Food preference and interspecific interactions in fungus-growing termite assemblage in a West African savanna

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An experiment was conducted to study food preference and interspecific interactions in a fungus-growing termite community at the Lamto Savanna Ecological Station in Ivory Coast. Food consumption of four termite species (*Macrotermes bellicosus*, *Ancistrotermes cavithorax*, *Microtermes toumodiensis* and *Odontotermes* aff. *pauperans*) was compared at baits of different sizes, belonging to the two most abundant tree species in this savanna, viz. *Crossopteryx febrifuga* and *Piliostigma thonningii*. All species preferred larger wood pieces. *A. cavithorax* was the most active forager on baits. Foraging activity of the mound builder, *M. bellicosus* was clearly influenced by the foraging patterns of the two underground fungus-growing species, *A. cavithorax* and *O.* aff. *pauperans*, thereby questioning the competitive ability of *M. bellicosus*, as against the activities of its competitors. *M. bellicosus* seems to be at the bottom of a possible competition hierarchy with regard to food niche. This imbalance in favour of underground species could have been increased by the fire regime in Lamto savanna, artificially occurring each year in the middle of the dry season and minimizing the abundance of large wood items, most preferred by *Macrotermes*.

Keywords: Baits, interspecific interaction, fungus-growing termites, food consumption.

A NUMBER of studies are available illustrating the food preferences and foraging strategies of different termite species and populations in different ecological regions of the world[1,2]. As termites are an important component of the savanna ecosystem[3], they have also been the focus of a number of population-level studies[4]. However, community-level assessment of food preferences and interspecific interactions of the savanna termites is lacking. Such an assessment among termite species at food source would help in understanding various aspects of the savanna system processes.

Although various studies are available on the role of fungus-growing termite populations (Macrotermitinae) of the Lamto savanna in Ivory Coast[5–12], a community-level assessment is lacking, as mentioned above is such an

assessment of the Lamto savanna fungus-growing termite community assumes extra importance, as there are studies reporting a decline in the termite species *Macrotermes*[13]. The present study attempted to make a community-level assessment of the food preferences and interspecific interactions within the fungus-growing termite community.

Study site

The field study was undertaken at Lamto, a savanna field station run by the University of Abobo-Adjamé, Abidjan in Côte d'Ivoire, West Africa. This pre-forest humid savanna is located approximately 200 km from Abidjan (5°02′W, 6°13′N). The site comprised of grass, shrub and woody savannas, intermingled with gallery and semi-deciduous plateau forests[14]. Average annual precipitation in the savanna is 1210 mm yr^{-1} (refs 15, 16).

Materials and methods

An experiment was designed to compare the foraging activities and food preferences of four fungus-growing termite species: the mound builder *Macrotermes bellicosus* Smeathman and three subterranean species: *Ancistrotermes cavithorax* (Sjöstedt), *Odontotermes* aff. *pauperans* (Silvestri) and *Microtermes toumodiensis* Wasmann.

Food types

Six different types of locally abundant wood litter belonging to two species were offered to the termite community as bait to find out their preferences. The selected wood species were *Piliostigma thonningii* and *Crossopteryx febrifuga*. Items of these two species were again subdivided into small, medium and large diameter categories. A total of 40 bait items of each were placed as bait. Total biomass and average individual weight of each type is given in Table 1.

Experimental design

Bait layout: As our experiment was designed to compare the foraging strategies of the four Macrotermitinae
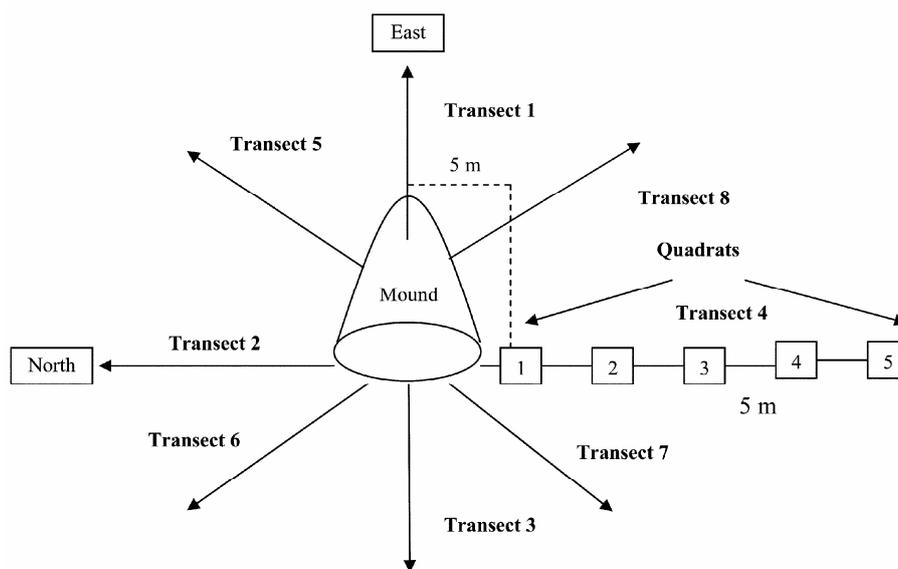
Figure 1. Bait layout showing different transects with respect to the mound.

Table 1. Initial total average weight of wood litter placed as bait

Type	Size class	Average weight (g) $N = 40$
Piliostigma thonningii	Small	3.52 (Range = 1.8–6.7 g)
	Medium	21.21 (Range = 10.3–34.4 g)
	Large	81.90 (Range = 35.3–146.0 g)
Crossopteryx febrifuga	Small	5.94 (Range = 2.2–10.8 g)
	Medium	19.74 (Range = 10.6–30.9 g)
	Large	51.60 (Range = 32.6–91.2 g)

Bait sampling: (a) Each bait item was monitored every day for 13 consecutive sampling days and the activity of any termite species present was recorded. The species present on bait was identified in the field, thus causing minimum disturbance to the bait item. (b) On each day, 25% of the total number of termite-attacked baits was removed randomly from the quadrats and all the individual termites present on the bait, and the soil deposited by them, were collected. This was done to estimate (i) the abundances of different termite species and (ii) the soil turned over at the bait item. After removing the individual termites and weighing the soil deposited on them, the bait item was replaced back in the quadrat. (c) The termites were later separated into different species and categories, e.g. (i) minor worker, (ii) major worker, (iii) minor soldier, (iv) major soldier and (v) reproductive and counted. (d) Soil deposited on each of the baits was dried and weighed.

species and as live *Macrotermes* mounds are rare in the savanna, one large *M. bellicosus* mound was selected in a shrub savanna habitat in order to include *M. bellicosus* within the ambit of the present study. Eight equidistant radial transects were laid in eight different directions around the mound at the beginning of the rainy season (Figure 1). Five 25×25 cm quadrats were laid at 5 m intervals along each of the eight transects. Each quadrat was cleared of all the above-ground plant biomass, including grass. Six baits were placed in each such quadrat in a random order: small, medium and large baits of the two chosen wood species. Forty bait items in each of the six categories were chosen at random. Each bait item was tagged and weighed before placing it in the quadrat. A total of 240 bait items were placed (6 food types/ quadrat × 5 quadrats/transect × 8 transects).

Data analysis

Variance in termite activity, both overall and species-wise, was tested with respect to the distance of the quadrat from the termite mound, to different transects, different bait types and bait size categories. ANOVA was done for individual variables and also for possible inter-actions of the same. Average frequency of occurrence of termites (both overall and species-wise) per transect was fitted with polynomial curves and regressed.

Hierarchial cluster analysis was done with species occurrence data at different baits to test for any food preference. Termite activity was tested for correlation with the bait initial weight, final weight and weight removed, and also the weight of the soil deposited on the baits. Log-standardized initial weights of the baits were

regressed with log-standardized quantities of soil deposited on the bait. Abundances of various castes on the removed baits were correlated with each other and also with the quantity of soil deposited, and the initial and final weights of the baits. Since *A. cavithorax* appeared to be the dominant species in the community, activities of other species were regressed against it. The number of times a species displaced another from different baits was estimated.

Results

Overall termite activity

Out of a total of 240 bait items placed (Table 1), 183 were attacked by termites (76.25% of the total number of baits). Of the total 3120 observations made during daily inspection of the baits (240 bait items/per day × 13 days), termite activity was recorded in 1056 observations.

The number of times baits were found to have *A. cavithorax* activity was 582 (55.11% of the total observations), that of *M. toumodiensis* was 296 (28.03%), *O.* aff. *pauperans* was 93 (8.80%), and *M. bellicosus* was 23 (2.17%) (Table 2). Considering the frequency of attack on the baits, *A. cavithorax* appeared to be the dominant species in the community.

Temporal distribution of termite activity

To check if bait removal had any effect on the activity of termites, difference between the frequency of bait items attacked on the day of removal and frequency of attacks on the same bait items the day after removal was compared using a *t* test. The difference was found to be non-significant. Termite activity followed a nonlinear pattern during the total period of observation. It was low initially and increased subsequently, but started to decline towards the end of the observation period. The pattern was found to fit best with a second-order curve ($R^2 = 0.89$, $P < 0.001$; $Y = 0.345 + 3.849X – 0.275X^2$). Activity of *A. cavithorax*

varied significantly with the number days after setting baits ($F = 3.070$, $df = 12$, $P < 0.001$). Its activity also showed a quadratic temporal relationship ($R^2 = 0.78$, $P < 0.01$; $Y = 0.466 + 2.289X – 0.153X^2$). The two other species, *M. toumodiensis* and *O.* aff. *pauperans,* also showed significant relationship with the number of days elapsed. The observed pattern fitted best with a third-order equation ($R^2 = 0.78$, $P < 0.01$, $Y = 2.491 – 0.64X + 0.21X^2 – 0.013X^3$, and $R^2 = 0.67$, $P < 0.05$, $Y = 0.023 + 0.78X – 0.11X^2 + 0.004X^3$ respectively).

Spatial distribution of the activity

Termite activity did not vary significantly between transects, but did so among quadrats at different distances from the mound on all transects combined ($F = 2.752$, $P < 0.05$). Maximum activity was observed in the first quadrat followed by the third and fourth quadrats (Figure 2). Although activity (frequency of occurrence) frequency did not vary significantly among different quadrats for *A. cavithorax*, it varied significantly for *M. toumodiensis*. ($F = 4.733$, $P < 0.005$) and weakly for *O.* aff. *pauperans* ($F = 2.443$, $P < 0.07$). *M. bellicosus* was observed only in quadrat 3 in the transects.

Overall termite activity at removed baits

A total of 138 bait items were removed at regular intervals, of which 63 had termite activity at the time of collection. *A. cavithorax* was found in 55 of 63 bait items that were removed. *M. toumodiensis* and *O.* aff. *pauperans* were present only in four removed bait items each.

Weight of the baits and termite activity

Total number of termites on the removed baits correlated significantly with the final weights of the baits ($r = 0.267$, $P < 0.05$). There was a stronger correlation between the initial weights of the removed baits and the number of

Table 2. Number of occurrences (observations during daily inspection at different baits placed along transects) of different species. Total number of times baits were found to have termite activity = 1056

Transect	ANC	MIC	OD	MB
1	53	5	30	0
2	49	59	5	0
3	110	25	0	16
4	94	37	8	5
5	28	72	4	0
6	51	61	18	0
7	61	30	12	2
8	136	12	16	0
Total	582	296	93	23

ANC = *Ancistrotermes cavithorax*, OD = *Odontotermes* aff. *pauperans*, MIC = *Microtermes toumodiensis*, MB = *Macrotermes bellicosus*.
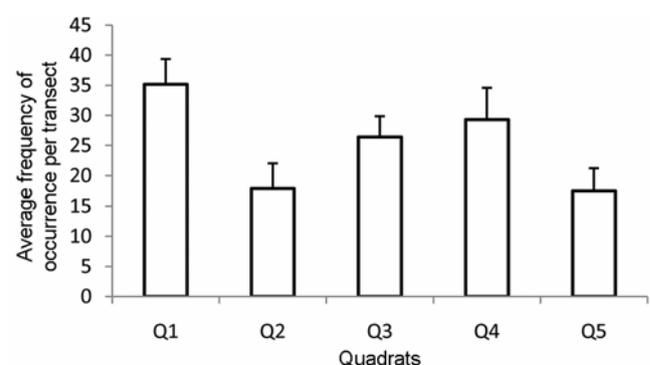

Figure 2. Species-wise average frequency of occurrence per transect over the sampling period. Data pooled for each species on all baits.

small workers (pooled for all species) found on the bait ($r = 0.432$, $P < 0.01$), indicating higher termite activity at larger bait items. Average number of individuals (averaged for different quadrats and transects) in different castes varied significantly with the species and bait type ($F = 7.98$, $P < 0.01$). Maximum number of individuals was observed for *A. cavithorax* in large *C. febrifuga* baits. *M. toumodiensis* and *O.* aff. *pauperans* had maximum number of individuals in *P. thonningii* baits.

Amount of soil turned at removed baits and termite activity

Total amount of soil deposited on all the baits amounted to 965.24 g. The initial weight of the baits (log standardized) determined the amount of soil deposited on them (log standardized; $N = 138$, $R^2 = 0.23$, $P < 0.001$). There was no significant relationship between bait type and soils deposited on them. *A. cavithorax* deposited significantly more soil compared to *M. toumodiensis* ($t = 4.784$, d$f = 25$, $P < 0.001$).

Quantity of bait consumed and termite activity

Initial weight of the baits also significantly determined the consumption (all species combined; $R^2 = 0.88$, $P < 0.01$). Quantity of bait consumed by the termites (estimated from the difference between the initial and the final weights of the bait) was positively correlated with the number of small workers present at the bait ($r = 0.263$, $P < 0.05$). There was positive correlation between consumption on medium-sized *C. febrifuga* baits and number of large workers ($r = 0.47$, $P < 0.05$). Total number of individuals of *A. cavithorax* correlated strongly with consumption ($r = 0.597$, $P < 0.001$).

Occurrence of different species at baits

A dendrogram (Figure 3) drawn on the basis of hierarchical cluster analysis with species occurrence data at different baits shows maximum similarity in food preference between *M. toumodiensis* and *M. bellicosus*. *O.* aff. *pauperans* was the next close species to this group. *A. cavithorax* was distinct from the other three in its food preference.

A. cavithorax seemed to prefer large food items as is apparent from its proportional occurrence at different baits (Figure 4 *a*; $F = 4.479$, $P < 0.03$). For *A. cavithorax* interaction between the number of days elapsed and bait type was found to be significant ($F = 2.329$, d$f = 12$, $P < 0.01$). Also, the interactive effect of the number of days, type of bait and distance from the *M. bellicosus* mound was highly significant ($F = 3.026$, d$f = 12$, $P < 0.001$). *A. cavithorax* seemed to prefer *C. febrifuga* over *Piliostigma* sp. (Figure 3; $t = -1.952$, $P < 0.03$).

Size and type of bait item influenced the activity of *M. toumodiensis* ($N = 324$, $F = 12.130$; d$f = 1$, $P < 0.01$). *M. toumodiensis* preferred *Piliostigma* over *Crossopteryx* ($t = 2.807$, $P < 0.01$; Figure 4 *b*). Interaction between the time elapsed after placement of the bait and distance of the bait from the *M. bellicosus* mound also significantly influenced the activity of *M. toumodiensis* ($F = 17.250$, d$f = 8$, $P < 0.001$).

Activity (proportional occurrence at different baits) of *O.* aff. *pauperans* had a significant preference towards *Piliostigma* sp. ($t = 2.483$, $P < 0.01$; Figure 3). Size of the bait item significantly influenced the activity of *O.* aff. *pauperans*, as it seemed to prefer large food items ($F = 9.592$, d$f = 2$; $P < 0.01$; Figure 4 *c*).

Maximum activity of *M. bellicosus* was found at 10 m from the mound (third quadrat) in all the three transects where it was active ($N = 23$, $F = 18.893$, d$f = 4$, $P < 0.001$). Although *M. bellicosus* seemed to prefer large *Piliostigma* baits, it was not statistically significant (Figure 4 *d*).

Species interactions

Activity of *A. cavithorax* seemed to affect the activities of other species. Activity of *M. toumodiensis* was significantly reduced by the activity of *A. cavithorax* ($R^2 = 0.397$, $P < 0.01$). Activity of *A. cavithorax* also significantly reduced the activity of *M. bellicosus* ($R^2 = 0.413$, $P < 0.02$). However, activity of *O.* aff. *pauperans* was not influenced by that of *A. cavithorax*. Activity of *M. bellicosus* was significantly reduced by the abundance of *O.* aff. *pauperans* ($R^2 = 0.489$, $P < 0.005$).

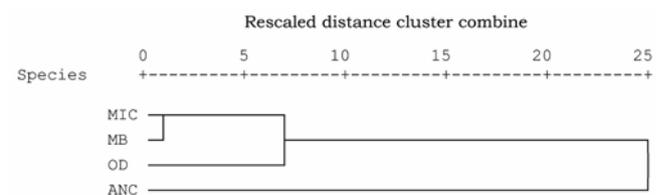When one species numerically replaced another that was occurring till the previous observation, it was

Figure 3. Dendrogram showing similarities in food preference of different species. Hierarchical cluster analysis using nearest neighbour method was used for anlysis. OD, *Odontotermes* aff. *pauperans*; MB, *Macrotermes bellicosus*; MIC, *Microtermes toumodiensis*; ANC, *Ancistrotermes cavithorax*.

Table 3. Displacement of one species by another at the bait

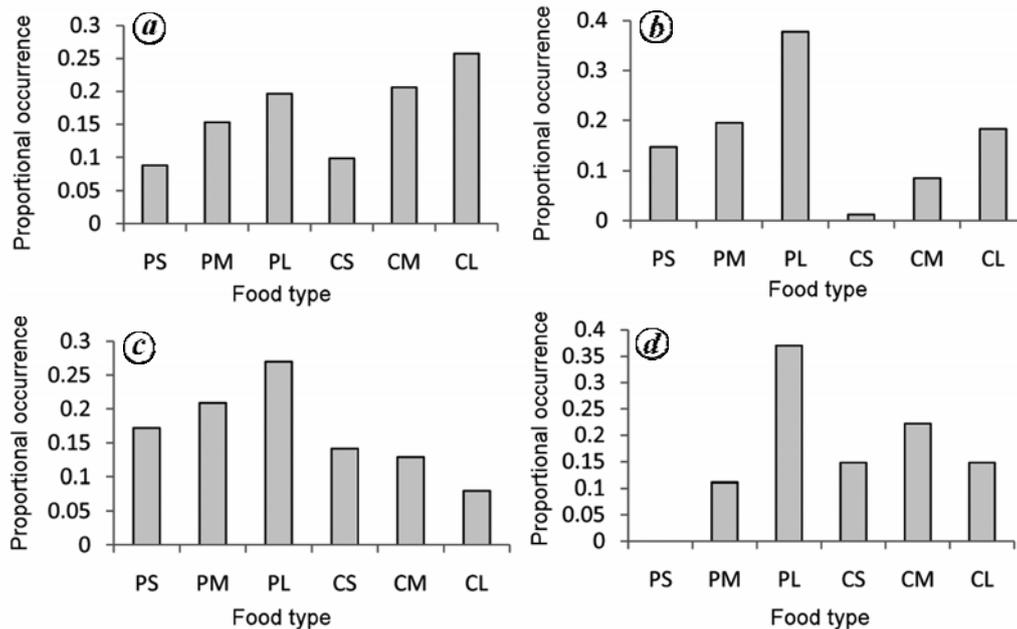| | Number of times displaced | | | |
Displaced by	ANC	MIC	OD	MB
ANC		30	9	4
MIC	20		5	0
OD	5	1		0
MB	4	1	2	

Figure 4. Proportional occurrences (proportion at a particular bait of the total occurrences) of different species towards different food types. *a*, *A. cavithorax*; *b*, *M. toumodiensis*; *c*, *O.* aff. *pauperans* and *d*, *M. bellicosus*. P, *Piliostigma* litter; C, *Crossopteryx* litter; S, Small; M, Medium and L, Large.

considered as displacement of the previous species by the latter. Such incidence of displacement occurred totally 80 times. Highest proportion of such displacement was shown by *A. cavithorax* followed by *M. toumodiensis* (Figure 3). On most occasions, *A. cavithorax* displaced another species from the *Piliostigma* bait. *M. toumodiensis* also followed such a pattern. Most of the displacements by *A. cavithorax* was directed towards *M. toumodiensis* compared to *O.* aff. *pauperans* ($t = 2.308$, d$f = 12$, $P < 0.02$) and *M. bellicosus* ($t = 4.309$, d$f = 9$, $P < 0.001$). There was no significant difference between the number of times *A. cavithorax* displaced *M. toumodiensis*, and vice versa. *M. toumodiensis* also displaced *A. cavithorax* more number of times than to *O.* aff. *pauperans* ($t = 4.949$, d$f = 9$, $P < 0.001$), while it never displaced *M. bellicosus*.

Discussion

Assemblage structure

The present study confirms a species assemblage of four fungus-growing and wood-feeding termite species[5,9,17-19]. In Tsavo Park, Kenya, Buxton[17] found that over 90% of wood litter was removed by three fungus growers. Ferrar[18] found four fungus-growing species in his study in Nylsvey, South Africa and Zeidler *et al.*[19] identified four fungus growers in northern Namibia.

The results of the present study bring out important clues regarding the structure of the fungus-growing termite assemblage and relative utilization of the food niche in Lamto savanna. With regard to the abundance on the baits, *A. cavithorax* was decisively the most dominant

species in the community followed by *M. toumodiensis* and *O.* aff. *pauperans*. The dominant position of *A. cavithorax* in this savanna type (open shrub savanna) confirmed the population and biomass estimates made by Josens[5,6]. Differences between species foraging patterns and feeding choice within the sub-family Macrotermitinae, underscore the relevance of the functional group concept, as pointed out by Jouquet *et al.*[20] considering the influence of fungus-growing termites on grass communities.

Temporal patterns

Overall termite activity was found to follow a hump-shaped temporal distribution that fitted best with a quadratic (second order) model. Following the rise in bait occupancy after discovery and recruitment, the frequency of occurrence in the baits fell, possibly due to depletion of the bait. Collins[21,22] indicated a drop in termite activity as a result of bait removal in baiting experiments. However, in the present study there was no significant difference between the frequency of attack on the day of removing the baits and the day after, thereby ruling out the possibility of bait removal affecting termite activity.

The same temporal distribution pattern was shown by *A. cavithorax*, while *M. toumodiensis* and *O.* aff. *pauperans* fitted best with a third-order curve. Since *A. cavithorax* dominated the community, its distribution pattern was reflected in the overall distribution pattern. Activities of *M. toumodiensis* and *O.* aff. *pauperans* peaked as the activity of *A. cavithorax* started to decline. This could be interpreted as indicating competitive release, or can also be attributed to interspecific differences in foraging

cycles. Rouland *et al.*[23] also observed a different temporal distribution pattern of foraging between *Macrotermes subhyalinus* and *Odontotermes nilensis* in Senegal.

Food consumption, soil deposition and caste

The result shows a strong relationship between the initial weight of the baits and food consumption. Clearly, different species preferred large baits over smaller ones for higher resource quality. Significant correlation between the number of individuals and the final weight indicates higher recruitment at the baits where consumption was greater. The three species found on the removed baits, *A. cavithorax*, *O.* aff. *pauperans* and *M. toumodiensis* did not have significant variance in terms of small workers. Significantly the caste investment in terms of recruitment of small workers was higher for different species on their preferred food type. *A. cavithorax* had more individuals belonging to different castes on large *Crossopteryx* sp. bait items, their preferred food, whereas other species preferred *Piliostigma* sp. There was a strong correlation between abundance of small workers and initial weight of the removed baits. Interestingly, even though *O.* aff. *pauperans* seemed to be lower down a possible competition hierarchy than *M. toumodiensis*, it deposited more soil than the latter. This reflects the relative abilities of soil deposition of different species and perhaps suggests that foraging activity may not always directly correspond to soil deposition and varies according to species. The average group size and caste composition in termite foraging groups are known to vary according to the nature and weight of the foraging substrate[24].

Resource utilization by different species

All the species preferred larger food items. There was a clear indication of food-type partitioning by different species with the dominant species. *A. cavithorax* preferred *Crossopteryx* wood litter whereas all the others, including *M. bellicosus* preferred *Piliostigma* wood litter. In their study of food preferences based on the carbon isotopic composition of the fungus combs belonging to Macrotermitinae species in Lamto, Lepage *et al.*[25] concluded that *Ancistrotermes* sp. gets a higher proportion of tree material in its diet (47–87%), whereas the proportion was 43–60% for *Microtermes* sp. and only 28–34% for *Odontotermes* sp. In a field study using baits, Garcia[26] also found that *Ancistrotermes* sp. exhibited a slight preference towards *Crossopteryx*; same with *Microtermes* sp., whereas *Odontotermes* sp. preferred *Piliostigma*. In a laboratory study, Cesselin *et al.*[27] showed the same preference of *A. cavithorax* towards *Crossopteryx* wood litter. In a recent study on food preference of termites at Sahelo-Sudanese savanna, Rouland *et al.*[23] found that *M. subhyalinus* preferred cane and millet stubbles, whereas *O. nilensis* preferred *Acacia* leaf litter and cattle manure.

Resource competition

The present study also showed that *A. cavithorax* deposited more soil on the bait than *O.* aff. *pauperans* or *M. toumodiensis*. A previous comparative laboratory study on *A. cavithorax* and *O.* aff. *pauperans* had predicted the exclusion of the latter species by *A. cavithorax* under field conditions[27], because of the higher investment in termite number and soil deposited by the latter species. The present study validates that prediction and indicates that *A. cavithorax* displaced other species from their preferred baits under field conditions. *M. toumodiensis* seems to be next in a possible competition hierarchy and interestingly, *A. cavithorax* seemed to displace it the maximum number of times compared to other species. Our finding that *A. cavithorax* and *M. toumodiensis* displaced each other significantly more times relative to the number of times they displaced other species suggests them to be the direct competitors. *O.* aff. *pauperans* is possibly an opportunistic exploiter of resources which might be modulating their foraging in tune with the top two competitors in the assemblage; but this requires to be further probed. The presence of *A. cavithorax* also significantly reduced the activities of *M. bellicosus* and *M. toumodiensis*. In a laboratory study with incipient colonies, Konaté[10] noticed that the aggressiveness of *Ancistrotermes* displaced *Odontotermes* from its preferred food when the two colonies were connected to the same arena. Interspecific aggression in termites was observed in several studies[28–30] and such ecological consequences of the aggressive abilities of species were also pointed out by Baroni-Urbani *et al.*[31]. Activities of *M. bellicosus* were also influenced by *O.* aff. *pauperans*. Facing the competitive abilities of fungus-growing underground species, whose foraging strategies seem more opportunistic and efficient, *M. bellicosus*, the only important mound-builder in the community seems to be at the bottom of a possible competition hierarchy based on food. This imbalance in favour of underground species may be attributed to the fire regime in Lamto savanna. Occurrence of fire is common every year in the middle of the dry season and this causes depletion of larger wood litter, most preferred by all species and particularly *Macrotermes* sp. In a Guinean savanna of Côte d'Ivoire, Korb and Linsenmair[32] found that litter is a limiting resource for termites early in the rainy season and could result in interspecific competition.

It appears that there is a clear interspecific competition hierarchy in this assemblage with *A. cavithorax* at the top, followed by *M. toumodiensis*, indicating that *A. cavithorax* and *M. toumodiensis* competed with each other for food. Both *A. cavithorax* and *M. toumodiensis* displaced each other significantly more times compared to the other species. Further studies and statistical analyses are necessary to assess the nature of these interactions and factors involved in the interactions between termite

species and the community structure[2]. The seasonal effect on the interactions also needs to be studied[33]. Foraging pattern and interspecific interactions, mostly aggressive interactions as related to food preferences, within the fungus-growing termite functional group, deserve further investigations to explain the community organization, co-existence and resource partitioning in the termite community.

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