

Beta-Diversity of Termite Assemblages Among Primary French Guiana Rain Forests

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ABSTRACT

Termites are an important component of tropical rain forests, and have been included in many studies focusing on the influence of human disturbance. Their distribution among primary rain forest has, however, rarely been investigated. Here we studied the termite fauna in seven mostly undisturbed forest sites, representing several rain forest types. Overall, approximately 70 percent of species were soil-feeders and 25 percent were wood-feeders, the remaining 5 percent being classified here as litter-feeders. Termite species richness did not differ significantly among sites, but sites differed in termite abundance. The palm swamp and the low forest situated on the foothills of an inselberg, hosted different termite communities to the other sites. These two sites presented a singular physiognomy suggesting that forest type is an important factor influencing species composition. We found no correlation between termite species composition and distance between sites, highlighting that at the scale of our study (about 100 km), forest sites share a similar species pool.

Key words: biodiversity; inselberg; Isoptera; Nouragues; tropical forest.

SOCIAL INSECTS, ESPECIALLY ANTS AND TERMITES, ARE AMONG THE MOST ABUNDANT ANIMALS IN TROPICAL RAIN FORESTS, where they account for a large percentage of the total animal biomass (Martius 1994, Eggleton *et al.* 1996, Ellwood *et al.* 2002). While ants are conspicuous, termites are more cryptic, but abound in wood and in the topsoil layers in which they constitute major organic matter decomposers (Holt & Lepage 2000, Sugimoto *et al.* 2000). Despite their tremendous impact and abundance, the species richness of termites remains well below that of mega-diverse insect orders such as Diptera or Coleoptera, and the richest areas sampled to date comprise no more than 150 species of termites (Davies *et al.* 2003a).

Following concern about the alarming destruction of tropical rain forests, many studies have focused on the variations of termite assemblages across forests subject to various degree of fragmentation (DeSouza & Brown 1994, Davies 2002, Sena *et al.* 2003), or along a gradient of forest disturbance (Davies *et al.* 1999, Okwakol 2000, Eggleton *et al.* 2002, Bandeira *et al.* 2003, Jones *et al.* 2003, Ackerman *et al.* 2009). They generally conclude that termite diversity decreases along the sequence primary forest → secondary forest → crops and cultivated fields—the latter stage generally being severely depauperate (Okwakol 2000). Differences in termite communities at a geographical scale among primary ecosystems are much less known, even though some studies highlighted faunal variation along altitudinal gradients (Gathorne-Hardy *et al.* 2001, Donovan *et al.* 2002) or according to the biogeographical location (review in Davies *et al.* 2003a). At a finer spatial scale, vertical stratification from soil to canopy level was recently demonstrated for wood-feeders (Roisin *et al.* 2006), as well as the influence of environmental factors such as the presence of palm trees (Davies 2002) or terrestrial bromeliads (Roisin & Leponce 2004).

With few exceptions, such as the lichen-feeding *Constrictotermes*, termites feed at some point along the wood–soil decompo-

sition gradient (Abe 1979, Tayasu *et al.* 1997). Studies in South America generally distinguish wood-, soil- and litter-feeders (*e.g.*, Davies 2002, Davies *et al.* 2003a). A fourth category including species feeding at the interface between wood and soil is also recognized (*e.g.*, Bandeira *et al.* 2003, da Cunha *et al.* 2006). Although the classification of species into distinct feeding groups necessarily involves arbitrary limits, these categories are ecologically relevant. Wood-feeding termites are more resilient to ecosystem perturbation than soil-feeding ones, which require more stable conditions (Wood *et al.* 1982, Eggleton *et al.* 2002, Jones *et al.* 2003).

Tropical rain forest structure varies according to multiple factors such as soil type and nutrient availability (Tuomisto & Ruokolainen 1994, Tuomisto & Poulsen 1996), topography (Austin *et al.* 1996, Webb *et al.* 1999) or biotic factors such as abundance and diversity of lianas (Schnitzer & Bongers 2002). Rain forests are therefore heterogeneous and are often composed of a mosaic of more or less dissimilar forest patches. For example, in the Nouragues Nature Reserve (French Guiana), high mature forest with a fairly open understory is intermingled with low forest patches characterized by the abundance of lianas and a dense understory, and with forested swamps (Poncy *et al.* 2001). High environmental heterogeneity is often pinpointed as a key factor favoring the maintenance of a diverse animal community (*e.g.*, Keller *et al.* 2009). In South America, seasonally flooded forests along the Amazon River host peculiar termite assemblages that differ considerably from those of *terra firme* forests (Mill 1982, Constantino 1992).

French Guiana hosts one of the most diverse termite faunas, with over 100 species belonging to four families (Davies 2002, Bourguignon *et al.* 2009a), and as such is a suitable place to study termite β -diversity. In this study, we investigated termite species composition at seven sites spread over three localities in French Guiana, with the following objectives: (1) Wood-feeding termites have been suggested to be more resilient than soil-feeding termites

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to ecosystem perturbation (Eggleton *et al.* 2002, Jones *et al.* 2003). Here, we hypothesize that higher sensitivity of soil-feeders to perturbation might also result from a higher degree of specialization to particular forest types. (2) For herbivorous insects, species composition has been observed to change subtly over large distances, suggesting that factors such as host specificity (generally at the family or genus level), or faunal shifts along environmental gradients (*e.g.*, altitude, vertical stratification from understory to canopy), are more likely to explain the high biodiversity of tropical ecosystems than speciation by distance (Novotny *et al.* 2002, 2005, 2007; Basset *et al.* 2003). We test whether faunal dissimilarities between termite communities are, as in herbivorous insects, mainly explained by forest type rather than by geographic distance.

METHODS

STUDY SITES.—Seven sites were sampled in three French Guiana localities: (i) three in the forest surrounding the Petit Saut dam (05°04' N, 52°59' W) (*Plow1*, *Plow2* and *Pswa*); (ii) three in the Nouragues Nature Reserve, including one at the Nouragues inselberg site (*Nlo*, *Nins* and *Nlian*) (04°05' N, 52°41' W); and one in the Kaw Mountain (04°32' N, 52°09' W) (*Kaw*). Petit Saut is about 110 km away from the Nouragues and Kaw stations, which are about 80 km away from each other. The three Petit Saut sampling sites were separated from each other by < 10 km and the three Nouragues sampling sites by < 5 km. The sites were selected in order to encompass geographically distant primary forests on the one hand, and different type of forests on the other. Sites *Nlo*, *Nlian*, *Plow1*, *Kaw* and *Plow2* were in mature lowland forest growing on well-drained soil, with an average canopy height reaching 30–40 m. *Nlian* differs the most from the other four primary forests, having a high density of lianas (Schnitzer & Bongers 2002). In *Kaw*, the ground layer mainly consisted of shallow soil patches intermingled with bare rock. Many tree species possessed superficial roots directly fixed on the rock, spreading up to 15 m from the trunk. *Pswa* sampling took place in a palm-rich forest growing on poorly drained soil, which is periodically flooded. Beside these sporadic events, several small rivers flow through the area and ephemeral ponds appear after brief rainfall events. The dominant vegetation comprises mainly palm trees of various genera, including *Euterpe* spp. The last sampled site (*Nins*) was a low forest growing on the foothills of the Nouragues inselberg, transitional between lowland rain forest and the rock savanna growing on the granitic outcrop. This short-stature forest was dominated by *Clusia minor* (Clusiaceae) intermingled with other low trees reaching not more than 10 m.

All forests experience about 3000 mm of rainfall per year, mostly distributed between January and June. The mean annual temperature is 26°C. The sampling plots in Petit Saut were free of severe disturbance. The Nouragues is almost completely unaffected by anthropogenic disturbances, while Kaw Mountain has undisturbed forest intermingled with patches that have been exploited for timber.

SAMPLING METHOD.—Termite sampling was carried out using a standard transect protocol. Each transect consisted of 49 or 50

quadrats of 5 m² (2.24 × 2.24 m). Each quadrat was investigated for 0.5 man-h, searching for termites in all favorable microhabitats (*e.g.*, epigeous mounds, dead wood, litter, soil, standing trees up to a height of 2 m). Quadrats were always located within the relevant single forest type with a minimum distance of 10 m between successive sampling points, as recommended by Roisin and Leponce (2004).

Termite specimens were collected in 80 percent alcohol. They were first classified into morphospecies based on the morphology of soldiers and workers then identified to genus and species level used various taxonomic works (Emerson 1925, Mathews 1977), keys (Constantino 2002) and comparisons with type material for the Rhinotermitidae, Termitinae and Apicotermitinae. Samples consisting of wingless adults only, recently settled after the nuptial flight, were discarded from later analysis because they did not represent established colonies. Because the distribution of social insects is highly aggregative, we considered presence/absence data per quadrat (occurrences). The number of occurrences per transect reveals the probability of encountering a given species, and was used as a proxy for species abundance. Termite species were allocated to soil-, wood-, or litter-feeder categories according to Davies *et al.* (2003b). We included *Ruptitermes* in this latter category (see Mathews 1977). We did not recognize wood–soil interface-feeders as a valid category distinct from true soil-feeders.

DATA ANALYSIS.—Litter-feeders were not analyzed as a separate guild because they were very rarely encountered and included too few species for analysis. They were, however, included in the analyses carried out on all termites or on particular termite taxa. To test if there was a difference in wood- and soil-feeder composition between sites, we computed χ^2 tests on the total number of species and on the total occurrences encountered in all sites. In the same way, we tested for differences in taxonomic composition between sites, using χ^2 tests on the total number of species and occurrences of the Rhinotermitidae family and on the four Termitidae subfamilies (*i.e.*, Apicotermitinae, Nasutermitinae, Syntermitinae and Termitinae). We calculated species rarefaction curves and Mao-Tau confidence intervals (CIs) (for full transect data) using the freeware EstimateS 8.00 (Colwell 2005), wood- and soil-feeders being treated separately. The curves were scaled using either samples (quadrats) or occurrences as abscissa. The first method gives a good estimate of the site biodiversity but does not distinguish between species abundance and richness, whereas the second only retains richness information (Gotelli & Colwell 2001). Detrended correspondence analysis (DCA) was used to investigate species-site association patterns. The analysis was carried out on the species by sites matrix as represented in Table S1. Two ordination plots were computed: one depicting all termites simultaneously; and one for soil-feeders alone. Taxonomic and ecological group differences along the first axis were investigated by comparing species scores by one-way ANOVA and Student's *t*-test, respectively. The analyses were carried out using the CANOCO software with the option detrending by segment (ter Braak & Šmilauer 1998). Species that were encountered on fewer than four occasions across the transects were discarded from the analysis as the detection of species-site

association is dubious when it relies upon too few records. The influence of rare species was later investigated using NNESS indexes. To emphasize site differences according to the termite community they host, we computed NNESS index for all pairs of sites using the freeware BiodivR (Hardy 2009). The NNESS estimator is based on theoretical expectations of species overlap under resampling of k individuals with replacement. When $k = 1$, the index is highly influenced by abundant species and is equivalent to the Morisita–Horn index, whereas when k rises, more weight is given to rare species (Grassle & Smith 1976). We computed NNESS index for $k = 1, 2, 4, 8, 16$ and 32 . To test if site similarity differed according to the weight given to rare species, we carried out a repeated measures ANOVA comparing each series of k values, using site mean as data input, on wood- and soil-feeders separately. We used Bartlett's K -test to determine if soil- and wood-feeder variability differed in their NNESS value. We computed a Mantel test, using distance (km) and Morisita–Horn index ($=\text{NNESS}_{k=1}$) as matrices, to determine if difference in species composition among sites differed according to distance.

RESULTS

Overall, 851 termite occurrences representing 95 species were collected, among which 477 occurrences and 68 species were assigned to soil-feeders, and 364 occurrences representing 24 species were wood-feeders (Table S1). The remaining four species, *Syntermes* sp. A, *Ruptitermes* nr. *xanthochiton*, *Velocitermes beeli* and *Velocitermes* sp. B, are leaf litter-feeders (Mathews 1977). Three families were represented, among which the Termitidae was the most ubiquitous with 89 species and about 88 percent of all occurrences. By contrast, with three species from only five occurrences, the Kalotermitidae family was scarcely collected. The last family, the Rhinotermitidae, was represented by four species and 102 occurrences (Table S1).

We found no between-site differences either in total species richness or occurrences ($\chi^2 = 1.81\text{--}6.33$, $df = 6$, $P = 0.387\text{--}0.936$). Wood-feeding termites were homogeneously distributed in terms of species richness among the seven sampled forests ($\chi^2 = 1.00$, $df = 6$, $P = 0.99$) and no significant difference was found for soil-feeders ($\chi^2 = 5.13$, $df = 6$, $P = 0.53$). When considering the total species occurrences, both wood- and soil-feeders were, however, unequally distributed among forests (wood-feeders: $\chi^2 = 42.92$, $df = 6$, $P < 0.001$; soil-feeders: $\chi^2 = 20.03$, $df = 6$, $P = 0.003$) (Fig. 1).

The species richness of the four Termitidae subfamilies did not differ between sites ($\chi^2 = 2.89\text{--}8.87$, $df = 6$, $P = 0.18\text{--}0.89$), whereas when occurrence was considered, the Apicotermittinae ($\chi^2 = 31.69$, $df = 6$, $P < 0.001$), Nasutitermittinae ($\chi^2 = 38.64$, $df = 6$, $P < 0.001$) and Syntermittinae ($\chi^2 = 23.56$, $df = 6$, $P < 0.001$) were all unequally distributed among sites. This contrasts with the Rhinotermitidae and Termitinae for which no significant difference was found ($\chi^2 = 9.63\text{--}11.78$, $df = 6$, $P = 0.07\text{--}0.14$) (Fig. 1).

Species rarefaction curves suggested lower soil-feeder species richness in *Nins* and *Pswa* compared with other sampled sites, especially *Nlian* and *Plow1* (Fig. 2). This lower richness in soil-

feeders was balanced by higher richness in wood-feeders, which were less abundant in *Nlian* and *Plow1*. The other three sites had intermediate richness, both for wood and soil-feeders. These curves do not, however, clearly differ from each other, as evidenced by the 95% CIs. When all transects were pooled, rarefaction curves did not level off and kept on rising with sampling effort.

When computed for soil and wood-feeders simultaneously, the first and second axis of DCA, respectively, captured 33.0 percent and 4.1 percent of the total variation (Fig. S1). The first axis depicted sites along a sequence beginning by *Nins* (short-stature forest) and ending by *Pswa* (palm swamp). The second axis was characterized by a low eigenvalue and was thus likely to contain only minor information. Whereas no difference exists between wood- and soil-feeders in the first axis scores (t -test: $t = -0.673$, $df = 52$, $P = 0.504$), we found significant differences between taxonomic groups ($F_{4,49} = 3.154$, $P = 0.022$), but Tukey test comparisons were only significant for the pair Termitinae–Apicotermittinae ($q = 4.405$, $P = 0.025$). The DCA computed with wood- and soil-feeders simultaneously did not obviously separate the sites, although when soil-feeders were analyzed separately, *Pswa* is separated from other sites (Fig. S2).

When we increased the weight given to rare species, through computing NNESS index with increasing k values, site similarity did not change for soil-feeders (ANOVA: $F_{5,36} = 100.54$, $P = 0.076$), but did so for wood-feeders (ANOVA: $F_{5,36} = 289.93$, $P = 0.045$). Rare species, therefore, slightly influence site dissimilarity. We compared wood- and soil-feeders only for NNESS with $k = 1$, and found wood-feeding termite communities varied less between sites than soil-feeding termite communities ($K = 5.313$, $df = 1$, $P = 0.0212$). As suggested by DCA, *Pswa* and *Nins* appear to host a particular termite fauna with generally low Morisita–Horn values (Table 1). Mantel test did not indicate any correlation between-site distance and their species composition ($r = 0.100$, $P = 0.337$).

DISCUSSION

Our results confirmed the scarcity of Kalotermitidae in the ground strata as we collected only three species accounting for less than 1 percent of the total termite captures. The sampled specimens were found inside short pieces of wood, possibly having fallen from tree-crowns, as this group is thought to be a specialist in tree canopies (Roisin *et al.* 2006). With only four species, the Rhinotermitidae is also poorly diversified, although quite abundant, with *Heterotermes tenuis* accounting for seven percent of all the records. Two more species, *Rhinotermes marginalis* and *Acorhinotermes subfusciceps*, are known from French Guiana (Davies 2002) but were not sampled here. These are either rare species or live in inaccessible habitats such as the central core of live tree trunks (Apolinário & Martius 2004). The last family, Termitidae, was far richer than the other two, and its subfamily species richness can be ranked as: Apicotermittinae > Nasutitermittinae > Termitinae > Syntermittinae. Interestingly, the Apicotermittinae, which account for 35 percent of collected species in our samples are the poorest in terms of described species (Constantino 1998), supporting the idea that

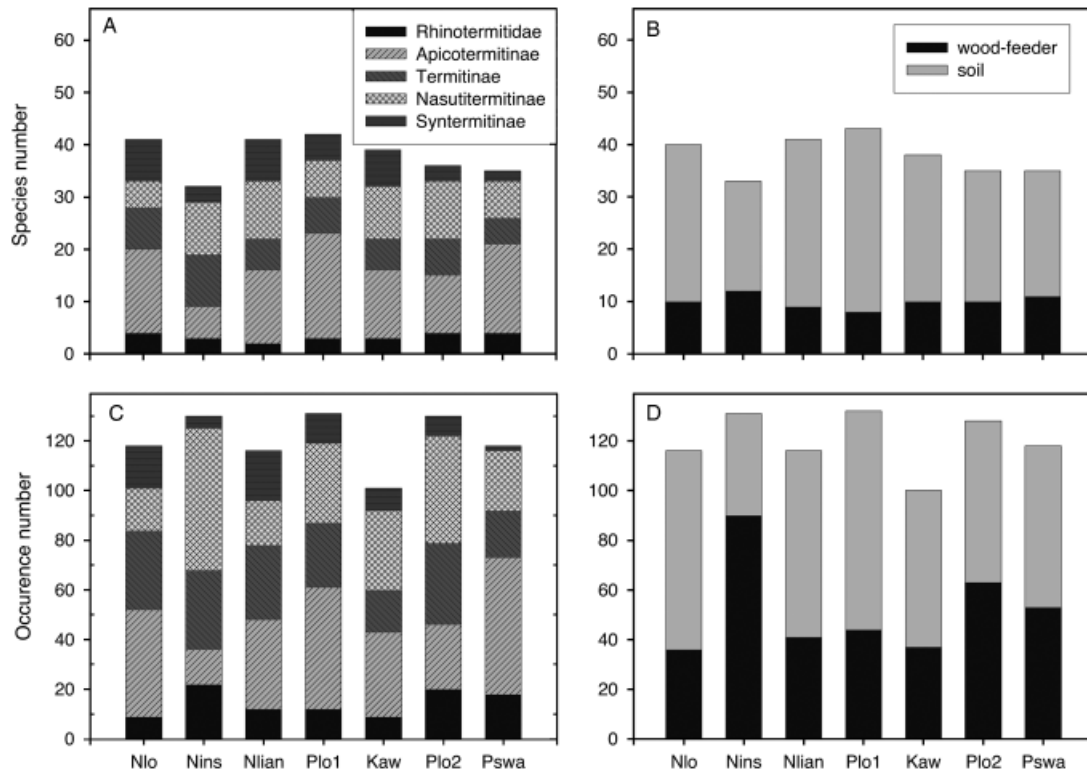


FIGURE 1. Taxonomic composition of termites in seven primary forests: (A) family and subfamily species richness, (B) wood- and soil-feeder species richness, (C) family and subfamily abundance and (D) wood- and soil-feeder abundance.

a complete revision of the group could yield many new species (Bourguignon *et al.* 2009b).

Despite differences in forest structure, species richness of wood- and soil-feeders did not vary across sites, even in the species-poor low forest and palm swamp. About a quarter of species were represented by 'singletons' (a single occurrence across all sampling units) and rarefaction curves continued to increase steeply after 50 sampled quadrats, indicating that continued sampling would yield many more species. Therefore, total species richness could not be reliably compared between sites. By contrast, we found strong differences between sites in termite occurrence number for both wood- and soil-feeders. In this aspect, the low forest (*Nins*) appeared the most distinctive as it hosted approximately twice as many wood-feeders and half as many soil-feeders as the other sites, probably on account of the shallow soil depth on the inselberg outcrop (Sarhou & Villiers 1998). Other sites all host similar numbers of termite ecological groups.

As for wood- and soil-feeders, we did not find any between-site differences in species richness for families and subfamilies of termites, although species richness varied greatly among sites in some subfamilies, and especially in Apicotermitinae whose species number ranged from six to 20 across sites. When total occurrence was considered, differences between sites were found for Apicotermitinae, Nasutitermitinae and Syntermitinae. Apicotermitinae were the most abundant in the palm swamp (*Pswa*) and the rarest in the low forest, following the trend of a low abundance of soil-feeders in this site.

Overall, species abundance (expressed in terms of number of occurrences across plots) allowed better site distinction than species richness. This could either result from undersampling bias, which is likely to affect species richness much more than total occurrence, or reveal the actual pattern that undisturbed sites mainly differ in species abundance rather than in species richness. Anyway, our results suggest that total occurrence number could better highlight site differences than species richness.

DCA plots indicated that termite communities are mainly distributed along the first axis, with sites lining up along a sequence beginning with *Nins* (low forest) and ending with *Pswa* (palm swamp). This sequence can be interpreted as a gradient of humidity, a factor that was already known to explain between-site variations in species composition (Davies *et al.* 2003b). Species situated on the lower end of this gradient occurred mainly in the low forest, such as *Termes* sp. A, *T. fatalis*, *Cavitermes tuberosus* and *Nasutitermes* sp. G. Species situated on the high side were mainly collected in the palm swamp, which appeared to host a specialized termite fauna comprising several unnamed *Anoplotermes*-group species and the nest builder *Anoplotermes banksi*. Other sites are situated in between and did not host a particular fauna. The second axis is more difficult to interpret; it accounted for a far lower amount of variation than the first axis and is thus less informative.

Previous studies, based on visible nests and wood-dwelling species, pointed out that seasonally flooded forests differ markedly from *terra firme* forests in termite species diversity and composition (Mill 1982, Constantino 1992). We also found between-site

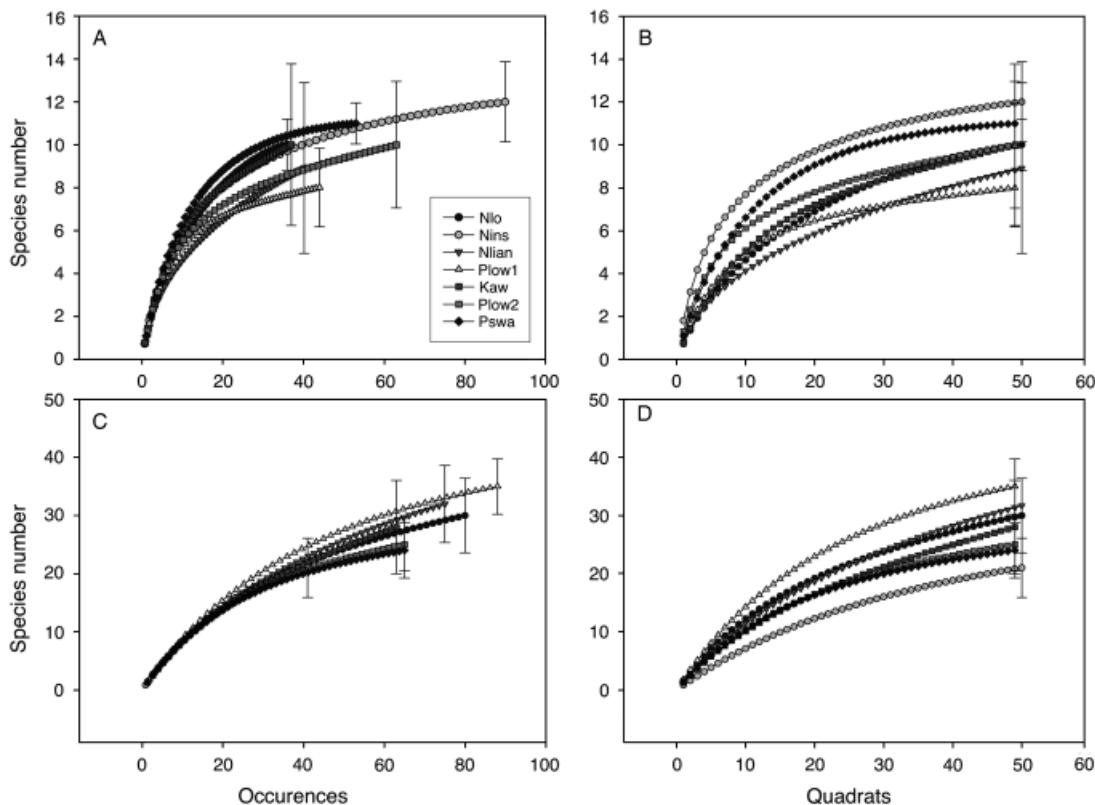


FIGURE 2. Species rarefaction curves for termite assemblages collected in seven forests: (A) curves scaled on occurrence number for wood-feeders, (B) curves scaled on quadrats for wood-feeders, (C) curves scaled on occurrence for soil-feeders, (D) curves scaled on quadrats for soil-feeders. Error bars are 95% confidence limits calculated by the Mao-Tau method (Colwell *et al.* 2004).

differences, especially for the palm swamp and the low forest, as depicted by the low NNESS indexes for these two sites (see Table 1). Soil-feeders better highlight these differences, as evidenced by a generally lower Morisita–Horn index for these two sites. The composition of wood-feeders is rather similar across sites, and specific species-site associations (*e.g.*, between *Nasutitermes* sp. G and low forest) are few. Wood-feeding termites therefore appear more generalist than soil-feeding termites, though this may not be true for rare species since increasing the weight given to rare species in sim-

ilarity index computation revealed lower indices, suggesting hidden species-site associations. The few extremely abundant species such as *Cylindrotermes parvignathus*, *H. tenuis*, and *Nasutitermes* sp. E, which altogether account for approximately 25 percent of the total termite occurrences, blur the pattern for rare species, which appear slightly more site-specific than abundant species. Overall, the higher specialization of soil-feeders is consistent with their higher sensitivity to anthropogenic disturbance (Wood *et al.* 1982, Eggleton *et al.* 2002, Jones *et al.* 2003). This is valid for tropical rain forests but deserve further investigation in other biomes, like the semi-arid Caatinga where wood-feeders were recently found more sensitive to perturbation (Vasconcellos *et al.* 2010).

As our sampling sites were distant either by about 100 km or by < 10 km, we can distinguish local and regional scales across which spatial autocorrelation might be expected. The Morisita–Horn index emphasized the dissimilarity of *Nins* and *Pswa*, suggesting that at the regional scale species distribution is shaped by forest types and not distance. This is also supported by the Mantel test that failed to reveal a correlation between-site distance and species composition. Overall, our results are congruent with studies on herbivorous insects, which put forward the low β -diversity of New Guinean forests, site dissimilarities being mainly explained by environmental parameters (Novotny *et al.* 2005, 2007; Hulcr *et al.* 2008).

TABLE 1. *Morisita–Horn index (NNESS for k = 1) for all pairs of sites. Bold font: wood-feeders; normal font: soil-feeders.*

Soil/Wood	<i>Nlo</i>	<i>Nins</i>	<i>Nlian</i>	<i>Plow1</i>	<i>Kaw</i>	<i>Plow2</i>	<i>Pswa</i>
<i>Nlo</i>	1	0.685	0.88	0.889	0.793	0.785	0.755
<i>Nins</i>	0.283	1	0.575	0.869	0.606	0.898	0.609
<i>Nlian</i>	0.708	0.349	1	0.791	0.583	0.796	0.791
<i>Plow1</i>	0.691	0.38	0.742	1	0.804	0.891	0.782
<i>Kaw</i>	0.546	0.258	0.556	0.56	1	0.616	0.738
<i>Plow2</i>	0.495	0.285	0.593	0.685	0.619	1	0.772
<i>Pswa</i>	0.274	0.194	0.281	0.301	0.347	0.245	1

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Termite occurrences in the seven sampled primary forests.*
 FIGURE S1. DCA bi-plot of termite species and primary forest sites.
 FIGURE S2. DCA bi-plot of soil-feeding termite species and primary forest sites.

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