Journal of Tropical Ecology (2010) **26**:323–334. Copyright © Cambridge University Press 2010
doi:10.1017/S0266467410000015

Termite diversity and abundance across fire-induced habitat variability in a tropical moist savanna (Lamto, Central Côte d'Ivoire)

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(*Accepted 29 December 2009*)

Abstract: At Lamto, little is known about animal community responses to habitat variability resulting from fires and the mosaic pattern of the vegetation in general and in particular about that of termites which play key roles in this ecosystem. With a standardized method, data were collected on termites from four habitats differing in their vegetation cover and fire-history: annually burned savanna, savanna woodland, forest island and gallery forest. A range of environmental variables was measured and correlated with species abundances. The number of termite species collected in the savanna woodland was very close to that found in the gallery forest while the forest island was the richest habitat. The species richness of the savanna woodland and forest island seemed partly due to their heterogeneous and transitional vegetation structures and variable food resources. With regard to the fire-history of habitats, Connell's intermediate disturbance hypothesis offers an explanation for differences in the patterns of habitat-specific species richness. Variation in species abundances was significantly correlated with only two environmental variables (soil pH and woody plant species richness). The pH appeared as the most influential factor for fungus-growers while tree invasion in the savanna strongly reduces the abundance of grass-feeding species (e.g. *Trinervitermes geminatus*). Although not significantly correlated with species abundances, soil carbon showed a positive correlation with the dominant soil-feeder *Basidentitermes potens*. As for wood-feeders, they were not strongly correlated with woody plant species richness; this fact might be linked to their use for other sources of nourishment. Overall, it appears that habitat variability in the Lamto reserve contributes to the maintenance of different subsets of the termite community.

Key Words: feeding group, habitat variability, intermediate disturbance hypothesis, Lamto, moist savanna, species distribution, termite community

INTRODUCTION

One of the conspicuous features of the savanna landscape at Lamto in central Côte d'Ivoire is its spatial heterogeneity. The vegetation is composed of evergreen (gallery forest) and semi-deciduous forests (forest islands) embedded in the savanna which itself is composed of several subtypes differing in the densities of shrubs and trees (Ménaut & Abbadie 2006). The savanna subtypes are differently impacted in the structure of their vegetation by annual fires causing high habitat variability (Gignoux 1994, Ménaut 1971, Monnier 1968, Mordelet 1993). Such habitat heterogeneity may influence the diversity and spatial dynamics of the savanna-dwelling communities (Gillison *et al.* 2003). As one of the main concerns for comprehending the ecology of animals consists in understanding the relationships between community dynamics and landscape structure (Boulinier *et al.* 1998), it is necessary to study community responses to habitat variability (Ramankutty & Foley 1999). Since fires are of special importance for the structure and dynamics of savannas, quite a number of studies have been undertaken to elucidate their effects on these ecosystems (Bond 1997, Sankaran *et al.* 2005, 2008; Tainton & Mentis 1984, Trollope *et al.* 1998). However, we still lack much important information on several aspects of fire impact on savanna ecosystems (Parr & Chown 2003, Trollope 1984).

At Lamto, although fire is the most important and frequently employed management tool for the maintenance of the savannas, very little is known about the consequences of the fire-induced habitat variability on the faunal diversity in general and that of termites in particular. Termites, as true ecosystem engineers

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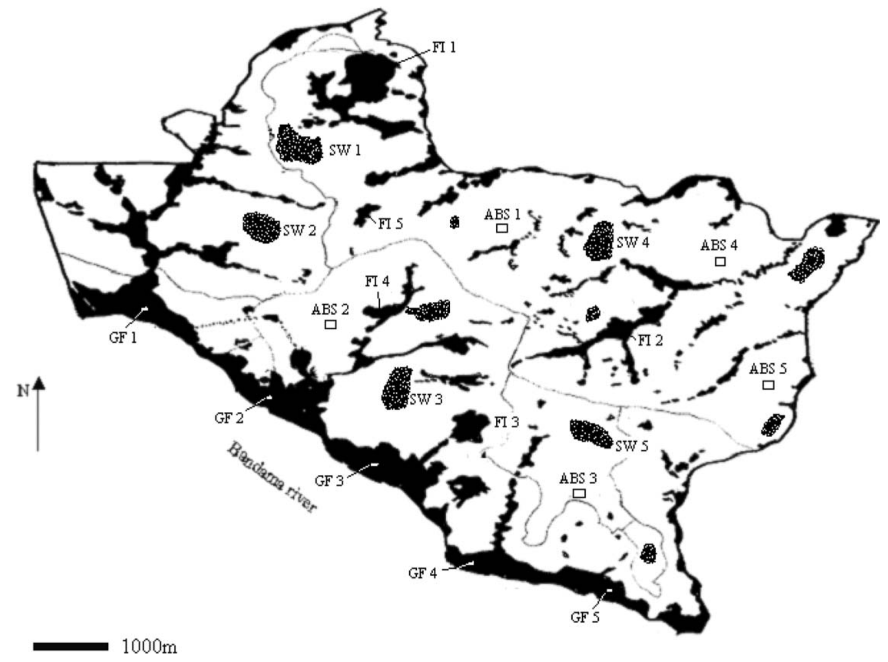

Figure 1. Map of the Lamto reserve showing habitat variability (modified from Gautier 1990). Transects are numbered from 1 to 5. Habitat abbreviations: ABS, annually burned savanna; SW, savanna woodland; FI, forest island and GF, gallery forest.

(cf. Jones *et al.* 1994), play key roles in the dynamics of this savanna landscape (Konaté 1998, Le Roux *et al.* 2006). Among others, these roles concern soil bioturbation and formation, modification of soil texture and nutrient content (Holt & Lepage 2000, Konaté *et al.* 1999, Lee & Wood 1971), decomposition of plant material (Josens 1983, Wood & Sands 1978) and emission of carbon dioxide (and also methane) (Konaté *et al.* 2003). Additionally, they represent good bio-indicators in tropical ecosystems with regard to their sensitivity to habitat disturbance causing changes in their species richness, composition and functional characteristics (Davies 1997, Eggleton *et al.* 2002, Konaté *et al.* 2005). With regard to these important ecological functions of termites, understanding their responses to the spatial structure of habitats is essential in view of the functioning of the Lamto protected area.

In this study, we investigated two hypotheses: (1) termite guilds respond variously to habitat variability maintained by regular fires at Lamto. Due to their specific ecological and biological characteristics, each species is expected to respond in its own way to changes in habitat structure; (2) much of the variation in species abundances is explicable in terms of environmental variables decisive for the establishment and success of termite colonies. To examine these hypotheses, we collected data on termite diversity and abundance from four habitat types differing in their vegetation cover and fire-history, and we also measured some environmental variables in order to correlate them with relative abundances of the different species.

METHODS

Study area

The study was carried out in the Lamto reserve (6°13′N, 5°02′W) representing a typical Guinean (i.e. humid) savanna in central Côte d'Ivoire. In this area, fire has been held responsible for the unexpected presence of savannas where climate should be able to sustain rain forests (Monnier 1968). The ample water availability supports the development of a rich vegetation which becomes, with drying up, a copious fuel source for the fires. As a result, these fires are relatively severe and occur every year (usually mid-January). They exert a stabilizing effect on the habitat mosaic by preventing massive tree invasion into the savanna, thereby hindering the re-establishment of forests and freezing the forest–savanna boundary in a historical position (Gillon 1983). Although these fires have a strong negative effect on newly recruited woody plants, the regular human-lit fires at Lamto cannot entirely prevent woody plant invasions because they are, as mid-dry-season fires, not hot enough and not covering the whole area to kill all tree and shrub species before they are tall enough to resist fires (Abbadie *et al.* 2006). This moist savanna possesses for most of the year a dense and high grass layer where scattered trees and bushes vary considerably in their abundance, leading to a high spatial heterogeneity (Figure 1). The annual precipitation attains 1200 mm and the dry season lasts less than 2 mo (Ménaut 1983). A long rainy season occurs from February to November and is usually interrupted by a

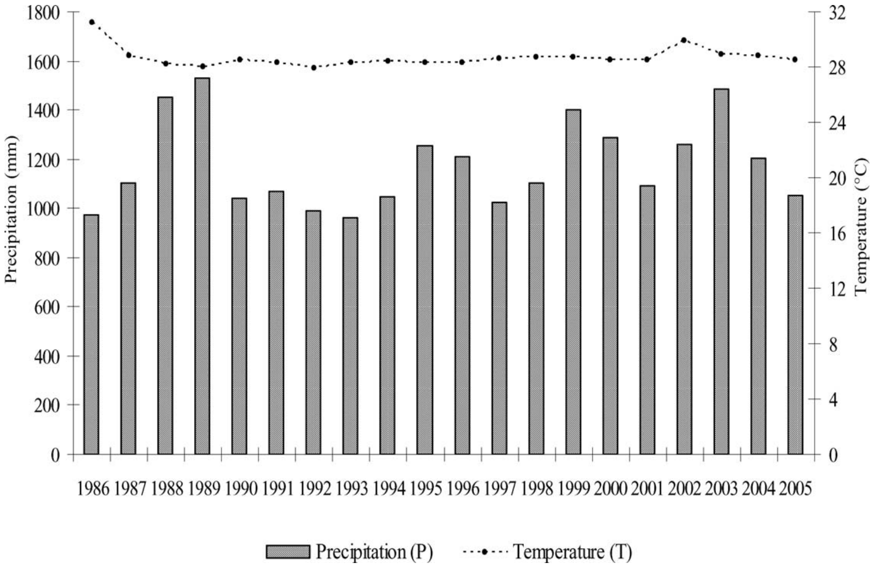

Figure 2. Total annual precipitation and mean annual temperature at Lamto over the two decades before the study (1986–2005) (data source: Station of Geophysics of Lamto).

short dry season in August; this is followed by a longer dry season in December and January. The analysis of climatic features over the two previous decades indicates that the precipitation range is 1000–1500 mm y^{-1} and the mean annual temperature is stable (Figure 2).

The habitats studied were chosen according to vegetation type and fire-history, each of them having its own characteristics. In the annually burned savanna, the tree cover ranges between 7% and 36% (Gautier 1990). This fuel-rich habitat is burned deliberately every year apart from the plots set and followed up for experiments on fire exclusion. This savanna type covers the lower part of slopes and the hydromorphic plateaux (Ménaut & Abbadie 2006). The savanna woodlands studied consisted of savanna patches randomly unburned for 5 y and strongly subjected to tree invasion (Vuattoux 1970, 1976). With a tree cover of 60%, the vegetation was a mixture of grass, tree and shrub layers (Gautier 1990). This savanna type appears mostly on slopes (Ménaut & César 1979). The impact of fire depends on the strength of the seasonal drought and mainly on the amount of fuel produced since the last fire event. The forest islands were semi-deciduous forests entirely surrounded by savannas. As these forests were not dense, their canopy was discontinuous. They possessed partly transitional vegetation comprising both forest and savanna tree species. This forest type is not impacted by fire in the interior because the grass stratum is lacking, replaced by a thin layer of leaf-litter which does not offer enough fuel to allow the fire to invade deeply inside. Only, the periphery is impacted. The gallery forest is located along the permanent Bandama River. This evergreen forest has a fully closed canopy and open undergrowth with abundant leaf litter. With regard to the physical structure, its vegetation is homogeneous and composed of only forest tree species. Although this habitat is partly in contact with the savanna, it is the best protected against fire and much more humid than the forest island.

Sampling design

Termites were sampled using a standardized method designed for rapid assessment of termite diversity by Jones & Eggleton (2000). Five separate blocks of each habitat type were sampled by delimiting at random one transect 100 m long and 2 m wide through each block. As transects were the sampling units, they were oriented so as to cover all the heterogeneity within the respective habitats. In the annually burned savanna and gallery forest which are spatially continuous, transects were separated by at least 200 m in such a manner as to be representative of the areas. Each transect was subdivided into 20 contiguous quadrats of 10 m^2 (5 × 2 m) each in order to standardize the sampling effort. In all quadrats, we hand-searched all microhabitats (logs, litter, stumps, twigs, nests, runways sheeting, fallen branches, etc.) up to a height of 2 m above ground level. As this method was designed for use in forests, we made modifications in the savanna by searching for termites between grass tufts or by uprooting them. All termites encountered were collected. Twelve samples of surface soil (each about 12 × 12 cm to 10 cm depth) were dug out in the quadrat at random locations. The soil was hand-sorted in situ and a representative sample of the termites (around 10 individuals of each termite caste present) was sorted and put into 70% ethyl alcohol. Termites collected were both of the soldier and worker castes; the alates were excluded because they did not necessarily imply the presence of a viable colony. In order to sample all 20 quadrats in one day, four trained collectors were deployed, with two people at a time sampling 10 quadrats for 30 min per quadrat. Following Andersen (1991), samplings were based on the occurrence of individuals (presence–absence) rather than their number with respect to the social habit of termites. The field work took place in July and August of 2005. This period, corresponding with the short dry season at Lamto, was especially favourable for sampling. In our area, foraging activities of termites are more evident during dry seasons as they consume preferentially dry plant matter; this allowed us easy access to a great number of species.

Identification and feeding group classification

All sampled termites were identified at the Royal Museum for Central Africa in Tervuren (Belgium). Specimens were identified to the level of species or, where this proved impossible, to numbered morphospecies using standard determination keys such as those of Webb (1961), Bouillon & Mathot (1965, 1966, 1971) and the descriptions made by Grassé (1986). After the identification, each species was placed into one of four feeding groups (fungus-growers, soil-feeders, wood-feeders and grass-feeders) defined according to termite diet (Josens 1972), mandible morphology (Deligne 1966) and gut content in the worker caste (Sands 1998). All fungus-growers belong to the subfamily Macrotermitinae. They consume grass, dung, wood and litter via an exo-symbiosis with the fungus *Termitomyces* for the decomposition of plant matter. The soil-feeders feed on soil organic matter and occasionally on very decayed wood. Most wood-feeders consume dead wood but some species feed on living plants. The grass-feeders are exclusive consumers of grassy litter. The species of the Lamto savanna belong exclusively to the genus *Trinervitermes*.

Environmental variables

Five equidistant vegetation survey plots of 100 m^2 (10 × 10 m) were established along each transect to describe the structure, diversity (on species level) and abundance of woody plants. As this component is more sensitive to fire than grasses, it is very decisive for the constancy of the respective ecosystems (Hien 1995, Sankaran *et al.* 2005). The plots were directly adjacent to the transects in order to investigate the relationship between vegetation dynamics and termite abundances. The methodology consisted in identifying and counting plant species in each plot. Plant species richness and density were used as references to detect differences in vegetation structures. At habitat level, plant species richness was defined as the mean number of species identified per transect and plant density as the average of the medians calculated per transect.

Along each transect, five soil sample composites (0–20 cm depth) were obtained by taking soils at three random locations within each plot of 10 m^2 and mixing them. These samples were air-dried and passed through a 2-mm sieve before analysing their physico-chemical properties in the laboratory as follows: $pH_{(water)}$ values were measured electronically on soil-to-water suspensions (Baize 2000), soil organic carbon was determined by the method of Anne (AFNOR 1996), total nitrogen and particle size (clay, silt and sand) by Kjeldahl and Robinson methods respectively (Anderson & Ingram 1993).

Data analysis

Sampling completeness was tested by constructing sample-based species accumulation curves and by recording the auto-similarity which is the mean similarity between transects of the same habitat type. The observed (S_{obs}) and estimated (Chao2) species accumulation curves were constructed after randomizing 500 times the sample order to ensure the statistical representation of the target community (Cao *et al.* 2002, Colwell & Coddington 1994). The mathematical formulations of the curves may be found by consulting the user guide of the online program EstimateS 7.50 (http://purl.oclc.org/estimates).

The species richness of termites was determined by enumerating the number of species observed over the whole transect. As we used presence-absence data, the relative abundance was defined as the number of encounters per transect, where the presence of one species in a quadrat represented one encounter (Magurran 2004). Following the description of Colwell & Coddington (1994) for incidence data, the second order and non-parametric estimator Chao2 was used as estimator of the species richness. It takes into account the distribution of species among quadrats and it needs for its calculation only the number of species found in just one quadrat and the number of species in exactly two. Simpson's index served to measure the diversity of the termite community. This index and its evenness were computed using the program 'Ecological Methodology' (www.Zoology.ubc.ca/Krebs). To better visualize the similarity of transects and habitats, the Unweighted Pair-Group clustering method using arithmetic Averages (UPGMA) was performed with the software STATISTICA version 6 (www.statsoft.com). The complementarity between communities allowed the description of the differences between habitats in terms of the species identity they support (Vane-Wright *et al.* 1991). We termed as 'dominant species' those whose total number of occurrences (from all habitats) equalled or exceeded the mean number of occurrences per habitat (= 20). The variation of feeding group abundances across habitats was analysed using the one-way analysis of variance whereas LSD (Least Significant Difference) post hoc comparison tests were performed to detect differences between these abundances.

Redundancy Analysis (RDA) was used to investigate the effects of environmental variables (woody plant species richness, woody plant density, soil pH, soil carbon, soil nitrogen, clay, silt and sand) on species abundances (ter Braak & Smilauer 2002) using CANOCO for windows 4.5 (www.canoco.com). For the clarity of the ordination and because of a strong colinearity between some variables, we made first a detailed examination of the correlation matrix of environmental variables in order to identify the subset to be introduced in the ordination by removing one of highly correlated variables in relative composition data from the RDA.

RESULTS

Sampling efficiency

The curves corresponding to observed species accumulation with increasing sampled area and estimated species richness were very similar for all habitats (Figure 3). Thus, the species richness observed was considered a very good estimate of that expected in each habitat. The values of auto-similarity varied little from one habitat to the next (Table 1). Transects did not differ in their taxonomic composition within the annually burned savanna, the gallery forest and the forest island for which auto-similarity values were 0.51, 0.54 and 0.48 respectively. In contrast, with 0.38 as auto-similarity value, transects belonging to the savanna woodland differed slightly among each other. The values of sampling coverage were high for all habitats (at least 83%). Overall, these findings point to a better estimation of the habitat-specific species pool of the termite communities after running five transects within each of the four habitats.

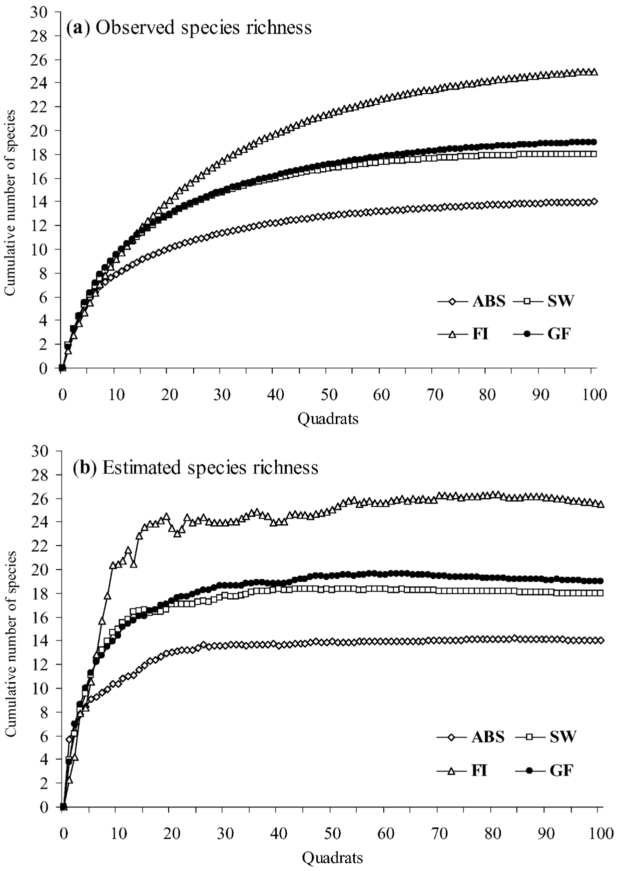

Figure 3. Sample-based accumulation curves of observed (a) and estimated species richness (b) of termites in the four habitats. Abbreviations are defined in Figure 1.

Species richness, species diversity and spatial distribution of termites

Overall, 31 species and morphospecies were found in all habitats combined (Appendix 1). By considering habitats separately, the forest island (25 species) was significantly richer than the annually burned savanna (14 species) (LSD test, $P < 0.01$, $n = 5$) and the savanna woodland (18 species) (LSD test, $P < 0.05$, $n = 5$). In contrast, the gallery forest (20 species) did not differ statistically from the savannas (Figure 4). Although the number of species varied from one habitat to the other, Simpson's diversity index was similarly high for all habitats. However, evenness was low for the savanna woodland and the forest

Table 1. Sample coverage, auto-similarity and metrics of termite diversity in the different habitats (sample coverage = ratio of the observed species richness as per cent of the estimated species richness in each habitat, auto-similarity = mean similarity between transects of each habitat, uniques = species collected only once in each habitat).

Habitats	Number of species observed	Sample coverage	Auto-similarity	Simpson's index	Evenness	Uniques
Annually burned savanna	14	93.3	0.51	0.84	0.43	1
Savanna woodland	18	85.7	0.38	0.80	0.27	3
Forest island	25	94	0.48	0.88	0.31	2
Gallery forest	20	83.3	0.54	0.9	0.46	4

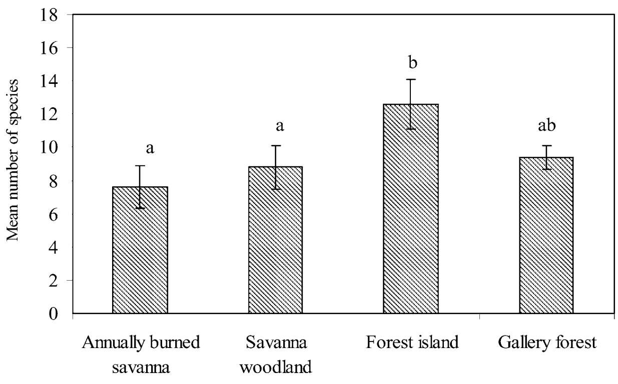

Figure 4. Termite mean species richness in habitats. Histograms with same letters did not differ significantly at P = 0.05 level (LSD post hoc comparison tests, n = 5). Bars are standard errors.

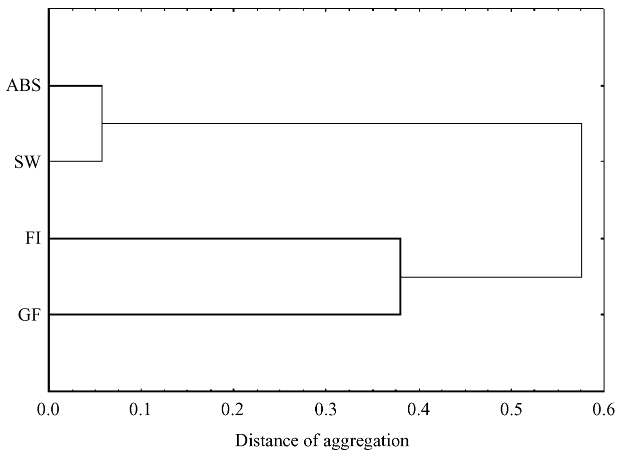

Figure 5. Classification of habitats based on their termite species composition with UPGMA (Unweighted Pair-Group Method using Arithmetic averages) using 1-Jaccard index as the distance between groups. Abbreviations are defined in Figure 1.

island and high for the annually burned savanna and the gallery forest (Table 1).

To discover how widely termite species were distributed in the habitats, we performed a cluster analysis at transect and habitat levels. At the transect level, the clusters were not formed according to the habitat type (figure not shown). In contrast, at the habitat level, two distinctive groups were formed clearly (Figure 5), each composed of habitats belonging to the two main ecosystems (i.e. savanna and forest). The complementarity showed that the termite community compositions were closely overlapping for the gallery forest and the forest island. In contrast, these two forests were very dissimilar to the annually burned savanna but only slightly so to the savanna woodland (Table 2). The annually burned savanna shared only 11 species out of 23 with the gallery forest and 12 species out of 27 with the forest island. Only two and three species collected in this regularly burned habitat were absent in the forest island and the gallery forest respectively. Out of the 18 species collected in the savanna woodland, four and six were not found in the two forest habitats respectively.

Table 2. Community complementarity (1-Jaccard's similarity index) between habitats. Data in cells are reported as follows: species in both habitats/species shared/complementarity.

Habitats	Annually burned savanna	Savanna woodland	Forest island	Gallery forest
Annually burned savanna	×			
Savanna woodland	20/12/0.40	×		
Forest island	27/12/0.56	29/14/0.48	×	
Gallery forest	23/11/0.52	25/12/0.48	26/17/0.27	×

Relative abundance of termites across habitats

According to their feeding habit, termite species were assigned to the four feeding groups listed in Table 3. The total abundance of fungus-growers did not vary significantly across habitats. However, their abundance in the savanna woodland was significantly higher than in the annually burned savanna (LSD test, $P < 0.05$, $n = 5$), the forest island (LSD test, $P < 0.05$, $n = 5$) and the gallery forest (LSD test, $P < 0.05$, $n = 5$). With significant variation across habitats, soil-feeders were less abundant in the savanna woodland than in the annually burned savanna (LSD test, $P < 0.01$, $n = 5$), the forest island (LSD test, $P < 0.01$, $n = 5$) and the gallery forest (LSD test, $P < 0.01$, $n = 5$). Better represented in forests than in savannas, the total abundance of wood-feeding species varied significantly. They were more abundant in the forest island and the gallery forest than in the annually burned savanna (LSD test, $P < 0.01$ and 0.001 respectively, $n = 5$) and in the savanna woodland (LSD test, $P < 0.05$ and 0.01 respectively, $n = 5$). In grass-feeders restricted to the annually burned savanna, the total abundance obviously varied significantly across habitats.

Using our criterion for dominant species, 8 (25.8%) out of the 31 species collected were dominant representing 461 out of 626 species occurrences. These dominant species were representative of all four feeding groups. Of the 13 fungus-growers, three were dominant (*Ancistrotermes cavithorax*, *Microtermes toumodiensis* and *Pseudacanthotermes militaris*) and represented 278 species occurrences (76.6%) out of 363. The number of occurrences of these species did not change significantly across habitats. The dominant soil-feeders were *Adaiphrotermes* sp., *Aderitotermes* sp. and *Basidentitermes potens* totalling 127 occurrences out of 156, i.e. 81.4%. Their occurrences across habitats did not vary significantly. The single dominant wood-feeding

Table 3. Variation of the relative abundances of termite feeding groups across habitats (using one-way ANOVA).

Feeding groups	Annually burned savanna	Savanna woodland	Forest island	Gallery forest	F	P-value
Fungus-growers	77	139	79	68	2.67	0.83
Soil-feeders	54	10	43	49	11.1	0.01
Wood-feeders	3	9	29	36	8.67	0.001
Grass-feeders	28	2	0	0	15.4	0.001

species (*Microcerotermes parvus*) was significantly more abundant in the two forests than in the two savanna habitats. Of overall 77 encounters with the wood-feeding species 28 were with *M. parvus* (36.4%). The grass-feeder *Trinervitermes geminatus* was restricted to the savannas and mainly to the annually burned savanna.

Effect of environmental variables on species distributions

Preliminary analysis of the correlation matrix of environmental variables allowed selecting five of the eight variables measured for redundancy analysis; these were: woody plant species richness (vegetation parameter), soil pH, soil carbon (organic matter), clay and silt (soil texture).

The ordination (RDA) of species abundances with the selected variables yielded eigenvalues of 0.143 for the first axis and 0.107 for the second while lower eigenvalues were found for the third and the fourth axes (0.057 and 0.031 respectively). All axes showed high correlations between species and variables; the coefficients were 0.888, 0.863, 0.851 and 0.783 respectively (Table 4). Of the variables included in the ordination, only two (pH and woody plant species richness) explained significant variation in species abundances (Monte-Carlo permutation tests for the pH: $F = 2.13$, $P < 0.01$, for woody plant species richness: $F = 1.96$, $P < 0.05$) (Figure 6). As the cosine of the angle between the arrows of a species and an environmental variable is an approximation of the correlation coefficient between the species and the environmental variable, some species (*P.* aff. *spiniger*, *P. militaris*, *Odontotermes* sp. 2, *Odontotermes* sp. 1, *F. tenebricus*, *A. guineensis*, *A. cavithorax*, *A. evuncifer* and *Astratotermes* sp.) were inferred to be positively correlated with the pH. If arrows are drawn for these species, they make sharp angles with the arrow for pH. This inference was better supported for *P.* aff. *spiniger*, *P. militaris*, *Odontotermes* sp. 2, *Odontotermes* sp. 1, *F. tenebricus*, *A. guineensis* and *A. cavithorax* than for *A. evuncifer* and *Astratotermes* sp. because the former species lie much further from the centre of the diagram than the latter two species. In contrast, *M. fuscotibialis*, *Odontotermes* sp. 3 and *N. latifrons* were negatively correlated with the pH. As for woody plant species richness, it showed strong negative correlations with the grass-feeders *T. geminatus* and *T. oeconomus* and the soil-feeders *Adaiphrotermes* sp. and *Aderitotermes* sp.; all those species were better represented in the annually burned savanna than in other habitats. Surprisingly, some wood-feeding species (*N. arborum*, *N. latifrons*, *M. fuscotibialis* and *M. parvus*) did not show significant correlations with this vegetation parameter. Although not decisive in the overall variation of species abundances, soil carbon was clearly positively correlated with the soil feeder *B. potens*. Overall, a number of species showed little change in their abundance in relation to environmental variables; this fact was illustrated by their positions towards the centre of the diagram.

DISCUSSION

Sampling efficiency

We evaluated sampling efficacy with sample-based species accumulation curves and auto-similarity of transects within the same habitats. With 100 quadrats of 10 m^2 the termite species richness was efficiently assessed in most habitats. This fact was illustrated on the one hand by the plateaux attained by the observed species accumulation curves, and on the other hand by high auto-similarity values for the gallery forest, the annually burned savanna and the forest island. Our data were close to those of Roisin & Leponce (2004) concerning the link between the species accumulation curves and the number of unique species. In fact, the

Table 4. Summary statistics for RDA with the environmental variables.

Axes	1	2	3	4
Eigenvalues	0.143	0.107	0.057	0.031
Species-variable correlations	0.888	0.863	0.851	0.783
Cumulative % variance of species data	14.3	25	30.7	33.8
Cumulative % variance of species-variable relationships	40.7	71.2	87.5	96.3
Sum of all unconstrained eigenvalues: 1.000				
Sum of all canonical eigenvalues: 0.351				

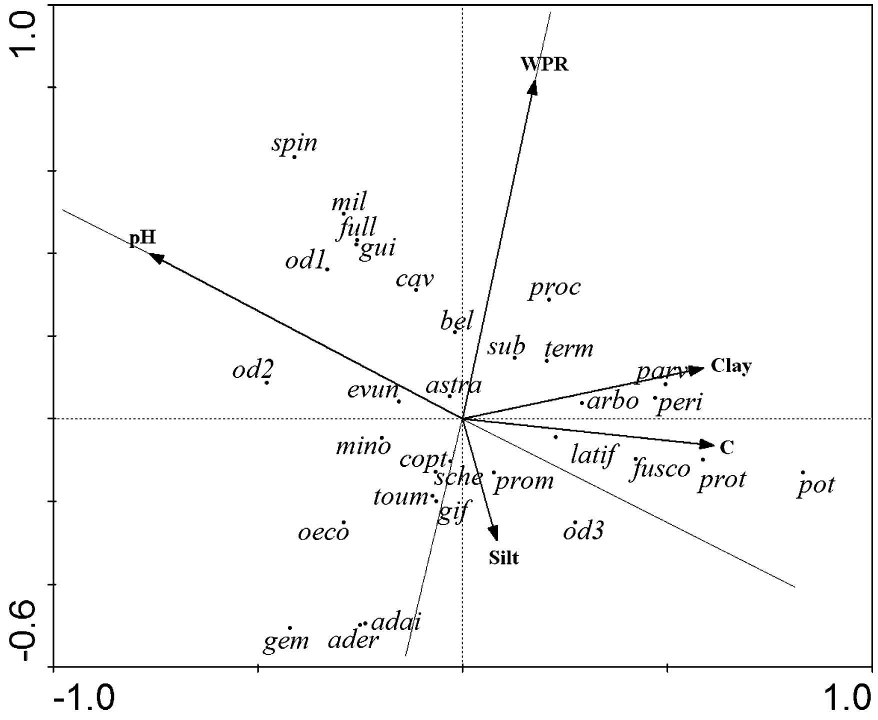

Figure 6. Diagram of RDA ordination of termite species abundances and environmental variables (data with arrows). Species abbreviations: cav, *Ancistrotermes cavithorax*; gui, *Ancistrotermes guineensis*; bel, *Macrotermes bellicosus*; sub, *Macrotermes subhyalinus*; gif: *Megaprotermes giffardii*; toum, *Microtermes toumodiensis*; od1, *Odontotermes* sp. 1; od2, *Odontotermes* sp. 2; od3, *Odontotermes* sp. 3; mil, *Pseudacanthotermes militaris*; mino, *Pseudacanthotermes* aff. *minor*; spin, *Pseudacanthotermes* aff. *spiniger*; evun, *Amitermes evuncifer*; adai, *Adaiphrotermes* sp., ader, *Aderitotermes* sp.; astra, *Astratotermes* sp.; pot, *Basidentitermes potens*; peri, *Pericapritermes* sp.; proc, *Procubitermes* sp.; prom, *Promirotermes* sp.; term, *Termes* sp.; copt, *Coptotermes* sp.; full, *Fulleritermes tenebricus*; fusco, *Microcerotermes fuscotibialis*; parv, *Microcerotermes parvus*; arbo, *Nasutitermes arborum*; latf, *Nasutitermes latifrons*; lama, *Schedorhinotermes lamanianus*; gem, *Trinervitermes geminatus*; oeco, *Trinervitermes oeconomus*. Variable abbreviations: WPR, woody plant species richness, C, soil carbon.

species accumulation curves level off when the number of unique species starts decreasing, which was observed in our study with regard to the low number of unique species in habitats despite the high sample coverage.

Our data provided also a good picture of termite species composition with five transects per habitat contrary to Jones & Eggleton (2000) who used only one transect. At least 80% of the expected termite species were sampled in each habitat while these authors found only 31–36% of the known local pool of termite species. They were satisfied with this in the sense that the taxonomic and functional group composition of the transect samples did not differ significantly from that of the known local fauna. In this study, the far more complete assessment of termite species richness and diversity in the savanna systems resulted on the one hand from the modification made (searches of termites between grass tufts or by uprooting them), and on the other hand from the increase of sampling effort by sampling more transects per habitat.

Thus, after successfully testing the efficiency of the method, our objective of assessing termite diversity and abundance across four habitats of the Lamto reserve differing in the vegetation cover and the fire-history could be addressed.

Species richness and species diversity of termites

As expected, more species were collected in the gallery forest and the forest island than in the annually burned savanna and the savanna woodland. Given that the two forests are not impacted by fire considered as the major cause of disturbance in the study area, their termite community was expected to vary little (Farji-Brener *et al.* 2002, Hoffmann 2003, Parr *et al.* 2002). The forest island was even significantly richer than the annually burned savanna and the savanna woodland. As this forest is embedded in the savanna, it may harbour many termites by serving as refuge for species sensitive to regular fire occurrences and also by providing variable sources of nourishment with regard to its transitional (i.e. mixed savanna and forest) vegetation (Grassé 1986). In contrast, the number of species found in the gallery forest was close to that of the savanna woodland and it did not even differ to that of the annually burned savanna. With fire being the major cause of disturbance in the Lamto savanna (Ménaut & Abbadie 2006, Ménaut & César 1982, Ménaut *et al.* 1990, Monnier 1968), our findings suggests to refer to the intermediate disturbance hypothesis of Connell (1978) for explaining this pattern of termite species richness. It states that the maximum species richness occurs at an intermediate intensity and frequency of natural disturbance. In agreement with this statement, the development of species richness within the different habitats may be explained by the fact that the annually burned savanna allows the persistence of only disturbance-adapted species, while the most protected gallery forest might favour competitive dominance of some species preventing other species from successful settling. Nearby these two contrasting habitats, there are savanna woodlands and forest islands which are only impacted by intermediate levels of disturbance allowing the maintenance of many species. The assessment of community complementarity pointed to their intermediate species compositions with the savanna woodland still close to the annually burned savanna and the forest island closer to the gallery forest.

The species diversity index was high and almost identical for all habitats. This result suggests considering additional causal factors beside vegetation type and fire-history, for instance decomposers and predators, to better understand the pattern of termite diversity in the Lamto ecosystem. Analogous observations were made on ants across differing fire-treated habitats in the Kruger National Park (South Africa) by Parr *et al.* (2004). While the mean ant species richness and abundance did not vary significantly between treatments, significant differences were observed between regularly burned and unburned plots in the community composition. However, our results contrasted to those of other authors (Scholes & Walker 1993, van Langevelde *et al.* 2003) who considered fire to cause only important damage to biodiversity in savanna systems. Regarding the evenness values, termite specimens were more equitably distributed between species in the homogeneous habitats i.e. the annually burned savanna and the gallery forest. In contrast, in the savanna woodland and the forest island, possessing more heterogeneous and transitional structures, termites were not evenly distributed. This finding suggests that habitat structure may be of great importance for the spatial dynamics of termites (Farji-Brener *et al.* 2002, Gillison *et al.* 2003, Lawton 1983, McCoy & Bell 1991, Tews *et al.* 2004).

Termite abundances and effects of environmental variables

With 58% of the total occurrences, fungus-growers were the best-represented feeding group across habitats. Neither their total abundance nor that of the dominant species (*A. cavithorax*, *M. toumodiensis* and *P. militaris*) varied significantly. Thus, they were not strongly affected by habitat variability; probably because of their high ecological plasticity partly based on the homeostatic properties of their mounds and the association with symbiotic fungi (Konaté 1998). The pH was the most influential variable, for instance for *A. cavithorax*, *A. guineensis*, *Odontotermes* sp. 1, *Odontotermes* sp. 2, *P. militaris* and *P.* aff. *spiniger*. Alkaline environments seem to favour fungus-growing species, which agrees with Boyer (1973) who found high concentrations of basic elements in the mounds of the genus *Macrotermes.* They consume very large amounts of litter in tropical savannas (Josens 1974); so much that Watson (1977) attributed to them the poverty of these soils in organic matter. In other respects, the species *Protermes* sp. found exclusively in the gallery forest was negatively correlated with this factor. It was not collected in savannas but its exact feeding and habitat preferences are still unknown.

As for soil-feeders, the total abundance varied significantly across habitats but that of the three dominant species (*Adaiphrotermes* sp., *Aderitotermes* sp. and *B. potens*) did not. Surprisingly, this feeding group was more represented in the annually burned savanna (the habitat poorest in organic matter) than in the two forest types (Abbadie & Nacro 2006). This result agrees with Tano (1993) who found this group abundantly in the Sudanian savanna of Booro-Borotou (north-western Côte d'Ivoire) which is also poor in resources. Such observations were made in other African areas; for instance, in the surroundings of Lubumbashi (Democratic Republic of Congo) where their biomass attained 5.26 kg m^{-2} in the savanna against 2.17 kg m^{-2} in the semi-deciduous forest and 0.17 kg m^{-2} in the primary forest (Freson *et al.* 1974). Although they feed preferentially on organic matter, only one species (*B. potens*) showed significant positive correlation with soil carbon. In the annually burned savanna, the organic matter is irregularly distributed through the soil profile due to the absence of dense tree root systems that maintain organic material in the superficial layers (Pirovano 1996). Following Braumann *et al.* (2000), the dominance of *Adaiphrotermes* sp. and *Aderitotermes* sp. in this savanna could be explained by the fact that they feed not only on relatively well-dispersed soil organic matter but also on highly fragmented plant tissues and refractory debris such as lignified cell walls, old xylem vessels and their dismembered secondary thickenings.

As expected, the relative abundance of wood-feeders was higher in the forests than in the savannas because of large amounts of dead wood, dead stumps, leaf litter and living woody plants (Jones *et al.* 2003). This pattern was most pronounced in the only dominant species (*M. parvus*). However, none of the wood-feeding species (*N. arborum*, *N. latifrons*, *M. fuscotibialis* and *M. parvus*) showed a significant correlation with woody plant species richness. As these species feed also on dead wood and litter (Josens 1972) one would expect them to be more tolerant to moderate tree invasion.

The grass-feeding species (*T. geminatus* and *T. oeconomus*) were restricted to savanna habitats and particularly to the annually burned savanna which provides very large quantities of grass. Tree invasion is a negative factor for grass-feeders as shown by the significant negative correlation between these species abundances and woody plant species richness.

ACKNOWLEDGEMENTS

We thank Kouassi Kouassi JB, N'Goran Bernard, Koffi Toussaint and Koffi Louis for their technical assistance in the field. We are grateful to Professor Jean Deligne (Royal Museum for Central Africa, Belgium) for his supervision during the identification of termites and to Professor Maurice Leponce (Royal Belgian Institute of Natural Sciences) for his helpful comments on the first draft of this manuscript. This study was conducted in the frame of the BIOTA-West project funded by the German Federal Ministry of Education and Research (BMBF).

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Appendix 1. List of species and morphospecies collected and their frequency of occurrences in the habitats. The dominant species are in bold and the symbol * indicates those whose frequency of occurrences varied significantly across habitats. Abbreviations: fg, fungus-growers; sf, soil-feeders; wf, wood-feeders; gf, grass-feeders.

Species or morphospecies	Feeding groups	Annually burned savanna	Savanna woodland	Forest island	Gallery forest
Ancistrotermes cavithorax (Sjöstedt) 1899	fg	44	65	48	34
Ancistrotermes guineensis (Silvestri) 1912	fg	0	7	4	0
Macrotermes bellicosus (Smeathman) 1781	fg	2	8	1	4
Macrotermes subhyalinus (Rambur) 1842	fg	0	0	6	0
Megaprotermes giffardii Ruelle 1978	fg	0	0	0	2
Microtermes toumodiens Grassé 1937	fg	21	11	10	12
Odontotermes sp. 1	fg	5	9	2	2
Odontotermes sp. 2	fg	2	8	1	1
Odontotermes sp. 3	fg	0	0	2	1
Protermes sp.	fg	0	0	2	6
Pseudacanthotermes militaris (Hagen) 1858	fg	3	21	3	6
Pseudacanthotermes aff. *minor* (Sjöstedt) 1913	fg	0	1	0	0
Pseudacanthotermes aff. *spiniger* Sjöstedt 1926	fg	0	9	0	0
Adaiphrotermes sp.	sf	18	2	6	15
Aderitotermes sp.	sf	29	5	3	9
Amitermes evuncifer Silvestri 1912	sf	2	2	5	1
Astratotermes sp.	sf	1	0	4	0
Basidentitermes potens Silvestri 1914	sf	4	1	13	22
Pericapritermes sp.	sf	0	0	4	2
Procubitermes sp.	sf	0	0	3	0
Promirotermes sp.	sf	0	0	3	0
Termes sp.	sf	0	0	2	0
Coptotermes sp.	wf	0	0	2	3
Fulleritermes tenebricus (Silvestri) 1914	wf	0	2	0	0
Microcerotermes fuscotibialis (Sjöstedt) 1896	wf	0	3	3	5
Microcerotermes parvus $*$ (Haviland) 1898	wf	3	3	7	15
Nasutitermes arborum (Smeathman) 1781	wf	0	0	7	10
Nasutitermes latifrons (Söstedt) 1896	wf	0	1	8	1
Schedorhinotermes lamanianus (Sjöstedt) 1911	wf	0	0	2	2
Trinervitermes geminatus $*$ (Wasmann) 1897	gf	26	2	0	0
Trinervitermes oeconomus (Trägardh) 1904	gf	2	0	0	0