35400-000, MG, Brazil. E-mail: spribeiro@iceb.ufop.br*

*Nádia B. Espírito Santo, Laboratório Ecologia Evolutiva de Insetos de Dossel e Sucessão Natural, Departamento de Biodiversidade, Evolução e Meio Ambiente / ICEB, Universidade Federal de Ouro Preto, Ouro Preto, MG, Brazil; now at Departamento de Biologia Animal, Instituto de Biologia, UNICAMP, Campinas 13083-970, SP, Brazil. E-mail: nadiabarbosa@yahoo.com.br*

*Jacques H.C. Delabie, Laboratório de Mirmecologia, Convênio UESC / CEPLAC, Centro de Pesquisa do Cacau, CEP: 45600-000, Itabuna, BA, Brazil. E-mail: delabie@cepec.gov.br*

*Jonathan D. Majer, Curtin Institute for Biodiversity and Climate, Curtin University, Perth, Western Australia 6845, Australia. E-mail: J.Majer@curtin.edu.au*

### Introduction

Ever since the term was originally coined by ROOM (1971), MAJER (1972) and LESTON (1978), the concept of the canopy ant mosaic has been intensively studied and debated (see, for example, RIBAS & SCHOEREDER 2002, SANDERS & al. 2007). It has been described as the presence of large ant territories in the canopy, resulting from the patrolling of dominant and aggressive ant species which alternate, one with the other, among the tree crowns. A number of co-dominant, sub-dominant or cryptic species may co-occur, and dominant ant species may have their own characteristic ant and invertebrate assemblages (MAJER 1992, MAJER & DELABIE 1993, MAJER & al. 1994).

Ant mosaics may not have a continuous distribution, and dominant ants may not always be a barrier to other species, as resources are not evenly distributed and thus not neces-

sarily worth defending to the same extent in different areas. The lack of mosaic continuity is strikingly illustrated for a northern Australian agro-ecosystem by MAJER & CAMER-PESCI (1991), in which portions of mango plantations support a mosaic of *Oecophylla* and *Crematogaster*, while other areas lack any dominant ants. Also, although ant mosaics are well-documented in plantations (MAJER 1992), a number of authors have failed to detect such mosaics in samples taken from natural, tall-tree forests (FLOREN & LINSENMAIR 2000, 2005, RIBAS & SCHOEREDER 2002). As a result, some researchers have assumed that the mosaic is an anthropogenic pattern, confined to artificial or highly simplified forests (FLOREN & LINSENMAIR 2000).

The debate on ant mosaics reached a climax with RIBAS & SCHOEREDER's (2002) paper which, based on null mod-

els, indicates that half of 14 journal articles surveyed would in fact have identified no acceptable mosaic structure, nor clear evidence of competition as a driving force in defining ant exclusion. Furthermore, the physical difficulty in measuring and detecting mosaics increases with canopy complexity and height, so the sampling that has been performed in tropical forests may reflect an inability to detect mosaics, rather than confirmation of the absence of such a pattern (BLÜTHGEN & STORK 2007). Although of importance in presenting what can and what cannot be proven, Ribas & Schoederer's paper did not separate actual lack of competition from lack of data capable of detecting competition (see also BLÜTHGEN & STORK 2007). We acknowledge that forest canopy patches free of mosaic-like territories within a mosaic-dominated canopy certainly do occur, but this has never been formalized in the literature or quantified properly. Failing to distinguish a section of canopy that lacks an ant territory from one that is inaccessible or only partially accessible may jeopardise most of the mechanistic conclusions about ant mosaics so far published. To answer whether the literature reflects a lack of precision in describing territories in hard-to-access habitats, or whether there is an actual absence of defended territories, is an essential question to resolve in order to understand why some natural forests seem not to have ant mosaics.

In the present study, we introduce a pairwise, upper versus lower canopy sampling design, capable of detecting ant mosaic sizes and boundaries over contiguous tree crowns within a large and complex tropical forest canopy. This method allows us to compare ant activity and defensive behaviour towards resources within two canopy strata; lower and upper. In order to map the dominant ant distribution (ecological dominance, sensu DAVIDSON 1998, PARR & GIBB 2009), we sampled at relatively evenly-spaced, paired points of upper and lower canopy and took exact measurements of all co-ordinates (X, Y and height). This sampling design is relatively easy to execute from a research crane.

We defined which species are the dominant ants by assessing defensive behaviour at baits, and also defined their territory sizes and shapes. In addition, we tested the hypothesis that even when there is a canopy mosaic, there exist territory-free spaces (i.e., tree crowns with various non-territorial ant species) and shared territories, where dominant species may occur without competitive exclusion; such areas are hereafter referred to as "permeable mosaic areas". Our prediction is that permeability should be more frequent towards the lower canopy, due to a combination of more costly patrolling conditions (due to larger and less intimately connected branches) and less profitable resources, such as extra-floral nectaries and trophobionts.

## Methods

The study was undertaken in February 2008 during the dry season using a research crane in the Parque Natural Metropolitan, a Smithsonian Research Institute facility in the Republic of Panama. The crane is situated in a semi-deciduous forest in Panama City (8° 59' 46" N, 79° 32' 48" W). Further details about the study site are given in WRIGHT & al. (2003). The canopy is dominated by large trees, mostly *Anacardium excelsum* (Anacardiaceae). Of the 25 sample pairs we measured (see below), 45% were taken on *A. excelsum*, and the remainder on ten other tree or liane species.

The positioning of samples was randomly defined from the crane's gondola. From a starting position above the canopy, set after 30 seconds moving to the right, we requested the crane operator to stop and descend. We took the closest first ramification of the tree (main branch, hereafter) as the lower canopy position, and set a sample point on one of the secondary trunks. Exactly above, on the branches ending at the foliage of the canopy surface, we positioned the upper canopy sample of the pair. Using a compass, we then moved westward by 15 metres to the next sampling location and repeated the operation on the closest tree / branch to that point. Then, the exact distance from the first point was taken with a measuring tape, as was the height from the ground for each sampling point in the pair. This was repeated over 100 m along three 15 m apart swathes of canopy until an entire 100 × 30 m plot had been baited (Fig. 1). A total 25 sampling pair points were set on 22 trees (from nine tree species plus two liana species). The resulting pattern of sampling points conformed, as far as possible, to a grid, although unlike in regularly spaced tree plantations, this was not perfectly arrayed due to restrictions posed by positioning and availability of suitable tree canopies. Since baiting was performed during a short time period, any further uncontrolled variance in ecological conditions equally affected both upper and lower canopy habitats at a given point.

This sampling design aimed to represent, as far as possible, a continuous expanse of canopy, with relatively similar distances between points and paired upper-lower canopy samples. However, in order to test our present hypothesis, which is based on sampling defensive behaviour rather than assemblage diversity, we assumed that each sample was equally independent of the others for the targeted sampling unit, namely individual ant workers. In other words, we assumed that a defensive act or recruitment in response to one particular sample was not affected by behavioural acts or recruiting in other samples. Thus, we assumed that distances, even within a tree, were large enough to collect ants foraging independently, regardless of whether they were coming from the same colony or not. This enabled us to quantify their territory and the differences in defensive efforts in each part of it.

The baiting procedure involved sardine-honey bait "cafeterias", which were set on a paper towel at each upper and lower canopy sampling point. Baits were left for 45 minutes and then removed, along with all ants recruiting to them. Samples were collected between 10:00 and 15:00 h on a sunny and warm day. When collecting up the baits, we also carefully searched for and collected ants around them, as some may have moved off the bait when we approached (often the case with *Pseudomyrmex* and *Cephalotes*). If we could not catch the ant, we visually recorded it to genus level. The samples were named according to BOLTON's (2012) nomenclature, by consulting LONGINO (2010) and also by consulting GUERRERO & al. (2010). Vouchers of the ants were deposited in the Centro de Pesquisa do Cacau and Universidade Federal de Ouro Preto, Brazil collections.

Ant species which occurred continuously among samples / trees, recruited massively to baits, and which were found mostly on their own or with very few individuals from other species in the samples, were considered to be dominant or sub-dominant (sensu MAJER & al. 1994, DE-



Fig. 1: Ant mosaic in the tree crown, showing sampling height within each crown.

JEAN & al. 2003) species. Other ants of low abundance and frequency were considered non-dominant. Some apparently sub-dominant species, being of high abundance but extremely localised, were found at the edge of our sampling grid and their territory may well be larger and extending outward from where we sampled, meaning that they are in fact dominants.

**Statistical test for the mosaic spatial structure:** Trees are numbered in the text and figures to simplify data presentation; their species names are found at the foot of Table 1. As our sampling distances were pre-defined, three of the very large trees housed two sampling pairs on opposite sides of their crowns (in these cases, trees are referred to as tree no. 2 - 3 etc., Fig. 1).

Pairwise and ranking comparisons of ant species abundance were made using non-parametric tests in order to detect the following patterns: (1) Competition hierarchies – chi-square contingency tables were used to test whether individual species occurred in separate or overlapping situations, resulting in their classification as "dominant", "sub-dominant" and "other species grouped"; numbers within these classifications were compared by Mann-Whitney tests ( $n = 25$ ). (2) Variation between strata – Mann-Whitney tests ( $n = 25$ ) were used to compare upper and lower canopy abundances of dominant, territorial species, using the assumption of a global independency of sampling points, as previously described. Finally, (3) permeable mosaic areas and territory-free-spaces were described from the spatial ant species occurrence and boundaries.

## Results

**Ant species abundances and distribution:** A total of 23 ant species and 476 foraging ant workers were sampled. *Azteca* was by far the most abundant genus recruiting in the canopy, with a total of 299 (63%) individuals, comprising four species (*A. trigona*, *A. velox*, *A. nr. chartifex*, and *A. snellingi*). Three of these species, namely *A. trigona* ( $n = 168$ ), *A. snellingi* ( $n = 56$ ) and *A. velox* ( $n = 48$ ), were

clearly distributed in mosaic territories, although *Azteca nr. chartifex* and *A. velox* were limited to one tree each (Fig. 1).

**Competition hierarchies:** The exclusion of other ants where *Azteca* was present, especially those from the same genus (100% avoidance), was noticeable at both studied scales (i.e., forest patches and trees) (Fig. 1). Similarly, *Camponotus (Myrmobrachys) sp. 1* also showed a statistically significant exclusion of other ant species over 95% of its occurrence. Likewise, *Cephalotes umbraculatus*, *Dolichoderus bispinosus* and *Azteca nr. chartifex* exhibited exclusion behaviours (Chi-Square<sub>1,2</sub> = 11.16,  $p < 0.005$ ). The exclusion between dominant or sub-dominant species was strong everywhere, but coexistence was seldom observed in the upper canopy, where we found only one case of overlap between two dominant ants. Interestingly, non-dominant species were much more common in the lower canopy. Only five samples in the upper canopy had non-dominant species (20%), compared with 13 (52%) in the lower canopy (Mann-Whitney,  $W = 531.0$ ,  $p = 0.016$ ). The actual exclusion on baits occupied by the dominant ant was also more severe in the upper canopy, where overlap with non-dominant species was only 12%, compared with 32% in the lower canopy.

**Variation between strata:** Mosaic territories and potential competitive exclusion were more evident in the upper than lower canopy. Although we found a similar frequency of dominant / territorial ants in the upper and lower canopy (76% of upper samples versus 72% of lower samples, Mann-Whitney,  $W = 630.5$ ,  $p = 0.87$ ), there was more evidence of competitive exclusion in the former.

**Permeable mosaic areas:** The mosaic was permeable in two places. First, *Azteca trigona* shared resources with *Cephalotes umbraculatus* and four other species in tree 34, the most easterly tree, and shared the lower branches of tree 29 with *Camponotus (Myrmobrachys) sp. 1* and *C. senex* (Fig. 1, Tab. 1). However, these two trees were the only crowns dominated by *A. trigona* which were sepa-

Tab. 1: Numbers of the various ant species sampled at baits from 25 paired upper (U) and lower (L) sampling points on trees and lianes (listed on lower part of Table) within the Parque Metropolitan Smithsonian Crane site, Panama.

Sample point	1	2	3	4	5	6	7	8	9	10	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35					
<b>Ant species</b>	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L	U	L				
<i>Azteca nr. chartifex</i>										14	13																			
<i>Azteca snellingi</i>	10	0										13	13	18	1	0	1													
<i>Azteca trigona</i>					24	8	15	21	0	3					12	0	1	0			20	11		20	1	21	11			
<i>Azteca velox</i>																										36	12			
<i>Camponotus (Myrmobrachys) sp. 1</i>			0	1						5	4			2	2			1	5	0	4	0	5	3	0	1	0	0	1	
<i>Camponotus crassus</i>															0	1	3	0						9	0	1	0			
<i>Camponotus senex</i>																		1	3		0	1	3	0			0	1		
<i>Camponotus sp. 3</i>																								0	7					
<i>Camponotus sp. 5</i>																							0	2						
<i>Camponotus sp. 6</i>													0	6													0	1		
<i>Camponotus sp. 7</i>																											0	1		
<i>Cephalotes atratus</i>												0	4											1	0	0	3			
<i>Cephalotes umbraculatus</i>			4	0					11	0	10	13												6	2					
<i>Cephalotes sp. 2</i>	4	0			0	5																								
<i>Crematogaster sp. 1</i>											0	11																		
<i>Dolichoderus bispinosus</i>		8	10		0	6																								
<i>Ectatomma tuberculatum</i>				1	0																									
<i>Pachycondyla sp. 1</i>	0	2																												
<i>Pachycondyla sp. 2</i>																									1	0				
<i>Pheidole sp. 1</i>	0	4																												
<i>Pseudomyrmex sp. 1</i>	0	1																												
<i>Pseudomyrmex sp. 2</i>										2																				
<i>Pseudomyrmex sp. 3</i>																										0	1			
<b>Plant species</b>																														
<i>Anacardium excelsum</i>		x	x	x	x	x	x	x			x	x	x	x			x	x		x	x	x	x			x	x			
<i>Castilla elastica</i>												x	x																	
<i>Chrysophyllum cainito</i>	x	x																												
<i>Cordia alliodora</i>																												x	x	
<i>Enterolobium sp. + Merremia sp. (liana)</i>																											x	x		
<i>Ficus elastica</i>								x	x	x	x					x	x													
<i>Guauma ulmifolia</i>				x	x																									
<i>Luehea seemannii</i>														x	x															
<i>Luehea seemannii + Amphilobium sp. (liana)</i>																											x	x		
<i>Merremia sp. (liana)</i>												x	x																	
<i>Spondias mombin</i>																											x	x		

rated from the rest of the territory by "empty" trees. Permeable mosaic areas were always restricted to a single tree, but *A. trigona* had permeable borders, considering the pattern above. For instance, tree 34 was very close to a noticeably "territory-free space" (trees 33 and 21, both adjacent to tree 34, see below), and thus may represent an outer extremity of the territory of *A. trigona*.

All species with territories larger than one tree had an exclusive occupancy in their core area. *Camponotus (Myrmobrachys) sp. 1*, despite its relatively low abundance at baits, had the second greatest frequency (12 samples – 24%), just after *Azteca trigona* (26% of samples). This *Camponotus* species occurred alone in ten samples, and shared baits with *Camponotus crassus*, and the dominants *A. snellingi* and *A. trigona*, in mosaic-permeable areas at the borders of the territories of these species, in the lower canopy.

The presence of *Crematogaster sp. 1* near to one of these permeable areas may either reflect some previous aggressive activity of this genus in the area, or a lack of resources worth defending. Finally, *Azteca snellingi* had a less exclusive territory, with 50% of its occurrence shared with other species, including once with *Camponotus (Myr-*

*mobrachys) sp. 1* in its territory border at the lower canopy of tree 24 (Fig. 1).

**Territory-free-spaces:** Two trees appeared as territory-free-spaces, as they were occupied by distinct species, but were without dominant or sub-dominant ones. Eight species were sampled exclusively in the territory-free space (34%). Also, territory-free spaces supported all the observed occurrences of *Cephalotes atratus*, which is large but rarely demonstrates aggressive behaviour. Furthermore, all three *Pseudomyrmex* (*P. oculatus*, *P. filiformis*, and one unidentified species), two *Pachycondyla*, *Crematogaster sp. 1*, and one *Pheidole* species were found in this small dominant ant-free zone. Besides this, we found *Ectatomma tuberculatum* co-occurring with *Dolichoderus bispinosus*, but only where the latter was in low numbers (i.e., a single individual at the bait).

## Discussion

We have described a snapshot of the distribution of ant workers in response to resources made available at relatively regular distances, both vertical and horizontally in the canopy. The features of these ant assemblages in the upper and lower canopy, as measured by our baiting procedure,

Tab. 2: Summary of ant assemblage parameters measured by baiting at paired points in the upper and lower canopy within the Parque Metropolitano Smithsonian Crane site, Panama. \* = proportion of all points with any overlap between the locally dominant species (owner of a continuous territory) and any other (dominant or non-dominant) species.

Habitat layer	Number of ant species	Number of ant individuals	Number of dominant ant species	Frequency of dominant ant species	Overlap between dominant ant species	Samples with non-dominant ant species	Exclusion of non-dominant by dominants at baits	Permeable areas in the mosaic*
Upper canopy	13	282	7	76%	4%	20%	88%	20%
Lower canopy	21	203	7	72%	12%	52%	68%	36%

are summarised in Table 2. It should be noted that, as with any studies where canopy crane access is involved, our sample size was restricted by the accessible perimeter of the crane, as well as by the time consuming movement of the gondola to reach random samples within the canopy. This poses limitations on the certainty of our findings, but this is a common problem of most canopy research. We therefore acknowledge that more detailed investigations are ultimately required to confirm our findings.

We observed exclusive use of these resources by a few dominant or sub-dominant species across large canopy volumes. More precisely, we detected solo species recruitment along continuous sections of the canopy, reflecting a mosaic type of distribution. Four *Azteca* species, one *Camponotus*, one *Cephalotes* and one *Dolichoderus* were the main dominant or sub-dominant species. Furthermore, by having the samples orthogonally placed both in the lower and upper canopy, we were able to detect where within a species' territory most of defensive behaviours occurred. Clearly, the upper canopy was better protected than the lower, and was thus more exclusively occupied. Large spaces between territory boundaries and permeable territory borders occurred in the lower canopy, which consequently lead to greater ant species diversity in this stratum.

ADAMS (1994) has already described ant mosaics involving *Azteca trigona* and *A. velox* in Panamanian mangrove. He described territory patrolling and defence, and hence the competitive territory delimitation between these two species and also between *Azteca* and *Crematogaster brevispinosa*. Our results confirm that these species have the same pattern of clear-cut, severely excluding territories, resulting in a sharp ant mosaic pattern in the tall tropical forest canopy of Parque Natural Metropolitano, not far from the previously studied mangroves of ADAMS (1994).

Mosaic permeable areas and territory-free spaces have been properly characterised for the first time in this study. Previous papers have considered the existence of territory gaps, or co-dominance in places / crowns where the cost-benefit of excluding competition was too high (DEJEAN & al. 2007). However, the dynamics of a shared territory border or the occupancy of a crown beyond a protected territory may not have been sufficiently described before (see "no-ants land", sensu HÖLLDOBLER 1979, HÖLLDOBLER & WILSON 1990).

The importance of ant competition in structuring ecological communities in tropical forests has been described at the understorey level. HÖLLDOBLER & LUMSDEN (1980) described in detail the territory limits and "no-ant lands" (see also HÖLLDOBLER & WILSON 1990) resulting from

strongly defended edge spaces of colonies of *Oecophylla* species (see another example for *Camponotus gigas* in PFEIFFER & LINSSENMAIR 2001). Also, DEJEAN & BEUGNON (1991) and BEUGNON & DEJEAN (1992) described the existence of noticeably permanent territory landmarks affecting species' distributions at the borders of ant territories.

At the canopy level, the actual importance of competition or, more precisely of the strength of mosaic distribution, has been challenged (RIBAS & SCHOEREDER 2002, SANDERS & al. 2007). Canopy surface roughness, crown contact, and liana interconnection at mosaic gaps between ant territories may interfere with the process of competition (see BLÜTHGEN & al. 2000, YANOVIK & KASPARI 2000), thus affecting the chances of detecting it, even in cases where competition is indeed a structuring force (PARR & GIBB 2009). The role of these factors in ant species distribution has, at best, only been speculatively discussed in the literature (reviewed by DEJEAN & al. 2007). In the present study, microhabitat variation (at the tree crown level scale) was controlled by the way the sampling was designed. Beyond the mosaic distribution, a clear pattern of more intense defensive behaviours in the upper canopy suggests that competition, whether a structuring force or not, functions unevenly in the canopy.

Why might the upper layers of the forest be better defended by ants? Figure 2 provides a schematic representation of conditions in the upper and lower canopy of a hypothetical tropical rainforest. The upper canopy is highly insolated, resulting in warm conditions (FITZJARRALD & MOORE 1995, PARKER 1995), and exhibits high photosynthesis, high primary productivity (HOLBROOK & LUND 1995) and, at certain times of the year, high leaf flushing (LOWMAN 1995). The tender new foliage would tend to support high levels of herbivores (LOWMAN 1995), high honeydew-producing hemipteran populations (BLÜTHGEN & al. 2000, GOITÍA & JAFFÉ 2009), and consequently high invertebrate predator loads (BASSET & al. 1992, CAMPOS & al. 2006), all of which provide abundant food for ants. Furthermore, nectar sources from extra-floral nectaries (EFN) and solid pearl bodies, which are clearly associated with ant defence of young growing tissues (BLÜTHGEN & al. 2000, SCHUPP & FEENER 1991), are abundant in the upper canopy and on emergent branches / trees (CAMPOS & al. 2006, JAFFÉ & al. 2003), providing additional resources for nectar-feeding ants.

All of these features would tend to attenuate lower down in the canopy as interception of solar radiation leads to darker, cooler conditions. The greater insolation and war-

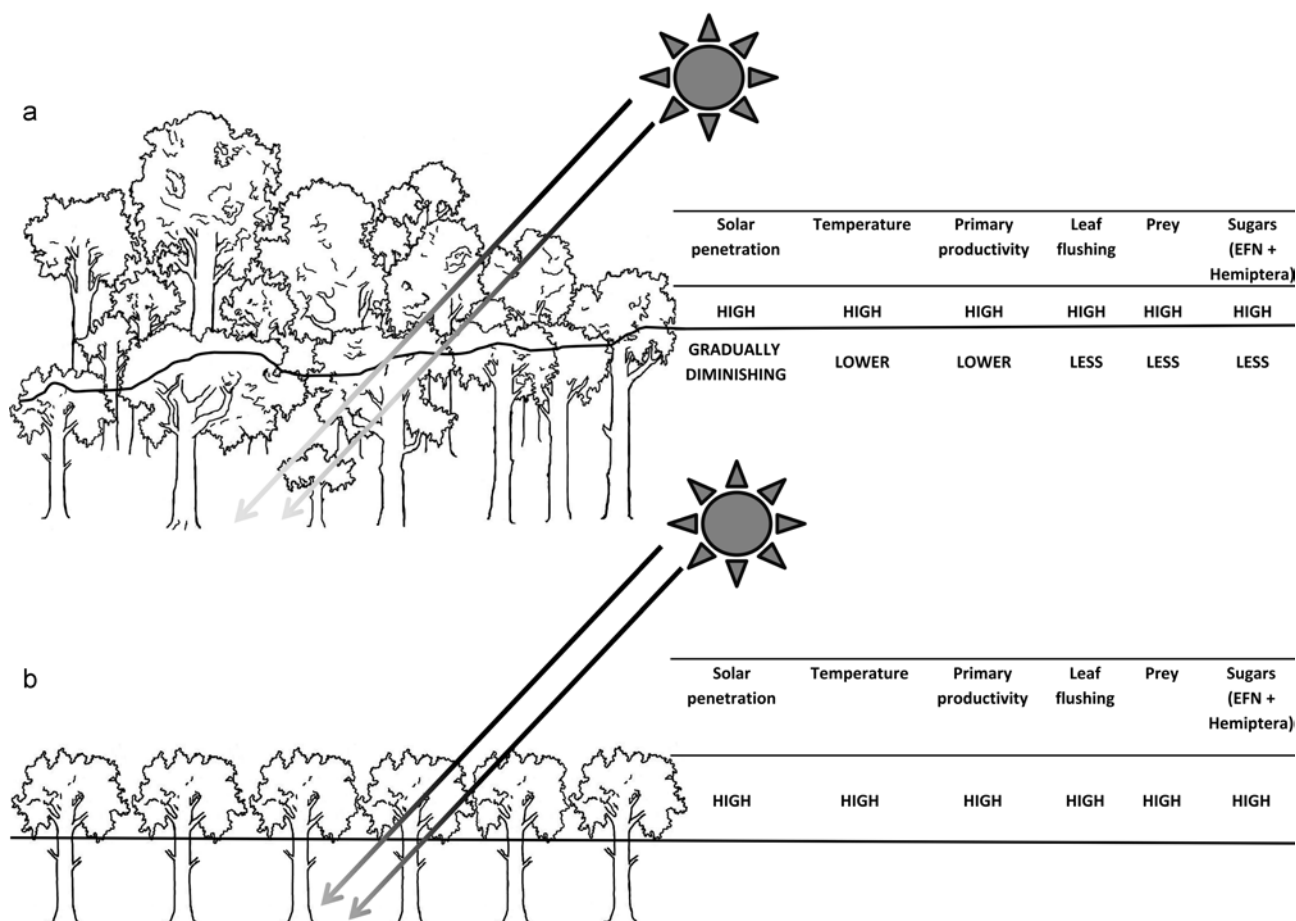


Fig. 2: Schematic diagram of environmental conditions in the canopy of a) rainforest and b) a typical tree crop plantation.

mer conditions in the upper canopy, along with the associated abundant food resources, could thus favour enhanced ant activity. This particular condition makes defence more costly and less effective in the lower canopy than it would be closer to predictable, profitable sources of energy near the canopy surface. There would be a progressive change in environmental conditions and resource availability passing down through the canopy, so the observed differences in mosaic characteristics observed here would probably represent a gradation through the canopy rather than a dichotomy between upper and lower canopy. It is important to note that the current survey was carried out during the dry season, when canopy thinning is likely to have occurred. HAHN & WHEELER (2002), also working in Panama, found that arboreal ants were more abundant on tree trunks sampled at breast height during the dry than the wet season, a phenomenon they attributed to the need to search more actively for protein during this climatically-stressed period. Our interpretation differs in that greater light penetration, and its associated influence on food resources and ant foraging, might also be a factor. Nevertheless, HAHN & WHEELER's (2002) observations indicate that it is possible that the gradation in mosaic characteristics observed here might change, or even be stronger, when the canopy thickens during the wet season.

The present findings could also account for the previously accepted gradient of decreasing ant species diversity from ground to canopy (YANOVIK & KASPARI 2000, DEJEAN & al. 2007), along with the great abundance of ants

in the canopies as a whole (STORK 1991, TOBIN 1995), which may be more precisely described now. A smooth gradient from ground, understory, lower canopy, to upper canopy of decreasing diversity and increasing dominance is likely to exist in various tropical forests. Although this gradient may partially result from the fact that ground dwelling predators and scavenger ants are, evolutionarily speaking, older guilds with more time for speciation compared with canopy-adapted ant species or guilds (DEJEAN & al. 2007), competition may be a relevant mechanism in ecological time affecting this within-canopy gradient (YANOVIK & KASPARI 2000).

All of these features contrast with the situation in tree crop plantations, such as cocoa or oil palm, where the thickness of the canopy equates to the outer canopy surface of the rainforest and, provided that shade trees are not present or too dense, means that the whole tree crop canopy mimics the upper canopy of the rainforest. The distribution of ants may therefore be equivalent to what would be found in the relatively inaccessible parts of the upper canopy, brought down to a level where it may be readily observed and described. This may be the reason for the contention about whether or not ant mosaics exist in rainforest canopies, even though they may exist in nearby plantations. The same situation for plantations could also apply to low-growing mangroves.

A future challenge is to quantify the valuable resources and how they are distributed in the upper canopy in order to justify such stronger patrolling by ants. The well-known

effect of sugar availability from EFN and homopteran-ant interactions in maintaining ant territory strength has also been described for tropical high canopies (BLÜTHGEN & FELDHAAR 2009). Extra-floral nectaries and semi-permanent homopteran-ant mutualisms are typical upper canopy features, and their importance for ant mosaics was predicted by DELABIE (2001), as well as by BLÜTHGEN & al. (2000, 2004), all of whom have indicated their importance in species distribution and richness. Studies by DEL CLARO & OLIVEIRA (1993, 1996, 2000) in the low Brazilian cerrado vegetation corroborate the fact that EFN and homopterans are resources needed for territory maintenance. In the cerrado, they are typically found in what may be seen as a savanna upper canopy (see RIBEIRO 2003). Recently, FAGUNDES & al. (2012) have shown experimentally that the absence of Homoptera during the winter weakens the canopy mosaic in a low savanna type of canopy.

Besides food resources, nesting and habitat structures are expected to define a great deal of ant distribution in the canopy (BLÜTHGEN & FELDHAAR 2009). CAMPOS & al. (2006) have discussed the relative importance of EFN versus other canopy parameters, such as tree height, crown complexity and host tree age. Along with ant interactions with micro-habitat, such as dwelling spaces for nesting, a resource-rich canopy seems to define the existence and strength of an ant mosaic (DEJEAN & al. 2007), and may clearly be related to the predominance of exclusion territories in the upper canopy.

The fact that a canopy ant mosaic exists in the upper canopy, and is much more pronounced than in lower strata, is corroborated by observations in north Queensland rainforest by one of us (JDM). A search of the lower strata on foot yielded low numbers of ants on trunks, and certainly no evidence of dominance. A subsequent inspection of the upper canopy from the canopy crane revealed enormous nests of *Oecophylla smaragdina* (and probably other dominants) in the uppermost part of the canopy, the part most exposed to solar radiation. It is also consistent with the recent observations of TANAKA & al. (2012), who accessed upper rain forest canopy in Borneo from a walkway and observed that a fern-associated dominant, *Crematogaster difformis* abounds and influences the community structure of other canopy ant species. Thus, to reiterate, we suggest that mosaics are so evident in tree crop plantations such as cocoa because their canopies represent the canopy surface of the rainforest, brought down to near ground level where they are more readily observed and where solar-driven interactions are also brought down to this level. Most of the searches for existence of ant mosaics in tropical forests have been performed from below, rather than above the canopy, in an ecosystem where solar radiation is so readily intercepted that only 1% reaches ground level (RICHARDS 1952).

In conclusion, most of the upper canopy may actually be within some mosaic of exclusion territories, and small species-rich crown spots in between territories are essential for canopy forest ecology and conservation. As shown by CAMPOS & al. (2006), the size and height of tree crowns ought to be of great importance for ant species diversity, due to increasing numbers of available microhabitats. In addition to that, we conclude that large crowns are also needed to release competitive pressure on territory borders, thus indirectly allowing the survival of non-aggres-

sive ant species in territory-free-space. These canopy features are of great conservation relevance, as their existence may challenge the current wisdom that intermediate disturbance, such as caused by removal of old large trees, could be more important for forest diversity than emergent, upper canopy habitats.

### Acknowledgements

We are indebted to Yves Basset for the offering of some of his crane hours, and by facilitating our research in the Smithsonian Research Institute; Héctor Barrios for identifying the tree species; Maurice Leponce, for criticism of our first draft; and anonymous referees for commenting on later drafts. We also thank Héctor Barrios and Oliver Misa for helping with the sampling. Mirele Brant is the artist who prepared Figure 1. SPR and JHCD acknowledge their research grants from CNPq.

### References

- ADAMS, E.S. 1994: Territory defense by the ant *Azteca trigona* – maintenance of an arboreal ant mosaic. – *Oecologia* 97: 202-208.
- BASSET, Y., ABERLENC, H.P. & DELVARE, G. 1992: Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon. – *Ecological Entomology* 17: 310-318.
- BEUGNON, G. & DEJEAN, A. 1992: Adaptative properties of the chemical trail system of the African weaver ant *Oecophylla longinoda*, LATREILLE (Hymenoptera: Formicidae). – *Insectes Sociaux* 39: 341-346.
- BLÜTHGEN, N. & FELDHAAR, H. 2009 [2010]: Food and shelter: how resources influence ant ecology. In: LACH, L., PARR, C. L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, pp. 115-136.
- BLÜTHGEN, N. & STORK, N.E. 2007: Ant mosaics in a tropical rainforest in Australia and elsewhere: a critical review. – *Austral Ecology* 32: 93-104.
- BLÜTHGEN, N., STORK, N.E. & FIEDLER, K. 2004: Bottom-up control and co-occurrence in complex communities: Honeydew and nectar determine a rainforest ant mosaic. – *Oikos* 106: 344-358.
- BLÜTHGEN, N., VERHAAGH, M., GOITÍA, W., JAFFÉ, K., MORAWETZ, W. & BARTHLOTT, W. 2000: How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. – *Oecologia* 125: 229-240.
- BOLTON, B. 2012: AntCat. An online catalog of the ants of the world. – <<http://www.antcat.org>>, retrieved on 15 December 2010.
- CAMPOS, R.I., VASCONCELOS, H.L., RIBEIRO, S.P., NEVES, F.S. & SOARES, J.P. 2006: Effect of tree size on insect assemblages associated with *Anadenanthera macrocarpa*: a case of ontogenetic succession. – *Ecography* 29: 442-450.
- DAVIDSON, D.W. 1998: Ecological studies of Neotropical ant gardens. – *Ecology* 69: 1138-1153.
- DEJEAN, A. & BEUGNON, G. 1991: Persistent intercolonial trunk route marking in the African weaver ant *Oecophylla longinoda*, LATREILLE (Hymenoptera: Formicidae) – Tom Thumb's versus Ariadne's orienting strategies. – *Ethology* 88: 89-98.
- DEJEAN, A., CORBARA, B., FERNÁNDEZ, F. & DELABIE, J.H.C. 2003: Mosaicos de hormigas arbóreas en bosques y plantaciones tropicales. In: FERNÁNDEZ, F. (Ed.): *Introducción a las hormigas de la región Neotropical*. – Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, pp. 149-158.
- DEJEAN, A., CORBARA, B., ORIVEL, J. & LEPONCE, M. 2007: Rainforest canopy ants: the implications of territoriality and pre-

- datory behavior. – *Functional Ecosystems and Communities* 1: 105-120.
- DELABIE, J.H.C. 2001: Trophobiosis between Formicidae and Hemiptera (Sternorrhyncha and Auchenorrhyncha): an overview. – *Neotropical Entomology* 30: 501-516.
- DEL CLARO, K. & OLIVEIRA, P.S. 1993: Ant-Homoptera interaction: Do alternative sugar sources distract tending ants? – *Oikos* 68: 202-206.
- DEL CLARO, K. & OLIVEIRA, P.S. 1996: Honeydew flicking by treehoppers provides cues to potential tending ants. – *Animal Behaviour* 51: 1071-1075.
- DEL CLARO, K. & OLIVEIRA, P.S. 2000: Conditional outcomes in a Neotropical treehopper-ant association: temporal and species-specific variation in ant protection and homopteran fecundity. – *Oecologia* 124: 156-165.
- FAGUNDES, F., DEL-CLARO, K. & RIBEIRO, S.P. 2012: Effects of the trophobiont herbivore *Calloconophora pugionata* (Hemiptera) on ant fauna associated with *Myrcia obovata* (Myrtaceae) in a montane tropical forest. – *Psyche* 2012: Article ID 783945.
- FITZJARRALD, D.R. & MOORE, K.E. 1995: Physical methods of heat and mass exchange between forests and the atmosphere. In: LOWMAN, M.D. & NADKARNI, N.M. (Eds.): *Forest canopies*. – Academic Press, San Diego, CA, pp. 45-72.
- FLOREN, A. & LINSENMAIR, K.E. 2000: Do ant mosaics exist in pristine lowland rainforests? – *Oecologia* 123: 129-137.
- FLOREN, A. & LINSENMAIR, K.E. 2005: The importance of primary tropical rain forest for species diversity: an investigation using arboreal ants as an example. – *Ecosystems* 8: 559-567.
- GOITÍA, W. & JAFFÉ, K. 2009: Ant-plant associations in different forests in Venezuela. – *Neotropical Entomology* 38: 1-41.
- GUERRERO, R.J., DELABIE, J.H.C. & DEJEAN, A. 2010: Taxonomic contribution to the *Aurita* group of the ant genus *Azteca* (Formicidae: Dolichoderinae). – *Journal of Hymenopteran Research* 19: 51-65.
- HAHN, D.A. & WHEELER, D.E. 2002: Seasonal foraging activity and bait preferences of ants on Barro Colorado Island, Panama. – *Biotropica* 34: 348-356.
- HOLBROOK, N.M. & LUND, C.P. 1995: Photosynthesis in forest canopies. In: LOWMAN, M.D. & NADKARNI, N.M. (Eds.): *Forest canopies*. – Academic Press, San Diego, CA, pp. 411-430.
- HÖLLDOBLER, B. 1979: Territoriality among *Oecophylla*. – *National Geographic Society Research Reports 1977*: 369-372.
- HÖLLDOBLER, B. & LUMSDEN, C.J. 1980: Territorial strategies in ants. – *Science* 210: 732-739.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: *The ants*. – The Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.
- JAFFÉ, K., HERNANDEZ, J.V., GOITÍA, W., OSIO, A., OSBORN, F., CERDA, H., ARAB, A., RINCONES, J., GAJARDO, R., CARABALLO, L., ANDARA, C. & LOPEZ, H. 2003: Flower ecology in the Neotropics: a flower-ant love-hate relationship. In: BASSET, Y., NOVOTNY, V., MILLER, S. & KITCHING, R. (Eds.): *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. – Cambridge University Press, Cambridge, UK, pp. 213-219.
- LESTON, D. 1978: A Neotropical ant mosaic. – *Annals of the Entomological Society of America* 71: 649-653.
- LONGINO, J.T. 2010: John T. Longino. Specializing in Neotropical myrmecology. – <<http://academic.evergreen.edu/projects/ants/>>, retrieved on 15 December 2010.
- LOWMAN, M.D. 1995: Herbivory as a canopy process in rain forest trees. In: LOWMAN, M.D. & NADKARNI, N.M. (Eds.): *Forest canopies*. – Academic Press, San Diego, CA, pp. 431-455.
- MAJER, J.D. 1972: The ant mosaic in Ghana cocoa farms. – *Bulletin of Entomological Research* 62: 151-160.
- MAJER, J.D. 1992: Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia – its structure and influence on ant diversity. In: LASALLE, J. & GAULD, I. (Eds.): *Hymenoptera and biodiversity*. – CAB International, Wallingford, UK, pp. 115-141.
- MAJER, J.D. & CAMERPESCI, P. 1991: Ant species on tropical Australian tree crop and native ecosystems – is there a mosaic? – *Biotropica* 23: 173-181.
- MAJER, J.D. & DELABIE, J.H.C. 1993: An evaluation of Brazilian cocoa farm ants as potential biological control agents. – *Journal of Plant Protection in the Tropics* 10: 43-49.
- MAJER, J.D., DELABIE, J.H.C. & SMITH, M.R.B. 1994: Arboreal ant community patterns in Brazilian cocoa farms. – *Biotropica* 26: 73-83.
- PARKER, G.G. 1995: Structure and microclimate of forest canopies. In: LOWMAN, M.D. & NADKARNI, N.M. (Eds.): *Forest canopies*. – Academic Press, San Diego, CA, pp. 73-106.
- PARR, C.L. & GIBB, H. 2009 [2010]: Competition and the role of dominant ants. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): *Ant ecology*. – Oxford University Press, Oxford, pp. 115-136.
- PFEIFFER, M. & LINSENMAIR, K.E. 2001: Territoriality in the Malaysian giant ant *Camponotus gigas* (Hymenoptera / Formicidae). – *Journal of Ethology* 19: 75-85.
- RIBAS, C. & SCHOEREDER, J.H. 2002: Are all ant mosaics caused by competition? – *Oecologia* 131: 606-611.
- RIBEIRO, S.P. 2003: Insect herbivores in the canopies of savannas and rainforests. In: BASSET, Y., NOVOTNY, V., MILLER, S. & KITCHING, R. (Eds.): *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. – Cambridge University Press, Cambridge, UK, pp. 348-359.
- RICHARDS, P.W. 1952: *The tropical rainforest*. – Cambridge University Press, Cambridge, UK, 450 pp.
- ROOM, P.M. 1971: The relative distribution of ant species in Ghana's cocoa farms. – *Journal of Animal Ecology* 40: 735-751.
- SANDERS, N.J., CRUTSINGER, G.M., DUNN, R.R., MAJER, J.D. & DELABIE, J.H.C. 2007: An ant mosaic revisited: Dominant ant species disassemble arboreal ant communities but co-occur randomly. – *Biotropica* 39: 422-427.
- SCHUPP, E.W. & FEENER, Jr. D.H. 1991: Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. In: HUXLEY, C.R. & CUTLER, D.F. (Eds.): *Ant-plant interactions*. – Oxford Science Publications, Oxford, pp. 175-197.
- STORK, N.E. 1991: The composition of the arthropod fauna of Bornean lowland rain forest trees. – *Journal of Tropical Ecology* 7: 161-180.
- TANAKA, H.O., YAMANE, S. & ITIOKA, T. 2012: Effects of a fern-dwelling ant species *Crematogaster difformis*, on the ant assemblages of emergent trees in a Bornean rainforest. – *Annals of the Entomological Society of America* 105: 592-598.
- TOBIN, J.E. 1995: Ecology and diversity of tropical forest canopy ants. In: LOWMAN, M.D. & NADKARNI, N. (Eds.): *Forest canopies*. – Academic Press, London, pp. 129-147.
- WRIGHT, S.J., HORLYCK, V., BASSET, Y. 2003: Tropical canopy biology program, Republic of Panama. In: BASSET, Y., HORLYCK, V. & WRIGHT, S.J. (Eds.): *Studying forest canopies from above: the International Canopy Crane Network*. – Smithsonian Tropical Research Institute and UNEP, Panama City, Panama, pp. 138-158.
- YANOVIK, S.P. & KASPARI, M. 2000: Community structure and the habitat templet: ants in the tropical forest canopy and litter. – *Oikos* 89: 256-266.