

Feeding ecology and phylogenetic structure of a complex neotropical termite assemblage, revealed by nitrogen stable isotope ratios

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Abstract

1. In the current ecological classification of termites, four feeding groups (I-IV) are recognised, corresponding to a gradient of decomposition from sound wood to highly mineralised organic matter in the soil.
2. Nitrogen stable isotopes (hereafter $\delta^{15}\text{N}$) were used to place termites from French Guiana rainforests along a wood-soil decomposition gradient, to test (i) whether feeding group assignation based on morphological characters was accurate and actually represented diet specialisation thresholds, and (ii) to what extent the dietary specialization of species is explained by phylogeny (phylogenetic autocorrelation).
3. $\delta^{15}\text{N}$ values vary over a range of 13‰, suggesting that diet diversification contributes to the high species diversity in French Guiana. $\delta^{15}\text{N}$ values span a similar interval in all Termitidae subfamilies. Ranges of different subfamilies broadly overlap, although each of them diversified preferentially on one side of the wood-soil decomposition gradient. Congeneric species share similar feeding habits, whereas distant species tend to feed on distinct substrates.
4. Feeding groups did not completely match stable isotope data: there was no discontinuity between Groups III and IV, and no correlation between anatomical criteria used to distinguish these groups and $\delta^{15}\text{N}$ values. Nor was there any consistent difference in $\delta^{15}\text{N}$ values between wood feeders of the families Rhinotermitidae (Group I) and Termitidae (Group II). We also suggest that species feeding outside the wood-soil gradient should be distinguished for their peculiar feeding requirements.

Keywords : Diet diversity ; feeding groups ; Isoptera ; phylogenetic autocorrelation.

Introduction

In comparison to the tremendous arthropod diversity found in tropical rainforests, termites represent a minor order, comprising no more than 150 species in the richest sampling sites (Davies *et al.*, 2003a). The opposite is true for their ecological significance as they represent one of the most important groups in terms of biomass (Fittkau & Klinge, 1973; Martius, 1994; Eggleton *et al.*, 1996) and are the principal animal decomposers of organic matter and ecosystem engineers in the tropics (Holt & Lepage, 2000; Sugimoto *et al.*, 2000; Jouquet *et al.*, 2006). In contrast to many insects living in close association with their host plants (Novotny *et al.*, 2002; Weiblen, 2002), termites are generalists in terms of the tree taxa they feed on. However, each species specialises on one kind of organic matter quality, ranging from sound wood or leaf litter to highly humified residues in the soil. The diversity of their diet is highest in the family Termitidae, whose representatives can exploit sound or decayed wood, litter, grasses, lichens, soil, or fungi that they cultivate in their nests (Abe, 1979). This food source diversification is not randomly distributed on the termite phylogenetic tree, as some lineages are specialised towards a particular kind of feeding substrate (Inward *et al.*, 2007). For example, the Macrotermitinae are the only fungus-growing termites, and most Apicotermitinae are soil-feeders. By contrast, such a diversity in feeding habits does not exist in other termite families, whose species are all wood feeders, with the exception of the Hodotermitidae, which feed on grasses (Bignell & Eggleton, 2000).

A convenient way to classify biological diversity is to order it into groups of related taxa. Similarly, ecologists have defined groups of species which are not obligatorily related but share ecological traits. Two ecological classifications reflecting different features of termite biology have been proposed: (i) Abe (1987) recognised the single-piece nesters, the intermediate nesters and the separate-piece nesters according to the degree of

association between nest sites and food sources, (ii) Termite species have also been classified into four groups (I-IV, representative of stages of organic decomposition from sound wood to soil organic matter) according to the materials they consume, as determined by gut content analysis (Donovan *et al.*, 2001). These feeding groups are supposed to correlate with a few morphological characters, which can be assessed without the need of gut content analysis. These groups have been used in several studies and sometimes integrated into further classifications (e.g. 'lifeways' in Eggleton & Tayasu, 2001; 'functional taxonomic groups' in Davies *et al.*, 2003a; Jones & Eggleton, 2011) and are still currently in use (e.g. Jones *et al.*, 2010; Ruckamp *et al.*, 2010). However, we recently found that the criteria used to distribute species between groups III and IV, when applied to neotropical Apicotermatinae, did not correlate with feeding niches (Bourguignon *et al.*, 2009).

Ratios of stable isotopes of nitrogen (hereafter $\delta^{15}\text{N}$) constitute an extremely useful tool for studying food webs, especially those involving arthropod communities where individual interactions are often difficult to investigate through direct observation (Hood-Nowotny & Knols 2007). Typically, their use relies upon the fact that stable isotope composition of an individual is the weighted average of the isotopic compositions of its potential food source, allowing the food pathway to be identified (Post, 2002; Vanderklift & Ponsard, 2003; Hyodo *et al.*, 2010). A gradual enrichment in ^{15}N along a humification gradient, from sound wood to heavily mineralised organic matter, is observed and allows us to distinguish these different food sources and their use by the termite species (Martinelli *et al.*, 1999, Krull *et al.*, 2002; Tiunov, 2007). The ^{15}N enrichment results from a combination of interrelated mechanisms, which are not fully understood yet, including the activities of microorganisms and plant roots (Högberg, 1997; Kramer *et al.*, 2003; Dijkstra *et al.*, 2008). This property of $\delta^{15}\text{N}$ is decisive to infer the trophic position of termites (Tayasu *et al.*, 1997, 1998, 2002; Bourguignon *et al.*, 2009). In the Mbalmayo forest, Cameroon, $\delta^{15}\text{N}$ values are below 8‰ for wood feeders, but reach above 12‰ for true soil feeders (Tayasu *et al.*, 1997). The same is true for termites from the Darwin area (northern Australia), but with globally lower $\delta^{15}\text{N}$ values: wood feeders fall below 3‰, soil feeders are above 5.5‰, and interface feeders are somewhere in between (Tayasu *et al.*, 1998). More recently, species-specific patterns were demonstrated in the soil-feeding species from the *Anoplotermes*-group (Bourguignon *et al.*, 2009). Altogether, these studies clearly demonstrate the suitability of stable isotope analysis in identifying food webs and in situating termite niches along a humification gradient.

With over 100 species representing the four feeding groups, French Guiana hosts one of the most diverse termite assemblages (Davies *et al.*, 2003b; Bourguignon *et al.*, 2011). In the present study, we examined the $\delta^{15}\text{N}$ signatures of termite species collected from two French Guiana forests. Our aim was threefold:

- 1 With the exception of our recent study on feeding niche diversification in neotropical *Anoplotermes*-group members (Bourguignon *et al.*, 2009), neotropical termite feeding habits have never been investigated with stable isotopes. Here, we provide further insights into the feeding ecology of neotropical termites and make a comparison with other continents.
- 2 Termite food source diversification reaches its maximum among species of Termitidae. However, it is still not known how commonly the shift from one food source to another has occurred (i.e. in how many clades), and if diet specialisation can act as a driver of speciation. To provide some clues, we investigate to what extent ecological niche evolution is conservative, making closely related taxa share similar niches (Losos, 2008).
- 3 Termite feeding groups, as defined by Donovan *et al.* (2001) from gut content analysis, are a tool to categorise ecologically similar species, but stable isotopes should provide useful additional data and corroboration. Here we test the feeding group concept (Donovan *et al.*, 2001) and its derivatives (lifeway groups: Eggleton & Tayasu, 2001; functional taxonomic groups: Davies *et al.*, 2003a) with isotopic data.

Materials and methods

Study site

Field work was conducted in two French Guiana forests: (i) near the Petit Saut dam (N05°04', W 52°59') between 18 January and 21 February 2008; and (ii) in the Nouragues Nature Reserve (N04°05', W52°41') between 13 and 23 April 2008. Both forests experience about 3000 mm of rainfall per year, mostly occurring between January and June and with a dry season from July to November. The mean annual temperature is 26 °C. Both sites are covered by mature lowland forest on well-drained soil, with an average canopy height reaching 30-40 m. Petit Saut was undisturbed until 1988, when construction of the hydroelectric dam began (for further details, see Cosson *et al.*, 1999). The Nouragues Nature Reserve is uninhabited and almost completely preserved from human-related disturbances.

Sampling

All possible habitats likely to host termites were thoroughly investigated, e.g. soil, pieces of wood or nests. For each foraging party encountered, two subsamples were taken: one series of individuals was prepared for isotopic analysis, as described below, whereas a voucher sample was kept in 80% alcohol for species identification. Termite samples were first classified into morpho-species based on the morphology of soldiers and workers. To help in identifying samples to genus and species levels, we referred to extensive taxonomic studies (Emerson, 1925; Mathews, 1977), keys (Constantino, 2002), revisions of particular taxa (Krishna & Araujo, 1968) and comparisons with type material for the Rhinotermitidae, Termitinae, and Apicotermitinae. Termites were allocated to one of the four feeding groups defined by Donovan *et al.* (2001), either after examination of the worker mandibles and digestive tract or according to group assignments by Davies *et al.* (2003b).

Isotopic analysis

Between 10 and 50 termite workers, depending on size, were collected and pooled to obtain a sufficient amount of material for isotopic analysis. To obtain comparable isotopic values between species, only workers were analysed and other castes were not taken into account. To avoid contamination by ingested material, all the termite specimens were dissected and the digestive tract removed. Then, specimens were dried at 60 °C for 24 h and air-freighted to Belgium. Dried samples were weighed in tin capsules and stored in a desiccator until used for analysis. Nitrogen stable isotope ratios ($\delta^{15}\text{N}$) were measured on a V.G. Optima (Isoprime, UK) IR-MS coupled to an N-C-S elemental analyser (Carlo Erba, Italy). Stable isotope ratios were expressed as a delta (δ) in ‰ according to:

$$\delta^{15}\text{N} = \left[\frac{(^{15}\text{N}/^{14}\text{N})_{\text{sample}}}{(^{15}\text{N}/^{14}\text{N})_{\text{standard}}} - 1 \right] \times 1000 \quad (1)$$

where $(^{15}\text{N}/^{14}\text{N})_{\text{standard}}$ is the isotopic ratio of the international standard (atmospheric N_2). The reference material was IAEA-N1 ($\delta^{15}\text{N} = +0.4 \pm 0.2\text{‰}$). Experimental precision (based on the standard deviation of one termite sample used as an internal standard) was within 0.30‰. We did not take $\delta^{13}\text{C}$ into account because it is poorly informative concerning the degradation level of the organic matter termites feed on (Bourguignon *et al.*, 2009).

Data analysis

Representatives of four termite families were collected for this study: Kalotermitidae, Serritermitidae, Rhinotermitidae, and Termitidae. In the last family, which encompasses species with the most diversified feeding habits, we recorded four subfamilies: Apicotermitinae, Termitinae, Syntermitinae, and Nasutitermitinae. We computed a Bartlett test using species mean $\delta^{15}\text{N}$ values to determine if variance differed among subfamilies, and thereby investigate if a similar variation in the feeding substrates occurred for every Termitidae subfamily. We also computed a one-way ANOVA to determine if average species mean values differed among subfamilies. If significant, we computed a Tukey *post hoc* test to compare pairs of subfamilies. The analyses were carried out on Petit Saut and Nouragues data separately.

To investigate phylogenetic patterns of termite diet, we computed phylogenetic correlograms of species mean $\delta^{15}\text{N}$ using Moran's I index as autocorrelation coefficient (Diniz-Filho, 2001). Using taxonomy as a proxy for phylogeny, we distinguished three non-overlapping phylogenetic distance classes: intra-generic, intra-subfamily, and inter-subfamily (or intra-family), to which we gave divergence limits of 1, 2, and 3 respectively. A significantly positive (respectively negative) Moran's I index for a given class means that the species being compared within this class are on average more (respectively less) similar than two random species in the sample considered. Statistical significance under the null hypothesis of random distribution of species ecological traits was tested for each class by comparing the observed Moran's I index with its distribution obtained for 999 permutations of mean $\delta^{15}\text{N}$ values among species, breaking the phylogenetic signal. Analyses were performed on Nouragues and Petit Saut data separately, using the software SPACoDi0.10 (Hardy, 2010).

To test whether termite species from the four feeding groups really differed in their feeding habits, we compared them using a one-way ANOVA applied on the species mean $\delta^{15}\text{N}$ values. A Tukey *post hoc* test was then carried out to compare each pair of feeding groups separately. The analyses were carried out on Petit Saut and Nouragues data separately.

Results

Altogether, we collected 289 termite samples representing 70 species: 136 samples representing 44 species were collected around the Petit Saut dam, whereas 153 samples and 56 species were collected in the Nouragues Nature Reserve. The $\delta^{15}\text{N}$ ranged from 0.4‰ to 13.3‰ at Petit Saut (Fig. 1) and from 3.1‰ to 16.5‰ in Nouragues (Fig. 2).

Unlike Kalotermitidae and Serritermitidae, which were only found at Petit Saut, all the subfamilies of Termitidae were found both at Petit Saut and in Nouragues (Figs 1, 2). The variance of mean species $\delta^{15}\text{N}$ values did not differ between Termitidae subfamilies (Bartlett's test: Petit Saut: $\chi^2 = 2.14$, d.f. = 3, $P = 0.54$; Nouragues: $\chi^2 = 1.80$, d.f. = 3, $P = 0.62$) but the average mean values did (one-way ANOVA: Petit Saut: $F_{3,43} = 30.45$, $P < 0.001$; Nouragues: $F_{3,48} = 9.44$, $P < 0.001$). Comparisons between subfamily pairs using a Tukey's *post hoc* test revealed that only Apicotermitinae differed from Termitinae ($P = 0.001$) and Nasutitermitinae ($P < 0.001$) in Nouragues, whereas all the comparisons differed in Petit Saut ($P < 0.005$), except the one between Apicotermitinae and Syntermitinae ($P = 0.96$).

Phylogenetic correlograms indicated significantly positive phylogenetic autocorrelation at the genus level for species mean $\delta^{15}\text{N}$ values (Nouragues: Moran's $I = 0.83$, $P < 0.001$; Petit Saut: Moran's $I = 0.60$, $P < 0.001$). The same was true at the subfamily level, but only in Petit Saut (Moran's $I = 0.21$, $P = 0.015$), whereas the signal was not significant in Nouragues (Moran's $I = -0.01$, $P = 0.863$). Conversely, species from distinct subfamilies tend to feed on distinct substrates (Nouragues: Moran's $I = -0.16$, $P < 0.001$; Petit Saut: Moran's $I = -0.12$, $P < 0.001$). In other words, the more related the species, the more similar their diet (Fig. 3).

Species from the four feeding groups differed significantly in their $\delta^{15}\text{N}$ values, both at Petit Saut (ANOVA: $F_{3,41} = 21.93$, $P < 0.001$) and in Nouragues (ANOVA: $F_{3,52} = 22.16$, $P < 0.001$) (Fig. 4); however, a Tukey's *post hoc* test revealed that not all groups differed significantly from one another: Group I did not differ from Group II (Petit Saut: $P = 0.998$; Nouragues: $P = 0.999$) and Group III did not differ from Group IV (Nouragues: $P = 0.987$; Petit Saut: $P = 0.31$). The other comparisons were all found to be significant ($P < 0.001$).

Fig. 1. Distribution of $\delta^{15}\text{N}$ values (mean \pm SD) for termite species collected from Petit Saut, grouped by family or subfamily. SD is depicted for all species with three or more occurrences.

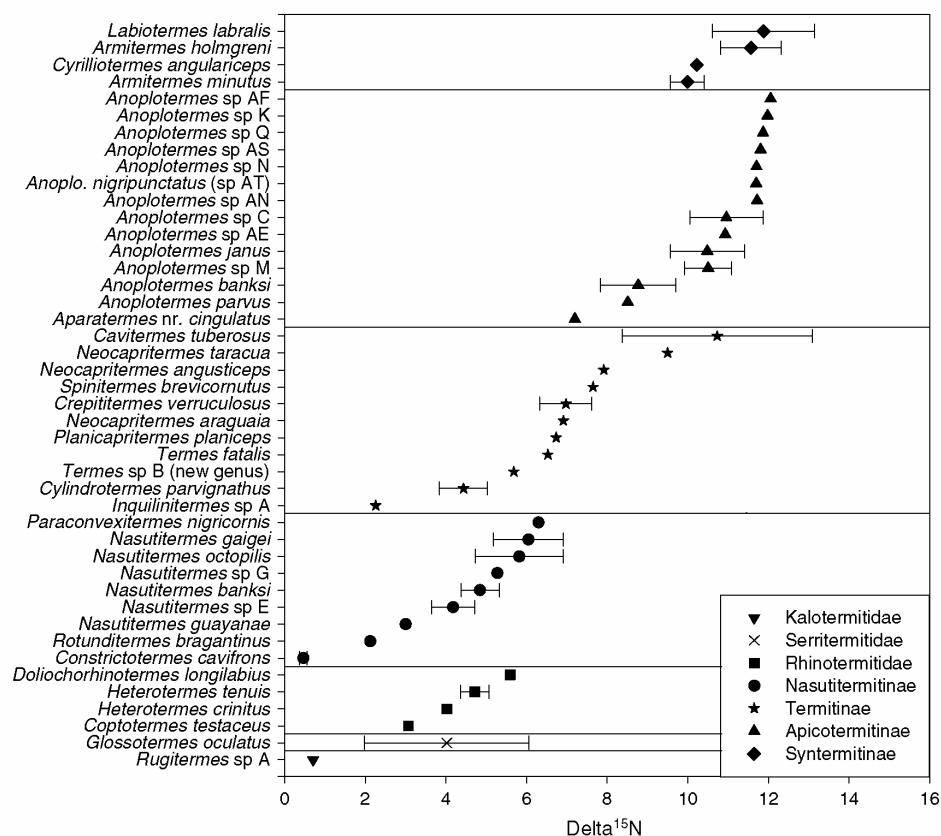


Fig. 2. Distribution of $\delta^{15}\text{N}$ values (mean \pm SD) for termite species collected from the Nouragues Nature Reserve, grouped by family or subfamily. SD is depicted for all species with three or more occurrences.

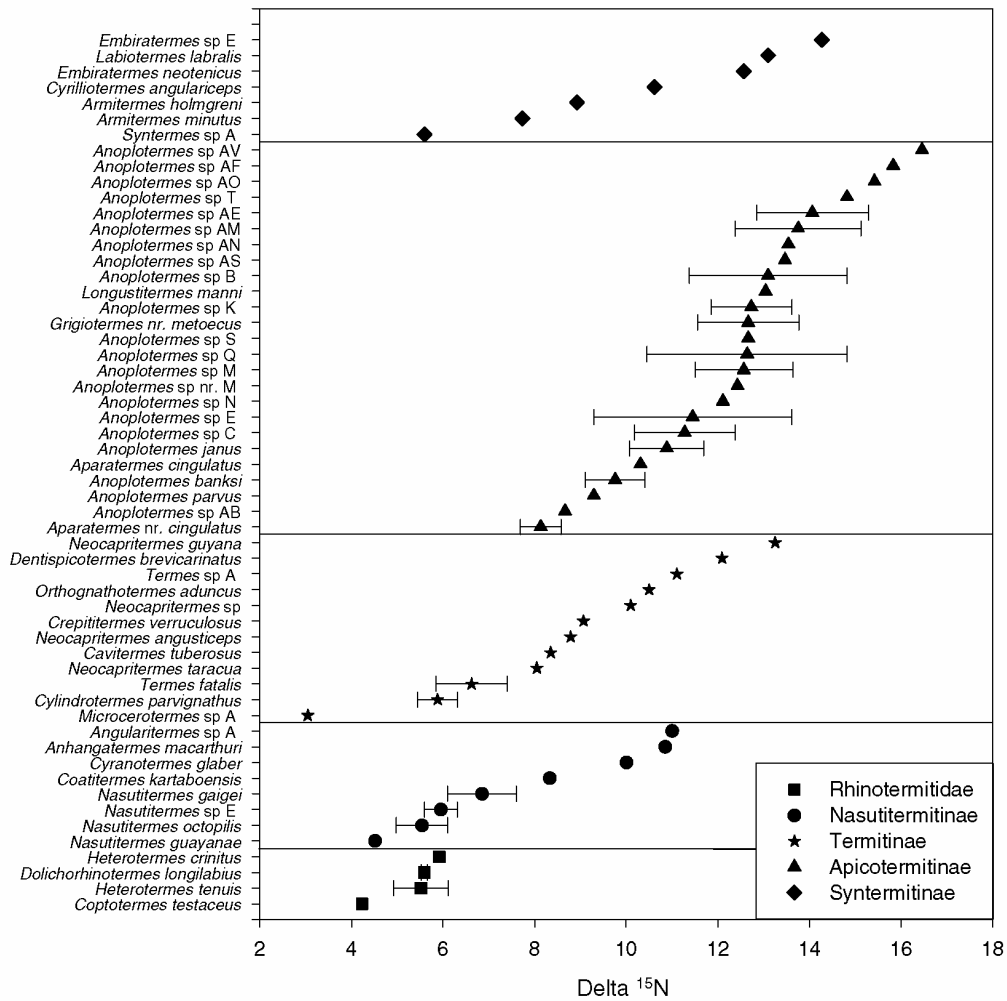


Fig. 3. Phylogenetic correlogram of $\delta^{15}\text{N}$ values pooled per species using Moran's I coefficients for three taxonomic distances between species. Analyses were undertaken on 38 and 52 species in Petit Saut and in Nouragues, respectively. Moran's $I > 0$ indicates phylogenetic clumping, $I < 0$ indicates overdispersion. The significance of the deviation from $I = 0$ is given as P -values next to the symbols.

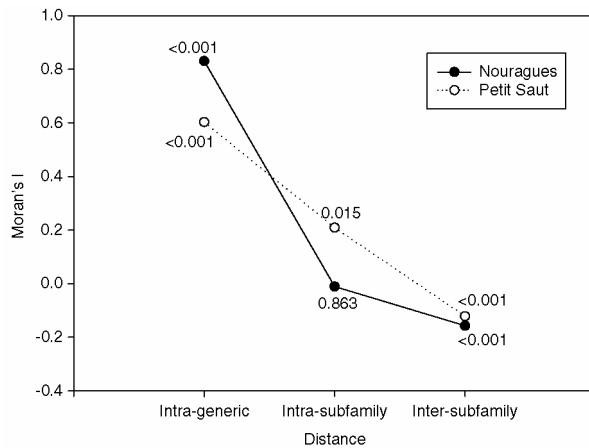
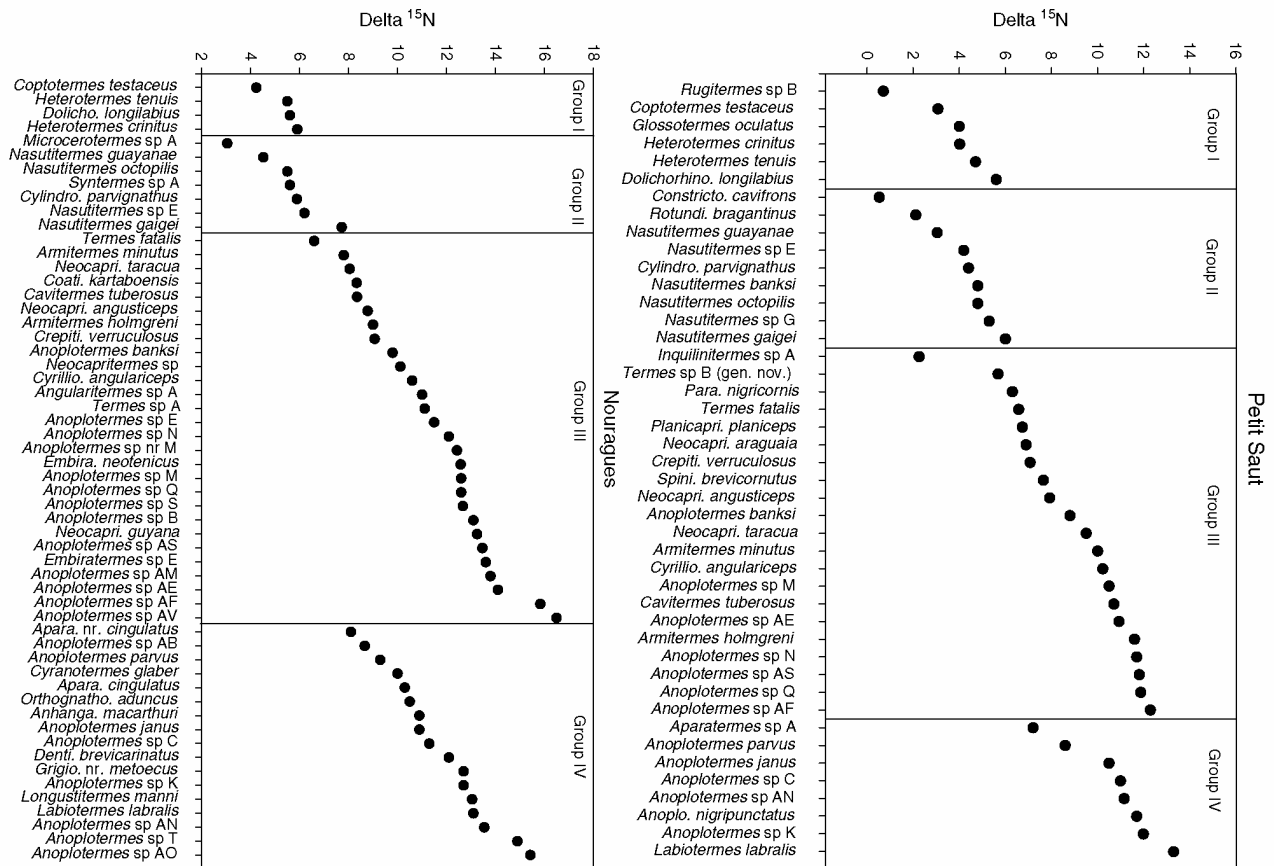


Fig. 4. Distribution of $\delta^{15}\text{N}$ values (mean \pm SD) for termite species collected from Petit Saut and from the Nouragues Nature Reserve, classified by feeding group according to Donovan et al. (2001).



Discussion

Feeding ecology of French Guiana termites

Nitrogen isotope ratios varied roughly over a range of 13‰, both at Petit Saut and in the Nouragues Nature Reserve, with a general trend for higher values in the latter site. If we only retain the species feeding on the wood-soil decomposition gradient (by removing the lichen feeder *Constrictotermes cavifrons*) and remove the lower termites, which do not display an important food source diversification as the Termitidae do, then the $\delta^{15}\text{N}$ range falls to 11‰ in Petit Saut. Following the same criteria, previous studies found $\delta^{15}\text{N}$ ranging over 7‰ in Australia (Tayasu et al., 1998), 13-16‰ in Africa (Tayasu et al., 1997; Hyodo et al., 2008), and 11‰ in Thailand (Tayasu et al., 2002). South America thus hosts an ecologically diversified Termitidae community, comparable in richness to those of Africa and Southeast Asia, although their taxonomical and functional structure differs (Jones & Eggleton, 2011).

With species feeding on various substrates such as wood, soil, litter, lichens or fungi, the family Termitidae has the most diversified diet (Abe, 1979). However, Termitidae subfamilies are not all equivalent and some seem more specialised towards one part of the wood-soil gradient than others, but they all present comparable ranges of food source diversification (Macrotermitinae are absent in South America). As such, the Apicotermitinae were never found feeding on wood but include species with the highest $\delta^{15}\text{N}$ values that likely feed on recalcitrant compounds of the organo-mineral complex. On the other hand, the Nasutitermitinae and the Termitinae include several wood-feeding species but have soil-feeders with $\delta^{15}\text{N}$ values comparatively lower than the average Apicotermitinae species. However, stable isotopes may fail in describing the precise feeding range of termitid subfamilies because other factors influence $\delta^{15}\text{N}$ ratios along the wood-soil gradient: (i) Wood-feeding termites, especially the N-limited ones such as the single piece nesting Kalotermitidae, may supplement their nitrogen-depleted diet by atmospheric fixation with the help of symbiotic bacteria (Breznak, 2000), causing a decrease in their $\delta^{15}\text{N}$ values (Tayasu et al., 1994, 1997). Their $\delta^{15}\text{N}$ is thus pulled down and is similar to their food source,

contrary to the ratio of soil-feeding species which are presumed not to fix atmospheric nitrogen (Tayasu *et al.*, 1997). (ii) $\delta^{15}\text{N}$ enrichment of consumer is generally between 1‰ and 3‰ compared with their food source (McCutchan *et al.*, 2003; Vanderklift & Ponsard, 2003), whereas in soil-feeding termites, $\delta^{15}\text{N}$ is roughly between 5‰ and 9‰ higher than the surrounding soil (Tayasu *et al.*, 1997). This could be because of the selection of small particles which are richer in adsorbed organic matter but have higher $\delta^{15}\text{N}$ ratios (Nadelhoffer & Fry, 1994).

Another factor which may influence our results is a differential association between termite species and their associated gut microflora. All termites are intimately associated with symbiotic bacteria but it is not clear if different species rely upon distinct symbiotic processes (Bignell & Eggleton, 2000). Therefore, the isotopic effect could differ among taxa reflecting different relationship between the termites and their associated microbes (Brauman *et al.*, 2000). However, the precise interaction between termites and their gut microflora is still not fully understood.

The food requirements of many species are roughly known but stable isotopes may provide further precision to identify the kind of organic matter species feed on. Species with $\delta^{15}\text{N}$ below 6‰ in Petit Saut and 7‰ in the Nouragues are generally wood-feeders, such as *Glossotermes oculatus* in spite of its high left mandibular index (>1.5), generally characteristic of soil feeders (e.g. Deligne, 1966; Fontes, 1987). However, some species have low $\delta^{15}\text{N}$ but are not wood-feeders: (i) *Syntermes* sp.A which feeds on leaf litter; (ii) *Constrictotermes cavifrons* which feeds on lichens, a typically ^{15}N -depleted resource; and (iii) *Inquilinitermes* sp.A, whose $\delta^{15}\text{N}$ value confirms that its food source consists of the mound material of *Constrictotermes cavifrons* nests (Cunha *et al.*, 2003). Other species are clearly soil-feeders when their $\delta^{15}\text{N}$ is above 9‰ in Petit Saut and 10‰ in the Nouragues, whereas intermediate values are found in species feeding on very decayed wood such as *Aparatermes* nr. *cingulatus*, *Armitermes* sp., *Coatitermes kartaboensis* or *Crepititermes verruculosus*.

As exemplified by *Neocapritermes*, whose $\delta^{15}\text{N}$ varies from 8.0‰ to 13.3‰ depending on the species, soil-feeders are the most subject to feeding habit diversification, owing to a large range of organic matter decomposition states occurring in the soil, which favours niche differentiation (Bourguignon *et al.*, 2009). On the other hand, the species identified as wood-feeders have very similar $\delta^{15}\text{N}$ values, suggesting indeed that they all feed on sound, non-decayed wood. Consequently, we found almost no differentiation between wood-feeding species whose $\delta^{15}\text{N}$ varies between 2‰ and 6‰, with mean values around 4‰ at Petit Saut and 6‰ in the Nouragues Nature Reserve, respectively. However, species niche differentiation could occur, but is likely to involve different parameters such as wood water content or hardness. This small $\delta^{15}\text{N}$ variation appears to be the rule in other tropical areas as well (see Tayasu *et al.*, 1998, 2002), suggesting that all wood-feeding termites, especially widespread genera such as *Heterotermes* or *Microcerotermes*, could serve for inter-site calibration.

Evolution of feeding habits

Related taxa usually tend to share biological traits, inherited from common ancestry. For example, closely related species of South American owls are closer in size than more distant species (Diniz-Filho & Sant'Ana, 2000). In a similar way, relatives generally tend to share ecological traits (Losos, 2008). Our results highlight that related species of termite feed on more similar substrates than unrelated ones, which tend to feed on distinct substrates. This phylogenetic autocorrelation is mainly marked between species of the same genus. However, we only included three levels, and computing similar analysis with additional subdivisions or, better, with a fully resolved phylogeny, could reveal concealed patterns. If our results support that diet diversification was particularly outstanding among Termitidae subfamilies compared with basal lineages, some major shifts were likely crossed by only few lineages. For instance, all fungus-growing termites form a monophyletic group, and shifting from wood towards soil-feeding possibly occurred only few times during termite evolution (Inward *et al.*, 2007).

Feeding groups

Our results did not completely support the feeding group classification proposed by Donovan *et al.* (2001). Group I cannot be distinguished from group II, and group III cannot be distinguished from group IV, based on differences in level of humification of their food source. However, our group I samples included only Rhinotermitidae, *Glossotermes* (Serritermitidae, closely related to the Rhinotermitidae, see Lo *et al.*, 2004), and *Rugitermes* (Kalotermitidae). As a consequence, we can only affirm that the Rhinotermitidae (+ *Glossotermes*) are similar to wood-feeding Termitidae in their food requirements. Other families included in group I may differ by their feeding ecology. For instance, small-colony Kalotermitidae are likely to display lower $\delta^{15}\text{N}$ values because their nitrogen needs may be covered to a higher extent by atmospheric N_2 fixation (Tayasu *et al.*, 1994;

Tayasu, 1998). The morphological distribution of species between groups III and IV is based on the enteric valve armature and the mandibular molar ridges, characters which probably have functional importance (Donovan, 2002). However, our results confirm (i) that $\delta^{15}\text{N}$ values of soil-feeding termites are spread along a continuum which cannot be split unambiguously in two groups, and (ii) that the simple morphological criteria used to assign species to either group are not correlated with their $\delta^{15}\text{N}$ values. For instance, *Anoplotermes banksi* and *A. parvus* show similar $\delta^{15}\text{N}$ values, although the enteric valve of the former is visibly unarmed (group III) whereas the latter displays a conspicuous armature of long sclerotised spines (group IV) (Bourguignon *et al.*, 2010). Although stable isotope values may be influenced by species-specific symbionts and digestive processes, and thus only provide an indirect measure of trophic position, our results strongly suggest that the morphology of mandibles and the enteric valve of soil-feeding termites are not representative of the state of humification of their diet. Although valid for South American soil-feeders, our results should be confirmed for the African termite fauna whose group IV members are more abundant and diversified.

Altogether, stable isotopes support the morphological delineation (based on mandible molar plates) between wood- and soil-feeders (Eggleton & Tayasu, 2001; Tayasu *et al.*, 2002), but do not support further discrimination. Wood- and soil-feeders rely upon the two sides of the wood-soil decomposition gradient and form an arbitrary splitting of the actual continuum. For instance, species feeding on extremely rotten wood, such as *Coatitermes kartaboensis*, *Paraconvexitermes nigricornis* or some *Neocapritermes* are situated in between, even although morphologically placed in the soil-feeders. Nevertheless, this division is practical and ecologically relevant as the two groups are not subject to the same constraints and show distinct responses to ecosystem perturbation (Wood *et al.*, 1982; Eggleton *et al.*, 2002; Jones *et al.*, 2003).

Beside the species feeding on the wood-soil gradient, two other groups rely upon different substrates: the lichen- or algae-feeders such as *Hospitalitermes* and *Constrictotermes* (Miura & Matsumoto, 1997; Martius *et al.*, 2000), and the fungus-cultivating Macrotermitinae (Rouland-Lefèvre, 2000). An adequate classification of ecological feeding groups should recognise their peculiarity and distinguish them from species feeding on the wood-soil gradient.

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