Biotic and abiotic determinants of the formation of ant mosaics in primary Neotropical rainforests

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Abstract. 1. Ants are widespread in tropical rainforests, including in the canopy where territorially dominant arboreal species represent the main part of the arthropod biomass.

2. By mapping the territories of dominant arboreal ant species and using a null model analysis and a pairwise approach this study was able to show the presence of an ant mosaic on the upper canopy of a primary Neotropical rainforest (*c.* 1 ha sampled; 157 tall trees from 28 families). Although Neotropical rainforest canopies are frequently irregular, with tree crowns at different heights breaking the continuity of the territories of dominant ants, the latter are preserved via underground galleries or trails laid on the ground.

3. The distribution of the trees influences the structure of the ant mosaic, something related to the attractiveness of tree taxa for certain arboreal ant species rather than others.

4. Small-scale natural disturbances, most likely strong winds in the area studied (presence of canopy gaps), play a role by favouring the presence of two ant species typical of secondary formations: *Camponotus femoratus* and *Crematogaster levior*, which live in parabiosis (i.e. share territories and nests but lodge in different cavities) and build conspicuous ant gardens. In addition, pioneer *Cecropia* myrmecophytic trees were recorded.

Key words. Ant mosaics, connections on the ground, host tree attractiveness, indicators of disturbance, primary Neotropical rainforest, territoriality.

Introduction

Ants dominate the fauna of tropical rainforest canopies in terms of both biomass and number of individuals, an ecological success that is possible thanks to their entirely or partially herbivorous diet as they feed on extrafloral nectar, food bodies and hemipteran honeydew (Davidson *et al.*, 2003; Blüthgen *et al.*, 2004). Yet, only a limited number of ant species with large colonies are concerned, something corresponding to the notion of 'numerical dominance' (the predominance of a species in frequency of occurrence in the ant community). When combined with 'behavioural dominance' (dominance in interspecific

competition due to superior fighting and/or recruitment abilities) this results in 'ecological dominance' (see Davidson, 1998). Certain canopy ants correspond rather to the latter case as they are characterised by very populous colonies of up to several million workers, large and/or polydomous nests (see Fig. 1), and an absolute intra- and interspecific territoriality, so that they are called 'territorially dominant arboreal ant species' (TDAAs) (Majer, 1993).

Two TDAAs can share the same territory (i.e. 'co-dominance') when they have complementary rhythms of activity (i.e. one is diurnal, the other is nocturnal), when their workers avoid each other with only occasional conflicts for food, or during 'parabiosis' (i.e. two species share the same territories and nests, but lodge in different cavities of these nests) (Majer, 1993; Dejean *et al.*, 2007, 2012; Vicente & Izzo, 2017; Yusha *et al.*, 2017).

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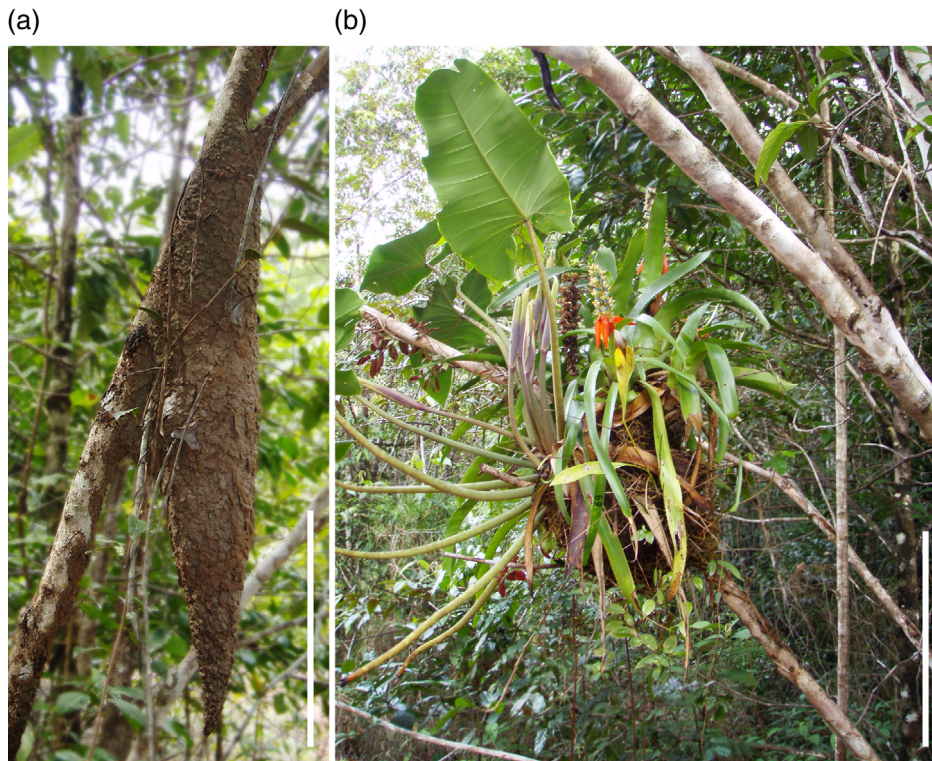
Fig. 1. (a) A large carton nest of *Azteca chartifex*. (b) A conspicuous ant garden resulting from the association between *Camponotus femoratus* and *Crematogaster levior*. Scale bar, 50 cm. [Colour figure can be viewed at wileyonlinelibrary.com].
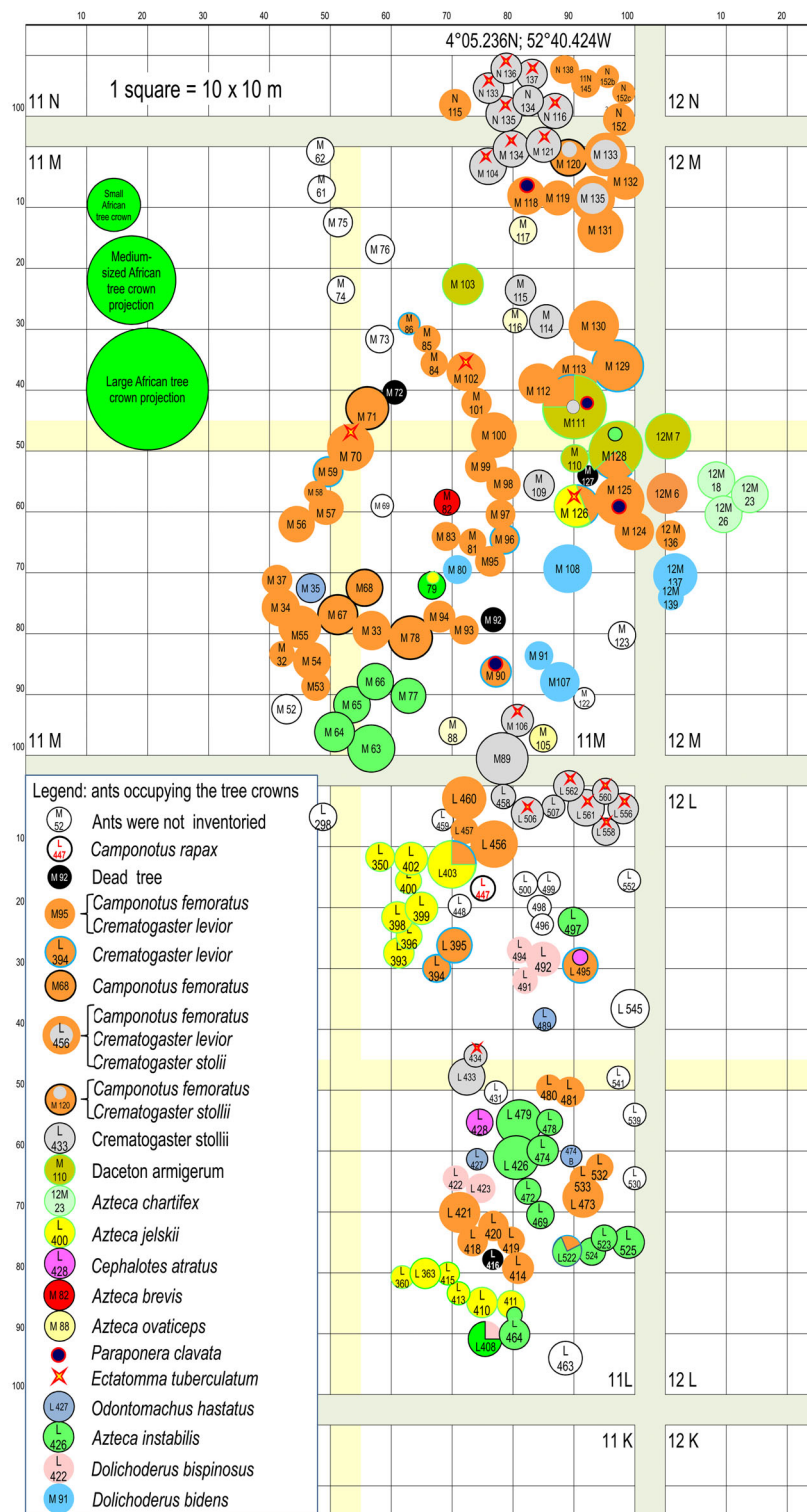
Territorially dominant arboreal ant species tolerate within their territories the presence of 'non-dominant' species with small colonies that represent only *c*. 5% of the ant biomass and individuals, but are species-rich (e.g. 43 species on one tree; 85 species on two trees) (Hölldobler & Wilson, 1994; Tobin, 1997). Exceptionally, colonies of non-dominant ants can become large enough to occupy and defend the crown of a tree; they are then called 'subdominants' (Majer, 1993; Majer *et al.*, 1994).

When the tree crowns are contiguous or interconnected by liana, the TDAAs' territories are distributed in a mosaic pattern, creating what has become known as 'arboreal ant mosaics' (Majer, 1972, 1993). That the arboreal ant fauna in tropical rainforests has a patchy distribution was first noted by Wilson (1958). The notion of 'ant mosaic' was later presented in studies conducted in African cocoa tree plantations whose canopy is easily attainable, permitting the rapid and efficient identification of the ant species occupying each individual tree (Room, 1971; Majer, 1972, 1993; Leston, 1973). Ant mosaics have been noted in the upper canopies of tropical African, Asian, Bornean, New Guinean and Neotropical rainforests (Adams, 1994; Dejean *et al.*, 1994, 2000, 2007, 2010, 2015, 2018; Armbrecht *et al.*, 2001; Blüthgen & Stork, 2007; Davidson *et al.*, 2007; Ribeiro *et al.*, 2013; Klimes, 2017; Yusah *et al.*, 2018; Leponce *et al.*, 2019). Nevertheless, ant mosaics are often absent from the 'sub-canopy', probably due to the scarcity of hemipterans whose honeydew is necessary to fuel the TDAA colonies (Floren & Linsenmair, 2000; Blüthgen & Stork, 2007; Dejean *et al.*, 2007, 2018; Ribeiro *et al.*, 2013; but see Klimes *et al.*, 2015). Yet,

very large TDAAs colonies can occupy vast spaces involving all canopy growth stages (Dejean *et al.*, 2007; Klimes *et al.*, 2015).

Founding queens do not install their colony by chance in tree crowns as selective plant attractiveness has been shown experimentally for both plant-ants and TDAAs (Djiéto-Lordon & Dejean, 1999a,b). Although tempered by the extension of the territories over adjacent trees (of different species) with the increasing size of the TDAAs' colonies, this effect remains perceptible (Dejean *et al.*, 2007, 2015, 2018; Fayle *et al.*, 2015). Also, an ontogenetic succession of ant species follows the sequence of stages in tree and vegetal formation development (Watt *et al.*, 2002; Kenne *et al.*, 2003; da Conceição *et al.*, 2014; Dejean *et al.*, 2016). Finally, the forest structure plays a role in the formation of ant mosaics. For example, tropical African rainforests have proportionately more 'large' trees (i.e. tall with a wide trunk and a large crown) than do the tropical forests of other continents, probably due to fewer disturbances over recent decades (Lewis *et al.*, 2013; see projections of African trees in Fig. 2). This explains why the Neotropical rainforest canopies are frequently irregular, with tree crowns at different heights probably resulting from treefall gaps, breaking the continuity of the territories of the TDAAs (Ribeiro *et al.*, 2013).

Studying ant mosaics is important because TDAAs prevent attended hemipterans from proliferating (Styrsky & Eubanks, 2007) and protect their host trees from defoliating insects through their predatory behaviour or by deterring them, either actively or simply through the presence of their long-lasting

Fig. 2. . Overhead view of the distribution of the trees and their associated territorially dominant ant species in the area studied in the Nouragues Ecological Field Station, French Guiana. Paths in this area follow an Hippodamian plan (grey lines representing the paths cutting at right angles and delimiting ha; the limits underlined in yellow serve to outline areas of 0.25 ha). The codes correspond to the trees listed in Appendix S1 (see also examples of the projection of African tree crowns for comparison). Note the co-occurrence of two mutually exclusive territorially dominant arboreal ant species in seven tree crowns (i.e. trees 11L403, 11L408, 11L411, 11L522, 11M111, 11M126, 11M128), and co-dominance in 29 trees. Certain co-occurrences of species are shown in the left part of the figure whereas others are represented by circles (e.g. *Cephalotes attratus* on a tree mostly occupied by *Crematogaster levior*; tree L495) or by red stars corresponding to *Ectatomma tuberculatum* tolerated by different ant species (e.g. trees M70, M104). [Colour figure can be viewed at wileyonlinelibrary.com].

landmarks (Majer, 1993; Dyer, 2002; Floren *et al.*, 2002; Dejean *et al.*, 2007; Offenberg, 2007).

Ant mosaics can be impacted by canopy gaps created by the death of a tree or trees downed by snapping or uprooting due to strong winds that are considered small-scale natural disturbances. An indirect impact also occurs during the formation of large gaps as they permit light-demanding tree species with low wood density (e.g. pioneer trees) to develop quickly from seeds (Schnitzer *et al.*, 2008).

In this study, conducted in a primary moist Neotropical rainforest situated in French Guiana, we aimed to determine: (i) if an ant mosaic exists in the upper canopy; (ii) if TDAA workers follow trails on the ground that interconnect neighbouring trees to compensate the irregularity of the canopy or if they use underground galleries; (iii) if the host tree taxa influence the TDAAs' distribution; and (iv) if locally strong winds due to the neighbouring presence of an inselberg affect the distribution of the TDAAs, favouring some of them.

Materials and methods

Study site, tree mapping and identification

The Nouragues Ecological Research Station (4°05′N, 52°41′W), dominated by a partly denuded inselberg (430 asl), is located within the Montagnes Balenfois massif typical of the Guiana Shield. Pollen coring and the radiocarbon dating of charcoal suggest that the forest cover has remained intact for > 3000 years at least, but with fires occurring *c*. 500 years ago. A variety of vegetal formations occur within a radius of 1.5 km, including: (i) those on the inselberg's summit; (ii) a low transition forest; (iii) a wide, forested plateau; and (iv) a liana forest whose origin might be due to strong winds or a microtornado. The climate is moist tropical, with a mean annual rainfall of 3000 mm distributed over *c*. 280 days, and the daily mean temperature is in the range 20.3–33.5 °C (Grimaldi & Riera, 2001; Tymen *et al.*, 2016).

In the Nouragues area, strong winds, probably due to the vicinity of the inselberg, generated on the plateau the formation of a liana forest and large gaps. Liana forests, caused by windthrow events resulting in gaps > 1 ha, generally persist for a long time, blocking the forest succession (van der Meer & Bongers, 1996; Stefan *et al.*, 2010; Tymen *et al.*, 2016).

Field studies were conducted on the plateau (2006–2010) where the staff of the Nouragues Ecological Research Station have established a grid of trails creating 1-ha forest plots over 70 ha; the trees have been mapped, measured, tagged, and identified (Poncy *et al.*, 2001).

Canopy access, gathering TDAA samples and mapping the ant mosaic

We used the single rope technique to reach the upper canopy tree crowns, permitting us to gather samples from 157 trees. To collect ant samples, we cut off two to four branches from different areas of the crowns (diameter 10–15 cm) of each tree. Because arboreal ants mark these branches as part of their territories (i.e. the workers deposit 'landmarks' that can last for more than 1 year; Beugnon & Dejean, 1992; Offenberg, 2007), several dozen to thousands of workers remained on them for more than 1 h after the sectioning of the branches (Dejean *et al.*, 2007, 2010, 2015). Using entomological aspirators, we were thus able to collect samples of the ants crawling on the fallen branches or hidden in hollow twigs.

In contrast to trapping methods permitting large numbers of species to be collected, this branch-clipping method allowed us to sample numerically dominant ants and obtain information on interspecific tolerance by noting the co-occurrence of these species on the same branches. Sampling ants by clipping branches does not provide a representative picture of 'non-dominant' ant species (not considered here), something needed in diversity studies.

We also verified at the bases of trees whether there were nests of *Ectatomma tuberculatum* or *Paraponera clavata*, two ground-nesting, arboreal foraging species known to be dominant or co-dominant (see studied ant nesting habits in Table 1).

The presence of arboreal ant trails on the ground was noted during a sampling of litter-dwelling ants in the area studied (Groc *et al.*, 2014). We therefore verified whether the trails interconnected the bases of different trees and whether certain workers transported brood and nestmates from one tree to another (see Orivel & Dejean, 2001). As most of the TDAAs in the area are diurnal, each hour between 08.00 and 18.00 hours during five non-consecutive sunny days we walked along a path selected to represent an area where the tree canopies were not interconnected but still shared the same TDAAs.

Because *E. tuberculatum* and *Crematogaster stollii* use underground galleries to interconnect trees (Table 1) when one or the other species was noted on groups of trees we sought to determine if these trees belonged to the same colony. We thus sprayed paint on workers from one nest (from *c*. 60 cm so that each ant had only some spots) and verified during the next 3 days if ants with spots of paint were present on the adjacent trees. For *E. tuberculatum*, we unearthed a nest from the base of a tree and sprayed blue paint, as the workers are yellowish. For *C. stollii*, we opened galleries at the base of a tree and sprayed yellow paint, as the workers are black; the verification required opening the galleries of adjacent trees.

All these techniques permitted us to pinpoint the exact limits of the TDAAs' territories, allowing the precise mapping of these territories (Fig. 2).

Ant samples were preserved in 70% ethanol for later identification; voucher specimens were deposited in the *Laboratório de Mirmecologia*, UESC/CEPLAC, Ilhéus, Bahia, Brazil, and in the Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Rarefaction curves of tree and ant assemblages

Diversity statistics were calculated using ESTIMATES 9.1 software (Colwell, 2013) with 100 randomisations of the sampling order without replacement. To estimate sampling completeness, the Chao1 (tree data, abundance-based) and Chao2 (ant data, occurrence-based) non-parametric estimators of total species richness were calculated (Colwell *et al.*, 2004).

Table 1. List of dominant ant species collected from 157 trees in the Nouragues Ecological Research Station (the total of the percentages is greater than 100% because one tree crown can shelter several dominant ant species due to cases of co-dominance).

Ant species	Occurrences	Frequency on trees	Nesting habits	
Crematogaster levior	69	43.95%	Carton nests, ant gardens, polydomous, parabiosis with *Camponotus femoratus*	Dejean *et al.* (2000); Vicente and Izzo (2017)
Camponotus femoratus	61	38.85%	Semi-spherical carton nests, ant gardens, polydomous, parabiosis with *Crematogaster levior*	Dejean *et al.* (2000); Vicente and Izzo (2017)
Crematogaster stollii	28	17.83%	Carton nests in cavities; galleries on tree trunks and branches; continue underground, interconnecting trees	Longino (2003)
Azteca instabilis	22	14.01%	Hemispherical carton nests against tree trunks or base of main branches, polydomous	De la Mora *et al.* (2008)
Ectatomma tuberculatum	19	12.10%	Ground-nesting at the base of trees, polydomous; galleries underground interconnecting trees	Delabie (1990); Hora *et al.* (2005)
Azteca jelskii	16	10.19%	Carton nests in cavities, polydomous	Longino (2007)
Dolichoderus bidens	6	3.82%	Numerous small carton nests under the leaves, polydomous	MacKay (1993); Delabie *et al.* (1991); Corbara *et al.* (2018)
Dolichoderus bispinosus	6	3.82%	Nests in cavities, polydomous	MacKay (1993)
Daceton armigerum	4	2.55%	Cavities in old branches of trees, polydomous	Dejean *et al.* (2012)
Azteca ovaticeps	4	2.55%	Nests in hollow trunks and branches of *Cecropia* spp. trees	Longino, 2007
Odontomachus hastatus	4	2.55%	Nests in trash baskets formed by palm trees or *Philodendron*	Gibernau *et al.* (2007); Camargo and Oliveira (2012)
Paraponera clavata	4	2.55%	Ground-nesting at the base of trees	Elahi (2005)
Azteca chartifex	3	1.91%	Large, triangular carton nests, polydomous	Delabie *et al.* (1991); Longino (2007)
Cephalotes atratus	2	1.27%	Large cavities in old branches of trees, polydomous	Bolton (2018)
Azteca brevis	1	0.63%	Carton nests in cavities; galleries on tree trunks and branches; continue underground, interconnecting trees	Longino, 2007; Schmidt & Dejean, 2018
Camponotus rapax	1	0.63%	Small colonies nesting in cavities in old branches of trees	Gibernau *et al.* (2007); AD, BC *pers. com*

Because ant mosaics correspond to non-random patterns of co-occurrence related to the mutual exclusion of TDAAs, we used a fixed-equiprobable null model and the C-score co-occurrence index with the sequential swap algorithm and 5000 iterations available in the ECOSIM software (Gotelli & Entsminger, 2004; Blüthgen & Stork, 2007; Fayle *et al.*, 2013). The fixed-equiprobable algorithm maintains the species occurrence frequencies and considers all sites (trees) equiprobable (Gotelli, 2000). The C-score index used in combination with the fixed-equiprobable algorithm generally has good statistical properties and is not prone to false positives (Gotelli, 2000). Specific associations between the most frequent ant species (i.e. present on > 10% of the 157 trees sampled) were tested using χ^2 tests with Yates' correction. When field observations revealed that a single tree crown belonged to two different territories ($n = 7$ cases), the species involved were encoded separately in the co-occurrences matrix (the whole results in a matrix of six ant species × 164 sampling units).

*Testing the relationships between tree family (or subfamily) and ant species*

To determine the influence of host trees in shaping the ant mosaic, the TDAAs recorded for each tree family (or subfamily

for the Fabaceae) allowed us to build a '10 ant species × 31 tree families' matrix. TDAAs found only occasionally were eliminated to avoid the effect of outliers, as were the 11 cases for which the trees were not identified, so that this study was conducted on 144 out of the 157 trees sampled.

To ordinate the host tree families based on the TDAAs they sheltered, we conducted a non-metric multidimensional scaling (NMDS) on a matrix of dissimilarity based on the Bray–Curtis dissimilarity index using 100 random starts. The final stress value of $0.06 < 0.1$ can be acknowledged as providing a good representation for a two-dimensional configuration. A hierarchical clustering using the 'complete' agglomeration method (NBCLUST package) on the dissimilarity matrix resulted in eight clusters of ant species; this was the best clustering scheme obtained using the 'majority rule' (24 indices computed). These analyses were conducted using the VEGAN and NBCLUST packages in R software (R Development Core Team, 2015).

Identifying different degrees of 'small-scale disturbance' between five Guianese rainforests

Because the parabiotic, ant-garden ants *Camponotus femoratus* (Formicinae) and *Crematogaster levior* (Myrmicinae) are
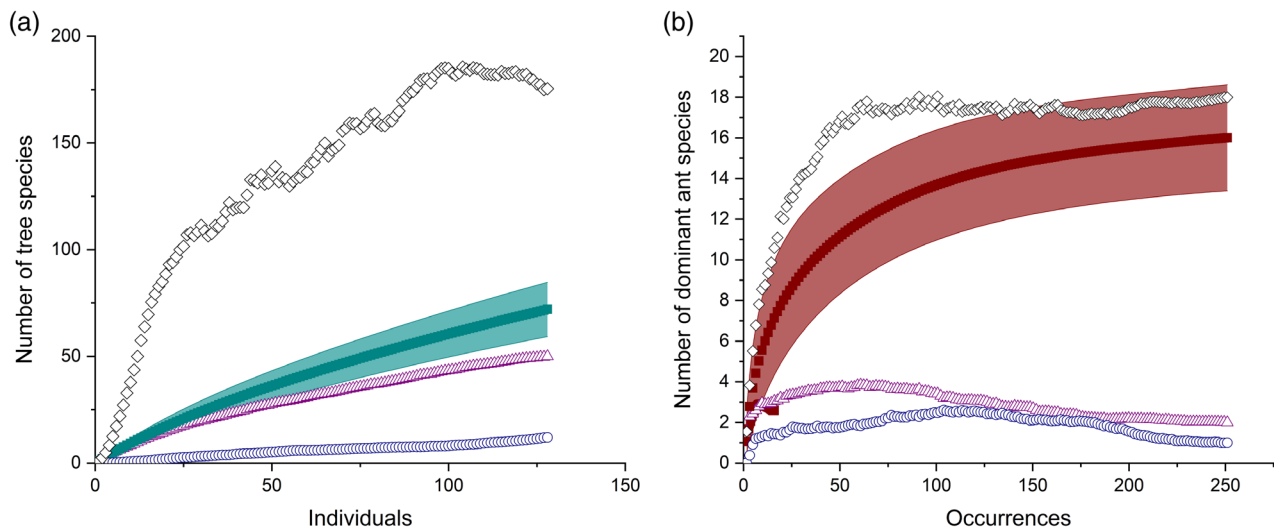
Fig. 3. (a) Individual-based rarefaction (Mao-Tau with 95% CI; solid lines) illustrating the incompleteness of the survey concerning the tree species (*N* = 141 trees identified), confirmed by the stability of the singletons (species observed with only one individual; triangles) and doubletons (species with only two individuals; circles). The estimated asymptotic richness of the assemblage obtained by Chao1 is shown as diamonds (Chao1 mean = 175 species; 95% CI: 119–298 tree species). Trees that could not be identified to the species level were excluded from this analysis. (b) Sample-based rarefaction (Mao-Tau with 95% CI; solid lines) illustrating the near-completeness of the survey concerning the ant species, confirmed by the decrease in uniques (species collected only once; triangles) and duplicates (species collected twice; circles). The estimated asymptotic richness of the assemblage obtained by Chao2 is shown as diamonds (*N* = 157 host trees). [Colour figure can be viewed at wileyonlinelibrary.com].

characteristic of pioneer formations but are also present in rainforest canopies, particularly around treefall gaps (Vicente & Izzo, 2017), they can serve as a basis for comparison to establish different degrees of 'small-scale natural disturbances' between rainforests. This needs to be distinguished from major disturbances such as those caused by hurricanes or by humans.

Thus, we compared the number of trees sheltering these ant garden ants with those sheltering the other dominant ants between five Guianese rainforests (data from the present study, two kinds of forests in Mitaraka, Petit Saut and Paracou) (Dejean *et al.*, 2018; Leponce *et al.*, 2019). A set of Fisher's exact tests was used for pairwise comparisons; simultaneous comparisons were adjusted using the false discovery rate, BH correction (Pike, 2011). We also compared the number of tree crowns sheltering these ant-garden ants between light-demanding and other types of trees on the Nouragues plateau as well as the frequency of light-demanding trees between the Nouragues plateau and Paracou, two terra firme rainforests (see data in Appendix S1A, B).

Results

General points

The 157 trees sampled represented 77 species belonging to 29 families, the Lecythidaceae (30 trees) being the most frequent, followed by the Fabaceae (28 trees) (Appendix S1), but we noted the incompleteness of the tree survey (Fig. 3a). The projected on-ground crown map (Fig. 2) corresponds to the location of individual trees in more or less circular horizontal projected crown areas whose diameters varied from 5–6 m to,

exceptionally, 14–15 m (see tree no. 11M11); one can note the presence of numerous gaps between these tall canopy trees.

A representative part of the dominant ant assemblage was inventoried (Fig. 3b). Among the 16 ant species recorded (nine genera from six subfamilies), only *Camponotus rapax* is a non-dominant species, here in the situation of sub-dominant on one tree: 11L447. The most frequent species, *C. levior*, noted on 43.95% of the tree crowns, generally nests in parabiosis with *C. femoratus*, both sharing ant gardens (Table 1; Figs 1, 2; Appendix S1).

Mapping the territorially dominant ant territories

Despite the absence of direct contact between certain tree crowns or their connection via lianas in many cases, the cohesion of these territories is possible thanks to the presence of trails on the ground that interconnect the trees. These trails are used during the warmest hours of the day (11.00–15.00 hours), the workers walking in both directions transporting larvae, nymphs and nestmates. This was noted for *Azteca jelskii* (connections between trees 11L403, 11L399, and 11L402), *Azteca instabilis* (trees 11M77 and 11M66), *C. femoratus* and *C. levior* (group of trees whose limits are 11M53, 11M37, 11M93, and 11M90; trees 11M111 and 11M128; Fig. 2). The nests of *Dolichoderus bidens* are interconnected by constantly used trails passing through low understorey vegetation. Also, spraying paint on *E. tuberculatum* or *C. stollii* workers confirmed that, via underground galleries, neighbouring trees sheltering these ant species belonged to the territory of one colony (e.g. for *C. stollii*, see groups 11M104, 11M135 and 11N136; 11L556, 11L458 and 11M106; Fig. 2).

Table 2. Associations between the most frequent species (frequency on the 157 trees sampled > 10%) by decreasing rank of occurrence and tested using χ^2 tests (1 d.f., Yates' correction).

		Frequency	1	2	3	4	5
1	*Crematogaster levior*	44%					
2	*Camponotus femoratus*	39%	+				
3	*Crematogaster stolli*	18%	−	−			
4	*Azteca instabilis*	14%	−	−	0		
5	*Ectatomma tuberculatum*	12%	−	−	+	0	
6	*Azteca jelskii*	10%	−	−	0	0	0

Symbols indicate the nature of the association: +, positive; −, negative; 0, not significant.

We also noted tree crowns divided into separate territories (e.g. 11L408, 11L411, 11L522, 11L403, 11M126, 11M128, 11M111; Fig. 2).

In addition to the cases of parabiosis between *C. femoratus* and *C. levior* noted on 56 tree crowns, co-dominance was frequent when involving *C. stollii*, which was often associated with *E. tuberculatum* (i.e. on 16 trees out of 28 sheltering *C. stollii*; Table 2; Fig. 2; Appendix S1). Other cases of co-dominance concerned *C. levior* and *Cephalotes atratus* (tree 11L495), *A. instabilis* and *A. jelskii* (trees 11L411 and 11M79), and *A. instabilis* and *Daceton armigerum* (tree 11M128) or *Dolichoderus bispinosus* (tree 11L408) (Fig. 2; Appendix S1).

The null model analysis confirmed the existence of a mosaic by revealing less species co-occurrence than expected by chance between the six most common ant species, indicating a competitively structured assemblage (observed *C*-score = 912.9, simulated *C*-score = 614.6; *P* < 0.001). The pairwise approach showed that *C. levior* and *C. femoratus* were positively associated with each other but negatively associated with all four other frequent species, whereas *C. stollii* was positively associated with *E. tuberculatum* (Table 2).

Influence of tree family (or subfamily) on the ant species distribution

The NMDS ordination of Bray−Curtis distances and the complete agglomeration method showed a strong host tree selectivity by the 10 most frequent dominant ant species as eight clusters were delimited with, as expected, the two parabiotic, ant-garden ants, *C. levior* and *C. femoratus*, being grouped together. *Azteca jelskii* was associated with *D. bispinosus*, whereas all other ant species were related to a specific set of tree taxa (Fig. 4; see also Fig. S1). Thus, the sampling size was large enough to obtain evidence that the formation of ant mosaics depends to some extent on the host trees.

Identifying different degrees of small-scale disturbances between five Guianese rainforests

The rate of presence of the ant-garden ants *C. femoratus* and *C. levior* on the Nouragues plateau (present study) and the Mitaraka swamp forest was not significant, but was significantly higher than the three other forests (Table 3). Among the latter, the difference between the forest of Paracou and the Mitaraka plateau was not significant, but was significant between them and the Petit Saut forest (ant-garden ants absent there) (Table 3).

The number of tree crowns sheltering *C. femoratus* and/or *C. levior* on the Nouragues plateau was not significant between light-demanding and other types of trees [8/20 cases (40%) vs. 59/120 (49.17%); Fisher's exact-test: *P* = 0.48]. Also, the comparison between the Guianese terra firme rainforests of the Nouragues plateau and Paracou resulted in non-significant differences in the relative numbers of light-demanding tree species (26/146 trees identified vs. 22/109; Fisher's exact-test: *P* = 0.87) (see Appendix S1).

Discussion

Ant mosaic characteristics and traits related to ant species dominance

Although Neotropical rainforest canopies are reputed to be irregular, breaking the continuity of the territories of TDAAs (Ribeiro *et al.*, 2013), we show the existence of an ant mosaic. This was demonstrated by mapping the spatial segregation of the numerically dominant ants in the upper canopy (Fig. 2), the use of a null model co-occurrence and a pairwise approach.

All already known cases of arboreal ant dominance were recorded, including classical TDAAs, co-dominance and even a colony of the non-dominant species *C. rapax* in the position of sub-dominance (small *C. rapax* colonies nest in old branches; Table 1). In addition to the parabiosis between *C. levior* and *C. femoratus*, most cases of co-dominance involved *C. stollii*, whose workers moreover defend territories vis-à-vis other TDAAs even though they mostly move inside carton galleries (Longino, 2007; Schmidt & Dejean, 2018). They were frequently associated with *E. tuberculatum* (Table 2). Some other cases of co-dominance correspond to tolerance between TDAA foraging workers (Fig. 2; Appendix S1).

A representative proportion of known dominant arboreal ants was inventoried in the upper canopy (Fig. 3), whereas this was not the case for trees for which a very large sampling effort might be necessary due to the hyperdiverse Amazonian rainforests (see Poncy *et al.*, 2001).

Importantly, although the TDAA territories frequently spread over several tree crowns, some tree crowns were divided into two or more separate territories (Fig. 2; Ribeiro *et al.*, 2013; Dejean *et al.*, 2018). This situation needs to be handled with
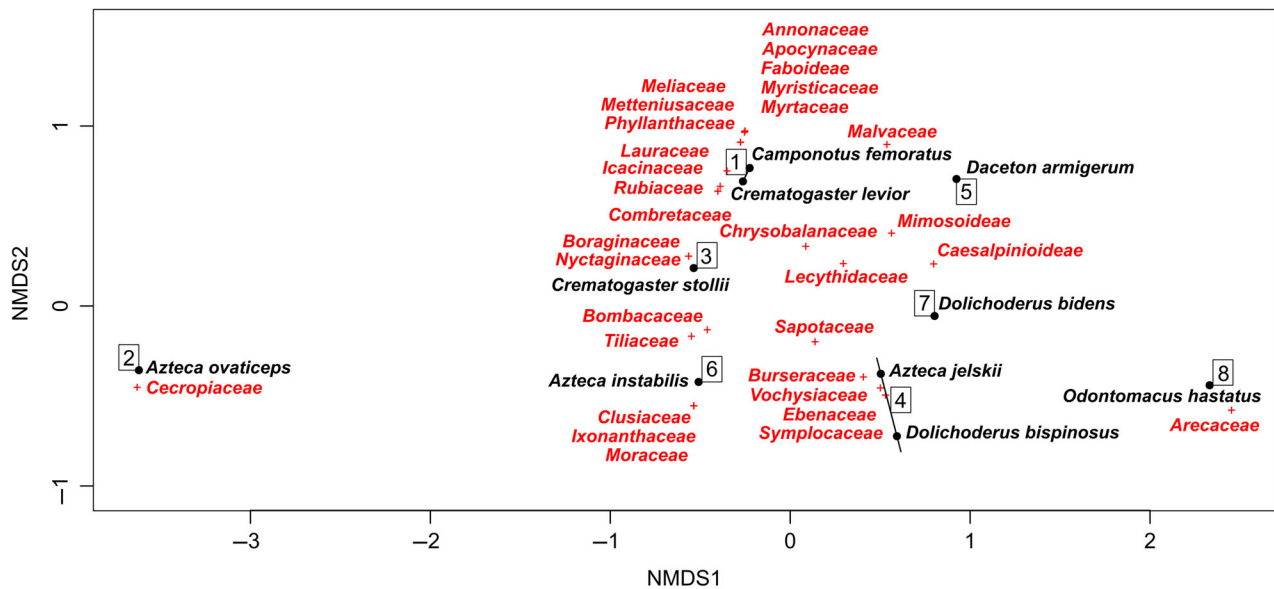
Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot showing the ant species (black dots) according to their host tree taxa (red dots) (Bray–Curtis distance). The 'complete' clustering of ant species in the ordination space according to host trees delimits eight clusters. The analysis was conducted on the 10 most frequent dominant ants and 31 tree families or subfamilies for the Fabaceae (this corresponds to 144 tree crowns out of the 157 sampled). The two interconnecting lines represent cases of associations between ant species. [Colour figure can be viewed at wileyonlinelibrary.com].

Table 3. Comparison of the parabiotic, ant-garden ants *Camponotus femoratus* and *Crematogaster levior* and all other territorially dominant arboreal ant species (TDAAs) between five Guianese rainforests.

	A: Nouragues (plateau)	B: Paracou	C: Mitaraka (plateau)	D: Mitaraka (swamp)	E: Petit Saut
Ant-garden ants	69 (45.7%)	27 (20.15%)	6 (20%)	15 (50%)	0 (0%)
All other TDAAs	82 (54.3%)	107 (79.85%)	24 (80%)	15 (50%)	45 (100%)
Total	151	134	30	30	45
	A×B	A×C	A×D	A×E	B×C
Fisher's exact test	$P < 0.001$	$P = 0.0088$	$P = 0.693$	$P = 0.0001$	$P = 1$
FDR adjustment	$P < 0.05$	$P < 0.05$	NS	$P < 0.05$	NS
	B×D	B×E	C×D	C×E	D×E
Fisher's exact test	$P = 0.002$	$P = 0.001$	$P = 0.0292$	$P = 0.0029$	$P < 0.0001$
FDR adjustment	$P < 0.05$	$P < 0.05$	$P < 0.05$	$P < 0.05$	$P < 0.05$

Statistical comparison: Fisher's exact tests and false discovery rate (FDR; BH correction) adjustment for simultaneous comparisons.

care to avoid confusing it with cases of co-dominance and which could cause the wrong data to be used in the statistical analyses, leading to erroneous interpretations.

A complementary survey conducted at ground level is necessary because it will allow trees whose crowns are not interconnected by contact or via lianas to be grouped in the same territory and, here too, avoid misinterpretations. Indeed, we showed that the workers of five TDAAs use trails on the ground or the low vegetation to interconnect trees whose crowns are not in contact, permitting them to exchange brood and workers and thus to maintain the colony odour, as is known for two ground-nesting ant species (Beugnon *et al.*, 2001; Orivel & Dejean, 2001). Furthermore, we confirmed that the colonies of *C. stollii* and *E. tuberculatum* interconnect neighbouring trees belonging to their territory via underground galleries.

Forest canopy functioning and ant mosaics

Among the functional traits of ant species involved in ant mosaics (e.g. colony size, territoriality, host-tree preference), the size of the colonies is primordial. For example, Camarota *et al.* (2016) demonstrated that, in the Brazilian Cerrado (a savanna with trees *c.* 6 m tall), null model analyses conducted on all ant species noted on trees resulted in random co-occurrence patterns. Yet, the same approach conducted on the most frequent species resulted in a segregated pattern, something confirmed through a pairwise approach [a pairwise approach also permitted Adams *et al.* (2017) to identify segregated TDAAs in a Panamanian rainforest]. Consequently, numerical dominance can be enough for null model analyses to illustrate a segregated pattern of occurrence (see other details in Blüthgen & Stork,

2007). Indeed, if ant abundance in tropical rainforest canopies surpasses that of all other animal taxa, this is due to dominant species because non-dominant ants, which are species-rich, represent only *c.* 5% of the ant biomass and individuals (Hölldobler & Wilson, 1994; Tobin, 1997).

Roles of host trees and small-scale disturbances on the distribution of dominant ants

Host tree specificity due to attractive chemicals acting on founding queens and workers, well known for myrmecophyte–ant relationships, was generalised to include TDAAs during ethological experiments showing the basis of nest-site selection by these arboreal ants (Djiéto-Lordon & Dejean, 1999a,b). This was also shown via the distribution of the dominant ants' territories, even though the latter expand as the colonies age (i.e. they occupy neighbouring trees whose taxa are distributed by chance) (Dejean *et al.*, 2007, 2015, 2018; this study). Our approach was valid as we, indeed, noted that the two ant-garden ants shared the same cluster and that the plant-ant *Azteca ovaticeps* was associated with its mutualist host mymecophyte, *Cecropia obtusa* (Cecropiaceae) (Fig. 4).

Another important characteristic is the dominance of the ant-garden ants *C. femoratus* and *C. levior* in the ant mosaic studied; these are two species typical of pioneer formations that are also frequent around treefall gaps and in plantations (Vicente & Izzo, 2017). Thus, their presence in primary rainforests (Dejean *et al.*, 2018; Leponce *et al.*, 2019; this study) might indicate some degree of past disturbances or frequent disturbances. The comparison between Guianese rainforests showed that the rate of presence of these two ant species was significantly higher on the Nouragues plateau than in other terra firme Guianese rainforests, but similar to that of a swamp forest (Table 3). Note that the characteristics of Neotropical swamp forests are similar to those of young, secondary forests and treefall gaps in old-growth forests (Souza & Martins, 2005).

Furthermore, the presence of the typical pioneer species *C. obtusa* shows that canopy gaps existed in the past; later these trees reached the canopy and so were recorded in this survey (Appendix S1; Fig. 2).

Relationships between small-scale natural disturbances and the presence of ant-garden ants

Because the comparison of the frequency of the ant-garden ants on the Nouragues plateau and the comparison of the numbers of light-demanding tree species between the Nouragues plateau and Paracou resulted in non-significant differences, we failed to show that these ants select 'light-demanding tree taxa' rather than others. Thus, the neighbouring presence of canopy gaps seems enough to favour the presence of these ants in the situation studied (i.e. whether the host trees are light-demanding or not).

Therefore, the abiotic disturbances represented by frequent strong winds and the formation of large canopy gaps are probably the main cause of the abundance of the ant-garden ants

C. femoratus and *C. levior* that withstand these effects better than do competing TDAAs (see Vicente & Izzo, 2017). Because they build conspicuous ant gardens that are easy to locate (Fig. 1), they might serve as indicators of different degrees of small-scale natural disturbances.

In conclusion, ant mosaics exist in Neotropical rainforests despite the irregularity of the canopy breaking the continuity of the territories of dominant ants due to frequent small-scale natural disturbances. The ant mosaics are ruled by the TDAAs' territoriality, host tree taxa selection, the need for contact between tree crowns or their interconnection via liana, plus the ability of certain TDAAs to interconnect trees belonging to their territories using trails on the ground or underground galleries. Furthermore, an abiotic influence plays a role in the form of strong winds and the formation of large canopy gaps.

Author contributions

AD, BC, and ML designed the experiments; AD and ML conducted the field study; JHCD identified the ants; AC and ML analysed the data; FA prepared the illustrations; AD wrote the paper, and all authors made significant contributions in terms of ideas and revisions. All authors have approved the manuscript and there are no conflicts of interest.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. (a) Identification of the 157 trees studied in the Nouragues Ecological Research Station and the dominant ant species they sheltered in their crowns (the codes are nailed to the trunks of the trees at *c.* 1.60 m in height). LD, light-demanding tree species including pioneer tree species (26 species out of 120 taxa identified). (b) For comparison, selection of LD tree species in the forest of Paracou, French Guiana (see Dejean *et al.*, 2018).

Fig. S1. Connectance diagram between tree species and ant species presented in Appendix S1.

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