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

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Complete List of Authors:	Dejean, Alain; CNRS-Guyane, Compin, Arthur; Universite Toulouse III Paul Sabatier, FSI Azémar, Frédéric; Universite Toulouse III Paul Sabatier, FSI Delabie, Jacques Hubert Charles; Cocoa Research Center, SEFIT; Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais Corbara, Bruno; Université Clermont Auvergne, CNRS, LMGE, F-63000 Clermont-Ferrand, France Leponce, Maurice; Royal Belgian Institute of Natural Sciences (RBINS), Rue Vautier 29, B-1000 Brussels (Belgium)
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1 **Biotic and abiotic determinants of the formation of ant mosaics in primary Neotropical**  
2 **rainforests**

3

4 Alain Dejean <sup>1,2</sup>, Arthur Compin <sup>1</sup>, Jacques H. C. Delabie <sup>3</sup>, Frédéric Azémar <sup>1</sup>, Bruno  
5 Corbara <sup>4</sup> and Maurice Leponce <sup>5,6</sup>

6

7 <sup>1</sup> Ecolab, Université de Toulouse, CNRS, Toulouse, France, <sup>2</sup> CNRS, UMR EcoFoG, AgroParisTech,  
8 Cirad, INRA Orcid ID: <https://orcid.org/0000-0002-3561-2248>, Université des Antilles, Université de  
9 Guyane, 97310 Kourou, France, <sup>3</sup> U.P.A. Laboratório de Mirmecologia, Convênio UESC/CEPLAC,  
10 C.P. 7, 45600-000 Itabuna, Bahia, Brazil, <sup>4</sup> Université Clermont Auvergne, CNRS, LMGE, F-63000  
11 Clermont-Ferrand, France, <sup>5</sup> Biodiversity Monitoring & Assessment, Royal Belgian Institute of  
12 Natural Sciences (RBINS), Rue Vautier 29, B-1000 Brussels, Belgium, <sup>6</sup> Behavioural & Evolutionary  
13 Ecology, Université Libre de Bruxelles (ULB), Av. F.D. Roosevelt 50, B-1050 Brussels, Belgium

14

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17 Correspondence: Alain Dejean, Ecolab, Université Toulouse 3, 118 route de Narbonne 31062,  
18 Toulouse cedex 9, France. E-mail: [alain.dejean@wanadoo.fr](mailto:alain.dejean@wanadoo.fr) Tel.: (33) 5 61 55 89 31

19

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

22 2. The mapping of the territories of dominant arboreal ant species, the use of a null model  
23 analysis and a pairwise approach permitted us to show the presence of an ant mosaic on the  
24 upper canopy of a primary Neotropical rainforest ( $\approx 1$  ha sampled; 157 tall trees from 28  
25 families). Although Neotropical rainforest canopies are frequently irregular with tree crowns  
26 at different heights breaking the continuity of the territories of dominant ants, the latter are  
27 preserved *via* trails laid on the ground or underground galleries.

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

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

35  
36 **Key words.** ant mosaics, connections on the ground, host tree attractiveness, indicators of  
37 disturbance, primary Neotropical rainforest, territoriality

38

## 39 **Introduction**

40

41 Ants dominate the fauna of tropical rainforest canopies both in terms of biomass and number  
42 of individuals, an ecological success possible thanks to their entirely or partially herbivorous  
43 diet as they feed on extrafloral nectar, food bodies and hemipteran honeydew (Blüthgen *et al.*,  
44 2004; Davidson *et al.*, 2003). Yet, only a limited number of ant species with large colonies are  
45 concerned, something corresponding to the notion of ‘numerical dominance’ (the  
46 predominance of a species in frequency of occurrence in the ant community). When combined  
47 with ‘behavioral dominance’ (dominance in interspecific competition due to superior fighting  
48 and/or recruitment abilities) this results in ‘ecological dominance’ (see Davidson, 1998).  
49 Certain canopy ants correspond rather to the latter case as they are characterized by very  
50 populous colonies of up to several million workers, large and/or polydomous nests (see Fig.  
51 1), and an absolute intra- and interspecific territoriality so that they are called ‘territorially  
52 dominant arboreal ant species’ (TDAAs) (Majer, 1993).

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

58 TDAAs tolerate within their territories the presence of ‘non-dominant’ species with small  
59 colonies that represent only  $\approx 5\%$  of the ant biomass and individuals, but are species-rich (e.g.,  
60 43 species on one tree; 85 species on two trees) (Hölldobler & Wilson, 1994; Tobin, 1997).  
61 Exceptionally, colonies of non-dominant ants can become large enough to occupy and defend  
62 the crown of a tree; they are then called ‘subdominants’ (Majer, 1993; Majer *et al.*, 1994).

63 When the tree crowns are contiguous or interconnected by liana, the TDAAs' territories are  
64 distributed in a mosaic pattern creating what has become known as 'arboreal ant mosaics'  
65 (Majer, 1972, 1993). Ant mosaics have been noted in the upper canopies of tropical African,  
66 Asian, Bornean, New Guinean and Neotropical rainforests and tree crop plantations (Majer,  
67 1993; Adams, 1994; Armbrecht *et al.*, 2001; Blüthgen & Stork, 2007; Davidson *et al.*, 2007;  
68 Dejean *et al.*, 2007, 2010, 2015, 2018; Pfeiffer, 2008; Fayle *et al.*, 2013; Ribeiro *et al.*, 2013;  
69 Klimes, 2017; Yusah *et al.*, 2018; Leponce *et al.*, 2019). Nevertheless, ant mosaics are often  
70 absent from the 'sub-canopy' likely due to the scarcity of hemipterans whose honeydew is  
71 necessary to fuel the TDAA colonies (Floren & Linsenmair, 2000; Blüthgen & Stork, 2007;  
72 Dejean *et al.*, 2007, 2018; Ribeiro *et al.*, 2013). Yet, very large TDAAs colonies can occupy  
73 vast spaces involving all canopy growth stages (Dejean *et al.*, 2007; Klimes *et al.*, 2015).

74 Founding queens do not install their colony by chance in tree crowns as selective plant  
75 attractiveness has been shown experimentally for both plant-ants and TDAAs (Djiéto-Lordon  
76 & Dejean, 1999a,b). Although tempered by the extension of the territories over adjacent trees  
77 (of different species) with the increasing size of the TDAAs' colonies, this effect remains  
78 perceptible (Dejean *et al.*, 2007, 2015, 2018; Fayle *et al.*, 2015). Also, an ontogenetic  
79 succession of ant species follows the sequence of stages in tree and vegetal formation  
80 development (Watt *et al.*, 2002; Kenne *et al.*, 2003; da Conceição *et al.*, 2015; Dejean *et al.*,  
81 2016). Finally, the forest structure plays a role in the formation of ant mosaics. For example,  
82 tropical African rainforests have proportionately more 'large' trees (i.e., tall with a wide trunk  
83 and a large crown) than do the tropical forests of other continents, likely due to fewer  
84 disturbances over recent decades (Lewis *et al.*, 2013; see projections of African trees in Fig.  
85 2). This explains why the Neotropical rainforest canopies are frequently irregular with tree  
86 crowns at different heights likely resulting from treefall gaps, breaking the continuity of the  
87 territories of the TDAAs (Ribeiro *et al.*, 2013).

88 Studying ant mosaics is important because TDAAAs prevent attended hemipterans from  
89 proliferating (Styrsky & Eubanks, 2007) and protect their host trees from defoliating insects  
90 through their predatory behavior or by deterring them either actively or simply through the  
91 presence of their long-lasting landmarks (Majer, 1993; Dyer, 2002; Floren *et al.*, 2002;  
92 Dejean *et al.*, 2007; Offenberg *et al.*, 2007).

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

98 In this study, conducted in a primary moist Neotropical rainforest situated in French  
99 Guiana, we aimed to determine: (1) if an ant mosaic exists in the upper canopy, (2) if TDAA  
100 workers follow trails on the ground that interconnect neighboring trees to compensate the  
101 irregularity of the canopy or if they use underground galleries, (3) if the host tree taxa  
102 influence the TDAAAs' distribution and (4) if locally strong winds due to the neighboring  
103 presence of an inselberg affect the distribution of the TDAAAs, favoring certain of them.

104

## 105 **Materials and methods**

106

### 107 *Study site, tree mapping and identification*

108 The Nouragues Ecological Research Station (4°05' N - 52°41'W), dominated by a partly  
109 denuded Inselberg (430 asl), is located within the *Montagnes Balenfois* massif typical of the  
110 Guiana Shield. The radiocarbon dating of charcoal and pollen coring suggest that the forest  
111 cover has remained intact over at least 3000 years, but with fires occurring ≈500 years ago. A  
112 variety of vegetal formations occur within a radius of 1.5 km, including: (1) the inselberg's

113 summit, (2) a low transition forest, (3) a wide, forested plateau, and (4) a liana forest whose  
114 origin might be due to strong winds or a microtornado. The climate is moist tropical, with a  
115 mean annual rainfall of 3000 mm distributed over  $\approx 280$  days; the daily mean temperature  
116 ranges from 20.3°C to 33.5°C (Grimaldi & Riera, 2001; Tymen *et al.*, 2016).

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

121 Field studies were conducted on the plateau (2006-2010) where the staff of the Nouragues  
122 Ecological Research Station has established grid trails every 100 m, creating 1 ha forest plots  
123 over 70 ha; the trees have been mapped, measured, tagged and identified (Poncy *et al.*, 2001).

#### 124 125 *Canopy access, gathering TDAA samples and mapping the ant mosaic*

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

134 In contrast to trapping methods permitting large numbers of species to be collected, this  
135 branch clipping method allows us to sample numerically dominant ants and obtain  
136 information on the co-occurrence of these species on the same branches, and so interspecific



137 tolerance. Thus, branch clipping does not permit to obtain a representative picture of ‘non-  
138 dominant’ ant species (not considered here), something needed in diversity studies.

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

142 The presence of arboreal ant trails on the ground was noted during a sampling of litter-  
143 dwelling ants in the area studied (Groc *et al.*, 2014). We therefore verified if the trails  
144 interconnected the bases of different trees and if certain workers transported brood and  
145 nestmates from one tree to another (see Orivel & Dejean, 2001). As most of the TDAAs in the  
146 area are diurnal, each hour between 8:00 and 18:00 during five non-consecutive sunny days,  
147 we walked along the same path that was chosen because it passed between trees whose  
148 canopies were not in contact whereas they share the same TDAAs.

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

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

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

162

163 *Rarefaction curves of tree and ant assemblages*

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

168 Because ant mosaics correspond to non-random patterns of co-occurrence related to the  
169 mutual exclusion of TDAAs, we used a fixed-equiprobable null model and the C-score co-  
170 occurrence index with the sequential swap algorithm and 5, 000 iterations available in the  
171 EcoSim software (Gotelli & Entsminger, 2004; Blüthgen & Stork, 2007; Fayle *et al.* 2013).  
172 The fixed-equiprobable algorithm maintains the species occurrence frequencies and considers  
173 all sites (trees) equiprobable (Gotelli, 2000). The C-score index used in combination with the  
174 fixed-equiprobable algorithm generally has good statistical properties and is not prone to false  
175 positives (Gotelli, 2000). Specific associations between the most frequent ant species (i.e.,  
176 present on more than 10% of the 157 trees sampled) were tested using *Chi*-square tests with  
177 Yates' correction. When field observations revealed that a single tree crown belonged to two  
178 different territories (n= 7 cases), the species involved were encoded separately in the co-  
179 occurrences matrix (the whole results in a matrix of 6 ant species x 164 sampling units).

180

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

182 To determine the influence of host trees in shaping the ant mosaic, the TDAAs recorded  
183 for each tree family (or subfamily for the Fabaceae) allowed us to build a '10 ant species x 31  
184 tree families' matrix. TDAAs found only occasionally were eliminated to avoid the effect of  
185 outliers as were the 11 cases for which the trees were not identified, so that this study was  
186 conducted on 144 out of the 157 trees sampled.

187 To ordinate the host tree families based on the TDAs they sheltered, we conducted a non-  
188 metric multidimensional scaling (NMDS) on a matrix of dissimilarity based on the Bray-  
189 Curtis dissimilarity index using 100 random starts. The final stress value of  $0.06 < 0.1$  can be  
190 acknowledged as providing a good representation for a 2-D configuration. A hierarchical  
191 clustering using the ‘complete’ agglomeration method (NbClust package) on the dissimilarity  
192 matrix resulted in eight clusters of ant species; this was the best clustering scheme obtained  
193 using the ‘majority rule’ (24 indices computed). These analyses were conducted using the  
194 Vegan and NbClust packages in R software (R Development Core Team, 2015).

195  
196 *Identifying different degrees of ‘small-scale disturbance’ between five Guianese rainforests*

197 Because the parabiotic, ant-garden ants *Camponotus femoratus* (Formicinae) and  
198 *Crematogaster levior* (Myrmicinae) are characteristic of pioneer formations (Dejean *et al.*,  
199 2000) but are also present in rainforest canopies, particularly around treefall gaps (Vicente &  
200 Izzo, 2017), they can serve as a basis for comparison to establish different degrees of ‘small-  
201 scale natural disturbances’ between rainforests. This needs to be distinguished from major  
202 disturbances such as those caused by hurricanes or by humans.

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

211

## 212 **Results**

213

### 214 *General points*

215 The 157 trees sampled represented 77 species belonging to 29 families, the Lecythidaceae  
216 (30 trees) being the most frequent followed by the Fabaceae (28 trees) (Appendix S1), but we  
217 noted the incompleteness of the tree survey (Fig. 3a). The projected on-ground crown map  
218 (Fig. 2) corresponds to the location of individual trees in more or less circular horizontal  
219 projected crown areas whose diameters varied from 5-6 m to, exceptionally, 14-15 m (see tree  
220 #11M11); one can note the presence of numerous gaps between these tall canopy trees.

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

226

### 227 *Mapping the territorially dominant ant territories*

228 Despite the absence of direct contact between certain tree crowns or their connection *via*  
229 lianas in many cases, the cohesion of these territories is possible thanks to the presence of  
230 trails on the ground that interconnect the trees. These trails are used during the warmest hours  
231 of the day (11:00-15:00), the workers walking in both directions transporting larvae, nymphs  
232 and nestmates. This was noted for *Az. jelskii* (connections between trees #11L403, #11L399  
233 and #11L402), *Az. instabilis* (trees #11M77 and #11M66), *Ca. femoratus* and *Cr. levior*  
234 (group of trees whose limits are #11M53, #11M37, #11M93 and #11M90; trees #11M111 and  
235 #11M128; Fig. 2). The nests of *Dolichoderus bidens* are interconnected by constantly-used  
236 trails passing through low understory vegetation. Also, spraying paint on *E. tuberculatum* or

237 *Cr. stollii* workers confirmed that *via* underground galleries neighboring trees sheltering these  
238 ant species belonged to the territory of one colony (e.g., for *Cr. stollii* see groups #11M104,  
239 #11M135 and #11N136; #11L556, #11L458 and #11M106; Fig. 2).

240 We also noted tree crowns divided into separate territories (e.g., #11L408, #11L411,  
241 #11L522, #11L403, #11M126, #11M128, #11M111; Fig. 2).

242 In addition to the cases of parabiosis between *Ca. femoratus* and *Cr. levior* noted on 56  
243 tree crowns, co-dominance was frequent when involving *Cr. stollii* which was often  
244 associated with *E. tuberculatum* (i.e., on 16 trees out of 28 sheltering *Cr. stollii*; Table 2; Fig.  
245 2; Appendix S1). Other cases of co-dominance concerned *Cr. levior* and *Cephalotes atratus*  
246 (tree #11L495), *Azteca instabilis* and *Az. jelskii* (trees #11L411 and #11M79), and *Az.*  
247 *instabilis* and *Daceton armigerum* (tree #11M128) or *Dolichoderus bispinosus* (tree #11L408)  
248 (Fig. 2; Appendix S1).

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

255

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

257 The NMDS ordination of Bray-Curtis distances and the complete agglomeration method  
258 showed a strong host tree selectivity by the 10 most frequent dominant ant species as eight  
259 clusters were delimited with, as expected, the two parabiotic, ant-garden ants, *Cr. levior* and  
260 *Ca. femoratus*, grouped together. *Azteca jelskii* was associated with *D. bispinosus*, whereas all  
261 other ant species were related to a specific set of tree taxa (Fig. 4). Thus, the sampling size

262 was large enough to obtain evidence that the formation of ant mosaics depends to some extent  
263 on the host trees.

264

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

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

271 The number of tree crowns sheltering *Ca. femoratus* and/or *Cr. levior* on the Nouragues  
272 plateau was not significant between light-demanding and other types of trees (8 cases out of  
273 20; 40% versus 59 out of 120; 49.17%; Fisher's exact-test:  $P = 0.48$ ). Also, the comparison  
274 between the Guianese terra firme rainforests of the Nouragues plateau and Paracou resulted in  
275 non-significant differences in the relative numbers of light-demanding tree species (26 out  
276 146 trees identified versus 22 out of 109; Fisher's exact-test:  $P = 0.87$ ) (see Appendix S1).

277

## 278 **Discussion**

279

280 *Ant mosaic characteristics and traits related to ant species dominance*

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

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

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

298 Importantly, although the TDA territories frequently spread over several tree crowns,  
299 some tree crowns were divided into two or more separate territories (Fig. 2; Ribeiro *et al.*,  
300 2013; Dejean *et al.*, 2018). This situation needs to be handled with care to avoid confusing it  
301 with cases of co-dominance causing wrong data to be used in the statistical analyses leading  
302 to erroneous interpretations.

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

311

312 *Forest canopy functioning and ant mosaics*

313 Among the functional traits of ant species involved in ant mosaics (e.g., colony size,  
314 territoriality, host-tree preference), the size of the colonies is primordial. For example,  
315 Camarota *et al.* (2016) demonstrated that, in the Brazilian Cerrado (a savanna with trees  $\approx 6$  m  
316 in height), null model analyses conducted on all ant species noted on trees resulted in random  
317 co-occurrence patterns. Yet, the same approach conducted on the most frequent species  
318 resulted in a segregated pattern, something confirmed through a pairwise approach (a pairwise  
319 approach also permitted Adams *et al.*, 2017 to identify segregated TDAs in a Panamanian  
320 rainforest). Consequently, numerical dominance can be enough for null model analyses to  
321 illustrate a segregated pattern of occurrence (see other details in Blüthgen & Stork, 2007).  
322 Indeed, if ant abundance in tropical rainforest canopies surpasses that of all other animal taxa,  
323 this is due to dominant species because non-dominant ants, that are species-rich, represent  
324 only  $\approx 5\%$  of the ant biomass and individuals (Hölldobler & Wilson, 1994; Tobin, 1997).

325

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

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



336 Another important characteristic is the dominance of the ant-garden ants *Ca. femoratus* and  
337 *Cr. levior* in the ant mosaic studied, two species typical of pioneer formations that are also  
338 frequent around treefall gaps and in plantations (Dejean *et al.*, 2000; Vicente & Izzo, 2017).  
339 Thus, their presence in primary rainforests (Dejean *et al.*, 2018; Leponce *et al.*, 2019; this  
340 study) might indicate some degrees of past disturbances or of frequent disturbances. The  
341 comparison between Guianese rainforests showed that the rate of presence of these two ant  
342 species was significantly higher on the Nouragues plateau than in other terra firme Guianese  
343 rainforests, but similar to that of a swamp forest (Table 3). Note that the characteristics of  
344 Neotropical swamp forests are similar to that of young, secondary forests and treefall gaps in  
345 old-growth forests (Souza & Martins 2005).

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

349

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

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

357 Therefore, the abiotic disturbances represented by frequent strong winds and the formation  
358 of large canopy gaps are likely the main cause of the abundance of the ant-garden ants *Ca.*  
359 *femoratus* and *Cr. levior* that withstand these effects better than do competitive TDAs (see

360 Vicente & Izzo, 2017). Because they build conspicuous ant gardens easy to locate (Fig. 1),  
361 they might serve as indicators of different degrees of small-scale natural disturbances.

362  
363 In conclusion, ant mosaics exist in Neotropical rainforests despite the frequent small-scale  
364 natural disturbances and absence of contact between tree crowns due to the structure of the  
365 trees. This is due to the TDAAs' territoriality, host tree taxa selection, contact between tree  
366 crowns and interconnection *via* liana, plus the ability of certain TDAAs to interconnect trees  
367 belonging to their territories using trails on the ground or underground galleries, whereas an  
368 abiotic influence plays a role in the form of strong winds and the formation of large canopy  
369 gaps.

370

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372

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384

### 385 **Supporting Information**

386

387 Additional Supporting Information may be found in the online version of this article under the DOI  
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389

390 Appendix S1. A. Identification of the 157 trees studied in the Nouragues Ecological Research Station  
391 and the dominant ant species they sheltered in their crowns (the codes are nailed to the trunks of the  
392 trees at  $\approx 1.60$  m in height). (LD): light-demanding tree species including pioneer tree species (26  
393 species out of 120 taxa identified). B. For comparison, selection of light-demanding tree species in the  
394 forest of Paracou, French Guiana (see Dejean et al., 2018).

395

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570 forest high canopy depend on spatial scale, time of day, and sampling method. *Peer J*, **6**, e4231.  
571

## 572 Figure legends

573  
574 Fig. 1. (a) A large carton nest of *Azteca chartifex*. (b) A conspicuous ant garden resulting from the  
575 association between *Camponotus femoratus* and *Crematogaster levior*. The scale bar represents 50cm.

576  
577 Fig. 2. Overhead view of the distribution of the trees and their associated territorially dominant ant  
578 species in the area studied in the Nouragues Ecological Field Station, French Guiana. The codes  
579 correspond to the trees listed in Appendix S1 (see also examples of the projection of African tree  
580 crowns for comparison). Note the co-occurrence of two mutually exclusive TDDAs in seven tree  
581 crowns (i.e., trees #11L403; #11L408; #11L411; #11L522; #11M111; #11M126; #11M128), and co-  
582 dominance in 29 trees.

583  
584 Fig. 3. (a) Individual-based rarefaction (Mao-Tau with 95 % CI, solid lines) illustrating the  
585 incompleteness of the survey concerning the tree species (N = 141 identified trees), confirmed by the  
586 stability of the singletons (species observed with only one individual, triangles) and doubletons  
587 (species with only two individuals, circles). The estimated asymptotic richness of the assemblage  
588 obtained by Chao1 is shown as diamonds (Chao1 mean = 175 species; CI95%: 119-298 tree species).  
589 Trees that could not be identified to the species level were excluded from this analysis. (b) Sample-  
590 based rarefaction (Mao-Tau with 95 % CI, solid lines) illustrating the near-completeness of the survey  
591 concerning the ant species, confirmed by the decrease in uniques (species collected only once,  
592 triangles) and duplicates (species collected twice, circles). The estimated asymptotic richness of the  
593 assemblage obtained by Chao2 is shown as diamonds (N = 157 supporting trees).

594  
595 Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot showing the ant species (black  
596 crosses) according to their host tree taxa (red dots) (Bray-Curtis distance). The 'complete' clustering  
597 of ant species in the ordination space according to host tree sample composition delimits eight clusters.  
598 The analysis was conducted on the 10 most frequent dominant ants and 31 tree families or subfamilies  
599 for the Fabaceae (this corresponds to 144 tree crowns out of the 157 sampled).

**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	
<i>Crematogaster levior</i>	69	43.95 %	Carton nests, ant gardens, polydomous, parabiosis with <i>Camponotus femoratus</i> .	Dejean <i>et al.</i> (2000); Vicente & Izzo (2017)
<i>Camponotus femoratus</i>	61	38.85 %	Semi-spherical carton nests, ant gardens, polydomous, parabiosis with <i>Crematogaster levior</i> .	Dejean <i>et al.</i> (2000); Vicente & Izzo (2017)
<i>Crematogaster stollii</i>	28	17.83 %	Carton nests in cavities; galleries on tree trunks and branches; continue underground, interconnecting trees.	Longino (2003)
<i>Azteca instabilis</i>	22	14.01 %	Hemispherical carton nests against tree trunks or base of main branches, polydomous.	De la Mora <i>et al.</i> (2008)
<i>Ectatomma tuberculatum</i>	19	12.10 %	Ground-nesting at the base of trees, polydomous; galleries underground interconnecting trees.	Delabie (1990); Hora <i>et al.</i> (2005)
<i>Azteca jelskii</i>	16	10.19 %	Carton nests in cavities, polydomous.	Longino (2007)
<i>Dolichoderus bidens</i>	6	3.82 %	Numerous small carton nests under the leaves, polydomous.	MacKay (1993); Delabie <i>et al.</i> (1991) Corbara <i>et al.</i> (2018)
<i>Dolichoderus bispinosus</i>	6	3.82 %	Nests in cavities, polydomous.	MacKay (1993)
<i>Daceton armigerum</i>	4	2.55 %	Cavities in old branches of trees, polydomous.	Dejean <i>et al.</i> (2012)
<i>Azteca ovaticeps</i>	4	2.55 %	Nests in hollow trunks and branches of <i>Cecropia</i> spp. trees.	Longino, 2007
<i>Odontomachus hastatus</i>	4	2.55 %	Nests in trash baskets formed by palm trees or <i>Philodendron</i> .	Gibernau <i>et al.</i> (2007); Camargo & Oliveira (2012)
<i>Paraponera clavata</i>	4	2.55 %	Ground-nesting at the base of trees.	Elahi (2015)
<i>Azteca chartifex</i>	3	1.91 %	Large, triangular carton nests, polydomous.	Delabie <i>et al.</i> (1991); Longino (2007)
<i>Cephalotes atratus</i>	2	1.27 %	Large cavities in old branches of trees, polydomous.	Bolton (2018)
<i>Azteca brevis</i>	1	0.63 %	Carton nests in cavities; galleries on tree trunks and branches; continue underground, interconnecting trees	Longino, 2007; Schmidt & Dejean, 2018)
<i>Camponotus rapax</i>	1	0.63 %	Small colonies nesting in cavities in old branches of trees.	Gibernau <i>et al.</i> (2007); AD, BC <i>pers. com</i>

**Table 2.** Associations between the most frequent species (frequency on the 157 trees sampled >10%) by decreasing rank of occurrence and tested using *Chi-square* tests (1 d.f., Yates' correction). Symbols indicate the nature of the association: "+" positive, "-" negative, "0" not significant.

	Frequency	1	2	3	4	5
1 <i>Crematogaster levior</i>	44%					
2 <i>Camponotus femoratus</i>	39%	+				
3 <i>Crematogaster stollii</i>	18%	-	-			
4 <i>Azteca instabilis</i>	14%	-	-	0		
5 <i>Ectatomma tuberculatum</i>	12%	-	-	+	0	
6 <i>Azteca jelskii</i>	10%	-	-	0	0	0

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

	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
	AxB	AxC	AxD	AxE	BxC
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
	BxD	BxE	CxD	CxE	DxE
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



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*. The scale bar represents 50cm.



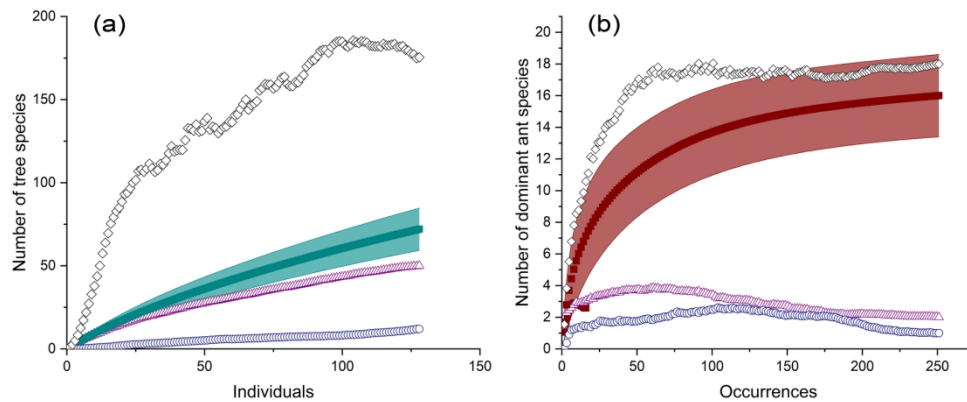


Fig. 3. (a) Individual-based rarefaction (Mao-Tau with 95 % CI, solid lines) illustrating the incompleteness of the survey concerning the tree species ( $N = 141$  identified trees), confirmed by the stability of the singletons (species observed with only one individual, triangles) and doubletons (species with only two individuals, circles). The estimated asymptotic richness of the assemblage obtained by Chao1 is shown as diamonds (Chao1 mean = 175 species; CI95%: 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 ( $N = 157$  supporting trees).

165x67mm (300 x 300 DPI)



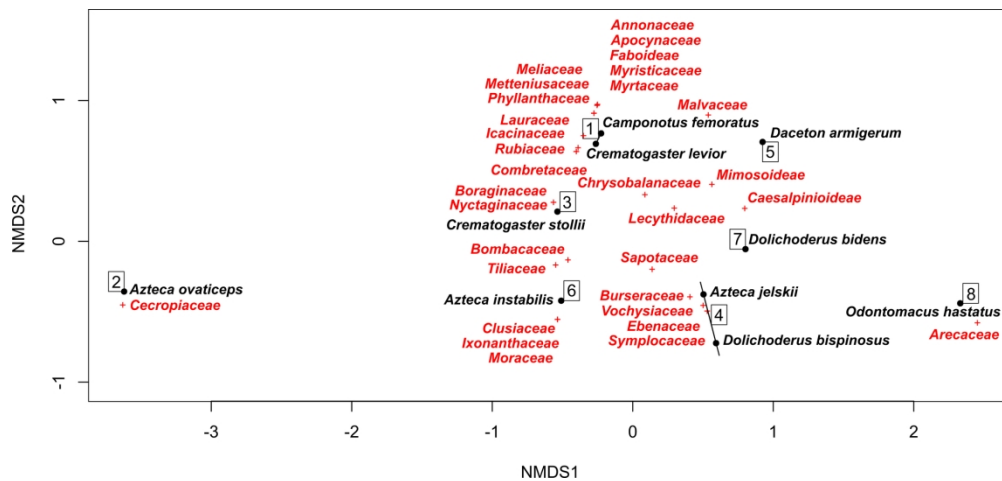


Fig. 4. Non-metric multidimensional scaling (NMDS) ordination plot showing the ant species (black crosses) according to their host tree taxa (red dots) (Bray-Curtis distance). The 'complete' clustering of ant species in the ordination space according to host tree sample composition delimits eight clusters. 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).

189x88mm (300 x 300 DPI)

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  $\approx 1.60$  m in height). (LD): light-demanding tree species including pioneer tree species (26 species out of 120 taxa identified).

Tree family	Tree species	CODE	Territorially dominant arboreal species
Vochysiaceae	<i>Qualea rosea</i>	11L350	<i>Azteca jelskii</i>
Lecythidaceae	<i>Lecythis persistens</i>	11L360	<i>Azteca jelskii</i>
Burseraceae	<i>Protium sagotianum</i>	11L363	<i>Azteca jelskii</i>
Lecythidaceae	<i>Lecythis poiteaui</i>	11L393	<i>Azteca jelskii</i>
Cardiopteridaceae	<i>Dendrobangia boliviana</i>	11L394	<i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11L395	<i>Crematogaster levior</i>
Lecythidaceae	<i>Lecythis poiteaui</i>	11L396	<i>Azteca jelskii</i>
Burseraceae	<i>Protium sagotianum</i>	11L398	<i>Azteca jelskii</i>
Sapotaceae	<i>Pouteria gonggrijpii</i>	11L399	<i>Azteca jelskii</i>
Chrysobalanaceae	<i>Licania canescens</i>	11L400	<i>Azteca jelskii</i>
Symplocaceae	<i>Symplocos martinicensis</i>	11L402	<i>Azteca jelskii</i>
Lecythidaceae	<i>Lecythis idatimon</i>	11L403	<i>Azteca jelskii</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11L408	<i>Azteca instabilis</i> , <i>Dolichoderus bispinosus</i>
Ebenaceae	<i>Diospyros capreifolia</i>	11L410	<i>Azteca jelskii</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11L411	<i>Azteca instabilis</i> , <i>Azteca jelskii</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11L413	<i>Azteca jelskii</i>
Annonaceae	<i>Fusaea longifolia</i>	11L414	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11L415	<i>Azteca jelskii</i>
Burseraceae	<i>Tetragastris altissima</i>	11L418	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Combretaceae	<i>Buchenavia</i> sp.	11L419	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Burseraceae	<i>Protium morii</i>	11L420	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11L421	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Sapotaceae	<i>Pouteria decorticans</i>	11L422	<i>Dolichoderus bispinosus</i>
Burseraceae	Unidentified	11L423	<i>Dolichoderus bispinosus</i>
Ixonanthaceae	<i>Cyrillopsis paraensis</i>	11L426	<i>Azteca instabilis</i>
Arecaceae	<i>Astrocaryum sciophilum</i>	11L427	<i>Odontomachus hastatus</i>
Burseraceae	<i>Protium opacum</i>	11L428	<i>Cephalotes atratus</i>
Lecythidaceae	<i>Lecythis persistens</i>	11L433	<i>Crematogaster stollii</i>
Nyctaginaceae	<i>Neea floribunda</i>	11L434	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Sapotaceae	<i>Micropholis cayennensis</i>	11L447	<i>Camponotus rapax</i>
Malvaceae	<i>Sterculia pruriens</i> (LD)	11L456	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lauraceae	<i>Ocotea percurrans</i>	11L457	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Combretaceae	<i>Buchenavia</i> sp.	11L458	<i>Crematogaster stollii</i>
Sapotaceae	<i>Pradosia ptychandra</i>	11L460	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Couratari oblongifolia</i>	11L464	<i>Azteca instabilis</i>
Cecropiaceae	<i>Pourouma tomentosa</i> (LD)	11L469	<i>Azteca instabilis</i>
Vochysiaceae	<i>Qualea rosea</i>	11L472	<i>Azteca instabilis</i>
Meliaceae	<i>Carapa procera</i>	11L473	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Mimosoideae	<i>Inga gracilifolia</i> (LD)	11L474	<i>Azteca instabilis</i>
Arecaceae	<i>Astrocaryum sciophilum</i>	11L474 B	<i>Odontomachus hastatus</i>

Clusiaceae	<i>Symphonia globulifera</i>	11L478	<i>Azteca instabilis</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11L479	<i>Azteca instabilis</i>
Lecythidaceae	<i>Eschweilera grandiflora</i>	11L480	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Lecythis persistens</i>	11L481	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Arecaceae	<i>Astrocaryum sciophilum</i>	11L489	<i>Odontomachus hastatus</i>
Vochysiaceae	<i>Erismia floribundum</i>	11L491	<i>Dolichoderus bispinosus</i>
Sapotaceae	<i>Manilkara bidentata</i>	11L492	<i>Dolichoderus bispinosus</i>
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	11L494	<i>Dolichoderus bispinosus</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11L495	<i>Crematogaster levior</i> , <i>Cephalotes atratus</i>
Mimosoideae	<i>Inga huberi</i> (LD)	11L497	<i>Azteca instabilis</i>
Vochysiaceae	<i>Qualea rosea</i>	11L506	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Sapotaceae	<i>Pouteria guianensis</i>	11L507	<i>Crematogaster stollii</i>
Bombacaceae	<i>Quararibea duckei</i>	11L522	<i>Azteca instabilis</i> , <i>Crematogaster levior</i>
Tiliaceae	<i>Apeiba glabra</i> (LD)	11L523	<i>Azteca instabilis</i>
Lecythidaceae	<i>Couratari multiflora</i>	11L524	<i>Azteca instabilis</i>
Sapotaceae	<i>Pouteria guianensis</i>	11L525	<i>Azteca instabilis</i>
Chrysobalanaceae	<i>Licania canescens</i>	11L532	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11L533	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Eschweilera grandiflora</i>	11L556	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Lecythidaceae	<i>Lecythis persistens</i>	11L558	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Cardiopteridaceae	<i>Dendrobangia boliviana</i>	11L560	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Cardiopteridaceae	<i>Dendrobangia boliviana</i>	11L561	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Lauraceae	<i>Ocotea</i> sp.	11L562	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Sapotaceae	<i>Chrysophyllum</i> sp.	11M32	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M33	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Myristicaceae	<i>Virola kwatae</i>	11M34	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M35	<i>Odontomachus hastatus</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11M37	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	11M53	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	11M54	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Myristicaceae	<i>Virola kwatae</i>	11M55	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11M56	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Sapotaceae	<i>Pouteria oblanceolata</i>	11M57	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Meliaceae	<i>Carapa</i> sp.	11M58	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Sapotaceae	<i>Micropholis guyanensis</i>	11M59	<i>Crematogaster levior</i>
Sapotaceae	<i>Chrysophyllum</i> sp.	11M63	<i>Azteca instabilis</i>
Lecythidaceae	sp.	11M64	<i>Azteca instabilis</i>
Moraceae	sp.	11M65	<i>Azteca instabilis</i>
Lecythidaceae	<i>Lecythis persistens</i>	11M66	<i>Azteca instabilis</i>
Sapotaceae	sp.	11M67	<i>Camponotus femoratus</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11M68	<i>Camponotus femoratus</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11M70	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Ectatomma tuberculatum</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M71	<i>Camponotus femoratus</i>
Sapotaceae	<i>Pradosia ptychandra</i>	11M77	<i>Azteca instabilis</i>
Myristicaceae	<i>Virola michelii</i>	11M78	<i>Camponotus femoratus</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M79	<i>Azteca instabilis</i> , <i>Azteca jelskii</i>

Caesalpinioideae	<i>Vouacapoua americana</i>	11M80	<i>Dolichoderus bidens</i>
Faboideae	<i>Swartzia benthamiana</i>	11M81	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11M82	<i>Azteca brevis</i>
Cardiopteridaceae	<i>Dendrobangia boliviana</i>	11M83	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	11M84	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Apocynaceae	<i>Aspidosperma helstonei</i>	11M85	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Phyllanthaceae	<i>Hyeronima alchorneoides</i>	11M86	<i>Crematogaster levior</i>
Cecropiaceae	<i>Cecropia obtusa</i> (LD)	11M88	<i>Azteca ovaticeps</i>
Sapotaceae	<i>Chrysophyllum lucentifolium</i>	11M89	<i>Crematogaster stollii</i>
Lecythidaceae	<i>Lecythis persistens</i>	11M90	<i>Crematogaster levior</i> , <i>Paraponera clavata</i>
Vochysiaceae	<i>Qualea rosea</i>	11M91	<i>Dolichoderus bidens</i>
Myristicaceae	<i>Iryanthera</i> sp.	11M93	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Apocynaceae	<i>Geissospermum</i> sp.	11M94	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Chrysobalanaceae	<i>Licania majuscula</i>	11M95	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Sclerobium melinonii</i>	11M96	<i>Crematogaster levior</i>
Myrtaceae	<i>Guettarda acreana</i>	11M97	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Not identified		11MM98	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11M99	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Myrtaceae	<i>Guettarda acreana</i>	11M100	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Mimosoideae	<i>Inga alba</i> (LD)	11M101	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Myrtaceae	<i>Guettarda acreana</i>	11M102	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Ectatomma tuberculatum</i>
Lecythidaceae	<i>Eschweilera grandiflora</i>	11M103	<i>Daceton armigerum</i>
Boraginaceae	<i>Cordia</i> sp.	11M104	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Cecropiaceae	<i>Cecropia obtusa</i> (LD)	11M105	<i>Azteca ovaticeps</i>
Cecropiaceae	<i>Pourouma</i> sp. (LD)	11M106	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Mimosoideae	<i>Inga melinonis</i> (LD)	11M107	<i>Dolichoderus bidens</i>
Lecythidaceae	<i>Eschweilera grandiflora</i>	11M108	<i>Dolichoderus bidens</i>
Lecythidaceae	<i>Eschweilera grandiflora</i>	11M109	<i>Crematogaster stollii</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11M110	<i>Daceton armigerum</i>
Caesalpinioideae	<i>Pseudopiptadenia suaveolens</i>	11M111	<i>Da. armigerum</i> , <i>Az. instabilis</i> , <i>Cre. levior</i> , <i>Para. clavata</i> , <i>Cre. stollii</i>
Sapotaceae	<i>Micropholis guyanensis</i>	11M112	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11M113	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp. (LD)	11M114	<i>Crematogaster stollii</i>
Lecythidaceae	<i>Couratari guianensis</i>	11M115	<i>Crematogaster stollii</i>
Cecropiaceae	<i>Cecropia obtusa</i> (LD)	11M116	<i>Azteca ovaticeps</i>
Cecropiaceae	<i>Cecropia obtusa</i> (LD)	11M117	<i>Azteca ovaticeps</i>
Meliaceae	<i>Carapa</i> sp.	11M118	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Paraponera clavata</i>
Lauraceae	sp.	11M119	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Parkia nitida</i>	11M120	<i>Camponotus femoratus</i> , <i>Crematogaster stollii</i>
Boraginaceae	<i>Cordia</i> sp.	11M121	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Sapotaceae	<i>Pouteria eugeniifolia</i>	11M124	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Apocynaceae	<i>Aspidosperma marcgravianum</i>	11M125	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Paraponera clavata</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M126	<i>Azteca jelskii</i> , <i>Crematogaster levior</i> , <i>Ectatomma tuberculatum</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11M128	<i>Azteca instabilis</i> , <i>Crematogaster levior</i> , <i>Daceton armigerum</i>
Mimosoideae	<i>Inga capitata</i> (LD)	11M129	<i>Crematogaster levior</i>
Mimosoideae	<i>Inga flagelliformis</i> (LD)	11M130	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>

Sapotaceae	<i>Chrysophyllum lucentifolium</i>	11M131	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Cardiopteridaceae	<i>Dendrobangia boliviana</i>	11M132	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Rubiaceae	<i>Guettarda acreana</i>	11M133	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Crematogaster stollii</i>
Tiliaceae	<i>Apeiba glabra</i> (LD)	11M134	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Not identified		11M135	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i> , <i>Crematogaster stollii</i>
Not identified		11N115	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Not identified		11N116	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Not identified		11N133	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Not identified		11N134	<i>Crematogaster stollii</i>
Mimosoideae	<i>Inga rubiginosa</i> (LD)	11N135	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Not identified		11N136	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Mimosoideae	<i>Inga leiocalycina</i> (LD)	11N137	<i>Crematogaster stollii</i> , <i>Ectatomma tuberculatum</i>
Not identified		11N138	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	11N145	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Not identified		11N152	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Not identified		11N152b	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Not identified		11N152c	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	12M6	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Mimosoideae	<i>Inga stipularis</i> (LD)	12M7	<i>Daceton armigerum</i>
Metteniusaceae	<i>Poraqueiba guianensis</i>	12M136	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Lecythidaceae	<i>Lecythis persistens</i>	12M137	<i>Dolichoderus bidens</i>
Mimosoideae	<i>Inga thibaudiana</i> (LD)	12M139	<i>Dolichoderus bidens</i>
Lecythidaceae	<i>Eschweilera coriacea</i>	12M18	<i>Azteca chartifex</i>
Caesalpinioideae	<i>Vouacapoua americana</i>	12M23	<i>Azteca chartifex</i> (very large nest)
Lecythidaceae	<i>Eschweilera coriacea</i>	12M26	<i>Azteca chartifex</i>

## 157 TREES

26 light-demanding tree species out of 146 trees identified; 17.8%

The myrmecophytic *Cecropia obtusa* was not considered in the statistics because it is specifically associated with *Azteca ovaticeps*.

B. For comparison, selection of light-demanding tree species in the forest of Paracou, French Guiana (see Dejean *et al.*, 2018).

Tree family	Tree species	CODE	Territorially dominant arboreal species
Anacardiaceae	<i>Tapirira</i> sp.	139	<i>Crematogaster levior</i>
Cecropiaceae	<i>Coussapoa</i> sp.	151	<i>Azteca instabilis</i>
Celastraceae	<i>Goupia glabra</i>	85	<i>Azteca chartifex</i>
Celastraceae	<i>Goupia glabra</i>	15	<i>Azteca chartifex</i>
Celastraceae	<i>Goupia glabra</i>	159	<i>Camponotus femoratus</i>
Faboideae	<i>Swartzia panacoco</i>	91	<i>Azteca instabilis</i>
Faboideae	<i>Swartzia panacoco</i>	92	<i>Azteca instabilis</i>
Faboideae	<i>Swartzia panacoco</i>	153	<i>Azteca instabilis</i>
Mimosoideae	<i>Inga alba</i>	40	<i>Azteca chartifex</i>
Mimosoideae	<i>Inga alba</i>	34	<i>Azteca instabilis</i>
Mimosoideae	<i>Inga huberi</i>	25	<i>Azteca jelskii</i>

Malvaceae	<i>Sterculia</i> sp.	163	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp.	164	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp.	168	<i>Camponotus femoratus</i> , <i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp.	162	<i>Neoponera goeldii</i>
Malvaceae	<i>Sterculia</i> sp.	138	<i>Crematogaster levior</i>
Malvaceae	<i>Sterculia</i> sp.	172	<i>Azteca jelskii</i>
Malvaceae	<i>Sterculia</i> sp.	178	<i>Azteca gnava</i>
Moraceae	<i>Brosimum guianense</i>	39	<i>Dolichoderus quadridenticulatus</i>
Moraceae	<i>Brosimum rubescens</i>	123	<i>Azteca jelskii</i>
Moraceae	<i>Heliocostylis pedunculata</i>	19	<i>Azteca instabilis</i>
Moraceae	<i>Heliocostylis pedunculata</i>	80	<i>Dolichoderus quadridenticulatus</i>

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22 light-demanding trees out of 131 identified; 16.79%; 134 trees monitored in total

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The discrimination of light-demanding tree species was based on Newbery *et al.* (1985), Roggy & Prévost (1999) and Gourlet-Fleury *et al.* (2004); we would like to acknowledge Dr. Jérôme Chave for verifying our list of tree species.

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