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Vertical stratification of the termite assemblage in a neotropical rainforest

Yves Roisin · Alain Dejean · Bruno Corbara ·
Jerôme Orivel · Mirna Samaniego ·
Maurice Leponce

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Abstract The importance of termites as decomposers in tropical forests has long been recognized. Studies on the richness and diversity of termite species and their ecological function have flourished in more recent times, but these have been mostly conducted in a thin stratum within a standing man's reach. Our aims were to evaluate the specific richness and composition of the termite assemblage in the canopy of a tropical rainforest and to determine its originality with respect to the sympatric ground-level fauna. We conducted systematic searches for canopy termites, together with conventional sampling of the sympatric ground-level fauna, in the San Lorenzo forest, Panama. We hypothesized that (1) the canopy accommodates two categories of wood-feeding termites (long-distance foragers and small-colony ''one-piece'' species) and possibly soil-feeders in suspended soil-like habitats; (2) due to the abundance of soil-feeders, the overall diversity of the ground fauna is higher than that of the canopy; (3) differences in microclimate and resource accessibility favour vertical stratification among wood-feeders. Sixty-three canopy samples yielded ten species of termites, all wood-feeders. Five of these were not found at ground level, although a total of 243 ground samples were collected, representing 29 species. In addition to long-distance foragers (*Microcerotermes* and *Nasutitermes* spp.) and small-colony termites (mostly Kalotermitidae), the canopy fauna included *Termes hispaniolae*, a wood-feeding Termitidae from an allegedly soil-feeding genus, living in large dead branches. Soil-feeders were absent from the canopy, probably because large epiphytes were scarce. As predicted, the ground fauna was much richer than that of the canopy, but the species richness of both habitats was similar when only wood-feeders were considered. Vertical stratification was strongly marked among wood-feeders, as all common species, apart from the arboreal-nesting *Microcerotermes arboreus*, could unequivocally be assigned to either a ground or a canopy group. The canopy, therefore, contributes significantly to the total species richness of the termite assemblage, and the diversity, abundance and ecological importance of canopy termites in tropical rainforests may be higher than previously recognized.

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Y. Roisin (✉)
Behavioural and Evolutionary Ecology, CP 160/12,
Université Libre de Bruxelles, Avenue F.D. Roosevelt 50,
1050 Brussels, Belgium
e-mail: yroisin@ulb.ac.be

A. Dejean · J. Orivel
Laboratoire d'Evolution et Diversité Biologique,
UMR-CNRS 5174, Bât. 4R3, Université Toulouse III,
118 Route de Narbonne, 31062 Toulouse Cedex 4, France

B. Corbara
Opération Canopée & LAPSCO, UMR-CNRS 6024,
Université Blaise Pascal, 34 Avenue Carnot,
63037 Clermont-Ferrand Cedex, France

M. Samaniego
Smithsonian Tropical Research Institute, Apartado Postal
0843-03092, Balboa-Ancon, Republic of Panama

M. Leponce
Section of Conservation Biology, Royal Belgian Institute
of Natural Sciences, Rue Vautier 29, 1000 Brussels, Belgium

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Introduction

Tropical rainforest canopies are a harsh environment, receiving much more sunlight and experiencing stronger variations in temperature and humidity than the understorey and ground strata below (Bohlman et al. 1995; Madigosky 2004). In the aftermath of pioneering studies of the biological diversity of various arthropod taxa in canopies (reviews in Stork et al. 1997; Basset et al. 2003a), a more comprehensive approach to forest communities, encompassing all strata from the ground to the upper canopy, is now emerging. Vertical differentiation between the understorey and the canopy has been demonstrated for leaf beetles and other herbivores (Basset et al. 2001, 2003b; Charles and Basset 2005). Other taxonomic groups, such as ants, Collembola, spiders or Acari, span the entire vertical range of the forest, from the humus layer to the outer canopy foliage and, therefore, constitute models of special interest for the study of vertical stratification (Paoletti et al. 1991; Rodgers and Kitching 1998; Yanoviak and Kaspari 2000; Prinzing and Woas 2003; Sørensen 2003; Fagan et al. 2006). Within the framework of the IBISCA-Panama project, an international initiative aimed at studying the vertical stratification and beta diversity of arthropods in a tropical rainforest (Springate and Basset 2004; see also http://www.naturalsciences.be/cb/ants/projects/ibisca_main.htm), we assessed the vertical distribution of termites (Isoptera), a pre-eminent group of decomposers of plant material in tropical ecosystems (Martius 1994; Bignell et al. 1997; Bignell and Eggleton 2000; Sugimoto et al. 2000).

Termite assemblages in pristine and/or degraded or partially degraded tropical forests have been extensively sampled in recent years (reviews in Eggleton and Bignell 1995; Davies et al. 2003a). However, most of these studies were restricted to a narrow stratum that extended from a few centimetres below the soil surface to a few metres above it. For instance, the widely used sampling protocol developed by Jones and Eggleton (2000) is limited to a height of 2 m. There are, however, ample possibilities for termite presence in the forest canopy. First, small-colony termites [Abe's (1987) "one-piece" life type] may colonize dead branches and spend their entire colony life cycle within them. Second, large-colony wood feeders, which are known to build their nest at various heights on tree trunks and to forage under an extensive network of wood carton tunnels, may be able to exploit dead wood sources at all levels of the forest. Third, "suspended soils" that form in and around large epiphytes or within hollow limbs (Paoletti et al. 1991) may provide opportunities for species feeding on decayed plant material.

Sampling such communities is, however, technically difficult, and data on the actual presence of termites in the upper forest strata remain limited (Martius 1994; Basset 2001). Standardized collecting techniques, such as fogging, provide poor results for termites (Adis et al. 1984; Eggleton and Bignell 1995; Basset et al. 2003c; Hurtado Guerrero et al. 2003). Consequently, the current knowledge base on termite canopy assemblages is mostly limited to a few casual captures or observations and single-species studies, with the focus on arboreal carton nest-builders and long-distance foragers of the family Termitidae (Abe 1978, 1979; Ellwood et al. 2002; Dejean et al. 2003; Gonçalves et al. 2005). In particular, the colonization of dead branches in tree crowns by small-colony species (especially of the family Kalotermitidae) remains poorly documented. However, the trapping of swarming alates in Amazonian forests suggests that several species, including some Kalotermitidae, must be canopy specialists because they escape detection when collecting is restricted to near-ground habitats (Rebello and Martius 1994; Martius 1997a).

The aim of this study was to evaluate the specific richness and composition of the termite assemblage in the canopy of a neotropical rainforest and to determine its originality with respect to the sympatric ground-level fauna. We put forward the following hypotheses.

1. Whereas the ground termite fauna of the San Lorenzo forest should comprise all characteristic elements of neotropical rainforests, including a large soil-feeding guild (Constantino 1992; Davies 2002; Davies et al. 2003a, b), two ecological categories are likely to predominate in the canopy: long-distance wood-feeding foragers (e.g. *Nasutitermes*, *Microcerotermes* spp.) and small-colony wood feeders (e.g. Kalotermitidae). In addition, soil feeders taking advantage of suspended soils may be present in the canopy as well.
2. Because soil-feeding species are known to constitute the major part of termite assemblages in neotropical rainforests, the species richness of the canopy fauna is expected to be much lower than that of the ground fauna.
3. However, because microclimatic conditions as well as dead wood distribution and accessibility (Bohlman et al. 1995; Yanoviak and Kaspari 2000; Madigosky 2004) differs between the ground and the canopy, the wood-feeding guild is likely to

comprise different species in each habitat. In particular, the canopy should accommodate species that are good colonizers and resistant to dry conditions; if present in the lower strata, such species should be more frequently encountered at the edge of the forest than in the interior (Toda 1992; Didham 1997).

Study site and methods

Field work took place in the San Lorenzo Protected Area (Colón Province, Republic of Panama), in the vicinity of the Fort Sherman canopy crane. This site averages 3000 mm of rainfall annually and an annual air temperature of 27°C. The climate is wet all year-round, with a drier season between January and mid-April. The forest has been mostly free of severe disturbance for the past 200 years and is evergreen, with less than 3% loss in canopy cover by the end of the dry season (Condit et al. 2000, 2004). Termites were sampled during two campaigns, one in September–October 2003, one in May 2004. In both years, we distinguished "ground" sampling (up to 2 m above the ground) from "canopy" sampling, here defined as encompassing all strata higher than 10 m above the ground. As suggested by Jones and Eggleton (2000), ground sampling was standardized by spending one man-hour per 10 m^2 searching for termites in all suitable microhabitats (dead wood, litter, termite-built mounds and galleries, humus, soil and trees up to a height of 2 m). Canopy sampling was carried out with the help of professional tree climbers. Whenever a tree was selected for sampling, the climbers were instructed to cut down as many dead branches as possible and to check for occupied termite galleries on the trunk and live branches. Small live branches, with flowers and fruit if present, were cut to allow identification of the tree species. Epiphytes were also taken down whenever possible, but large specimens were scarce. Cut branches, gallery fragments and epiphytes were thoroughly searched for termites. Due to constraints resulting from the need to coordinate various sampling programmes on different arthropod taxa, protocols differed slightly between 2003 and 2004.

In 2003, ground sampling was centred on three 20×20-m^2 plots, which were focal to other sampling programmes. The GPS coordinates of these squares, almost perfectly aligned in a W–E line, were as follows: 9°16.550′N, 79°58.628′W; 9°16.547′N, 79°58.590′W; 9°16.550′N, 79°58.565′W. We slightly modified the protocol developed by Jones and Eggleton (2000), who recommended sampling along a 100×2-m belt transect divided into 20 successive quadrats of 5×2 m. Rather than arranging sampling quadrats in a straight line, we placed them parallel to the sides of the focal 20×20-m^2 square, leaving a 10-m buffer distance to prevent interference with other programmes and avoiding the side through which access was provided. Each of our transects thus ran along three sides of a rectangle, which were 30, 40 and 30 m long, respectively. Each 5×2-m quadrat was searched for one man-hour as described above. Canopy sampling was carried out within a 170×40-m area, starting 10 m west of the first focal square and running W–E to completely encompass the three focal squares. A total of 80 trees, each more than 15 m tall and in contact with the outer canopy, were sampled as described above.

The 2004 campaign was more specifically aimed at termites. As recommended by Roisin and Leponce (2004), ground sampling quadrats were reduced to 5 m^2, positioned every 10 m along a 400-m-long transect, and each searched for one-half man-hour. The starting point (9°16.757′N, 79°58.465′W) was situated 790 m NE of the starting point of the 2003 canopy sampling area, and the transect proceeded W–E. Canopy sampling was carried out on 42 large, emergent trees, all within a 20-m-wide belt covering the ground quadrats.

Termite colony samples were collected in 80% alcohol. They were identified to species or morphospecies level with the help of original descriptions (see Constantino 1998 for a recent catalogue) and additional papers (Nickle and Collins 1992; Roisin 1995; Constantino 2001). The identification of *Termes panamaensis* (Snyder) was possible thanks to the examination of the type material (holotype, USNM type 00218; type colony, USNM 003075). The identification of *T. hispaniolae* (Banks) was facilitated by the loan of specimens from Galeta Island, whose determination was made by A.E. Emerson (USNM 004806), and by several samples from the West Indies (University of Florida collection). Samples consisting of wingless adults only, recently settled after the nuptial flight, were discarded from later analysis because they did not represent established colonies. Species were qualified according to the presence or absence of a specialized worker caste, and classified into feeding groups. The absence of specialized workers correlates with a small colony size, a flexible development of immatures and the ability of colonies to accommodate themselves into relatively small pieces of dead wood (Abe 1979; Higashi et al. 1991; Roisin 2000). Feeding groups were defined according to Donovan et al. (2001): group I are non-Termitidae (all wood-feeders), group II are Termitidae feeding on wood or solid litter items, group III feed at the soil/wood interface or on partly mineralized humus ("intermediate feeders", refer to DeSouza and Brown 1994; all from the family Termitidae) and group IV are true (mineral) soil-feeders (all from the family Termitidae). Because the distribution of social insects is highly aggregative, we considered presence/absence data per sampling unit (occurrences) rather than abundances. Ground sampling units were individual quadrats; canopy sampling units were individual trees. One occurrence was thus defined as the presence of one species in one sampling unit (quadrat or tree).

To overcome differences in protocols and allow comparisons between ground and canopy samples, graphs were scaled by individual occurrences rather than by sampling units (see Gotelli and Colwell 2001; Colwell et al. 2004). Rarefaction curves and biodiversity indices were calculated using EstimateS ver. 7.00 (Colwell 2005).

Results

In 2003, the sixty 10-m^2 quadrats yielded 157 occurrences, with 23 species represented. Canopy sampling provided 30 occurrences, representing nine species, from 26 trees. In 2004, the forty 5-m^2 quadrats yielded 86 occurrences, representing 21 species, of which six had not been found in 2003. Despite the difference in quadrat area, the distribution of the number of occurrences per quadrat did not significantly differ between 2003 and 2004, as both distributions matched a Poisson distribution with their common mean (2.43 occurrences per quadrat; 2003: χ^2=3.22, df=4, p>0.1; 2004: χ^2=5.17, df=3, p>0.1). From the canopy, we obtained 33 occurrences, representing eight species, from 19 trees. One of these species had not been found in 2003. Over the two campaigns, 29 species were found in ground samples, ten in canopy samples and 34 species in total (Table 1). Twenty species of trees supported termites in their canopy. Details of the canopy samples, including tree identifications, are given in the two tables of the Supplementary Material. We were unable to detect any specificity pattern in the relationship between canopy termites and trees.

Assigning species to feeding groups posed little difficulty. Our assignments generally agree with those of Donovan et al. (2001) and Davies et al. (2003b) at the genus level. *Anoplotermes*-group species were distributed between groups III and IV, with the most common species, *Anoplotermes parvus*, fitting in group IV. Only the genus *Termes* presented a difficulty. *Termes* species are presumed to be soil-feeders, or at least soil-wood interface feeders (intermediate feeders, refer to DeSouza and Brown 1994; group III, refer to Donovan et al. 2001; Davies 2002, Davies et al. 2003b). However, *T. hispaniolae* was found inside dead branches, and close examination of its worker mandibles clearly revealed a wood diet (group II). In contrast, the soil-dwelling *T. panamaensis* fits in group III.

The distribution of species and occurrences between the ground and the canopy (Fig. 1) clearly shows the predominance of Termitidae in both assemblages. However, Kalotermitidae constitute a substantial part of the canopy occurrences, while being almost absent from the ground records. The opposite situation occurs with the Rhinotermitidae. Small-colony species, devoid of a specialized worker caste (Kalotermitidae and *Prorhinotermes*), were almost exclusively found in the canopy. Groupings according to diet revealed the predominance of soil feeders (groups III–IV) in the ground fauna, whereas the canopy assemblage was exclusively composed of wood feeders (Table 1).

Despite differences in ground sampling protocols between 2003 and 2004, individual occurrence-based curves were similar for both years. Species accumulation rates and diversity indices (Fisher's alpha and Simpson's 1/D) strongly differed between the ground and the canopy (Figs. 2, 3): the canopy fauna displayed a significantly lower diversity than the ground fauna. In addition, the canopy rarefaction curve shows signs of levelling off, whereas ground curves remain almost straight on the log-linear graphs, which corresponds to a logarithmic phase of species accumulation. However, if only wood-feeding species are taken into account, the accumulation curves of the ground and canopy species become remarkably similar (Fig. 4).

Among wood feeders, the seven most frequently encountered species (≥14 occurrences) were not randomly distributed between the ground and canopy strata (χ^2 =99.44, df=6, p<0.001). These frequent species clearly comprise canopy specialists (*Calcaritermes brevicollis* and *Nasutitermes nigriceps*), ground specialists (*Heterotermes convexinotatus*, *Cylindrotermes macrognathus*, *Amitermes beaumonti* and *N. guayanae*) and an ubiquitous species, *Microcerotermes arboreus*. Among the less frequent species, the other Kalotermitidae and *T. hispaniolae* were exclusively found in the canopy (Table 1).

Discussion

Hypothesis 1: faunal composition of the canopy versus ground strata

Season and ground-level sampling protocols differed between 2003 and 2004, but both campaigns yielded similar results. Because the San Lorenzo forest

Table 1 List of observed termite species and their occurrences[a] in ground and canopy transects

Family/subfamily/species	Worker caste/ feeding group[b]	2003		2004		Total	
		Ground	Canopy	Ground	Canopy	Ground	Canopy
Kalotermitidae							
Glyptotermes angustus (Snyder)	No/I	–	2	–	1	–	3
Neotermes holmgreni Banks	No/I	–	1	–	1	–	2
Rugitermes panamae (Snyder)	No/I	–	1	–	3	–	4
Calcaritermes brevicollis (Banks)	No/I	1	3	–	10	1	13
Rhinotermitidae							
Prorhinotermes molinoi Snyder	No/I	–	1	–	–	–	1
Heterotermes convexinotatus (Snyder)	Yes/I	18	–	19	–	37	–
Coptotermes niger Snyder	Yes/I	3	–	2	–	5	–
Termitidae							
Termitinae							
Microcerotermes arboreus Emerson	Yes/II	5	4	8	7	13	11
Cylindrotermes macrognathus Snyder	Yes/II	13	–	7	–	20	–
Amitermes beaumonti Banks	Yes/II	15	–	2	–	17	–
Termes hispaniolae (Banks)	Yes/II	–	3	–	3	–	6
T. panamaensis (Snyder)	Yes/III	–	–	1	–	1	–
Orthognathotermes wheeleri Snyder	Yes/IV	7	–	4	–	11	–
Neocapritermes centralis (Snyder)	Yes/III	–	–	1	–	1	–
Syntermitinae							
Cornitermes walkeri Snyder	Yes/II	2	–	–	–	2	–
Embiratermes chagresi (Snyder)	Yes/III	13	–	4	–	17	–
Nasutitermitinae							
Nasutitermes nigriceps (Haldeman)	Yes/II	2	13	–	6	2	19
N. guayanae (Holmgren)	Yes/II	12	2	2	–	14	2
Nasutitermes sp.1	Yes/II	–	–	2	2	2	2
Subulitermes sp.1	Yes/III	7	–	7	–	14	–
Coatitermes clevelandi (Snyder)	Yes/ III	–	–	2	–	2	–
Apicotermitinae							
Anoplotermes parvus Snyder	Yes/IV	20	–	7	–	27	–
A. manni Snyder	Yes/IV	1	–	2	–	3	–
Anoplotermes sp.A	Yes/IV	5	–	6	–	11	–
Anoplotermes sp.B	Yes/IV	3	–	1	–	4	–
Anoplotermes sp.C	Yes/III	2	–	–	–	2	–
Anoplotermes sp.H	Yes/III	13	–	4	–	17	–
Anoplotermes sp.I	Yes/III	2	–	–	–	2	–
Anoplotermes sp.J	Yes/III	1	–	–	–	1	–
Anoplotermes sp.K	Yes/III	2	–	–	–	2	–
Anoplotermes sp.L	Yes/III	9	–	3	–	12	–
Anoplotermes sp.M	Yes/III	–	–	1	–	1	–
Anoplotermes sp.N	Yes/III	–	–	1	–	1	–
Ruptitermes sp.1	Yes/III	1	–	–	–	1	–
Occurrences (total = 306)		157	30	86	33	243	63
Species (total = 34)		23	9	21	8	29	10

[a] Numbers shown are occurrences; i.e. the number of sampling units (quadrats or trees) in which each species was present

[b] Feeding groups as defined by Donovan et al. (2001)

remains humid and experiences almost no loss of canopy cover during the January–April drier season (Condit et al. 2000), the ground-level fauna should hardly suffer from drought stress (Martius et al. 2004), and little difference would therefore be expected in termite activity between October and May. As was also predicted (Roisin and Leponce 2004), reducing the quadrat area from 10 to 5 m^2 had no tangible effect on the number of occurrences. The ground-level fauna was largely dominated by soil feeders (groups III and IV, refer to Donovan et al. 2001).

Few other studies – carried out in neotropical rainforests following a similar protocol – are available for comparison. From 13 transects in rainforest fragments of various sizes in French Guiana, Davies et al. (2003b) obtained 99 termite species. Although the Guianan survey revealed a higher species density than our study in Panama, the composition of the taxonomic and feeding groups of both assemblages were similar. In Davies et al.'s (2003b) study as in ours, Kalotermitidae were very scarce and Rhinotermitidae were poor with respect to species number, although a single

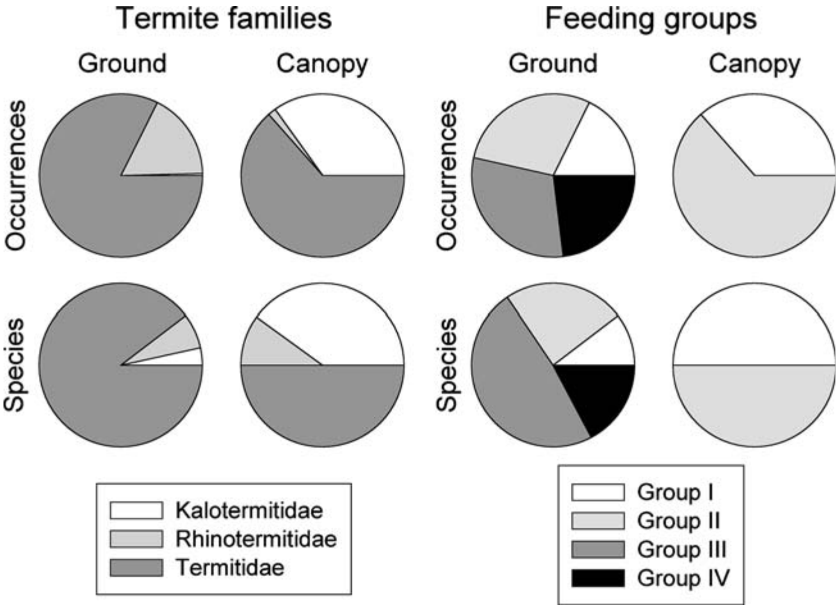

Fig. 1 Distribution of termite occurrences (*top*) and species (*bottom*) by family (*left*) or feeding group (*right*) in the ground and canopy samples. Feeding groups are as defined by Donovan et al. (2001)

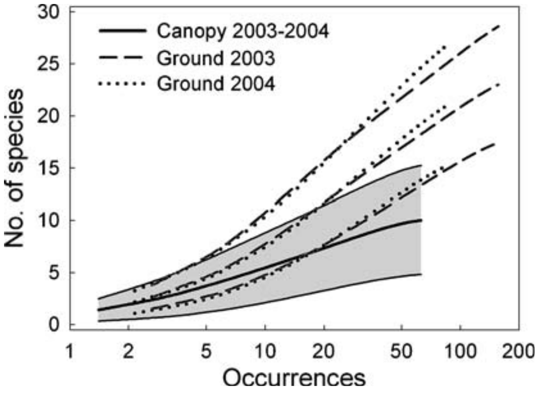

Fig. 2 Rarefaction curves for termite assemblages from canopy sampling (pooled 2003–2004 campaigns: *solid lines*, *shaded area*) compared with ground sampling campaigns (*dashed* and *dotted lines*). Graphs show most likely estimates and 95% confidence intervals, calculated by the Mao-Tau method (Colwell et al. 2004). The *abscissa* is scaled logarithmically to reveal more clearly the logarithmic or asymptotic nature of curves

Heterotermes species accounted for a large number of records. The family Termitidae, especially rich in soil-feeding species, was highly dominant. Soldierless Apicotermitinae (the *Anoplotermes* group) constituted about one-third of the observed species richness at both sites. In Brazilian Amazonia, DeSouza and Brown (1994) recorded termite occurrence in transects composed of successive 15-m^2 quadrats. They found relatively few soldierless species (9 out of 64), but this may be due to their sampling protocol, which did not include systematic searches of soil samples. Nevertheless, their study revealed a high species density (64 species in four 220×3-m transects), from which Kalotermitidae were absent. The scarcity of Kalotermitidae and the abundance of soldierless Apicotermitinae thus appear to be general traits of neotropical rainforest termite faunas, as long as near-ground sampling is involved. These traits equally apply to African

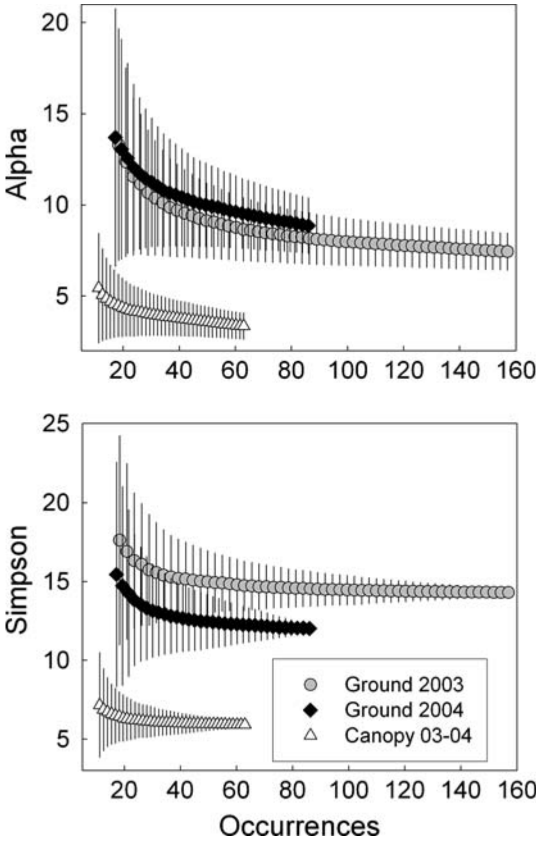

Fig. 3 Fisher's alpha (*top*) and Simpson's inverse index (1/*D*) (*bottom*) for ground and canopy samples (mean ± standard deviation)

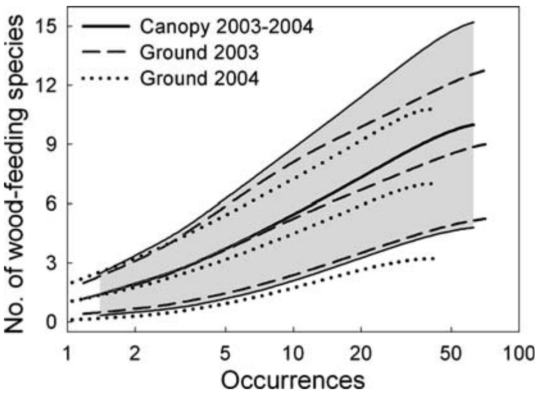

Fig. 4 Rarefaction curves for assemblages of wood-feeding termites from canopy sampling (pooled 2003–2004 campaigns: *solid lines*, *shaded area*) compared with ground sampling campaigns (*dashed* and *dotted lines*). Graphs show averages and 95% confidence intervals, calculated by the Mao-Tau method (Colwell et al. 2004). *Abscissa* is scaled logarithmically

rainforests, although these are also rich in soil-feeding Termitinae (Eggleton et al. 1996, 2002). Mainland rainforests of Southeast Asia also accommodate a low abundance of Kalotermitidae but are characterized by the absence of soldierless Apicotermitinae and the dominance of Termitinae in the soil-feeding guild (Eggleton et al. 1999; Eggleton 2000; Davies et al. 2003a).

Canopy sampling yielded ten species, all of which were wood feeders. Among these, the two expected ecological categories (see Hypothesis 1) were represented. Five species out of ten and one-third of the canopy occurrences were small-colony species, without a distinct worker caste (Kalotermitidae and the rhinotermitid *Prorhinotermes*). Our results suggest that the Kalotermitidae family may be much more abundant and species-rich in tropical rainforests than previously assumed on the basis of ground-level collecting efforts (Davies et al. 2003a). Accordingly, the role played by small-colony termites from the canopy in the wood decomposition process in tropical rainforests could be greater than previously recognized. This issue deserves further attention in all of the world's tropics.

Three genera of Termitidae were represented in the canopy. *Nasutitermes* and *Microcerotermes* are pantropical genera comprising arboreal as well as epigeous nesters. Arboreal species build foraging wood-carton tunnels over long distances, and these tunnels are common sights in tropical forests worldwide (Abe 1978, 1979; Leponce et al. 1997; Dejean et al. 2003; Gonçalves et al. 2005). The finding of *T. hispaniolae* in the canopy (six occurrences up to 35 m high; none at ground level) was unexpected, because *Termes* species are allegedly soil or soil-wood interface feeders (DeSouza and Brown 1994; Donovan et al. 2001). However, *T. hispaniolae* was found inside dead branches, feeding on sound wood. The fact that this species is widespread in the West Indies (Scheffrahn et al. 1994) is also consistent with its ability to live inside of wood and disperse by rafting over water gaps (Eggleton and Tayasu 2001). The occurrence of *T. hispaniolae* in the canopy is interesting for two reasons. First, this species does not fit into any of the pre-defined ecological categories of Hypothesis 1: it is a wood feeder, which neither fits into the small-colony ''one-piece'' category (like most Kalotermitidae), nor into the arboreal nest-building, long-distance foraging category (like *Nasutitermes* or *Microcerotermes* spp.). It suggests that another category of canopy termites, comprising large-colony Termitidae, is able to live their entire life cycle in large, dead branches. Such habitats should be stable enough to allow the development of termite colonies with a complex pattern of social polymorphism, including a permanent worker caste (Higashi et al. 1991). Second, *T. hispaniolae* may represent another instance of re-evolution of wood feeding from soil-feeding ancestors, a transition that allegedly occurred in several Termitidae lineages, such as those comprising *Amitermes*, *Microcerotermes* or *Nasutitermes* (Eggleton and Tayasu 2001). A better knowledge of the phylogeny of *Termes* and related genera could provide further evidence for (or against) this evolutionary scenario.

The absence of soil-feeders from the canopy can be explained by the near absence of large epiphytes able to accumulate litter and generate soil-like environments. Soil-feeding termites live on an energetic knife-edge (Eggleton and Tayasu 2001): soil is an energy-poor resource that must be ingested in large amounts at a low foraging cost to yield a positive energetic balance. It is therefore likely that only large aggregates of epiphyte-associated, soil-like habitats may be colonized by soil-feeding termites. Davies et al. (2003b) actually encountered *A. parvus* from the casual sampling of an epiphyte 25 m high in a forest in French Guiana. We can therefore predict that soil-feeding termites will be found on a regular basis in tropical canopies provided they are rich in epiphytes.

Hypothesis 2: specific richness of the ground versus canopy strata

Unavoidable differences in sampling protocols preclude direct comparisons of species richness and density between the ground and the canopy. Although the canopy area actually searched for termites (approx. 6800 m^2 in 2003 and 8000 m^2 in 2004) was much larger than the ground area (600 and 200 m^2, respectively), it yielded fewer occurrences and species. This suggests that the density of termite species in the canopy is relatively low compared with the ground, even if only wood-feeders are considered. Yet, despite the availability of professional tree climbers, canopy sampling remains technically difficult, time-consuming and necessarily less exhaustive than ground sampling. Altogether, only 36% of the trees were found to be colonized by termites. In the Brazilian Atlantic forest, Gonçalves et al. (2005) found a similar level of occupancy, although their study was limited to tunnel-building Termitidae (*Nasutitermes* spp. and *Microcerotermes* cf. *exiguus*). These authors report that tree circumference, height and branch density all correlate positively with the presence of arboreal termites. It is likely that these variables also correlate with the presence of dead wood in the canopy, which is exploited by tunnel-building Termitidae as well as by small-colony Kalotermitidae. The vertical distribution of available dead wood should be a key parameter for future studies aimed at quantifying the role of termites at various levels of the forest. In Amazonian forests, Martius (1997b) estimated that standing dead branches could represent as much volume as standing dead trees, but rigorous assessments are badly needed.

Consistent with Hypothesis 2, comparisons based on equal numbers of occurrences clearly demonstrated the higher diversity of the ground fauna, mostly due to the diversity of soil-feeders. Ground transects not only displayed a higher observed species richness than canopy transects, but their species accumulation curves did not show signs of saturation. Consequently, one could expect that extended sampling might lower the relative part of the canopy fauna in the total species richness of the termite assemblage below the presently observed proportion of 30%. However, when only the wood-feeding guild is considered, the canopy shows a diversity similar to that found at the ground level. Further collecting efforts are needed to obtain a more precise picture of the distribution of wood-feeding species at all levels of the forest. In addition, an unknown factor influencing the respective richness of ground and canopy termite faunas is their beta diversity. The diversity of trees may render the upper layers more heterogeneous and, therefore, more likely to vary with location than the ground environment (Basset et al. 2003b); on the other hand, the present study did not indicate any specificity in the relationship between canopy termites and tree species. The patchiness of canopy habitats may also require greater dispersal abilities, which should make canopy faunas more homogeneous over large spatial scales (Fagan et al. 2006). Whether canopy assemblages change more or less rapidly than the corresponding ground assemblages remains open to future investigation.

Hypothesis 3: vertical stratification of wood-feeding species

Although the diversity of the canopy fauna was similar to that of the wood-feeding guild encountered at ground level, these assemblages differed by their taxonomic composition. The termite fauna of the canopy is clearly more than just a subset of the wood-feeders encountered at ground level: it is a distinct assemblage, characterized by its richness in Kalotermitidae and by the presence of specialist species of Termitidae.

According to Hypothesis 3, the canopy should preferentially accommodate drought-resistant species, which are also likely to be present in forest edge habitats. The Kalotermitidae, long known to thrive in dry wood and colonize marginal habitats, clearly match those criteria. Dead branches theoretically constitute ideal habitats for such termites, whose colonies are limited in size and can spend their entire life cycle within a single piece of wood (Abe 1984, 1987; Higashi and Abe 1996; Eggleton 2000).

Among the Termitidae, *M. arboreus* was the only species commonly found at all heights within the forest. *Nasutitermes* species were unevenly distributed: *N. nigriceps* was preferentially found in the canopy, whereas *N. guayanae* was more common near ground level. Previous studies of the same genera in New Guinean coconut plantations revealed the competitive dominance of a large arboreal species, *N. princeps*, over the smaller *M. biroi*, whereas the latter proved faster at colonizing new sites (Leponce et al. 1996, 1997). Another nasute, *N. novarumhebridarum*, showed a preference for isolated, dead trees. Whether the same pattern of niche partitioning between arboreal *Nasutitermes* and *Microcerotermes* species occurs in San Lorenzo would require further examination. The fact that *M. arboreus* occurs at all heights indeed suggests that this species behaves in an opportunistic fashion.

The absence of *N. corniger* (or its synonym, *N. costalis*: see Scheffrahn et al. 2005) from our samples is noteworthy because this arboreal species is widespread and abundant in Panama, especially in second-growth habitats of the former Canal Zone (Thorne 1981) and mangroves along the Atlantic coast (Levings and Adams 1984). Casual sampling (unpublished results) actually revealed its presence in the San Lorenzo area. In French Guiana, this species was also found 20 m high in a dead, inundated (“ghost”) forest, albeit not in the rainforest itself (Davies et al. 2003b). The occurrence of this species in the canopy was thus expected. Its absence can be best explained by the spatial structure of the canopy and possible competition from congeneric species, particularly *N. nigriceps*. As judged from their foraging range (Levings and Adams 1984) and nest size (Thorne et al. 1994; Thorne and Haverty 2000), *N. nigriceps* is found on a much larger scale than *N. corniger* and would, therefore, be better adapted to large canopy trees, whereas *N. corniger* would thrive in the denser network of branches and vines encountered in second-growth areas. Although resemblances between the forest edge and canopy and common features of their faunas have been pointed out (Toda 1992; Didham 1997), the distributions of *N. corniger* and *N. nigriceps* suggest that differences in forest structure may be an important factor limiting such similarities. Further studies within the IBISCA framework should reveal whether the distribution of other arthropods follows a congruent pattern.

Perspectives: vertical stratification in other ecosystems

Because tall evergreen tropical forests are presumably the ecosystems in which abiotic and biotic gradients from the ground to the outer canopy are the strongest and most stable, vertical stratification can be expected to decline as one moves towards drier, higher or more seasonal ecosystems (Basset et al. 2003d). Unfortunately, comparative data on the vertical stratification of termites in other ecosystems are almost non-existent. Some recent data from drier tropical forest ecosystems, however, support this hypothesis. For instance, in a study of the Chacoan dry ‘‘monte’’, the Kalotermitidae represented 29% of the observed species and 19% of the occurrences (Roisin and Leponce 2004), whereas in a West African semi-deciduous forest, they represented 35% of the observed species and 6% of the encounters (Attignon et al. 2005). This suggests that taxa almost completely restricted to the canopy in evergreen forests may be common near ground level in more open, drier ecosystems. The direct sampling of the canopy in such ecosystems is, however, still wanting. Conversely, one may expect that taxa usually restricted to the ground level ascend to the higher strata in more humid forests, whose canopy is less subject to dessication and richer in epiphytes (e.g. lowland cloud forest: Gradstein 2006).

Finally, a more pronounced vertical stratification should be expected in sites showing a high stability and an even higher diversity of wood-feeding termites than the San Lorenzo forest. For instance, some sites in African forests yielded up to 15 species of wood-feeding Termitidae – in addition to many soil feeders – from a single 200-m^2 ground-level transect (Davies et al. 2003a). A specific search for canopy-dwelling species in such forests would be of utmost interest.

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