Journal of Tropical Ecology (2003) **19**:325–331. Copyright © 2003 Cambridge University Press
DOI:10.1017/S0266467403003353 Printed in the United Kingdom

Nest site selection by ants in a flooded Mexican mangrove, with special reference to the epiphytic orchid *Myrmecophila christinae*

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(*Accepted 16 June 2002*)

Abstract: The distribution of the arboreal ant community plus a termite species of the genus *Nasutitermes* was inventoried on 938 red mangrove, *Rhizophora mangle* L., trees in a completely flooded mangrove forest of the Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. Colonies sheltered in dry hollow branches of the trees and the pseudobulbs of the epiphytic orchid, *Myrmecophila christinae*. Two size classes of dry hollow tree branches were categorized in order to test differences in ant distribution. As some trees remained unoccupied by either an ant or a termite colony, we deduced that the competition for nesting sites was low. Differences in the composition of the ant community corresponded to the nature of the shelters (i.e. diameter of the hollow branches or orchid pseudobulbs). The ant fauna was richer in the large dry hollow branches of *R. mangle* than in the smaller ones, with certain ant species belonging to the subfamilies Ponerinae and Formicinae being significantly more frequent in the large dry hollow branches than in the small ones. *Cephalotes* and *Pseudomyrmex* were the most frequent ant genera inhabiting the dry branches of *R. mangle*, while *Dolichoderus bispinosus* was the most frequent ant species inhabiting the orchid pseudobulbs. Arboreal *Nasutitermes* sp. selected mostly the orchid pseudobulbs and thus indirectly interfered with ant nest-site selection. Our results highlight niche differentiation through the selection of nest sites among different types of shelter.

Key Words: ants, diversity, epiphytes, mangroves, Mexico, nest-site selection, termites

INTRODUCTION

Few tree species are adapted to coastal mangrove ecosystems and sometimes mangrove forests are monospecific. For example, only three mangrove tree species, *Avicennia germinans* L. (Avicenniaceae), *Laguncularia racemosa* Gaertn. (Combretaceae) and *Rhizophora mangle* L. (Rhizophoraceae), are present on the Mexican coastline. The latter species, also present along the African Atlantic coast, is dominant on tropical coastlines of the Americas (Day *et al.* 1996, Hutchings & Saenger 1987).

Ants have been described as the most important and influential group in mangrove insect communities and the tidal flush leads ants to limit their activity to the tree crowns (De Baar & Hockey 1993, Lopes & Aguiar dos Santos 1996). As a consequence, except for the mangrove mud-nesting ant *Polyrhachis sokolova* (Nielsen 1997*a*, *b*), mangrove ants are arboreal, most of them nesting in the hollow branches of trees. Also, certain species are associated with epiphytes, particularly in neotropical mangroves, while others build their own carton nests (Clay & Andersen 1996, Cole 1983*a*, *b*; De Baar & Hockey 1993, Delabie *et al.* 1998, Lopes & Aguiar dos Santos 1996, Nielsen 2000, Ozaki *et al.* 2000, Rico-Gray *et al.* 1998). Certain mangrove ant species correspond to the definition of 'dominants' (i.e. arboreal ants characterized by very populous colonies and a highly developed intra- as well as interspecific aggressiveness resulting in a mosaic-pattern distribution of their territories; Dejean & Corbara 2002, Majer 1993), with arboreal *Nasutitermes* termites also defending territories in mangroves resulting in an ant–termite mosaic (Adams & Levings 1987, Levings & Adams 1984).

Although the ant communities in mangrove forests have been well studied in terms of distribution, including the importance of island size on the presence of certain species (Clay & Andersen 1996, Cole 1983*b*), little has been published on their species diversity and their nest-site selection. We decided therefore to conduct a study in a completely flooded mangrove forest of the Atlantic coast of Mexico almost exclusively composed of *R. mangle*. We hypothesized that when selecting their nest site ants and/or termites are influenced by the nature of the shelters, such as epiphytic orchids and dry hollow *R. mangle* branches, including the diameter of the latter (see Fonseca 1999).

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METHODS

This study was carried out in Asuncion Bay situated on the Caribbean coast of the Biosphere Reserve of Sian Ka'an, Quintana Roo, Mexico (see Dejean & Olmsted 1997). This bay has a completely flooded mangrove forest only accessible by small boat. The studied mangrove is almost entirely monospecific with *R. mangle* heavily dominating. *Avicennia germinans*, *L. racemosa* and *Conocarpus erectus* L. are very rare, while *Metopium brownei* (Jacq.) Urban (Anacardiaceae) individuals have developed on some small islands. The epiphytic orchid *Myrmecophila christinae* G. Carnevali & Gómez-Juarez (formerly *Schomburgkia tibicinis*; Carnevali *et al.* 2001), known to shelter ants in hollow pseudobulbs (Dejean *et al.* 1995, Rico-Gray *et al.* 1989), was very frequent in this mangrove. Epiphytic bromeliads were rare, while in a neighbouring inundated forest both *M. christinae* and bromeliads abounded (Dejean *et al.* 1995).

The studied mangrove was composed of living trees, most of them isolated, so that their distribution corresponded to a heavily fragmented habitat unsuited for studies on ant territoriality. Due to frequent tropical storms, most of these trees have in the upper part of their crown several dry, hollow branches where ant and termite colonies sheltered. During sampling, we opened the dead branches of each tree by hand or with a saw in order to verify if they sheltered ant or *Nasutitermes* sp. colonies in their hollow centre. We opened the orchid pseudobulbs with pruning shears. Although we noted the quasi-permanent presence of small, unidentified termites, only *Nasutitermes* sp. colonies were taken into consideration in this study because they are known to compete with ants for nesting sites in mangrove trees (Levings & Adams 1984). The samples consisted of a dry branch or several orchid pseudobulbs containing a large part of an ant or *Nasutitermes* sp. colony that we put into a coded plastic bag. The branches and the pseudobulbs were then decorticated in the laboratory. We randomly sampled 938 isolated *R. mangle* trees, of which 305 had dry branches whose diameter was less than 7 cm (class R_{small}), and 300 others had larger dry branches of 7–15 cm in diameter (class R_{large}) (width of hollow centre less than 0.5 cm and 0.5–1.2 cm, respectively). The 333 remaining trees sheltered clusters of *M. christinae* pseudobulbs (class M). Along with *Nasutitermes* sp., we identified the ant species and noted their distribution among these three classes. We also noted the different categories of ant nesting affinities (see Dejean & Olmsted 1997): arboreal-nesting ant species (A), ant species previously known to nest in bromeliads (B) and ground-nesting ant species (G). Voucher specimens of ants were deposited in the Natural History Museum of Los Angeles County, California, USA.

The Jaccard similarity index, or the percentage of shared ant species, was calculated between each class. A Factorial Correspondence Analysis (FCA; Benzecri 1973) was conducted on the contingency table of ant and termite species and their distribution in the three classes of nesting sites using SPAD 3.01 software. Only the 13 ant species with an occurrence equal or greater than 10 (out of the 623 cases of colonies sheltering in dry branches or orchids) were included individually in the analysis, while the remaining 25 species (55 occurrences) were pooled in the category 'others'. We used the Fisher–Freeman–Halton exact-test from StatXact 3.1® software for the statistical comparison of the distribution of subfamilies, and the Fisher exact-test from SigmaStat 2.0® software for the comparisons between classes. Appropriate probabilities were adjusted for the number of simultaneous tests using the sequential Bonferroni procedure (Rice 1989).

RESULTS

Diversity in the arboreal stratum

The total occupancy rates of the *R. mangle* branches (R_{small} and R_{large}) were lower than those of the orchid pseudobulbs (M; Table 1). The dry hollow branches contained a total of 31 ant species out of 37 (20 species for R_{small} class and 24 species for R_{large} class), while 18 ant species occupied the hollow pseudobulbs of *M. christinae* (Appendix 1). The percentage of occupancy was not significantly different between the small and the large branches either for ants or for *Nasutitermes* sp. (Fisher exact-test; R_{small} vs. R_{large}: $P = 0.256$ and $P = 0.09$, respectively). Nevertheless, the comparison of the occupancy rates between the pooled dry hollow branches and the orchid pseudobulbs (R_{small} plus R_{large} vs. M) resulted in a significant difference for ants as well as for *Nasutitermes* sp. (Fisher exact-test; $P < 0.0001$).

Most recorded ant species are generalists that tend hemipterans, feed on plant exudates, on all kinds of debris, on dead insects and are able to capture prey. All ponerine species plus the two pseudomyrmecines are good predators that also exploit extrafloral nectar and hemipteran honeydew. *Cyphomyrmex minutus* is a fungus-growing ant, the mycelium developing on different kinds of debris, including dead insects. Note that we also recorded small colonies of several termite species other than *Nasutitermes* sp. that shared the trees with ants and generally served as prey.

Distribution of ants and termites

The R_{small} and R_{large} classes of branches shared 42% of the ant species, but with a variation in the distribution of subfamilies (see below), while the comparison of each class of hollow branches with *M. christinae* resulted in

Table 1. Total distribution of Nasutiterminae (*Nasutitermes* sp.) and ant subfamilies in the three classes of arboreal shelters sampled in a mangrove forest of the Sian Ka'an Biosphere Reserve, Mexico. Occupancy percentages are in parentheses. R_{small}: trees with dry hollow branches of *Rhizophora mangle* less than 7 cm in diameter; R_{large}: trees with dry hollow branches between 7–15 cm in diameter; M: pseudobulbs of *Myrmecophila christinae* (Fisher–Freeman–Halton tests with Bonferroni correction; R_{small} vs. R_{large}: $P = 0.0014$; R_{small} vs. M and R_{large} vs. M: $P < 10^{-5}$; $\alpha = 0.01$).

Family and subfamily	R_{small}	R_{large}	M
Termitidae			
Nasutiterminae (*Nasutitermes* sp.)	51 (26.4)	32 (18.5)	114 (44.4)
Formicidae			
Formicinae	25 (13)	41 (23.7)	33 (12.8)
Dolichoderinae	2 (0.0)	5 (2.9)	76 (29.6)
Myrmicinae	68 (35.2)	59 (34.1)	22 (8.6)
Pseudomyrmecinae	47 (24.4)	30 (17.3)	1 (0.0)
Ponerinae	0 (0.0)	6 (3.5)	11 (4.3)
Vacant trees	112 (36.7)	127 (42.3)	76 (22.8)
Inhabited trees	193 (62.3)	173 (58.6)	257 (77.2)
Total number of sampled trees	305	300	333
Total number of ant species	20	24	18

low similarity indices (Appendix 1). Otherwise, we noted a significant difference in the distribution of *Nasutitermes* sp. and ant subfamilies between the three compared classes of shelter (Table 1). Among the ant communities, the Myrmicinae were the best represented in both classes of hollow branch, while the Pseudomyrmecinae were in second position for class R_{small} and the Formicinae for class R_{large}. In contrast, *Nasutitermes* sp. was most frequent in *M. christinae* pseudobulbs, followed by the ant subfamily Dolichoderinae, with a strong presence of *Dolichoderus bispinosus* (Table 1; Appendix 1).

The FCA illustrated the graphical separation of the three nest-site types according to species composition (Figure 1). The first factor (88.4% of ϕ^2) separates small and large branches. Among the most frequent species, three main groups can be distinguished: (1) *D. bispinosus* (Dolichoderinae) and *Pachycondyla villosa* (Ponerinae) were mainly associated with *M. christinae* with founding queens and workers able to enlarge the entrances of the pseudobulbs; (2) the three *Cephalotes* species, the two *Pseudomyrmex* and *Wasmannia auropunctata* were mainly associated with the dry hollow branches. Within these species, *Pseudomyrmex nigropilosus* nested mostly in the small branches, *W. auropunctata* in the large branches; (3) the remaining four species (*Camponotus atriceps*, *C. planatus*, *Monomorium ebeninum* and *Tetramorium similinum*) represented opportunistic species.

'Bromeliad-ants' were significantly more frequent in orchid pseudobulbs, while known arboreal ant species and ground-nesting species were more common in hollow branches (Figure 2). Colonies of the arboreal-nesting category (A) were significantly more frequent in the small rather than in the large hollow branches. The converse was true for the ground-nesting category (G), while bromeliad-ant colonies (B) did not differ significantly between small and large branches.

DISCUSSION

Nest site selection by ants and termites

The competition for nesting was low in the studied flooded mangrove as numerous trees with dry hollow branches or orchids were unoccupied by ants or termites. It is also possible that the territory of certain colonies of 'dominant' ant or termite species extended to the vacant sampled trees if it escaped our attention that certain of the selected tree crowns came into contact with their nesting tree (see Adams & Levings 1987).

The relatively large ant species richness (37 ant species) is due to the presence of both arboreal and ground-nesting ant species. Known ground-nesting ant species have been previously noted in the hanging soils of epiphytes (Blüthgen *et al*. 2000*a*, *b*; Dejean & Olmsted 1997, Longino & Nadkarni 1990), while in this study they were found nesting in hollow branches. This unexpected result shows that these species are flexible in their nesting abilities and are able to find suitable food items in these flooded mangroves, probably thanks to the presence of termites. Among them, *W. auropunctata*, a tramp species of ecological importance in places where it has been introduced, shows once more its arboreal-nesting ability in its native area. Indeed, this species, recorded in hanging soils (Longino & Nadkarni 1990) or associated with epiphytes (Dejean *et al*. 1995), also competes with dominant arboreal ants (Armbrecht *et al*. 2001, Majer 1993).

The high frequency of *Pseudomyrmex* spp. and *Cephalotes* spp. in both classes of dry hollow branches is

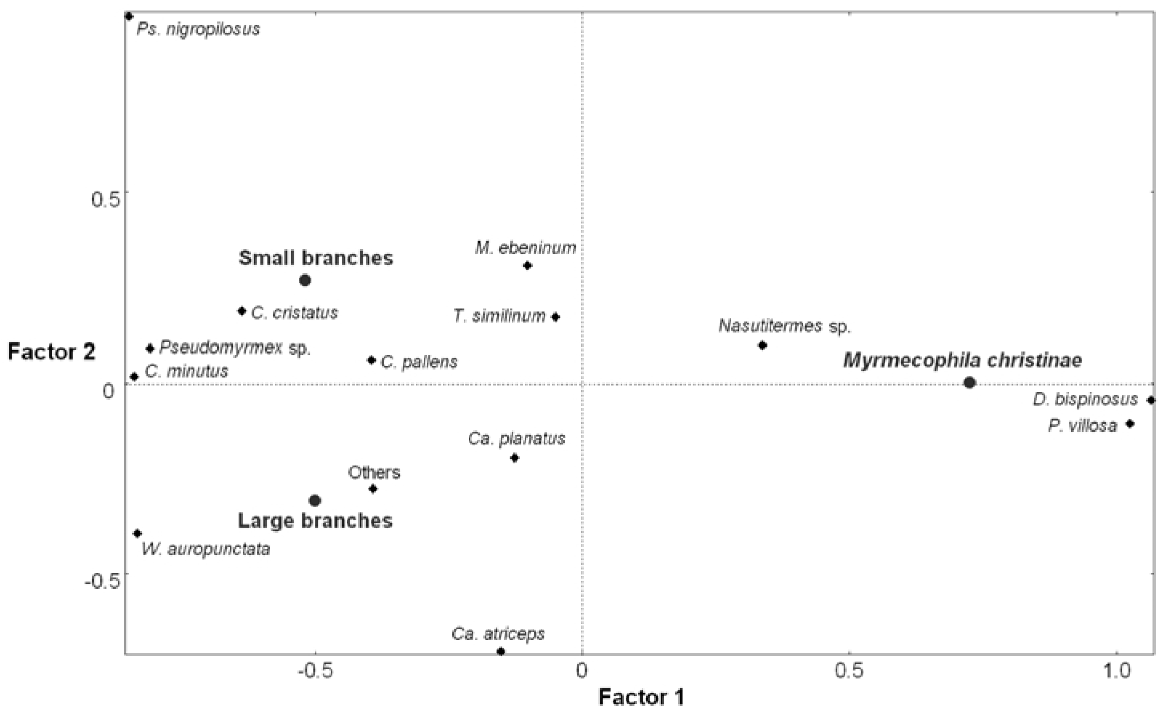


Figure 1. Factorial Correspondence Analysis of the distribution of ants, *Nasutitermes* sp. and nesting shelters. The first factor (88.4% of ϕ^2) clearly opposes *Myrmecophila christinae* and the two classes of hollow branches, while the second factor (11.6% of ϕ^2) separates small and large branches.

consistent with their known arboreal biology and nesting habits. Indeed, they are known as 'specialists' of hollow branches (Andrade & Baroni-Urbani 1999, Ward 1990, 1999). These ant species are often considered as weakly aggressive in intra- and interspecific relationships and so less active in the structure of an arboreal mosaic (Andrade & Baroni-Urbani 1999, Majer 1993, Ward 1990, 1999). *Camponotus planatus* must really be seen as an 'opportunist' according to Andersen's (1997) functional group definition since it occupies all the nest-site categories of this mangrove forest.

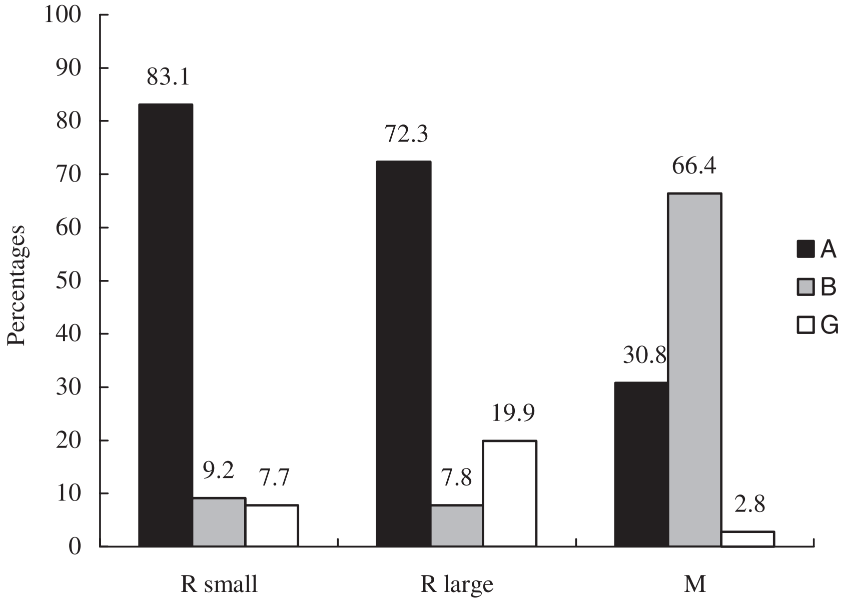
While in this mangrove *D. bispinosus* and *P. villosa* colonized the *M. christinae* pseudobulbs, they were associated with the epiphytic bromeliad *Aechmea bracteata* Swartz and defended exclusive territories in a neighbouring inundated forest where *M. christinae* was also present (Dejean & Olmsted 1997, Dejean *et al.* 1995). Choice tests conducted on *P. villosa* queens and workers have confirmed the attractiveness of *A. bracteata* (Dejean 1990). As a result, these species show behavioural flexibility and adaptability (they enlarge pseudobulb entrances), permitting them to colonize different epiphyte species and so have a wider distribution.

According to the FCA, *Nasutitermes* sp. could be defined as opportunistic but with some preference for *M. christinae* pseudobulbs. Although known for their ability to compete with ants for nest sites and territories (Adams & Levings 1987, Dejean & Olmsted 1997, Levings & Adams 1984, Lopes & Aguiar dos Santos 1996), arboreal *Nasutitermes* termites were unexpectedly the most frequent occupants of the hollow branches and orchid pseudobulbs. Further studies are therefore needed to understand how the ant/termite mosaic functions in contiguous mangrove trees.

Role of *Myrmecophila christinae*

The high frequency of *M. christinae* in Neotropical mangroves could be explained by its good adaptation to this extreme environment (i.e. exposure to sun, wind and high salinity), rather than to terra firma or inundated forests where bromeliad epiphytes are frequent competitors (Carnevali *et al.* 2001, Dejean *et al.* 1995, Rico-Gray *et al.* 1998). Also, associations with sheltered ants and termites favour the maintenance of *M. christinae* as they provide it with minerals. This epiphyte also produces extrafloral nectar, an energy source that helps to maintain a long-term relationship with ants (Koptur 1992, Rico-Gray *et al.* 1989, 1998). Like certain epiphytic *Philodendron* (Blüthgen *et al.* 2000*b*), *M. christinae* shaped the ant community in the studied mangrove through its frequent association with *D. bispinosus* and *P. villosa*, two dominant arboreal species (Dejean *et al.* 1995) rarely noted in the hollow branches.

In conclusion, we have shown that the presence of *Rhizophora* dry hollow branches and an epiphytic orchid in



Category / Classes	R_{small} *versus* R_{large}		M *versus* R	
A	P = 0.03	*	P < 0.0001	***
B	P = 0.83	ns	P < 0.0001	***
G	P = 0.001	**	P < 0.0001	***

Figure 2. Distribution of the ant species according to their previously known nesting habits (A: arboreal nesting ant species; B: ant species that usually nest in bromeliads; G: ground-nesting ant species) in the selected three classes of shelters of the mangrove forest (R_{small}: dry hollow branches of *Rhizophora mangle*, Ø < 7 cm; R_{large}: dry hollow branches of *R. mangle*, 7 < Ø > 15 cm; M: *Myrmecophila christinae* pseudobulbs). Statistical significance with Bonferroni correction: *: P < 0.05; **: P < 0.01; ***: P < 0.001.

a flooded mangrove permits ant and *Nasutitermes* sp. colonies to nest. As some trees remain unoccupied by such colonies, our results highlight an aspect of the niche differentiation of each species through the selection of its nest site between different shelters.

ACKNOWLEDGEMENTS

We are grateful to Elena Etchavaria and Jony-Fredi Camal for their participation to the field work and to Andrea Dejean, Christel Ferrand, Mogens G. Nielsen and two anonymous referees for constructive comments on the manuscript.

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Appendix 1. Total species composition of a mangrove forest of the Sian Ka'an Biosphere Reserve, Mexico. R_{small}: trees with dry hollow branches of *Rhizophora mangle* of less than 7 cm in diameter; R_{large}: trees with dry hollow branches of 7–15 cm in diameter; M: *Myrmecophila christinae* pseudobulbs. Nesting affinities: A, arboreal; B, bromeliad; G, ground.

Species	Nesting affinity	R_{small}	R_{large}	M
Termitidae				
Nasutitermes sp.	A	51	32	114
Formicidae				
Ponerinae				
Ectatomma tuberculatum Olivier	G	0	2	0
Pachycondyla crenata Roger	G	0	1	0
Pachycondyla unidentata Mayr	G	0	2	0
Pachycondyla villosa Fabr.	B	0	1	11
Pseudomyrmecinae				
Pseudomyrmex nigropilosus Emery	A	9	1	0
Pseudomyrmex sp.	A	38	29	1
Myrmicinae				
Cephalotes biguttatus Emery	A	0	2	0
Cephalotes cristatus Emery	A	11	7	2
Cephalotes maculatus F. Smith	A	2	0	0
Cephalotes minutus F.	A	14	12	0
Cephalotes pallens Klug	A	14	11	7
Crematogaster sculpturata Pergande	A	2	0	0
Crematogaster sp. *brevispinosa* group	A	0	2	0
Crematogaster sp. *limata* group	A	2	5	0
Cyphomyrmex minutus Mayr	G	0	1	0
Leptothorax anduzei Weber	A	0	0	1
Leptothorax echinatinodis Forel	G	2	0	0
Monomorium ebeninum Forel	B	5	2	4
Pheidole sp. *flavens* group	A	1	0	0
Solenopsis (*Diplorhoptrum*) sp.	A	0	0	1
Tetramorium similimum F. Smith	B	7	4	7
Wasmannia auropunctata Roger	G	8	13	0
Dolichoderinae				
Azteca instabilis F. Smith	A	0	0	1
Dolichoderus bispinosus Olivier	B	1	4	73
Dolichoderus championi Forel	A	0	1	0
Dolichoderus lutosus F. Smith	A	0	0	2
Forelius pruinosus Roger	A	1	0	0
Formicinae				
Camponotus atriceps F. Smith	GA	1	7	4
Camponotus auricomus Roger	A	0	0	2
Camonotus linnaei Forel	A	0	0	1
Camponotus novogranadensis Mayr	A	1	5	0
Camponotus planatus Roger	A	17	24	22
Camponotus rectangularis Emery	A	5	0	2
Camponotus sericiventris Guérin	G	0	2	0
Camponotus striatus F. Smith	A	0	1	0
Camponotus (*Pseudocolobopsis*) sp.	A	0	2	1
Paratrechina steinheili Forel	A	1	0	1
Total number of occupied samplings		193	173	257
Total number of ant species		20	24	18
Jaccard similarity index	R_{large}	0.42		
	M	0.29	0.29	