
Arboreal ant diversity (Hymenoptera: Formicidae) in a central African forest

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Abstract

Like many developing tropical areas, central Africa is subject to substantial anthropogenic disturbance associated with the large-scale harvesting of natural resources. We surveyed the ants of the forest canopy at an oil extraction site near Gamba, Gabon. Ants were collected by hand and with tuna baits from nine tree crowns in late secondary forest. Thirty-six ant species were collected in all. Michaelis–Menten and incidence-based richness coverage estimates indicate that this represents 65% of the arboreal ant species richness at the site. *Crematogaster* spp. generally were behaviourally aggressive and monopolized baits in most trees. Taxonomic similarity (classical Sørensen index) averaged 0.25 (range = 0.00–0.50) between trees and was not a function of the distances separating them. No edge effects were detected, but there was a tendency for trees within the same forest patch to show higher similarity in ant composition than trees in separate patches. Overall arboreal ant species richness and composition in the disturbed forests around Gamba were similar to those found in primary forests of the region.

Key words: biodiversity, canopy, disturbance, Gabon, tropical forest

Résumé

A l'instar de nombreuses régions tropicales en développement, l'Afrique centrale est sujette à des perturbations anthropogéniques substantielles associées à l'exploitation à grande échelle de ressources naturelles. Nous avons fait une étude sur les fourmis de la canopée forestière sur un

site d'extraction pétrolière proche de Gamba au Gabon. Les fourmis furent prélevées manuellement et avec des appâts faits de thon dans neufs couronnes d'arbres d'une forêt secondaire récente. En tout, trente six espèces de fourmis furent collectées. Le modèle de Michaelis-Menten et les estimations de richesse basées sur la fréquence indiquent que ceci représente 65% de la richesse spécifique des fourmis arboricoles dans ce site. *Crematogaster* spp. a manifesté généralement un comportement agressif et a monopolisé les appâts dans la plupart des arbres. La similitude taxonomique moyenne (index classique de Sørensen) était de 0.25 (écart = 0.00–0.50) entre les arbres et n'était pas fonction des distances entre eux. Aucun effet lisière ne fut détecté, mais il existe une tendance présentant une plus haute similarité en composition d'espèces de fourmis entre arbres d'un même bloc forestier qu'entre arbres de blocs séparés. Globalement, la composition et la richesse en espèces de fourmis arboricoles dans les forêts dérangées autour de Gamba étaient similaires à celles trouvées dans les forêts primaires de la région.

Introduction

As in most tropical regions around the world, natural areas in central Africa are under significant and increasing pressure from anthropogenic disturbance, especially deforestation (WRI, 2000). In particular, industrial-scale timber production poses a major threat to forests in central Africa, and is expected to increase as oil production declines in hydrocarbon-rich places like Gabon (WRI, 2000; Wilkie & Laporte, 2001; Laurance *et al.*, 2006). Oil extraction also has detrimental effects on forests and biodiversity, including the potential for large-scale chemical contamination, non-native species introductions, and forest fragmentation due to road and infrastructure development (e.g., Ayotamuno, Akor & Igho, 2002; San Sebastián

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& Hurtig, 2004; Walker, 2006). As part of an effort to document and mitigate these impacts, faunal and floral inventories, as well as behavioural and ecological studies of specific taxa, are being conducted in Gabon through a recent partnership between Shell Oil Company and the Smithsonian Institution (e.g., Basset *et al.*, 2004; Alonso *et al.*, 2006; Laurance *et al.*, 2006). This information will become increasingly valuable in the near future, as central Africa shifts away from oil-based economies and requires policy makers, landowners and conservation organizations to make critical decisions about land use. Here we contribute to this knowledge base by reporting the results of a preliminary survey of arboreal ants within the Shell industrial complex.

Ants are a functionally important element of tropical rain forests (e.g., Hölldobler & Wilson, 1990), and compose a substantial fraction of insect abundance and biomass in the canopy (Fittkau & Klinge, 1973; Davidson *et al.*, 2003). Inventories and surveys in lowland neotropical forests show that individual tree crowns frequently harbour >30 species of ants, and these ant assemblages tend to exhibit high β -diversity over relatively short distances (Wilson, 1987; Longino & Colwell, 1997; Yanoviak & Kaspari, 2000). Whereas comprehensive ant inventories exist or are in progress for some sites in the neotropics, less information is available regarding the arboreal ants of lowland afrotropical forests (Robertson, 2000; Fisher, 2004a). However, ecological studies of ant mosaics (Leston, 1978) provide comparative inventory data for agricultural plantations and forests in the region (e.g., Dejean & Corbara, 2003).

The primary objective of this study was to use easily replicable methods to generate a preliminary inventory of arboreal ants in a disturbed African forest-savanna mosaic. Large-scale oil extraction has been underway in the study area for *c.* 50 years. The site was also selectively logged in the past, so much of the existing nonflooded forest is late secondary growth (Basset *et al.*, 2004). Some of the forest at the site has been colonized by the non-native ant *Wasmannia auropunctata* (Roger), an invasive species that reduces the diversity of native ants where it occurs in the region (Walker, 2006). Our goal was to collect baseline data that will be able to be compared with future surveys conducted at the same site (e.g., as part of an ongoing *W. auropunctata* monitoring programme) (A. Mikheyev, unpublished data) as well as with less disturbed locations in the region (e.g., the Shell Rabi site and surrounding areas) (Ward *et al.*, 2003; Laurance *et al.*, 2006).

Additionally, we examined potential landscape-level patterns in the ant assemblages to determine how similarity in species composition may vary between trees according to their association with forest patches. Given that β -diversity tends to be high in tropical arboreal ant communities, we predicted that trees located within the same continuous patch of forest would have more similar ant assemblages than trees in separate patches.

Methods

This study was conducted within the Shell Oil Company hydrocarbon extraction concession in Gamba, Gabon (2°43'S, 10°00'E; Fig. 1). The site is an industrial conservation corridor linking two national parks: the Reserve de Petit Loango in the northwest and Moukalaba-Doudou National Park to the east. The Shell concession is an area of moderate anthropogenic disturbance within the Gamba Complex of protected areas, which is the largest tract of protected land in Gabon (Thibault, Fisher & Goodman, 2004). The landscape is a mosaic of regenerated forest patches (>50 years old) on sandy soils surrounded by savanna, and receives *c.* 2100 mm of rainfall per year, with a pronounced dry season occurring June–September. Data were collected during the wet-dry transition in April 2006. Additional details about climate, geology and biodiversity at the site are provided elsewhere (Ward *et al.*, 2003; Basset *et al.*, 2004; Fisher, 2004b; Alonso *et al.*, 2006; Laurance *et al.*, 2006).

We collected ants from the crowns of nine different mature canopy or emergent trees in nonflooding late secondary forest within the concession. Eight of the trees were climbed with the single-rope technique (Perry, 1978). Tree 9, a smaller mature midcanopy tree, was leaning such that its crown could be accessed without technical climbing. Distances between sampled trees ranged from 170 m (trees 4 and 6) to 5 km (trees 3 and 6; Fig. 1). For logistical reasons, most of the focal trees were located within 100 m of forest edge habitat (median = 50 m, range = 1–500 m). All nine trees were of different species, although only two were identified (tree 7 = *Aucoumea klaineana* Pierre, tree 9 = *Barteria nigritana* Hook.f.).

Ants were surveyed in each focal tree crown during daylight hours (between 08.00 hours and 18.00 hours) for a minimum total of 2 h over a period of 1–3 days by hand collecting and by placing tuna baits at various points along the branches and trunk. Collection was generally conducted from a single secure point near the centre of the

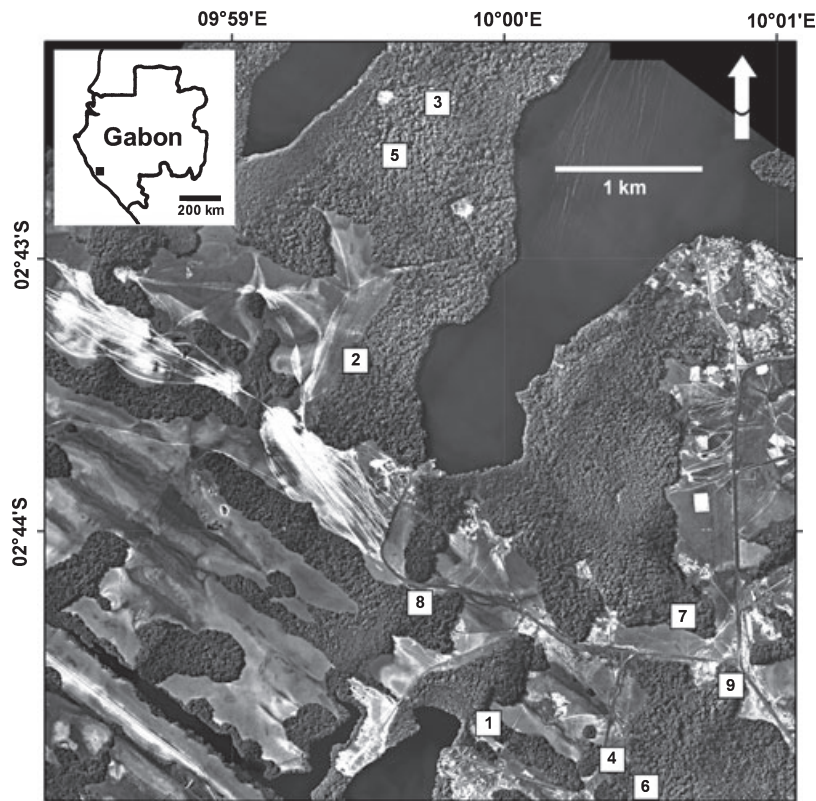


Fig 1 Map of the study area indicating locations of focal trees and the approximate location of the study site in Gabon (black square, inset map). Large homogeneous grey areas (e.g., beneath the scale bar) are water, mottled grey areas (e.g., in the SW quadrant) are savanna and white areas are open sand and disturbed sites in savannas

tree crown (i.e., the divergence of the largest branches), and the search area included all visible accessible surfaces within a radius of *c.* 2.5 m from that fixed point. In addition to collecting active foragers with forceps, we opened any dead twigs within reach and removed loose bark at various points along the trunk 5 m above the ground and higher. Because the linear nature of tree crowns tends to channel ant movements (e.g., Yanoviak & Kaspari, 2000), this approach captured the majority of the active ant fauna in each crown and enabled us to identify the behaviourally aggressive species in each tree.

We estimated arboreal ant species richness at the site with rarefaction techniques computed using EstimateS (Colwell, 2005) and we used the classical incidence-based Sørensen similarity index to assess taxonomic overlap in species composition among focal trees (Chao *et al.*, 2005). To examine the possible effects of patchiness on similarity in the ant communities, we assigned focal trees to three groups: 'Separate' included trees 1, 7 and 8, each of which is asso-

ciated with a separate forest patch; 'Patch 1' consisted of trees 2, 3 and 5, which exist in a largely contiguous expanse of older secondary forest in the northern part of the study area (= sites A and B of Basset *et al.*, 2004); and 'Patch 2' included trees 4, 6 and 9, which are located in a younger secondary forest patch in the south-eastern portion of the study area (Fig. 1). We used Wilcoxon rank sums (SAS Institute, 2002) to test two directional hypotheses: (i) lower similarity within the Separate group compared with within Patch 1 and Patch 2 (pooled), and (ii) lower similarity between Patch 1 and Patch 2 than within them (pooled).

Ants were mounted on points and identified using readily available keys such as Bolton (1973, 1987 and information compiled by Taylor (2006). A complete voucher collection was deposited at the California Academy of Sciences (San Francisco) and subsets were deposited at the Smithsonian laboratory in Gamba, the Museo de Historia Natural Javier Prado (Lima, Peru) and the U.S. National Museum (Washington, DC).

Table 1 Ant species collected in the study

Taxon	Frequency ^a	Behaviour ^b	Nest ^c
Cerapachyinae			
<i>Simopone conciliatrix</i> Brown ^d	1	I	Yes
Dolichoderinae			
<i>Plagiolepis alluaudi</i> Emery	5	S	Yes
<i>Tapinoma luridum longiceps</i> (Wheeler)	2	C	Yes
Formicinae			
<i>Camponotus</i> sp. 1	4	S	Yes
<i>Camponotus</i> sp. 2	2	C	Yes
<i>Camponotus</i> sp. 3	1	S	Yes
<i>Camponotus</i> sp. 4	2	N	Yes
<i>Camponotus</i> sp. 5	1	S	Yes
<i>Camponotus</i> sp. 6	1	S	Stray
<i>Camponotus</i> sp. 7	2	C	Yes
<i>Oecophylla longinoda</i> (Latreille)	1	N	Stray
<i>Paratrechina grisoni</i> (Forel)	1	S	Yes
<i>polyrhachis decemdentata</i> André	3	S	Yes
<i>Polyrhachis lanuginosa</i> Santschi ^d	1	S	Yes
<i>Polyrhachis latispina</i> Emery	5	I	Yes
Myrmicinae			
<i>Cataulacus erinaceus</i> Stütz	1	C	Yes
<i>Cataulacus guineensis</i> F. Smith	3	S	Yes
<i>Cataulacus mocquerysi</i> André	1	S	Stray
<i>Cataulacus</i> nr. <i>satrap</i> Bolton	6	S	Yes
<i>Cataulacus tardus</i> Santschi	2	S	Yes
<i>Crematogaster</i> (<i>Sphaerocrema</i>) sp. 1	1	M	Yes
<i>Crematogaster africana</i> Mayr	1	M	Yes
<i>Crematogaster ambigua</i> Santschi	1	M	yes
<i>Crematogaster buchneri</i> Forel	4	M	Yes
<i>Crematogaster depressa</i> (Latreille)	2	M	Yes
<i>Monomorium</i> sp. 1 (nr. <i>leopoldinum</i>)	3	S	Yes
<i>Monomorium</i> sp. 2 (nr. <i>floricola</i>)	2	S	Yes
<i>Monomorium</i> sp. 3	1	N	Stray
<i>Pyramica maynei</i> (Forel) ^d	3	S	Yes
<i>Tetramorium ictidum</i> Bolton	2	S	Yes
<i>Tetramorium occidentale</i> (Santschi)	1	N	Yes
<i>Tetramorium quadridentatum</i> Stütz	1	N	Stray
Ponerinae			
<i>Platythyrea conradti</i> Emery	5	I	Yes
<i>Platythyrea modesta</i> Emery	3	I	Yes
Pseudomyrmecinae			
<i>Tetraoponera mocquerysi</i> (André)	1	N	Stray
<i>Tetraoponera ophthalmica</i> (Emery)	3	N	Yes

Identifications and most taxonomic authorities are from Taylor (2006).

^aNumber of trees of nine in which a species was found.

^bM, generally monopolized baits; C, co-existed with other species at baits; S, subordinate to other species at baits; I, insinuator species (*sensu* Wilson, 1971); N, no observations at baits.

^cYes, clearly nesting in the focal tree; Stray, collected only as Stray individuals from undetermined nest sites.

^dSpecies not collected in Monts Doudou by Fisher (2004a).

Results

Thirty-six ant species were collected in this study. Three were not found in Fisher's (2004a) extensive survey of the nearby Monts Doudou forest (Table 1), and at least one (*Simopone conciliatrix*) is a new record for Gabon. Most were nesting in the crowns of the focal trees, but a few were represented by one or two stray foragers wandering across from adjacent trees (Table 1). As in other central African forests (e.g., Dejean *et al.*, 2000), *Crematogaster* spp. were behaviourally the most aggressive, monopolizing baits in almost all trees where they occurred (Table 1). Where *Crematogaster* were absent, *Catantopus erinaceus*, *Tapinoma longiceps* and *Camponotus* spp. monopolized or co-existed at tuna baits (Table 1). Although not previously recorded as a forest canopy species, we frequently found the dacetine *Pyramica maynei* nesting in the organic matter associated with root mats of vascular epiphytes at mid-canopy heights (c. 20 m) and above. We did not find the invasive species *W. auropunctata* in or around the trees we sampled.

Based on Michaelis–Menten and incidence-based richness coverage estimators, total arboreal ant richness at the site is predicted to be 52–58 species (Fig. 2). Thus, our collection effort captured c. 65% of the arboreal ant assemblage. Extrapolation from a logarithmic curve fit to the Mao Tau values ($R^2 = 0.99$) indicated that samples from another 14 trees would be required to capture 90% of the species at this site. Total collection time (i.e., not including preparation and climbing) averaged 3.2 h per tree (range = 2.0–5.5 h). The number of ant species collected per tree (mean \pm SE = 8.8 ± 1.23 , range = 3–14)

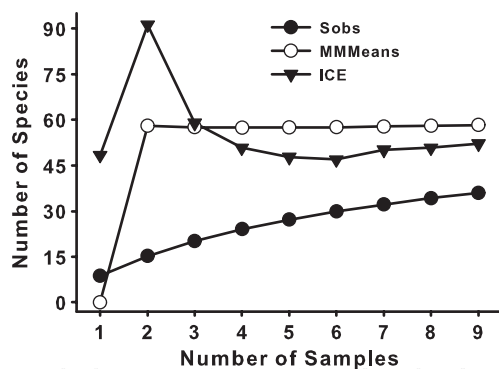


Fig. 2 Michaelis–Menten (MMMean), incidence-based richness estimate and Mao Tau observed (Sobs) species accumulation curves based on 50 randomized iterations of data from nine focal trees

was not a function of (log) distance from forest edge (linear regression: $F_{1,7} = 1.38$, $R^2 = 0.16$, $P > 0.27$) or of time spent collecting in each crown ($F_{1,7} = 1.79$, $R^2 = 0.20$, $P > 0.22$). The latter result indicates that the minimum 2 h spent per tree was sufficient to capture the common diurnal resident species.

The nine focal trees shared an average of 2.3 ant species (range = 0–6), and average Sørensen similarity between trees was 0.25 ($n = 36$ paired comparisons, range = 0.00–0.50). There was no significant relationship between similarity indices and the distance between sampled trees (linear regression: $F_{1,34} = 0.94$, $R^2 = 0.03$, $P > 0.33$). Although our sample sizes were minimal, there was a tendency for trees within Patches 1 and 2 to have larger average (\pm SD) Sørensen similarity values (0.33 ± 0.093 , $n = 6$) compared with trees in the separate group (0.19 ± 0.086 , $n = 3$; $z = 1.68$, $P = 0.05$, $\alpha = 0.02$). However, there was only a slight trend for greater similarity within Patches 1 and 2 (0.33 ± 0.093 , $n = 6$) than between them (0.25 ± 0.202 , $n = 9$; $z = 1.01$, $P = 0.16$). A few species appeared to be broadly distributed within forest patches. For example, *Plagiolepis alluaudi* occurred in all trees sampled in Patch 1, and *Camponotus* sp. 1 and *Crematogaster buchneri* occurred in all trees sampled in Patch 2, but no single ant species was shared among all trees in the Separate group.

Discussion

Our results indicate that arboreal ant communities in the secondary forests around Gamba are as diverse as those of the surrounding primary forests, and are similar to other central African sites in terms of species composition. Our richness estimate (52–58 species) may be somewhat inflated owing to the limited number of trees sampled, but comparison with more extensive surveys suggests that the overestimation is not extreme. Specifically, our estimate was consistent with that predicted for nearby primary forests of Monts Doudou (57 species, assuming that 27% of the species collected at Monts Doudou are arboreal) (Fisher, 2004a), and twice the number found in primary forest canopy in Cameroon (28 species) (Dejean *et al.*, 2000). Perhaps this is because of the proximity of primary forests, which probably serve as source pools of species for colonization of disturbed sites in Gamba. Alternatively, arboreal ant communities may not be especially sensitive to disturbance associated with selective harvesting (versus more catastrophic disturbance, such as clearcutting).

Regardless, additional studies are needed to determine if the ant communities in the secondary forests are similar to those of primary forest in terms of other ecological parameters, such as trophic structure (Davidson *et al.*, 2003) and resistance to invasion by exotic species (Walker, 2006).

Large-scale oil drilling tends to increase forest fragmentation via the development of roads and other infrastructure. The most likely ecological effect of such disturbance on arboreal ants is an increase in forest edge habitat, which differs from the forest interior in abiotic and biotic conditions (Laurance *et al.*, 1998). Ant communities associated with edges in Cameroon had lower species richness and differed in composition from those in adjacent primary forest canopy (Dejean & Gibernau, 2000; Dejean *et al.*, 2000). We did not find a similar relationship between distance from an edge and number of species present in a tree. However, the surveys in Cameroon focused on an artificial edge associated with a road, and included a broad range of vegetation types. In contrast, most forest edges around Gamba are part of a natural, older forest-savanna mosaic, and we sampled only the trunks and crowns of mature trees.

The lack of correlation between Sørensen similarity values and inter-tree distances in this study is not surprising given the heterogeneity of the landscape. For example, the absolute distance between trees 3 and 5 and between trees 7 and 9 is similar, but the perceived distance for a dispersing forest animal is presumably very different; the former pair of trees are separated by continuous forest whereas the latter are separated by savanna and a road (Fig. 1). Assuming (among other factors) that ants are generally more likely to colonize new sites in the same forest patch than to cross open areas, similarity in ant composition between trees within forest patches should be greater than between trees in different patches. Despite the small sample sizes, our results lend some support to this hypothesis.

The invasive ant *W. auropunctata* is established at several localities within the study area, but was not detected specifically in our arboreal samples. Although our survey is far from comprehensive, the focal trees are relatively widely dispersed and *W. auropunctata* is generally conspicuous where it occurs (Walsh *et al.*, 2004). Thus, if this species is widespread at the site, we probably would have encountered at least a few stray individuals in our collections or when walking through the forest in search of climbable trees. Nonetheless, more data are needed to

establish accurately its current distribution in the forests around Gamba.

In sum, large-scale oil drilling operations potentially influence communities of arboreal ants and other organisms via several mechanisms, including deforestation, forest fragmentation and exotic species introductions. Our survey provides a preliminary basis for examining the current and future impacts of these types of disturbance on central African canopy ants. Although far from comprehensive owing to low sample size and lack of nocturnal collections, the simple, standardized sampling technique we employed makes our results comparable with data from other forests. Many species we found have few prior collection records and some (e.g., *Tetramorium ictidum*) were previously known only from workers found in leaf litter samples, suggesting that many presumed 'litter' taxa may actually be nesting in the canopy. Thus, our results provide strong evidence that additional surveys, as well as behavioural and ecological studies, of central African ants would be scientifically fruitful.

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