Research article

Community interactions between ants and arboreal-nesting termites in New Guinea coconut plantations

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Summary. We investigated the incidence of inquiline ants and of arboreal-nesting ants on a community of three arboreal-nesting termites living in New Guinea coconut plantations. Inquiline ants were present in 10% of *Microcerotermes biroi* nests and in 4% of *Nasutitermes princeps* nests. Live termite nests inhabited by the most common inquiline ant, *Camponotus* sp. A, were generally left by the ant after several months. In some nests, *Camponotus* sp. A was observed coexisting with its host during the whole observation period (3 years). Therefore, *Camponotus* sp. A was apparently an opportunistic inquiline which did not affect significantly the mortality of termite colonies. The arboreal-nesting ant, *Crematogaster irritabilis*, was locally found occupying up to 99% of the trees present in 1 ha plots. In such hot spots, the overall abundance of termites was approximately half that of plots devoid of *Crematogaster irritabilis*. The high density of *Crematogaster irritabilis* may be an important limiting factor for the termite assemblage, by hastening the death or hindering the establishment of arboreal termite colonies.

Key words: Predation, inquilinism, Isoptera, *Crematogaster*, *Camponotus*.

Introduction

Ants and termites are major components of tropical ecosystems but little is known of how they interact. Ants are major, sometimes specialized, termite predators (Wheeler, 1936; Sheppe, 1970; Wood and Sands, 1978; Longhurst et al. 1978, 1979; Longhurst and Howse, 1979; Deligne et al., 1981; Nutting and Jones, 1990; Hölldobler and Wilson, 1990) but they may also be commensals or even mutualists (Higashi and Ito, 1989; Jaffe et al., 1995). Predation by ants on termite mounds in Africa and in Australia may be one of the major causes of termite mortality (Bodot, 1967; Lepage, 1981; Collins, 1981; Abe and Darlington, 1985; Darlington, 1985; Higashi and Ito, 1989).

Coconut plantations may harbour numerous ant species (e.g., 65 species recorded by Brown (1959) in the Solomon Islands, to the east of Papua New Guinea), the dominant species being distributed in mosaics (Greenslade, 1971; Majer, 1993). In Papua New Guinea, coconut trees may support termite nests from which covered galleries depart. These galleries reach either the top of the trees or the ground where they often proceed to adjacent trees. Along the north coast of New Guinea, the most abundant arboreal-nesting termite is *Microcerotermes biroi* (Desneux), followed by *Nasutitermes princeps* (Desneux) and *N. novarumhebridarum* (N. and K. Holmgren) (Leponce et al., 1997). Termite nests and/or covered galleries occupy from 25% of the trees in open plantations (density ≤ 100 trees/ha) to 56% of the trees in denser habitats (> 100 trees/ha) (Leponce et al., 1995). Several ant species, e.g. *Oecophylla smaragdina* (F.), are ubiquitous in the habitat but are only occasional termite predators, because termites seldom leave the shelter of their galleries or nests.

In this study we evaluated the effect of the presence of ants on the distribution and abundance of arboreal-nesting termites in coconut plantations of Papua New Guinea. We focused on the two categories of ants which are the most likely to interact with arboreal termites : inquiline ants, which inhabit live termite nests, and arboreal-nesting ants, which build their nest on trees like arboreal-nesting termites. We first assessed the frequency of inquiline ants in termite nests and monitored nests containing the commonest inquiline ant to record the outcome of the cohabitation between termites and ants. Second, we compared termite abundance in plots invaded by or devoid of the most abundant arboreal-nesting ant species and studied the dynamics of the cohabitation between ants and termites.

Materials and methods

The observations were conducted in coconut plantations along the north coast of New Guinea near Hansa Bay, Bogia district, Madang Province.

Inquiline ants

The presence of inquiline ants was systematically checked in all *M. biroi* and *N. princeps* nests present in eight plots of 1 ha randomly selected and in one plot of 3 ha chosen for the abundance of *N. princeps* nests (plot XVI in Leponce et al., 1995). *N. novarumhebridarum* nests were disregarded from this sampling because of their low abundance in plantations (see Leponce et al., 1995). Ants were detected by making superficial cuts (2–3 cm deep) all over the nest surface.

Ants coming out of the nest were collected and preserved in 70% ethanol for later identification. Voucher specimens were deposited at the "Institut Royal des Sciences Naturelles de Belgique", Brussels. Small populations of tiny ants, which did not seem to exert much influence on termite population, were disregarded from this sampling.

Twenty-two *M. biroi* and 12 *N. princeps* nests containing the most common inquiline ant were monitored for up to three years. To minimise the effects of the disturbance caused by sampling, the nests were only checked after long intervals of 6 to 30 months. As a control, 31 *M. biroi* and 12 *N. princeps* nests devoid of inquiline ants were monitored during the same period.

Arboreal-nesting ants

Coconut plantations around Hansa Bay were scanned for the presence of arboreal nesting ants. In order to evaluate the maximum interference of these ants with the termite community we selected two plots invaded by the commonest arboreal ant species: plot O of 0.8 ha in an open plantation (96 trees/ha, tall trees > 20 m in height, alias plot XIX in Leponce et al., 1995) and plot D of 1.0 ha in a dense plantation (202 trees/ha, trees 13–25 metres in height, alias plot XX in Leponce et al., 1995). Ant and termite nests and trails were mapped in September 1990, April 1993 and April 1994 in plot O and in April 1993 and April 1994 in plot D. Observations were performed during daytime in sunny weather to compare ant activity under similar conditions. Termite abundance in O and D was compared to termite abundance in, respectively, 5 open and 5 dense plots of approximately 1 ha mapped during the same period (plots I–V and XI–XV, respectively, in Leponce et al., 1995), devoid of arboreal ants but very similar in other respects.

Results

Inquiline ants

Inquiline ants were found in 44 of 462 (9.5%) *M. biroi* nests and in 5 of 120 (4.2%) *N. princeps* nests checked in 9 plots. The difference in proportion of inquiline ants between the two species is near the significance level (Chi-square = 3.55, df = 1, P = 0.060). Carpenter ants were the commonest inquilines : *Camponotus* sp. A was found in 23 *M. biroi* nests and in five *N. princeps* nests; *Camponotus* sp. B was found in nine *M. biroi* nests. *Philidris* (formerly *Iridomyrmex*) *cordatus* (Smith) was found in four *M. biroi* nests and in one *N. princeps* nest. Other species found in *M. biroi* nests included *Calomyrmex* sp. and *Tapinoma* sp. The presence of *Camponotus* sp. A could often be detected by the presence of a different building material than the termite carton on breaches in the nest envelope. These ants were found in apparently healthy termite colonies and in abandoned parts of old, large,

termite nests. Coccids were also present on the tree trunk inside termite nests and galleries invaded with *Camponotus* sp. A. This ant was sometimes found outside termite nests in rotten wood under the tree bark. Single queens of *Camponotus* sp. A were found in some *M. biroi* nests. *Camponotus* sp. A reared their brood in termite nests, but nest parts or galleries occupied by *Camponotus* sp. A were walled off by termites. When the nest was artificially opened, *Camponotus* sp. A attacked termites which either squirted their defensive secretion (*N. princeps*) or used their mandibles (*M. biroi*) against the ants.

Twenty-two *M. biroi* and 12 *N. princeps* nests found with *Camponotus* sp. A were monitored for up to 3 years. *Camponotus* sp. A either left or was expelled from the termite nest after a few months in most cases (in respectively 45% and 75% of the *M. biroi* and *N. princeps* nests). In about 15% of the nests of both species, *Camponotus* sp. A was observed coexisting for 6 to 19 months (*M. biroi*, n = 3 nests) or even 35 months (*N. princeps*, n = 2 nests) with its host. The proportion of termite nests which collapsed during the observation period was higher for *M. biroi* (9/22 = 41%) than for *N. princeps* (1/12 = 8%) but this difference is not statistically different (Fisher's Exact test, P = 0.061). The *N. princeps* nest monitored died for unknown reasons. Attacks by adjacent colonies of *N. princeps* were responsible for three deaths of *M. biroi* nests. The death of the other six *M. biroi* nests was difficult to explain but could be the consequence of the presence of *Camponotus* sp. A which still occupied three dead nests at the end of the observation period (the other three already had fallen down to the ground because of the lack of maintenance by termites). However the comparison with ant-free nests, not exposed to interspecific competition and surveyed during the same period, suggests that the mortality of *M. biroi* nests was independent of the presence of *Camponotus* sp. A (7/31 vs. 6/19 dead nests, Chi-square test, 1df, P > 0.05). The same was true for *N. princeps* (0/12 vs. 1/12 dead nests, Fisher's Exact test, P > 0.05).

Arboreal-nesting ants

Three arboreal-nesting ant species were observed in coconut plantations around Hansa Bay: *Crematogaster* (*Xiphocrema*) *flavitarsis* Emery, *Papyrius* (formerly *Iridomyrmex*) *nitidus* (Mayr) and *Crematogaster* (*Orthocrema*) *irritabilis* F. Smith. The first two species were sparsely distributed in coconut plantations. Observations in plots monitored to study the dynamics of the termite community (Leponce et al. 1997 and unpublished results) indicate that *Papyrius nitidus* was able to dislodge both *M. biroi* and *N. princeps* mature colonies by progressively invading the termite nest. Only *C. irritabilis* populations spread over more than 1 ha in coconut plantations; however, such heavily colonised spots were scarce. The factors responsible for the high density of ants remain to be identified, however the spots were always adjacent to cocoa plantations and to bushes which were apparently more favourable habitats. In coconut plantations, *C. irritabilis* built its nests on the trunk and on the palm leaves at the top of the

tree. The species attacked termites whose nest or galleries were artificially opened. On some occasions *C. irritabilis* was observed building its carton nest on a live termite nest which was then progressively invaded.

In plot O (open plantation) on average 86% of the 78 trees present were occupied by *C. irritabilis* and 12% by termites during the observation period (% ants/% termites: 1990: 77/11; 1993: 96/9; 1994: 84/15). None of the *M. biroi* colonies recorded in 1990 survived until 1993 but three nests, one of each termite species, developed in the meantime (Fig. 1). In site D (dense plantation) *C. irritabilis* nests or trails were found on 99% of the 202 trees in 1993 and on 96% in 1994; however the number of trees supporting ant nests increased from 146 to 161 (Fig. 2). During the same period trees

occupied by termites decreased from 27% to 21%. The breakdown/establishment of a termite nest between 1993 and 1994 was significantly related to the presence/absence of an ant nest on a tree in 1994 (Fisher's exact test P = 0.02). In plot O, such a relationship could not be investigated due to the small sample size. In both plots O and D, the absence/presence of termite nest at a particular time was independent of the presence/absence of an ant nest (Fisher's exact tests, P > 0.05).

In sites invaded by *C. irritabilis* the proportion of trees occupied by arboreal termites was half that in open or dense plantations without *C. irritabilis*: $12 \pm 3\%$ in site O versus $25 \pm 8\%$ in plots I-V and $24 \pm 4\%$ in site D versus $54 \pm 7\%$ in plots XI-XV (t-tests, P < 0.05).
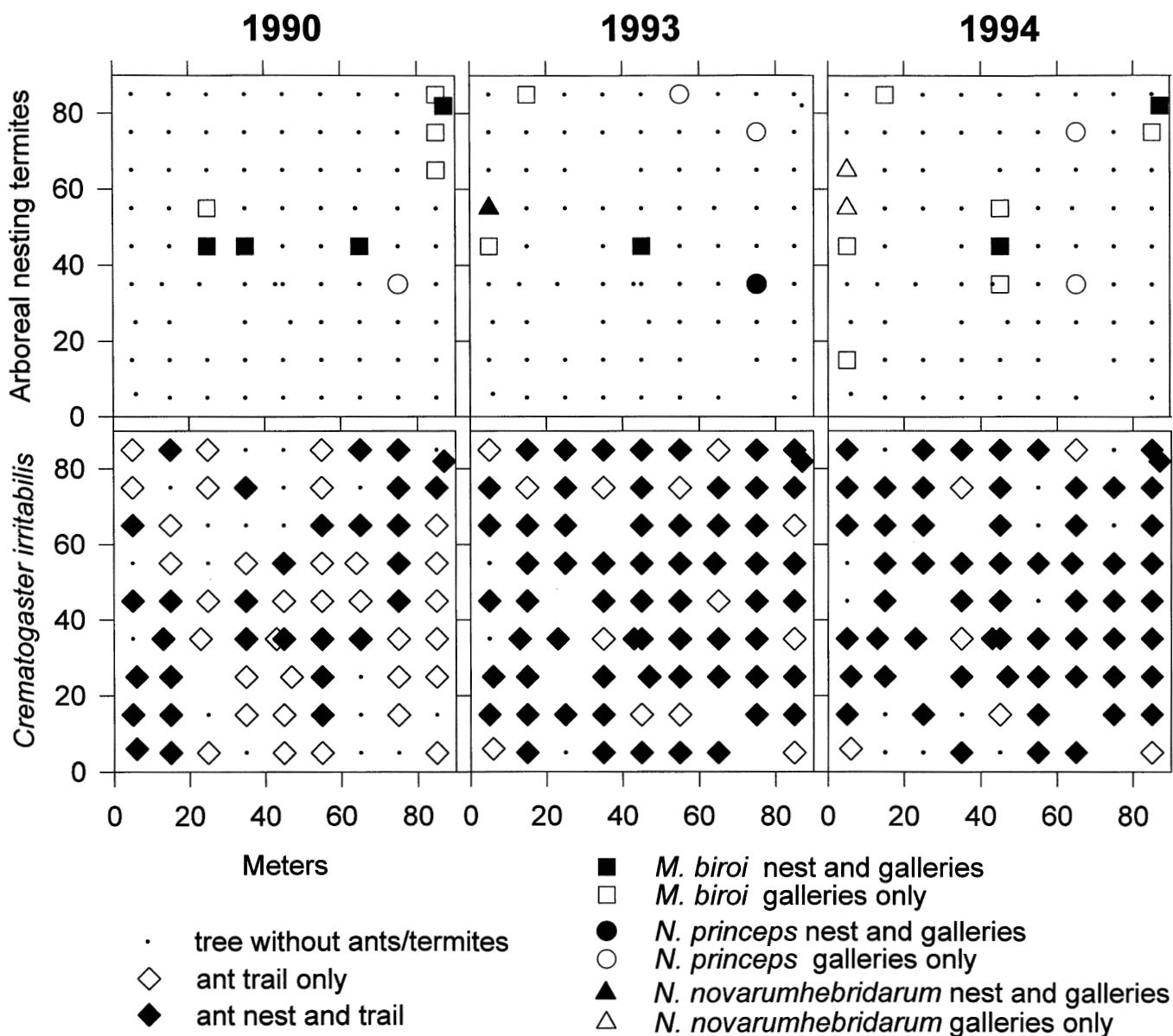

Figure 1. Map of occupation of site O by arboreal nesting termites and *Crematogaster irritabilis* in September 1990, April 1993 and April 1994. Maps of termite (at top) and ant (at bottom) colonies were separated for clarity
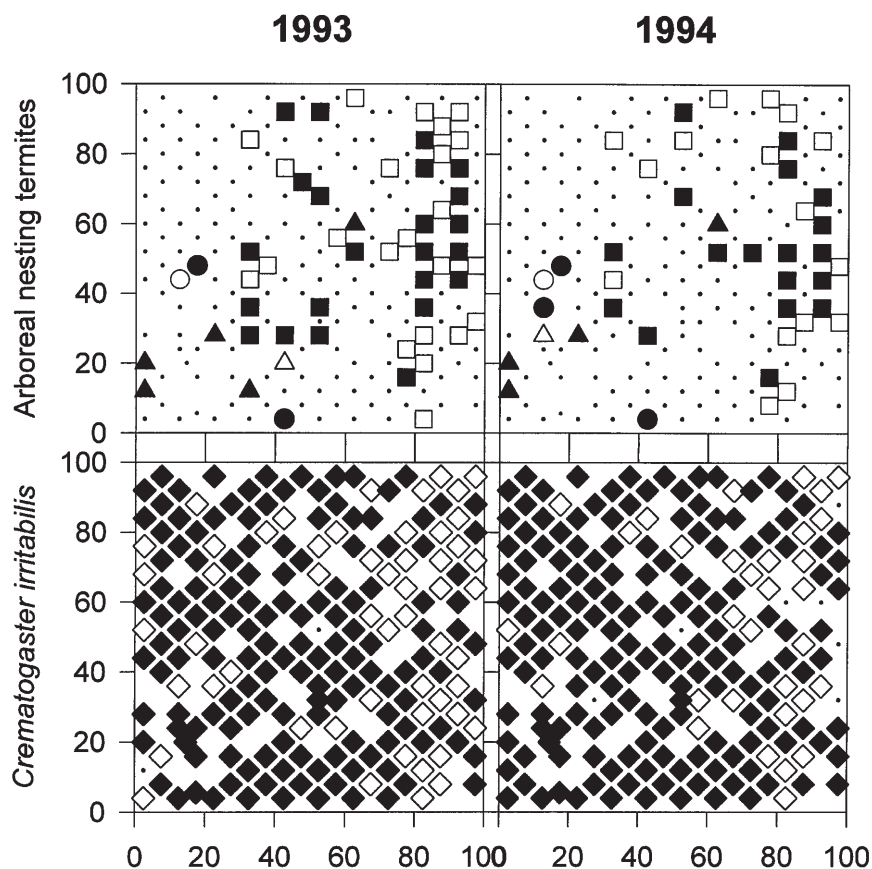
1993   **1994**

Figure 2. Map of occupation of site D by arboreal nesting termites and *Crematogaster irritabilis* in April 1993 and April 1994. Legend as in Fig. 1

Discussion

Carpenter ants were the most common inquilines of *M. biroi* and *N. princeps* nests in New Guinea. Arboreal *Microcerotermes* nests in Zambia also host *Camponotus* ants (Sheppe, 1970). The exact nature of the relationship with their host is difficult to assess: *Camponotus* sp. A probably seeks shelter and occasional food in termitaria which may also be used for foundations. Whether termitaria are preferred by ants to other nest sites remains to be investigated.

Two factors might explain why inquilines were found twice as often in nests of *M. biroi* as in nests of *N. princeps*. First, the defensive secretion of *Nasutitermes* soldiers has proved to be an effective weapon against ants (Eisner et al., 1976; Mill, 1983; Everaerts et al., 1988, 1990; Valterová et al., 1989) especially in species such as *N. princeps* where its pheromonal role allows a coordinated warfare between soldiers and workers (Roisin et al., 1990). Second, it might be more difficult for ants to isolate themselves from the termite colony in *N. princeps* nests where the openings between chambers are much wider than in *M. biroi* nests (Deligne and Pasteels, 1982). *Camponotus* sp. A was apparently the only species that inhabited *N. princeps* nests while *M. biroi* nests hosted at least five different ant species suggesting that invasion by ants may be easier in *M. biroi* nests than in *N. princeps* nests.

Nest mortality in *M. biroi* and *N. princeps* was independent of the presence of *Camponotus* sp. A. The only obvious cause of death of *M. biroi* colonies was the attack by an adjacent *N. princeps* colony (Leponce et al., 1997). Our data suggest that the incidence of inquiline ants across the termite assemblage is low: (i) inquiline ants were present in less than 10% of termite nests; (ii) the commonest inquiline, *Camponotus* sp. A, did not affect significantly the termite nest mortality during the observation period; (iii) *Camponotus* sp. A generally inhabited the termitaria for a limited period of time though on occasions the cohabitation with its host could last for up to 3 years.

Some patches of coconut plantations were dominated by the arboreal *Crematogaster irritabilis*. In the monitored plots there was a relatively stable but dynamic proportion of trees occupied by ants and termites over 2 to 3 years. The establishment of new termite nests was more successful on trees devoid of ant nests, but the absence of correlation between the presence of an ant nest and the presence of a termite nest indicate that ants have no difficulty to establish a nest on a tree occupied by termites. The termite global abundance was half lower where *C. irritabilis* was dominant.

The present study suggests that whereas inquiline ants have a low impact, the presence of arboreal ants such as *Crematogaster* can be locally an important limiting factor for the arboreal termite assemblage in coconut plantations and possibly in other tropical agroecosystems and native ecosystems where *Crematogaster* often dominate (Majer, 1993).

Acknowledgements

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