Invertebrate Diversity and the Ecological Role of Decomposer Assemblages in Natural and Plantation Forests in Southern Benin

Inauguraldissertation

zur
Erlangung der Würde eines Doktors der Philosophie
vorgelegt der
Philosophisch-Naturwissenschaftlichen Fakultät
der Universität Basel

von

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aus Cotonou, Benin

Basel, 2004

Genehmigt von der Philosophisch-Naturwissenschaftlichen Facultät auf Antrag von

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Basel, den 6. Juli 2004

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Chapter 1

General Introduction

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General Introduction

Tropical forests are disappearing at alarming rates worldwide (Laurance, 1999). The loss and fragmentation of tropical forests appears to be the single greatest threat to the world's biological diversity (Whitmore, 1990; Huston, 1994). One of the resolutions of the Convention on Biological Diversity is that measures have to be taken in order to conserve natural forests, especially tropical forests, which are among the biodiversity hotspots considered as a global priority for conservation (Sayer and Wegge, 1992; Myers et al., 2000). According to FAO (2000), the annual deforestation rate in Africa is about twice as high as the global rate (0.3 versus 0.7%).

Secondary forests and forest plantations make up an increasing proportion of the total forest cover, due to the continued destruction of natural forest by humans on the one hand and large-scale reforestation or afforestation on the other hand. For some countries, secondary and plantation forests may soon be all that remains (Castelletta et al., 2000). Since 1990, the area of tropical forest converted to plantation forest has considerably increased. Forest plantations may contribute to reducing deforestation and the degradation of natural forest (FAO, 2001). Therefore, there is a growing need for biodiversity studies in plantation forests. Some studies have demonstrated that these forests can support a rich and varied fauna and serve to conserve wildlife as well (Speight and Wylie, 2001). Conversion of natural forest to plantation forest may lead to a change in litter quality, composition and hence microbial and faunal decomposer assemblages (Ananthakrishnan, 1996). For a sustainable management of tropical forests, it is important to understand changes in key ecosystem processes such as decomposition and nutrient cycling that are encountered when converting natural forest or other land uses into plantation forests, or when rehabilitating natural forest (Attignon et al., 2004).

Litter decomposition in terrestrial ecosystems

In terrestrial ecosystems, the major part of the net primary production enters the detritus-based food web litter (Swift et al., 1979; Wardle and Lavelle, 1997). Therefore, litter decomposition is an important process regulating energy flow, nutrient cycles, and structures of ecosystems (Swift et al., 1979; Wachendorf et al., 1997). Many studies have shown that decomposition is influenced by litter quality, climatic factors and soil biota (Tian et al., 1997; Wachendorf et al., 1997; Wardle and Lavelle, 1997; Heneghan et al., 1999; Gonzalez and Seastedt, 2001). Some studies suggest that the soil fauna may have a greater effect on decomposition in tropical forests than in temperate ones (Heneghan et al., 1999; Gonzalez and Seastedt, 2001). However, decomposition rates vary greatly even among tropical forests, depending on factors such a climate and litter quality. Soil biota include microflora, Microinvertebrates and macroinvertebrates. Microflora (bacteria and fungi) is the major group that decomposes litter directly (Vossbrinck et al., 1979; Wardle and Lavelle, 1997). Microinvertebrates directly consume or indirectly regulate microfloral communities, thereby affecting decomposition rates (Vossbrinck et al., 1979; Reddy and Venkataiah, 1989). Macroinvertebrates influence decomposition through changing the abundance of microdecomposers (Lawrence and Wise, 2000).

Ecological role of soil invertebrates

Soil invertebrates are important components of tropical ecosystems. This diverse group of animals covers a range of taxa, the most important being protozoans, nematodes, earthworms, mites, springtails (Collembola), millipedes, centipedes and range of insects (mostly belonging to Diptera, Coleoptera and Isoptera). Soil invertebrates perform important functions related to the growth conditions of plants. For example, ecosystem engineers such as termites and earthworms increase soil porosity and average pore size by tunnelling through the soil (Edwards and Shipitalo, 1998). These invertebrates ingest considerable amounts of soil and dead plant material, thereby contributing to the mixing of organic matter and mineral soil. This improves aggregate stability and increases the surface of organic material so that it is more readily colonised and decomposed by soil bacteria and fungi (Lavelle et al., 1997). Examples have shown that soil fauna enhance nitrogen mineralization markedly by up to 25% (Seastedt, 1984; Verhoef and Brussard, 1990). Soil invertebrates are the dominant animal group in many terrestrial ecosystems and may have higher biomass on an area basis than above-ground herbivorous insects or vertebrates (Odum, 1971). Soil invertebrates represent, with their relatively high protein content, a significant pool of nutrients such as nitrogen, which may ultimately become available for primary production. Soil invertebrates are also important players in terrestrial food webs. They are an important food source for many predacious invertebrates and vertebrates (Bilde et al., 2000; McNabb et al., 2001).

Ecological significance of termites in tropical forest ecosystem

Macroinvertebrates have an important role in the maintenance of soil structural stability and fertility in many natural and man-modified habitats.

Being at the ecological centre of many tropical ecosystems (Wilson, 1992), termites are considered important insect indicators. In many tropical forest soils, termites are the most abundant and important decomposers (Wood and Sand, 1978; Matsumoto and Abe, 1979; Collins, 1983). Termites living in the tree canopy and on epiphytes may also attain high biomass (Ellwood and Foster, 2004). Termites are vital in maintaining decomposition processes (Collins, 1989), and play a central role as mediators of nutrient and carbon fluxes (Lawton et al., 1996; Bignell et al., 1997). The presence of termites increases soil permeability markedly and may improve soil structure, aeration, nutrient cycling and soil fertility. Termites fragment and comminute litter, thereby facilitating the action of microorganisms, which in turn transform litter organic compounds into mineral nutrients available to plants. The influence of termites on decomposition processes is governed to a large extent by the species composition and structural diversity of local assemblages (Lawton et al., 1996). However, there are still relatively few studies of termite assemblages in tropical forests.

This study was conducted in the Lama forest reserve in Benin. The reserve is situated in an area where savannahs have for a long time interrupted the forest belt extending along the West-African coast. This interruption is called the Dahomey Gap. The Lama forest reserve is the largest natural forest in southern Benin, and one of the last remnant forests within the Dahomey Gap (Nagel, 1987; Ern, 1988; Sokpon, 1995; Ballouche et al., 2000). It is composed of natural forest (2,500 ha), degraded forest/savannah (4,759 ha) and forest plantations (9,000), and has the protectional status of a "classified forest" since 1946. The forest is home to several endangered wildlife species and rare plants. Therefore, it is of primary concern for biodiversity conservation in Benin. Despite an urgent need for conserving the biodiversity of Lama forest, only few studies have been conducted so far, focusing on the natural forest. A preliminary list of insects was compiled (Boppré, 1994; Tchibozo, 1995; Emrich et al., 1999), and a butterfly inventory conducted (Fermon et al., 2001). However, despite the important ecological role of invertebrates in the functioning of forest ecosystems, they have received very little attention. Yet only an understanding of key ecosystem processes provides the basis for a more sustainable forest management.

This thesis consists of five manuscripts, hereafter referred to as Chapters 2– 6.
In **Chapter 2** (“Leaf litter breakdown in natural and plantation forests of the Lama forest reserve in Benin”), we show that the breakdown of litter in the Lama forest reserve strongly depends on litter and forest type. Litter breakdown was more rapid in natural forest than in plantation forests, and we found a significant litter × forest interaction. Litter of *Afzelia africana* decomposed faster than litter of *Tectona grandis*. With the exception of teak, decay rate coefficients (k) were higher in Lama forest than in most other tropical forests. The activity

(frequency of occurrence) of litter-dwelling invertebrates was higher in indigenous than in exotic litter, and also higher in natural than in plantation forests. Litter breakdown was strongly related to the activity of invertebrates.

In Chapter 3 ("Termite assemblages in a West-African semi-deciduous forest and teak plantations"), we present results of the first termite inventory in Lama forest, comparing termite assemblages in semi-deciduous forest and teak plantations in terms of species richness, abundance and trophic structure. Termites were monitored adapting a standardised belt transect method (100 × 2 m). We found that overall species richness was very low. This was related to the black cotton soil (vertisol) which excluded most soil-feeders of the soil/humus interface and all true soil-feeders. We found more species in semi-deciduous forest, with a dominance of Kalotermitidae. Teak plantations were dominated by fungus-growing species (Macrotermitinae). The density of fungus-growers was significantly higher in teak plantations than in semi-deciduous forest. Multiple regression identified two significant predictors of termite assemblages, soil water content (higher in natural forest) and leaf-litter biomass (higher in teak plantations). The high encounter density of fungus-growers in teak plantations was related mainly to these factors.

In **Chapter 4** ("Activity of termites and other epigeal and hypogeal invertebrates in natural semi-deciduous forest and plantation forests in Benin"), we present a cardboard baiting method to examine the activity of soil- and litter-dwelling termites and other invertebrates in semi-deciduous forest, teak plantations (old and young) and firewood plantations (*Senna siamea* mainly). We used the frequency of occurrence of invertebrates at cardboard baits as a measure of attraction, and tested for the effect of forest type and season. The overall frequency of occurrence of invertebrates was affected by forest type and was highest in natural forest, followed by firewood plantation, young and old teak plantations. The most frequent soil invertebrates were Collembola, Isopoda, Isoptera, Diplopoda, Araneae and Hymenoptera (ants). The activity of most of the abundant taxa (except Diplopoda and Araneae) varied among forest types, with the highest activity recorded in natural forest. Invertebrates showed a strong seasonal activity pattern, with a distinct low during the long dry season (except for termites). The highest activity of termites was found in old teak plantations. However, on species level we found only significant difference for *Microtermes? pusillus?* (final identification pending), with higher activity in old than in young teak plantations.

In **Chapter 5** ("*Stemmiulus (Diopsiulus) lama* n. sp., a new millipede from Benin (Myriapoda, Diplopoda, Stemmiulidae)"), we describe a new millipede species, *Stemmiulus lama* n. sp., from Lama forest. This species is the first record of a stemmiulid millipede in Benin.

In **Chapter 6** ("Diversity of true bugs (Heteroptera) in various habitats of the Lama forest reserve in southern Benin"), we report the results from a Heteroptera diversity assessment. True bugs were sampled over a 12-month period, using funnel traps, ground photo-eclectors, Malaise traps, flight traps and sweep-nets. We compared species richness, relative abundance and diversity indices for Heteroptera assemblages from nine different forest habitats, including natural forest, degraded forest, plantations as well as isolated forest fragments. A total of 893 specimens (imagoes) were collected, representing 104 species in 16 families. There was no significant effect of forest type on species richness and evenness. But Heteroptera abundance, Shannon-Wiener diversity and Berger-Parker dominance differed significantly among forest habitats. Moreover, Heteroptera assemblages in disturbed forest were significantly more diverse than those in undisturbed forest.

In **Chapter** 7, we summarize the main results of the five manuscripts and present our general conclusions.

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Chapter 2

Leaf Litter Breakdown in Natural and Plantation Forests of the Lama Forest Reserve in Benin.

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Applied Soil Ecology, in press

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Abstract

The Lama forest reserve in southern Benin, West Africa, comprises timber and fuelwood plantations as well as some of the country's last vestiges of semi-deciduous lowland forest. The reserve is intended to protect the fauna and flora and to promote the sustainable use of tree plantations. An important aspect in its management is the preservation of soil quality which in turn is related to key ecosystem processes such as decomposition. In the present study, we examined the breakdown of leaf litter from two indigenous (*Afzelia africana* and *Ceiba pentandra*) and two exotic tree species (*Tectona grandis* and *Senna siamea*), using the litterbag technique (1,920 litterbags altogether), and the relationship between litter breakdown and the relative abundance (frequency of occurrence) of litter-dwelling invertebrates. The study was conducted over a 140-day period, focusing on four different forest types: semi-deciduous natural forest, young teak, old teak and fuelwood (mainly *S. siamea*) plantations. Both main factors, litter species and forest type, had a significant effect on litter breakdown. The residual litter weight was lowest in *A. africana*, intermediate in *S. siamea* and *C. pentandra* and highest in *T. grandis*. Differences were significant for all but one pairwise comparison (*A. africana* vs. *S. siamea*). With regard to forest type, the breakdown was highest in natural forest, followed by young teak, old teak and firewood plantations. Except for teak plantations (young vs. old teak), all comparisons were significant. We also found a significant litter × forest interaction, indicating dissimilar changes in litter breakdown across forest types. With the exception of teak, decay rate coefficients (k) were higher than in most tropical forests, ranging from $k = 1.3$ (*T. grandis* in firewood plantations) to $k = 4.7$ (*A. africana* in natural forest). The frequency of occurrence of invertebrates differed among leaf litters and forests, while there was no significant litter × forest interaction. Higher frequencies were observed in indigenous than in exotic litter. Likewise, litterbags in natural forest attracted more invertebrates than those in forest plantations. We found a significant inverse linear relationship between invertebrate frequency and residual litter weight, indicating that the breakdown of litter was strongly related to the activity of invertebrates. Our study concludes that management practices should aim to enhance decomposer communities to safeguard the productivity and sustainable use of Lama forest.

Keywords: Natural forest; Plantation forests; Litter breakdown; Litter-dwelling invertebrates; Lama forest

1. Introduction

Litter production in the equatorial belt is two to three times higher than in temperate regions (Ambasht and Srivastava, 1995). In moist tropical lowland forests, the annual litterfall ranges between 6–12 t/ha (Sharma and Sharma, 1995). Leaves constitute the major part of the total litterfall, providing an important nutrient pool. Thus, the breakdown of leaf litter is a key component in nutrient cycling in tropical forests. Decomposition processes are regulated by a number of abiotic and biotic factors (Lavelle et al., 1993). These comprise (1) microclimate, mainly temperature and humidity (Meentemeyer, 1995), (2) litter quality, in particular nitrogen, lignin and polyphenol concentrations and ratios (Wood, 1995; Ananthakrishnan, 1996; Aerts, 1997; Heal et al., 1997; Sariyildiz and Anderson, 2003), (3) soil nutrient content (Verhoeven and Toth, 1995), and (4) the qualitative and quantitative composition of decomposer communities, including bacteria, fungi and invertebrates (Swift et al., 1979; Knoepp et al., 2000). In tropical forests, the biological activity of decomposers is concentrated in litter and the topsoil (Barros et al., 2002).

Mean annual decomposition rate constants – or decay rate coefficients – (k) for temperate and tropical forests have been estimated at $k = 0.9$ and $k = 1.8$, respectively (Torreta and Takeda, 1999). Within the tropics, there is some evidence of regionality in decomposition rates, with $k > 2$ (high) for most African forests and $k = 1–2$ (medium to high) for forests in Southeast Asia and the Neotropics (Anderson and Swift, 1983). Very high ($k \approx 4$) rates are observed mainly in African tropical forests (Olson, 1963), indicating rapid nutrient cycling. However, decay rates can be low ($k < 1$) even in tropical areas, depending on litter type, season and altitude (Verhoef and Gunadi, 2001).

Natural forests in the tropics support a high diversity of trees and show considerable variation in decomposer communities and litter decomposability (Anderson and Swift, 1983; Takeda, 1998). Large tracts of forest have been converted into other land uses, including forest plantations, leading to different litterfall and decomposition regimes. From 1990 to 2000, one percent (10 million ha) of all tropical forests were converted into tree plantations (FAO, 2001), a trend expected to continue in the next decades. By altering litter quality, composition and hence microbial and faunal decomposer assemblages, the conversion into forest plantations may affect soil fertility (Ananthakrishnan, 1996). For the sustainable management of tropical forests it is therefore important to understand changes in decomposition processes and nutrient cycling encountered when converting natural forest or other land uses into plantation forests – or when rehabilitating natural forest.

The present study examines the breakdown of leaf litter in Lama forest reserve, a mosaic of natural, degraded and plantation forest including some of the last vestiges of semi-deciduous lowland forest in southern Benin, West Africa (Ern 1988; Sokpon, 1995). The principal goal of the study was to provide baseline data for the sustainable management of Lama forest. The specific objectives were to study the effects of litter type (indigenous and exotic species) and forest system (natural and plantation forests) on the breakdown of leaf litter, and to relate decomposition rates to the activity of litter-dwelling invertebrate assemblages.

2. Materials and methods

2.1 Study area and experimental sites

Lama forest is situated in the so-called Dahomey gap, a discontinuity of the West African rainforest belt (Jenik, 1994). The reserve (*forêt classée*) lies in the Lama depression, about 80 km north of Cotonou (between 6°55.8–58.8'N and 2°4.2–10.8'E), covering 16,250 ha (Fig. 1). The study focused on four different forest ecosystems, hereafter coded with Roman numerals. (I) Remnants of semi-deciduous forest (Adjanohoun et al., 1989) are scattered within the *Noyau Central* (NC), the inner, now fully protected part of the reserve (4,800 ha) which is composed of a mosaic of natural forest (1,900 ha), secondary forest, *Chromolaena odorata* thickets and enrichment plantings (Specht, 2002). Dominant tree species of the semi-deciduous forest are *Afzelia africana, Albizia zygia, Anogeissus leiocarpus, Ceiba pentandra, Dialium guineense* and *Diospyros mespiliformis.* (II) Young teak plantations, *Tectona grandis*, were planted between 1985–1995. They enclose the NC nearly entirely, forming a buffer zone that separates the NC from surrounding cropland. In the present study, we only included stands planted between 1988−1991. (III) Old teak plantations are contiguous to young teak plantations, representing northerly and southerly extensions. They were established between 1963−1965. Old and young teak plantations cover about 10,000 hectares. (IV) Firewood plantations (2,400 ha) are located in the south-western part of Lama forest. They are composed of *Senna siamea* mixed with teak (ratio 3:1). The firewood plantations were planted between 1988−1996, of which we studied stands from 1990−1992.

Four replicate sites, each measuring about 1.0 × 7.5 m, were selected within each forest type (Fig. 1). All replicates were similar with respect to soil type, vegetation and – in case of plantations – tree age. The distance among replicate sites varied between 0.5 and 19.0 km, i.e., replicates were widely scattered over the respective forests to assure spatial representativeness. The minimum distance between sites and forest edges was 50 meters.

2.2 Climate

The climate in Lama forest is subequatorial, showing two rainy and two dry seasons. The mean annual precipitation is 1,100 mm. The highest rainfall occurs in June and the lowest in January. The annual precipitation deficit is about 200 mm, but relative humidity is always high. Average annual temperatures vary between 25–29°C, with a maximum in February and March (39°C) and a minimum in December (15°C). The data for Lama forest recorded during the study are shown in Fig. 2. Mean minimum and maximum temperatures were 24 and 27°C, respectively. Average relative humidity ranged between 84–94%, with a minimum of 50–60% and a maximum of 100%.

2.3 Soil and environment properties

Lama forest is named after the Portuguese word “lama” (mud). The name alludes to the characteristic vertisols in the Lama depression. Only towards the borders of the reserve (old teak plantations) are vertisols gradually replaced by sandy ferralsols (Specht, 2002). An overview of soil and other site characteristics registered during the study period is given in Table 1. Major features distinguishing semi-deciduous and plantation forests were differences in the carbon and nitrogen content of the soil (higher in semi-deciduous forest) as well as differences in litter cover (lower) and canopy cover (higher). Earthworm activity in semi-deciduous forest was very high, but this was also observed in young teak plantations.

2.4 Leaf litter

We examined leaf litter from two indigenous (*A. africana*, Leguminosae, and *C. pentandra*, Bombacaceae) and two exotic tree species (*T. grandis*, Verbenaceae, and *S. siamea*, Leguminosae). *A. africana* is a widespread species of fringing forest and drier parts of the African forest belt (Keay, 1989). *C. pentandra*, the kapok or silk-cotton tree, is distributed pantropically. Keay (1958) considers this tree an ancient introduction to Africa from tropical America, whereas other authors propose an American or African origin (Zeven and de Wet, 1982). Here we consider the kapok as an indigenous tree. Teak, *T. grandis* (timber), and the yellow cassia, *S. siamea* (fuelwood), are widely planted trees originating from Southeast Asia

(Keay, 1989). *S. siamea* is a non-nodulating legume and is therefore not associated with nitrogen-fixing *Rhizobium* bacteria (e.g., Ojo and Fagada, 2002). Basic physico-chemical litter characteristics are summarised in Table 2. The data indicate that litter quality was high in *A. africana*, low in teak and intermediate in *C. pentandra* and *S. siamea*. This ranking, however, is tentative since other components determining litter quality, in particular lignin and polyphenol, were not analysed.

Litter breakdown was studied using the litterbag method (Bocock and Gilbert, 1957; Bocock et al., 1960). This is the most widely used technique for examining litter decomposition in terrestrial ecosystems (Yamashita and Takeda 1998; Mesquita et al., 1998; Tian et al., 2000; Conn and Dighton 2000). During the dry season 2002 (February and March), freshly fallen leaves were collected from semi-deciduous forest (*A. africana* and *C. pentandra*), old teak plantations (*T. grandis*) and firewood plantations (*S. siamea*), respectively, air-dried and stored in a dry place. Before filling the litterbags, the leaves were oven-dried (120°C) for one hour to constant weight. For each species, 480 litterbags (20 × 20 cm, flat plastic-coated glass fibre material, mesh size 4 mm) were filled respectively with 6 g (*C. pentandra*), 8 g (*A. africana*) and 11 g (*T. grandis* and *S. siamea*) of leaf litter (total = 1,920 litterbags). The mesh size was sufficiently small to minimize losses of litter due to breakage – a general bias inherent to the litterbag technique – while being large enough to allow access of most litter-dwelling invertebrates into the bags (Loranger et al., 2002). The dissimilar filling weight (initial weight) was necessary to attain a similar, even distribution of the morphologically different leaves in the bags (i.e., approximately similar volumes). The initial weight was treated as a covariable in the data analysis.

In May 2002, at the beginning of the rainy season, 30 litterbags per leaf species (120 bags per site) were placed randomly onto the ground of each of the 16 experimental sites. Litter *in situ* was first removed and litterbags were secured with wire hooks to ensure close contact with the soil. Bags were individually marked and labelled with aluminium tags. Three litter bags per species and site (pooled sample = one set) were collected in random order in two-week intervals, the sampling period lasting from May to October 2002 (14−140 days post-exposure). Each set was carefully transferred into individual plastic bags and transported to the field laboratory. In a first step, invertebrates were extracted (see below). Subsequently, the dry litterbags of each set were emptied onto a tray and thoroughly cleared with fine brushes from extraneous material (adhering plants, plant debris and soil). The residual weight of the cleaned litter was recorded after one hour oven-drying at 120°C.

2.5 Extraction of litter-dwelling invertebrates

Invertebrates were extracted to relate decomposition rates directly to the relative abundance of litter-dwellers within litterbags. We used a modified Tullgren extractor consisting of two overlying wood panels (surface of panels 4 m^2, distance between panels 20 cm). Collecting vials (250 ml) were placed on the bottom panel, and extraction funnels into holes (14 cm in diameter) in the top panel. The extractor was equipped with 65 polyethylene funnels, the top measuring 22 cm in diameter and the exit tube leading into the collecting vials half filled with 75% ethanol. Black plastic sleeves (18 cm long, 20 cm in diameter) were placed on top of the funnels, serving as litterbag containers. In each sleeve, three litterbags (one set, vertical position) were extracted at a time. Electric bulbs (40 W), fitted in steel bowls as reflectors, were suspended from wooden bars about 10 cm above the sleeves. Sixty four sets (192 litterbags) were extracted on each sampling occasion. The extraction lasted for 72 hours, which was sufficient to extract most of the litter fauna according to preliminary tests. In these tests, collecting vials were replaced after 72 hours and the extraction was extended to 120 hours. Only in about 10% of the replacement vials were invertebrates found.

Invertebrates (detritivores, herbivores and predators) were sorted using a stereomicroscope. In view of the large number of samples (64 vials per extraction) and strong spatial and temporal fluctuations in invertebrate numbers among sets of litter bags it was impossible to count all specimens. For example, individual vials were sometimes flooded with mites, springtails, ants or dipteran larvae, whereas other samples contained no or only a few specimens. We therefore used the frequency of occurrence f (of $n = 10$ extractions per litter and forest type) as a measure of invertebrate activity over the 140-day study period. For example, $f = 1$ if ≥ 1 specimen of a particular taxon was extracted on a single sampling occasion, and $f = 10$ if ≥ 1 specimen was extracted on all sampling occasions. Binary sampling greatly facilitates the processing of large sample sizes (Peveling et al., 1999). Moreover, the method is robust towards strong fluctuations in invertebrate numbers, leading to low within-group variation and high statistical power. In this paper, we use binary sampling for the first time to quantify litter-dwelling invertebrates. No inferences can be drawn about the contribution of individual taxa to overall litter decay. This, however, is also true of complete enumeration techniques. Our objective was to compare the activity of individual taxa and of whole invertebrate assemblages among different types of litter and forest

2.6 Data analysis

We used a linearized, single exponential model to analyse litter breakdown, using litter and forest type as main factors and time (log days) and initial weight as covariables. The model allowed direct statistical comparison among individual regressions (breakdown over time) through analysis of covariance (ANCOVA). Levene's test and a lack of fit test were performed to test the homogeneity of variances and data fit, respectively (SPSS 11.0). Due to a highly variable distribution and amount of rainfall at the onset of the rainy season, litter breakdown was triggered at different times across forest types and replicates, resulting in heterogeneous variances. This analytical problem was overcome by omitting days 42 and 56, the sources of the heterogeneity of variances, from the analysis. On all other sampling days, variances were homogeneous, indicating that the differentiating effect of initial rainfall diminished as the rainy season progressed, resulting in similar decay conditions and dynamics in replicate sites.

We used the mean residual weight (percentage of initial weight remaining) of each set of litterbags (as defined above) as input data. It was therefore possible to compensate for missing data (4.5% of 1,920 litterbags). If one or two litterbags from a set were missing, we used the (mean) residual weight of the litterbag(s) remaining. If a full set got lost, which happened on two occasions, data points were regenerated by extrapolating breakdown trends from other samples. By regenerating missing data, we maintained a balanced design and could test for interactions. Sidak multiple comparison of means was employed if the main effects were significant, using an experimentwise error rate of $\alpha = 0.05$. Marginal means of the residual weight were estimated at the covariate *time* = 70 days (70-d post-exposure). Main effects were interpreted even if the litter × forest type interaction was significant (Sokal and Rohlf, 1997), provided that the interaction was considerably lower in magnitude than the main effects (Snedecor and Cochran, 1980).

Interactions were explored graphically by pairwise plotting of corrected cell means (Harwell, 1998).

Note that ANCOVA cannot be applied to fixed intercept models (Wieder and Lang, 1982). Therefore, and because we log-transformed time rather than residual weight to optimise data fit, decomposition rate constants cannot be inferred from our unfixed intercept model. For descriptive purposes, *k* values and decay half times ($t_{1/2}$ in months) were derived from Olson's (1963) single exponential decay model with fixed intercept, using mean residual weight data.

We used two-way analysis of variance (ANOVA) to compare individual frequencies of occurrence of all major litter-dwelling invertebrate taxa in relation to litter and forest type (main factors), followed by Student Newman Keuls *post hoc* test (Zar, 1999). Analyses were done with untransformed data in case of homogeneous variances. Otherwise, data were $\log_{10}(f+1)$-transformed to achieve homogeneity of variances or we switched to non-parametric Kruskal-Wallis analysis, followed by Nemenyi multiple range test when significant differences were found. We used Holm's sequential multiple test procedure to adjust significance levels for multiple testing (Manly 2001), at an error rate of $\alpha = 0.05$. Parametric ANOVA and Newman Keuls test were also conducted for the litter fauna as a whole, using the cumulative frequency of occurrence of all taxa as a measure of the overall activity of litter-dwelling invertebrates.

Linear regression was performed to analyse the relationship between the cumulative frequency of occurrence of invertebrates and litter breakdown (mean residual weight over time). For this analysis, litters within forests were pooled.

3. Results

3.1 Leaf litter breakdown

The initial litter weight had no significant effect on litter breakdown ($F_{1/494} = 0.36$; $P = 0.549$). This covariable was therefore omitted from the remaining analyses. Litter breakdown differed depending on litter and forest type (Fig. 3). Both main factors proved very highly significant ($F_{3/495} = 21.8$ and 36.7, respectively, for litter and forest type; $P < 0.001$). The mean residual weight of leaf litter at 70-day post-exposure was lowest in *A. africana* (51.1%), highest in *T. grandis* (66.8%) and intermediate in *S. siamea* (54.6%) and *C. pentandra* (60.8%), respectively. Differences among means were significant at $P < 0.05$ or lower for all but one (*A. africana* vs. *S. siamea*) of the pairwise comparisons (Fig. 4a). With regard to forest type, litter decay was highest in natural forest, revealing a mean residual weight of 45.4%, compared to 60.1, 61.7 and 66.1%, respectively, in young teak, old teak and firewood plantations (Fig. 4b). Except for teak plantations (young vs. old teak), all pairwise comparisons were significantly different at $P < 0.05$ or lower.

We also found a slight yet significant litter × forest interaction ($F_{9/495} = 1.9$; $P < 0.042$), indicating dissimilar changes in litter breakdown across forest types. For example, the breakdown of litter from *T. grandis* decreased from old teak to natural forest whereas *C. pentandra* showed the opposite trend (Fig. 5a). Moreover, in most pairwise comparisons, *C. pentandra* behaved contrary to *A. africana* (Fig. 5a–b, d–f).

Decay rate coefficients for *A. africana* were high in forest plantations (2.5–3.4) and very high (4.7) in natural forest (Table 3). The lowest decay rate coefficients were recorded for teak, with medium to high values in forest plantations (1.3–1.7) and a high value in natural forest (3.5). Thus, even the least decomposable litter, *T. grandis*, broke down relatively well in Lama forest. This is also reflected in the low decay half times which ranged from 1.8 months for *A. africana* in natural forest to 6.3 months for *T. grandis* in firewood plantations.

3.2 Litter invertebrates

Twenty three different litter-dwelling invertebrate taxa were distinguished, their mean frequency of occurrence (all litter and forest samples included, $n = 64$) ranging from 0.09 (± 0.04, standard error) in Embioptera (webspinners) to 7.0 (± 0.36) in Acari. The most frequent taxa ($f \geq 1.0$) were, in descending order, Acari, Diptera (larvae), Diplopoda, Coleoptera (imagines and larvae), Annelida (Oligochaeta), Pseudoscorpiones, Hymenoptera (mainly Formicidae), Collembola, Chilopoda, Araneae, Homoptera, Lepidoptera (caterpillars), Isoptera and Isopoda.

The overall frequency of litter-dwelling invertebrates differed significantly among leaf litters ($F_{3/48} = 17.6$; $P < 0.001$) and forests ($F_{3/48} = 16.9$; $P < 0.001$), while there was no significant litter × forest interaction ($F_{9/48} = 1.7$; $P = 0.115$). The mean cumulative frequency of occurrence was highest in litter from *A. africana* (53.6 ± 4.6, standard error) and lowest in litter from *T. grandis* (30.2 ± 2.7) (Fig. 6a). All differences between means were significant at $P < 0.05$ or lower except for *A. africana* (53.6 ± 4.6) and *C. pentandra* (52.2 ± 2.9). In summary, the frequency of invertebrates was higher in indigenous than in exotic litter. Comparing the two plantation species, *S. siamea* (41.6 ± 3.6) attracted more invertebrates than *T. grandis* (30.2 ± 2.7). With regard to forest type (Fig. 6b), invertebrates were nearly twice as frequent in natural forest (58.7 ± 3.7) than in firewood plantations (32.9 ± 3.4). Intermediate frequencies were found in young (42.8 ± 3.6) and old (43.3 ± 3.7) teak plantations. Except for young and old teak, all differences among means were statistically significant at $P < 0.05$ or lower.

Analyses for individual taxa yielding significant differences among leaf litter species are summarized in Table 4. Most taxa were more frequent in litter from *A. africana* or *C. pentandra* than in litter from *S. siamea* or *T. grandis*. Exceptions were Gastropoda and

Lepidoptera which dominated in *T. grandis* and *S. siamea* litter. Table 5 presents the corresponding results for the different forest types. Here all but two taxa (Isoptera and Lepidoptera) were more frequent in natural forest than in forest plantations. Old teak plantations had significantly more termites than any other forest type. The frequency of Lepidoptera was also highest, even though only significant compared to young teak plantations.

We found a significant inverse linear relationship between the mean cumulative frequency of occurrence of invertebrates (x) and the mean residual litter weight (y), indicating that the breakdown of litter increased with increasing frequency of occurrence and hence biological activity of litter-dwelling invertebrate assemblages (Fig. 7). The linear regression model was (standard errors in parentheses):

$y = -0.56\ (\pm\ 0.12)\ x + 83.35\ (\pm\ 5.76)\ (r^2 = 0.597;\ F_{1/14} = 20.7,\ P < 0.001)$.

4. Discussion

4.1 Litter quality

Of the four species of leaf litter, teak had by far the highest C:N ratio and specific leaf weight (Table 1), indicating low litter quality and decomposability (Torreta and Takeda, 1999; Beck, 2000; Xuluc-Tolosa et al., 2003). At ratios higher than 30–40, microbial activity is significantly reduced, leading to N-immobilisation and impeded decomposition (Torreta and Takeda, 1999). A high specific weight delays litter breakdown because the surface area for microbial colonisation is small. In view of these chemical and physical traits, litter from teak was expected to decompose more slowly than the other species. Conversely, *A. africana*, which had the lowest C:N ratio and a low specific weight, degraded fastest. Other comparisons, however, are less straightforward. For example, *C. pentandra* had a more favourable C:N ratio (34 vs. 40) but broke down less than *S. siamea*. This suggests that an assessment of the relationship between litter quality and breakdown requires analyses of other components such as lignin and polyphenols. Combining C:N ratios and lignin and polyphenol concentrations, Tian et al. (1995) developed a plant residue quality index (PRQI) to predict the decomposability of litter in Nigeria. Among 16 different types of leaf litter, *S. siamea* had one of the highest PRQIs, higher values indicating a more rapid breakdown. Our study confirms a high degradability of *S. siamea*, even though the C:N ratio in the variety grown in Lama forest was more than twice as high as in the Nigerian variety (Weibel, 2003). No PRQIs have been published as yet for the other species investigated in Lama forest.

4.2 Decay rate constants

Despite great variations among litter and forest types, litter breakdown was fast in all species but teak, whose decay rate constants in Lama forest plantations ($k = 1.3$–1.7) were lower than those observed in tropical teak plantations in India ($k = 2.0$–2.3; Sankaran, 1993). The lower rates may be due to the drier conditions in Lama forest. Nonetheless, even the more recalcitrant teak litter broke down rapidly in the closed canopy natural forest ($k = 3.5$). Canopy development and dense undergrowth enhance microbial and faunal activities by maintaining a favourable soil moisture regime (Seastedt, 1995). The highest decay rate was observed in litter from *A. africana* in natural forest ($k = 4.7$), indicating an optimal combination of litter quality and environmental conditions. Similar rates have rarely been reported for tropical or subtropical forests. Montanez (1998) found decay rates of $k = 3.5$–4.8 in Mexican horticultural trees. A rate of $k = 4.3$ has been reported for a Chinese subtropical forest (Cameron and Spencer, cited in Meentemeyer, 1995).

Comparison of annual decay rate constants, however, may be confounded by differences in the length of the observation period (Meentemeyer, 1995). Extrapolation of decay curves from short observation periods yields higher k values than extrapolation from long periods (Lisane and Michelsen, 1994). Studies of short duration range from 98 days (e.g., Tian et al., 1992, 1995, 1998) to 180 days (Yamashita and Takeda, 1998), those of long duration usually extend over more than one year (e.g., Sankaran, 1993; Lisane and Michelsen, 1994; Loranger et al., 2002). With an observation period of 140 days, our results compare best with those from short-term studies. In a 98-day study in Nigeria, about 300 km east of Lama forest, Tian et al. (1998) found a weekly decay rate constant of $k \approx 0.08$ for *S. siamea* leaf litter, corresponding to an annual rate of $k \approx 4.2$. This value is close to the one for natural forest in our 140-day study ($k = 4.0$), suggesting that eco-climatic conditions within the Dahomey gap favour high decay rates and supporting the hypothesis that maximum rates in the tropics occur at intermediate levels of precipitation (Seastedt, 1995).

4.3 Soil properties

Physico-chemical soil properties also influence the decomposition of leaf litter (Ananthakrishnan, 1996). Clay-rich vertisols are the prevailing soils in Lama forest. These hydromorphic soils undergo strong swelling-shrinking cycles, thereby enhancing bioturbation and the abiotic breakdown of litter (Lavelle, 2002). Even though litterbags may not be directly affected by such processes, there may be an effect on soil and litter organisms, hence on the colonisation of litterbags. Vertisols often support a high biomass of earthworms (Fragoso and Lavelle, 1995). We confirmed this in our study where elevated earthworm activities were noted in young teak plantations and natural forest (Table 1). Earthworms participate in the decomposition of organic matter directly and provide food resources and microhabitats for microarthropods (Loranger et al., 1998).

Due to reduced water infiltration, vertisols may become seasonally waterlogged. Litterbags in Lama forest were never submerged when collected, but we cannot rule out short-term inundation and hence a temporary involvement of aquatic macroinvertebrates in the breakdown of litter. Litterbag studies in mangrove systems revealed greatly accelerated decomposition rates due to macroinvertebrates (Ashton et al., 1999). This suggests that future studies should also look at the consequences of seasonal flooding.

4.4 Forest system

The breakdown of litter varied among forest systems. Decay rates were always highest in natural forest and lowest in fuelwood plantations (Fig. 3, Table 3). This is also reflected in the litter cover which was ≤ 50% in natural forest but up to 100% in plantations (Table 1). As mentioned above, closed canopy forests provide an optimum microclimate for the breakdown and mineralization of litter. Conditions encountered in the open canopy fuelwood plantations were much less favourable. In terms of intensity and frequency of woodcutting, these plantations bear the highest degree of human impact in Lama forest. Moreover, they are frequently affected by anthropogenic fires – though not during the study period. In view of this disturbance regime, an impeded biotic breakdown of litter was to be expected.

Litter breakdown in young and old teak plantations was much faster than in fuelwood plantations. Trees are felled at an older age, and human disturbances such as weeding and thinning are confined to the first years. Thereafter, plantations are allowed to mature, developing species-rich understorey vegetation which in turn may support high arthropod diversity (Lachat et al., submitted). Surprisingly, we found no difference in litter breakdown between young and mature teak plantations. This contradicts the observation that decomposition increases as forests mature (Xulux-Tolosa et al., 2003). A possible explanation lies in the different soil types. In Lama forest, young teak grows on vertisol and old teak on sandy ferralsol. The breakdown of litter is presumably faster on vertisol. Thus, a higher degree of disturbance may be compensated by more favourable soil conditions.

Contrary to our study, other studies found similar (Loranger et al., 2002) or even lower (Yamashita and Takeda, 1998) decomposition rates in tropical secondary forests than in plantations. However, in most studies different species of leaf litter were used in different forests. Thus, variations in decay rates are difficult to interpret because they may be due to litter quality or forest type. Loranger et al. (2002) found no difference in the decay rate of *Bursera simarouba* among natural and plantation forests and concluded that litter quality was a more important determinant of decomposition than forest type. This conclusion does not hold for Lama forest. Differences among forest types were as pronounced as those among litter types (c.f., Fig. 3).

We found a significant litter × forest type interaction. This implies that the potential of different forest ecosystems to decompose litter varies depending on litter species and can be interpreted as an adaptation of decomposer assemblages to particular types or assortments of litter. Similar observations were made in a riverine forest in Europe where allochthonous leaf litter degraded as slowly as at the place of origin in spite of high decomposer biomass (Beck, 2000).

4.5 Litter invertebrates

Our study found an inverse relationship between the cumulative frequency of occurrence of litter invertebrates and the residual weight of leaf litter (Fig. 7). We cannot dismiss the possibility that both variables were partly controlled by other variables. For example, a favourable microclimate may enhance the microbial breakdown and attract more invertebrates. Nevertheless, an increased activity of invertebrates, most of them detritivores, does have an effect on litter decay even if microbial decay is stimulated independently. In fact, both are interlinked processes: invertebrates directly consume microorganisms and/or convert litter into microfragments, thereby speeding up microbial decay (e.g., Reddy, 1995; Ananthakrishnan, 1996). Further evidence of the importance of invertebrates in litter breakdown has been gathered in a follow-up study which showed that litter breakdown was significantly reduced in litterbags with mesh sizes excluding meso- and macroinvertebrates (Joost, 2004).

A closer examination of our results reveals a complementary pattern of litter breakdown (Fig. 4) and invertebrate frequency (Fig. 6), the only difference being that *A. africana* and *C. pentandra* (invertebrate frequency) – rather than *A. africana* and *S. siamea* (litter breakdown) – were statistically similar. An interesting finding is the preference of most invertebrate taxa for native litter (Table 4). Only gastropods and caterpillars occurred more frequently in *S. siamea* and *T. grandis* than in native litter, presumably due to a suitable microclimate in the more slowly degrading litter.

Overall invertebrate frequencies were intermediate in *S. siamea* and lowest in teak. Comparisons with other studies are difficult because of different sampling methods. Even so, a study in India found lower diversity and density of microarthropods in teak litter than in litter from natural forest (Ananthakrishnan, 1996). In Nigeria, densities of soil/litter microarthropods in *S. siamea* plantations were higher than in *Acacia leptocarpa* and *Leucaena leucocephala* plantations (Adejuyigbe et al., 1999).

Cumulative invertebrate frequencies were highest in natural forest and lowest in firewood plantations. Again, we found deviations from this general pattern when looking at different taxonomic and trophic groups (Table 5). Termites had their maximum frequency in old teak plantations and not in natural forest. This could be related to more favourable soil conditions (sandy ferralsol). The construction of termitaria may be difficult in vertisols, due to their strong shrinking and swelling (Lee and Wood, 1971). In addition, there appears to be a link to the forest system. We found much higher densities of subterranean fungus growers (Macrotermitinae) in teak plantations than in natural forest (unpublished data).

Given the role of termites as ecosystem engineers (Lavelle et al. 1997), changes in termite assemblages are expected to alter the decomposition regime and hence the nutrient status of the soil, with possible long-term effects on forest productivity. In terms of abundance and biomass, termites are considered resilient to the conversion of primary or old growth secondary forest into tree plantations (Lavelle et al. 1997). However, plantations may induce changes in species turnover and relative abundance of trophic groups. In young rubber plantations in Côte d'Ivoire, termite assemblages were dominated by xylophagous taxa, due to the high biomass of decaying logs from the former forest, whereas fungus growers were getting more important in aging plantations (Gilot et al., 1995).

Termite/earthworm ratios may also change in relation to forest type. We found indications of high earthworm activity in young teak plantations and natural forest, yet this finding was not representative in time. More studies are needed that concurrently examine the effects of forest type and management system on the composition and biomass ratio of termite and earthworm assemblages.

5. Conclusions

The breakdown of leaf litter in Lama forest was generally fast, indicating a high biological activity and nutrient turnover. Even so, we observed great differences in decay rates, depending on litter quality and forest type. Indigenous and yellow cassia litter degraded faster than litter from teak, and higher decay rates were observed in natural than in plantation forests. Our results suggest that soil quality will develop differently in Lama forest, depending on tree species and forest management. In tree plantations, lower decay rates might eventually translate into reduced primary production, and possibly reduced timber or fuelwood yields – even though this outcome may be less likely in Lama forest because of the high fertility of vertisols. Knowledge of long-term effects of tree plantations on soil quality is a prerequisite for the sustainable management and use of forests (e.g., Tian et al., 2001). Management practices should aim to enhance the biological activity of decomposer communities so as to avoid soil degradation and to maintain productivity.

Acknowledgements.

This study was conducted within the scope of *BioLama*, a research partnership between *NLU-Biogeographie* and the *Faculté des Sciences Agronomiques*. The Swiss National Science Foundation and the Swiss Agency for Development and Cooperation are acknowledged for their financial support. A number of people provided assistance and advice in this study. We would like to thank C. Houngbédji, M. Guedegbé, L. Konetche, K. Bankolé (*BioLama*) and P. Houayé, R. Akossou, D. Honfozo, H. Hodonou, V. N'velin (*Office National du Bois*). We are also grateful to two referees for instructive comments on an earlier version of this manuscript.

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Table 1. Characteristics of the experimental sites in Lama forest. Values are means for replicate sites (*n* = 4; ± standard error) or ranges (after Weibel, 2003).

	Forest type			
Character	Semi-deciduous forest	Young teak plantations	Old teak plantations	Firewood plantations
Soil [a]				
Type	Vertisol	Vertisol	Sandy ferralsol	Vertisol
Soil cracks [b]	none	superficial	none	deep
pH mean	4.5 (0.5)	4.5 (0.5)	4.8 (0.6)	5.0 (0.6)
C (%)	4.1 (0.3)	2.5 (0.3)	1.4 (0.3)	3.2 (0.4)
N (%)	0.31 (0.01)	0.21 (0.01)	0.14 (0.01)	0.28 (0.02)
C:N ratio	13.2 (0.6)	11.3 (0.8)	9.1 (0.6)	11.4 (0.5)
Litter cover (%) [b]	< 25–50	50–100	< 25–100	50–100
Earthworm activity [b]	very high	very high	low	low
Canopy cover (%) [b]	100	30–50	50–80	< 30–50

[a] topsoil; [b] assessment conducted once only in August 2002

Table 2. Physico-chemical characteristics of leaf litter used in the decomposition study (after Weibel, 2003).

Species	C (%)	N (%)	C:N ratio	Specific weight [a] (mg/cm^2)
Afzelia africana	46.1	1.8	26	8.2
Ceiba pentandra	44.7	1.3	34	8.2
Senna siamea	44.4	1.1	40	8.8
Tectona grandis	41.5	0.7	57	16.5

[a] calculated according to Torreta and Takeda (1999)

Table 3. Litter decay rate coefficient (k, year), coefficient of determination (r^2) and decay half time ($t_{1/2}$ in months) in the Lama forest.

		Type of litter (species)			
Type of forest		*Tectona grandis*	*Senna siamea*	*Afzelia africana*	*Ceiba pentandra*
Natural forest	k	3.5	4.0	4.7	3.4
	r^2	0.68	0.76	0.88	0.95
	$t_{1/2}$	2.4	2.0	1.8	2.5
Young teak	k	1.7	2.9	3.4	1.8
	r^2	0.70	0.62	0.56	0.59
	$t_{1/2}$	5.0	2.9	2.4	4.5
Old teak	k	1.4	2.8	2.6	2.5
	r^2	0.81	0.79	0.75	0.85
	$t_{1/2}$	5.7	2.9	3.1	3.4
Firewood	k	1.3	1.9	2.5	2.0
	r^2	0.94	0.89	0.96	0.91
	$t_{1/2}$	6.3	4.3	3.3	4.1

Table 4. Mean frequency of occurrence of invertebrates in different types of litter (forests pooled). Only taxa with significant results (error rate $\alpha = 0.05$ adjusted for multiple testing) and $f \geq 0.9$ are listed. Means in rows not sharing a letter are significantly different at $P < 0.05$. Capital letters indicate parametric, small letters non-parametric analyses.

	Mean frequency of occurrence ($n = 16$; ± standard error)			
Taxon / Type of litter	*Afzelia africana*	*Ceiba pentandra*	*Senna siamea*	*Tectona grandis*
Gastropoda	0.1 (0.1) ^{a}	0.6 (0.3) ^{ab}	1.6 (0.3) ^{b}	1.4 (0.4) ^{b}
Annelida (Oligochaeta)	4.0 (0.7) ^{ab}	6.6 (0.6) ^{a}	3.2 (0.6) ^{b}	0.5 (0.2) ^{c}
Acari	7.7 (0.7) ^{ab}	8.9 (0.4) ^{b}	6.4 (0.7) ^{ac}	5.0 (0.7) ^{c}
Diplopoda	4.1 (0.7) ^{AB}	5.4 (0.6) ^{A}	4.1 (0.6) ^{AB}	2.4 (0.5) ^{B}
Chilopoda	0.9 (0.3) ^{A}	3.0 (0.4) ^{B}	1.9 (0.3) ^{AB}	0.9 (0.3) ^{A}
Collembola	5.6 (0.7) ^{a}	2.6 (0.4) ^{a}	1.1 (0.3) ^{b}	0.5 (0.2) ^{b}
Homoptera	1.6 (0.4) ^{a}	0.3 (0.1) ^{b}	1.4 (0.3) ^{a}	1.3 (0.3) ^{ab}
Lepidoptera	0.5 (0.2) ^{A}	0.2 (0.1) ^{A}	1.9 (0.3) ^{B}	1.6 (0.4) ^{B}
Diptera	7.6 (3.6) ^{A}	5.7 (0.5) ^{B}	4.6 (0.5) ^{B}	4.7 (0.5) ^{B}

Table 5. Mean frequency of occurrence of invertebrates in different types of forest (litter pooled). Only taxa with significant results (error rate $\alpha = 0.05$ adjusted for multiple testing) and $f \geq 0.9$ are listed. Means in rows not sharing a letter are significantly different at $P < 0.05$. Capital letters indicate parametric, small letters non-parametric analyses.

	Mean frequency of occurrence ($n = 16$; ± standard error)			
Taxon / Type of forest	Natural forest	Young teak	Old teak	Firewood
Isopoda	2.2 (0.4) ^{a}	0.4 (0.2) ^{b}	0.9 (0.3) ^{b}	0.5 (0.2) ^{b}
Acari	8.7 (0.4) ^{a}	8.4 (0.6) ^{ac}	4.9 (0.6) ^{b}	5.9 (0.7) ^{bc}
Pseudoscorpiones	5.3 (0.6) ^{a}	4.4 (0.6) ^{a}	2.8 (0.6) ^{b}	1.5 (0.4) ^{b}
Diplopoda	6.3 (0.6) ^{A}	3.7 (0.4) ^{B}	4.3 (0.5) ^{B}	1.7 (0.6) ^{C}
Isoptera	0.4 (0.1) ^{a}	0.4 (0.1) ^{a}	2.4 (0.4) ^{b}	0.9 (0.4) ^{a}
Coleoptera	5.0 (0.4) ^{A}	3.1 (0.4) ^{B}	4.1 (0.5) ^{AB}	2.6 (0.5) ^{B}
Hymenoptera	5.6 (0.4) ^{A}	2.9 (0.4) ^{B}	3.0 (0.5) ^{B}	2.4 (0.4) ^{B}

Legends

Fig. 1. Map of Lama forest reserve and location of sampling sites (after Specht, 2002); NC = noyau central, T = teak plantations, S = settlement areas, F = firewood plantations; diamond = semi-deciduous forest, open circle = young teak plantations, filled circle = old teak plantations, triangle = firewood plantations.

Fig. 2. Temperature (T), relative humidity (RH) and rainfall in Lama forest during the experimental period.

Fig. 3. Residual litter weight and corresponding decay curves for different types of litter in natural forest and forest plantations. Decay rate coefficients and coefficients of determination are given in Table 2.

Fig. 4. Mean residual weight ($n = 128$; ± standard error) of leaf litter (at covariate *time* = 70 days post-exposure) for different types of litter (a; forests pooled) and forest (b; litter pooled). Means marked with different letters are significantly different at $P < 0.05$ or lower.

Fig. 5. Interaction plots of corrected cell means for pairwise comparisons of leaf litter decomposition in different types of forest.

Fig. 6. Mean cumulative frequency of occurrence ($n = 16$; ± standard error) of litter-dwelling invertebrates in different types of litter (a; forests pooled) and forest (b; litter pooled). Means marked with different letters are significantly different at $P < 0.05$ or lower.

Fig. 7. Linear relationship between cumulative frequency of occurrence of invertebrates and litter decomposition (residual weight) in Lama forest.

Fig. 1.

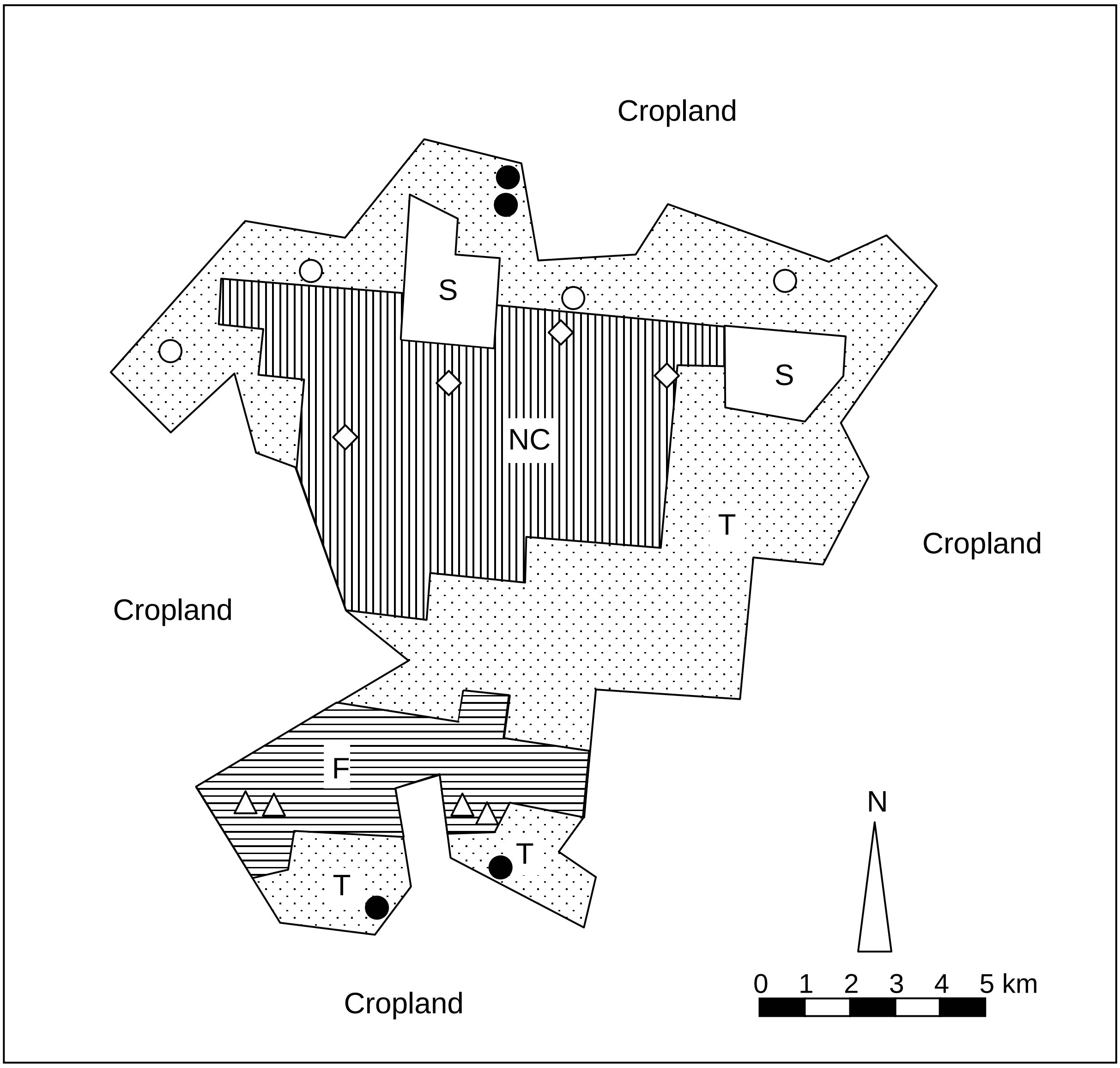


Fig. 2.

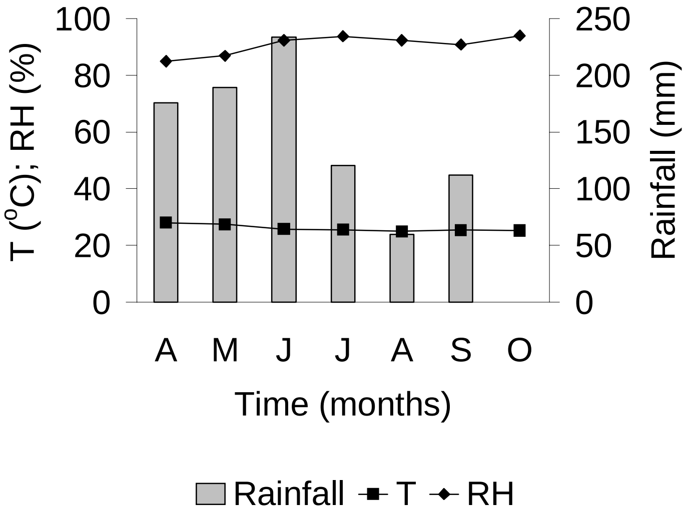

100
80
60
40
20
0
250
200
150
100
50
0
T (^{o}C); RH (%)
Rainfall (mm)
A
M
J
J
A
S
O
Time (months)
Rainfall
T
RH

Fig. 3.

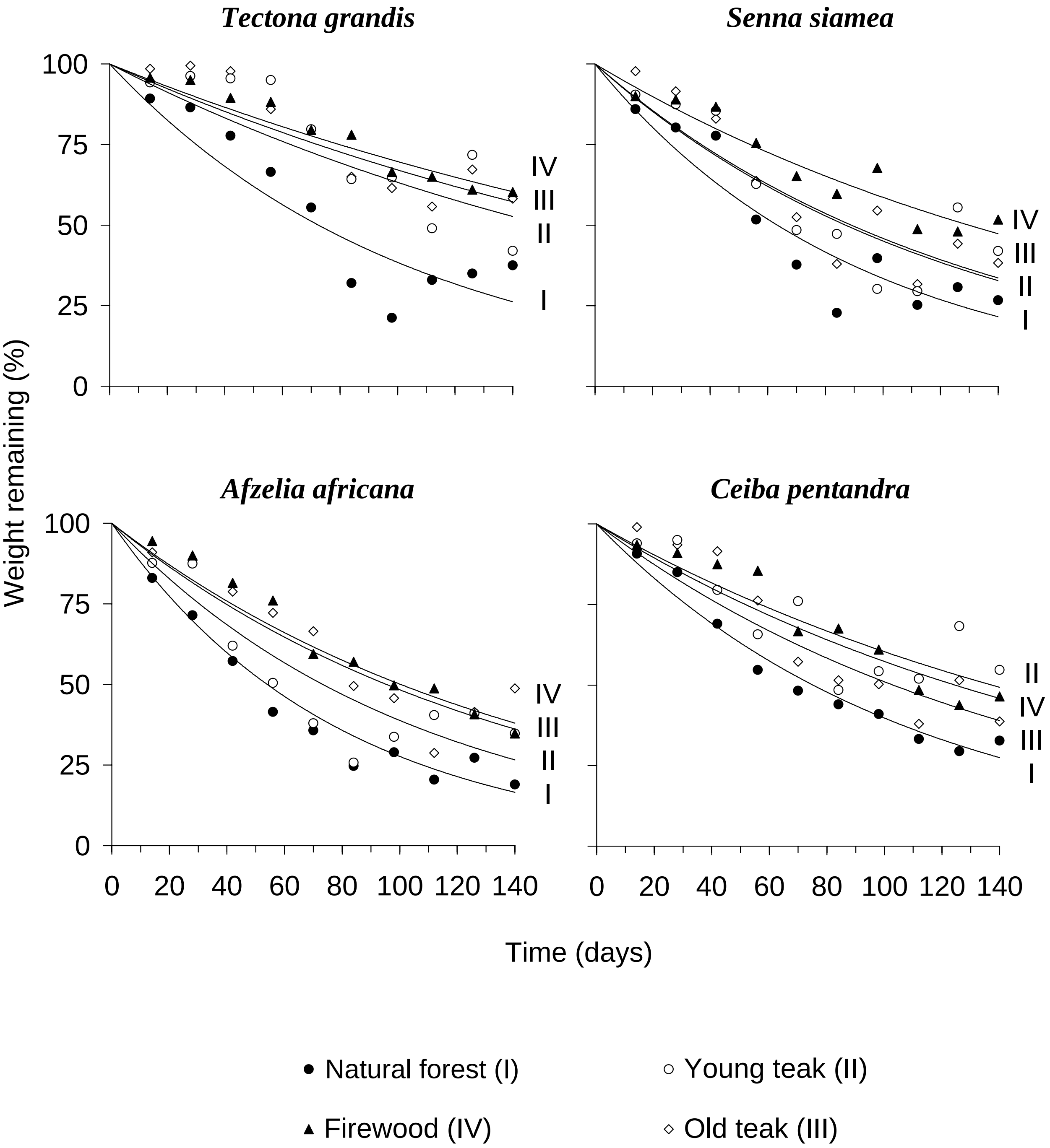

Tectona grandis
Senna siamea
Afzelia africana
Ceiba pentandra
Weight remaining (%)
Time (days)
0
25
50
75
100
0
20
40
60
80
100
120
140
I
II
III
IV
● Natural forest (I)
○ Young teak (II)
▲ Firewood (IV)
◇ Old teak (III)

Fig. 4.

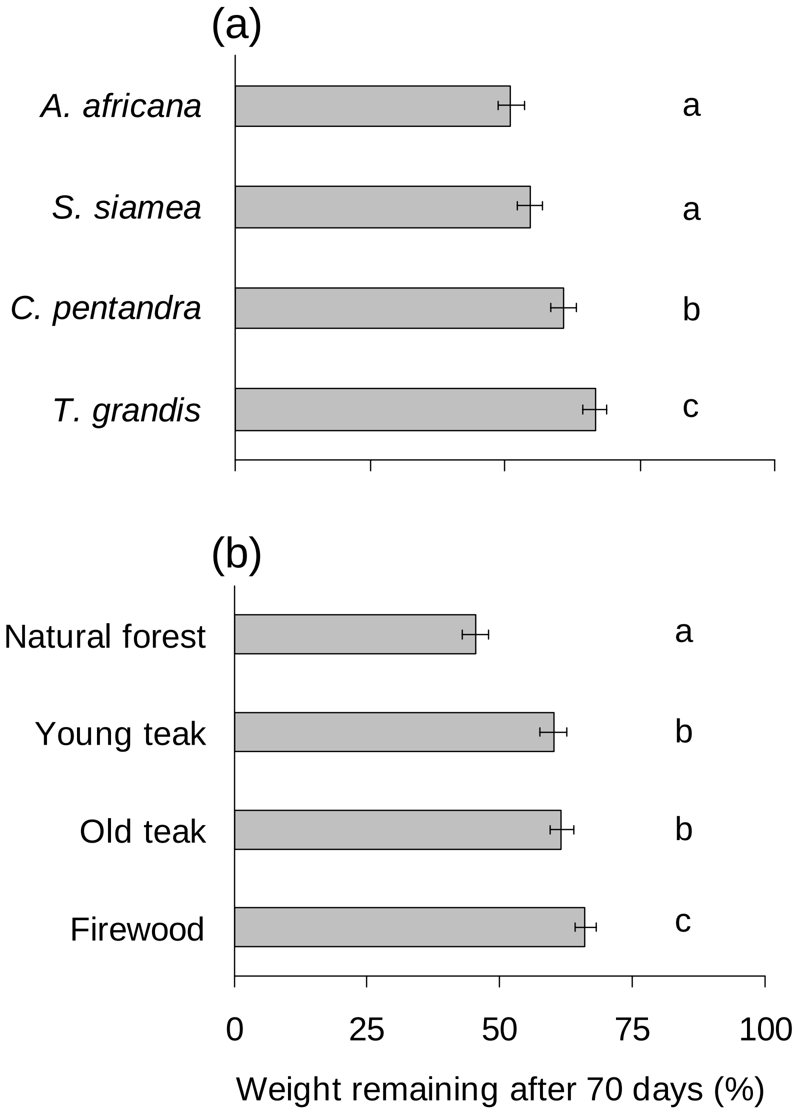

(a)
A. africana
S. siamea
C. pentandra
T. grandis
a
a
b
c
(b)
Natural forest
Young teak
Old teak
Firewood
a
b
b
c
0
25
50
75
100
Weight remaining after 70 days (%)

Fig. 5.

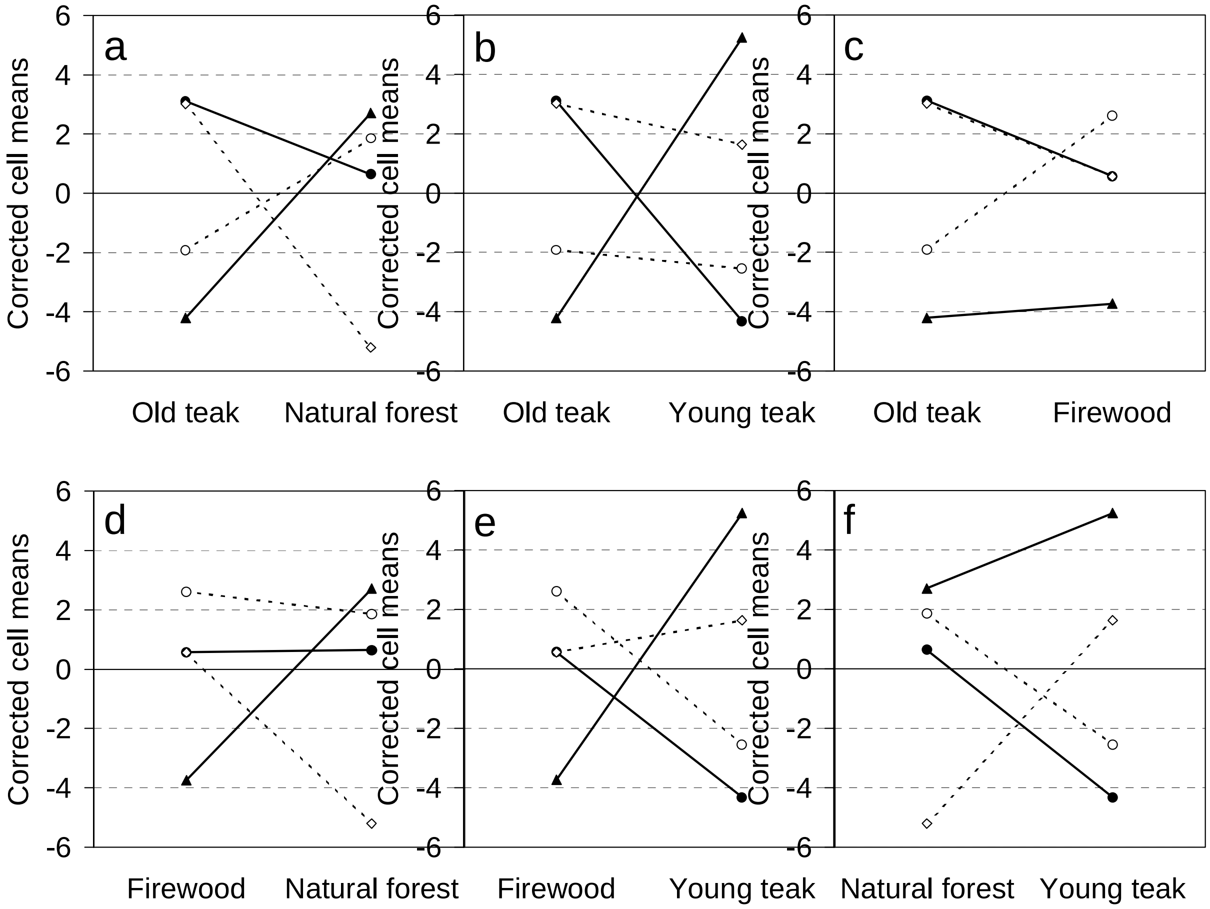

a
b
c
d
e
f
Corrected cell means
6
4
2
0
-2
-4
-6
Old teak
Natural forest
Young teak
Firewood

Fig. 6.

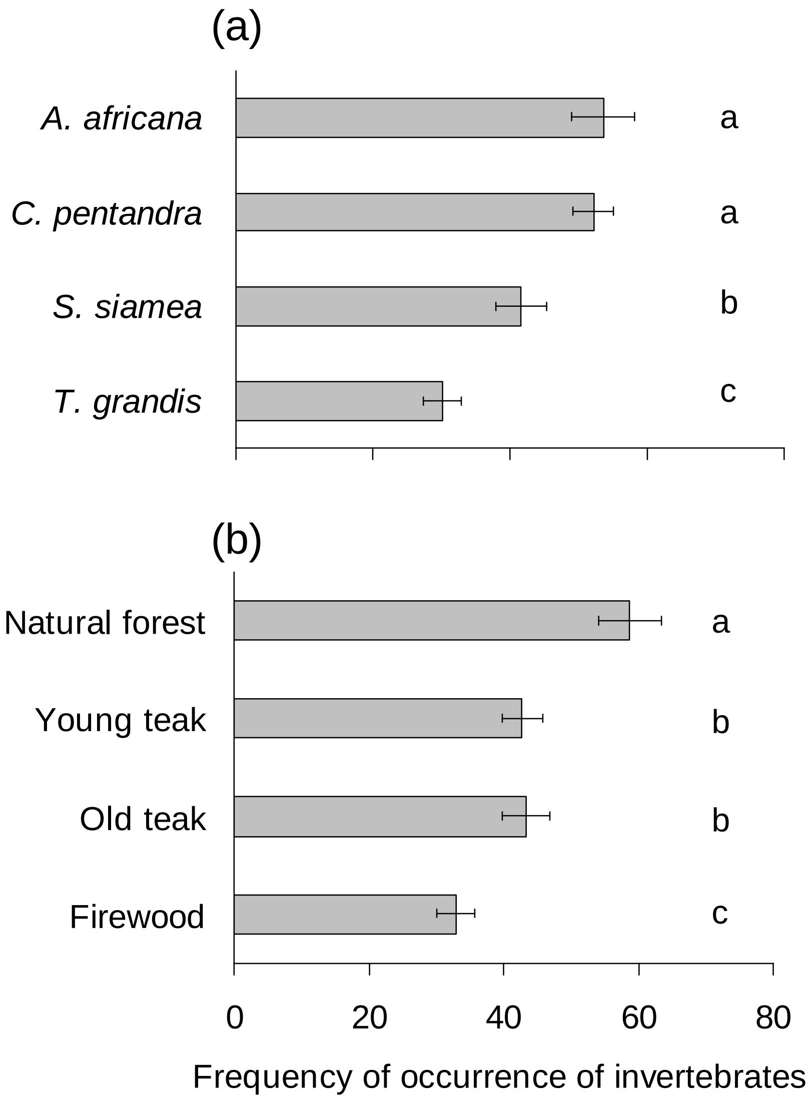
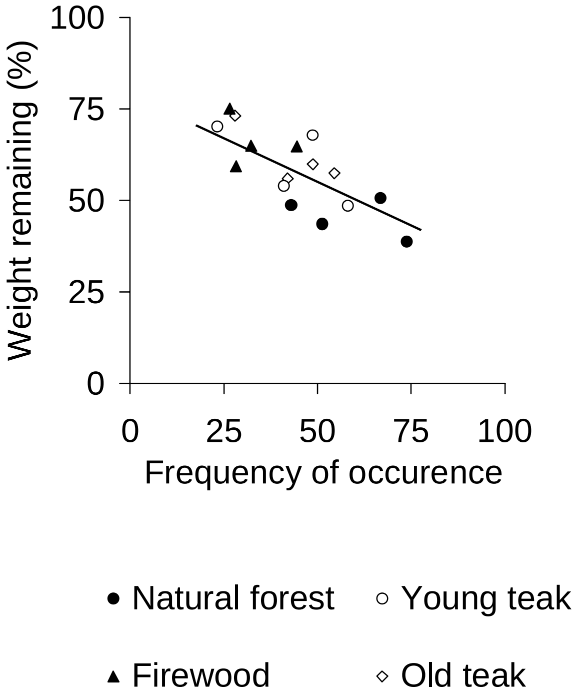

(a)
A. africana
C. pentandra
S. siamea
T. grandis
a
a
b
c
(b)
Natural forest
Young teak
Old teak
Firewood
a
b
b
c
0
20
40
60
80
Frequency of occurrence of invertebrates

Fig. 7.


Weight remaining (%)
100
75
50
25
0
0
25
50
75
100
Frequency of occurence
● Natural forest
○ Young teak
▲ Firewood
◇ Old teak

Chapter 3

Termite Assemblages in a West-African Semi-deciduous Forest and Teak plantations

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Abstract

The Lama forest reserve comprises one of the last tracts of natural forest in southern Benin, West Africa. It includes various types of forest subjected to different levels of disturbance, including remnants of natural and degraded semi-deciduous forest as well as teak plantations. We studied effects of the conversion of natural forest into teak plantations on the structure and functional diversity of termite assemblages. Termites were chosen because of their key role in tropical food webs and decomposition processes, and because of their sensitivity to forest disturbances. Four belt transect (2 m × 100 m) surveys were run in each of the two forest types, adopting a standardized termite diversity assessment protocol. Termite assemblages were remarkably species-poor, with only 19 species encountered on the eight transects. The low species richness was related to the black cotton soil (vertisol) which excluded most soil-feeders of the soil/humus interface and all true soil-feeders. This was also reflected by the complete absence of Apicotermitinae (soil-feeders). Mean species richness was significantly higher in natural forest (9.5 per transect) than in teak plantations (6.5), but mean termite encounters were significantly lower (96 versus 219 in teak plantations), equivalent to 0.43 and 1.09 encounters per square meter, respectively. Termite assemblage and feeding group structure differed significantly among forests. Kalotermitidae (wood-feeders) were only found in semi-deciduous forest. In contrast, Macrotermitinae (fungus-growing wood- and litter-feeders) were more species-rich and about four times more abundant in teak plantations. The feeding group structure was mirrored in significantly different weighted humification scores of the two assemblages (1.914 in natural forest versus 1.996 in teak plantations). Principal components analysis and multiple regression were combined to analyse the relationship between termite assemblages and environmental variables. The analysis identified two significant predictors of termite assemblages, soil water content (higher in natural forest) and leaf-litter biomass (higher in teak plantations). The high encounter density of fungus-growers in teak plantations seems to be related mainly to these factors. Indirect evidence also suggests that a lower predation pressure by ants in teak plantations may have contributed to the high density. Our results indicate that changes in termite assemblages brought about by the conversion of natural forest into teak plantations may eventually translate into changes in soil fertility, with possible consequences for teak productivity.

Keywords: Semi-deciduous tropical forest; Teak plantations; Forest disturbance; Termite assemblage; Termite diversity; Feeding groups.

1. Introduction

Deforestation and forest degradation are an unabated threat to biodiversity in the tropics. Therefore, implementation of sustainable forest management strategies remains a major task in biodiversity conservation and tropical resources management. This involves adoption of environmentally sound forest harvesting practices as well as establishment of plantation forests which are expected to increase tremendously over the next decades to satisfy the demand for timber, fuelwood and pulpwood (FAO, 2001).

An important question is if forest plantations can contribute to the conservation or restoration of biodiversity (Lamb, 1998). Knowledge about the effects of forest transition on soil fertility is key to answering this question. In tropical forest biomes, decomposition processes and soil fertility are closely linked with termite activity and biomass. Termite biomass may account for 95% of the total insect biomass in forest soils (Lavelle et al., 1997) and 21% of the total invertebrate biomass in forest canopy epiphytes (Ellwood and Foster, 2004). In Ghanaian rain forests, termites consume about 20% of the annual litter fall, and up to 10% of the annual primary production (Wagner et al., 1991). Thus, perturbations of the diversity, composition and functional characteristics of termite assemblages are likely to affect soil fertility (Jones, 1990; Eggleton et al., 2002).

Termite assemblages have been widely used as models for studying the effects of forest disturbance on ecosystem processes and biodiversity (de Souza et al., 1994; Eggleton et al., 1996, 1999; Davies et al., 1999; Davies, 2002). Several of these studies have shown that soil-feeding termites are particularly vulnerable to disturbances, whereas wood- and litter-feeders, in particular fungus-growers, may even show positive responses. At moderate levels of disturbance, total species richness may be relatively stable. In this situation, changes in the trophic structure of termite assemblages appear to be more sensitive disturbance indicators than changes in species richness (e.g. Davies, 2002).

The objective of the present study was to examine effects of the conversion of natural forest to teak plantations on the structure and functional diversity of termite assemblages in the Lama forest reserve, West Africa, adopting a standardized termite diversity assessment protocol (Jones and Eggleton, 2000). Preliminary evidence from a litter breakdown study indicated similar relative abundance of termites in semi-deciduous forest fragments and 15-year old teak plantations (Attignon et al., 2004). However, this study was not designed to investigate termite species richness and abundance.

2. Materials and Methods

2.1. Study area

The Lama forest reserve in Benin is located in the Lama depression about 80 km north of the Atlantic coast (6°55.8’ to 6°58.8’ N and 2°4.2’ to 2°10.8’ E; altitude 40–80 m above sea level). It has a mean annual precipitation of 1,100 mm. The reserve extends over an area of about 160 km^2 and is divided into a fully protected central part, the *Noyau central*, covering nearly one third of the total surface, and a cordon of forest plantations separating it from adjacent cropland (Fig. 1). The *Noyau central* comprises natural, degraded and secondary forest. The plantations are composed of teak, *Tectona grandis* (Verbenaceae), and fuelwood, *Senna siamea* and *Acacia auriculiformis* (Leguminosae). A more detailed overview of the various forest types is given in Specht (2002). The present study was conducted in remnants of natural semi-deciduous forest in the *Noyau central* and 15-year old teak plantations. Vertisols are the prevailing soils in these forests.

2.2. Termite sampling

We modified the standardized termite diversity assessment protocol developed by Jones and Eggleton (2000). The original protocol prescribes timed termite searches along 2 m × 100 m belt transects. Each transect is divided into 20 contiguous sections measuring 2 m × 5 m, and one person-hour is spent for each section to collect termites from all types of microhabitats, including twelve 12 cm × 12 cm surface soil samples (10 cm deep) and all other microhabitats up to a height of 2 m above ground level (logs, stumps, twigs, litter, nests, runway sheetings, etc.). The protocol has been adopted successfully in nearly one hundred transect surveys across five tropical regions (Davies et al., 2003). However, it was not workable in Lama forest because taking and searching the soil samples alone took about one person-hour (half an hour for two persons). This was due to difficulties to extract soil cores from the compact black cotton soil. We therefore modified the protocol by taking and searching the soil samples independent of time. This was achieved by pushing, by the weight of body, 12 cm × 12 cm × 12 cm iron-framed soil samplers with sharpened edges into the soil. The total soil surface surveyed in this way was 0.1728 m^2 per section (3.456 m^2 per transect). The soil cores were transferred onto plastic sheets and checked for the presence of termites. Thereafter, forty minutes (twenty minutes for two persons) per section were devoted to collecting termites from the remaining microhabitats, as foreseen in the protocol.

Four transects were run in each of the two forest types between August and September 2002 (Fig. 1). The transects were oriented so as to cover expanses of homogeneous forest. The distance among replicate transects in teak plantations ranged from 3–13 km, and the distance among replicate transects in semi-deciduous forest from 2–8 km. The nearest distance between teak plantation and natural forest transects was 1–4 km. Sampling was conducted between 0900–1800 hours. Termites of both workers and soldiers were collected. Specimens were preserved in 80% alcohol. In a few cases, fungus combs were found with no termites in them. These were registered as Macrotermitinae encounters.

2.3. Processing of samples

A reference collection was established of all morphospecies found on the transects or elsewhere in the forest. We also prepared a collection of worker mandibles glued to glass slides. The reference collection was used to sort and count the specimens sampled. Mandible characters were used to facilitate the identification of samples without soldiers. Identification to genus and sometimes to species was achieved by using standard determination keys, and by consulting termite specialists.

2.4. Environmental variables

Several environmental variables were recorded to analyse their influence on termite assemblages and to characterize the two forest ecosystems. Measurements were made during different seasons between 2002–2004. Some data were originally collected for other purposes but could be used as well for the present study. Thus, different methods were applied at different times.

The rainy season soil water content (percent g H_2O g^{-1} oven-dry soil) was measured in May 2003 from eight surface soil samples (between 2–10 cm depth) collected in each forest type. The dry season soil water content was measured in March 2004 from four soil samples taken in four sections of each transect. Rainy season temperatures and percent relative humidity were measured over a thirty-day period in June 2002, using one data logger (Hobo Pro RH/Temp) in each forest type. Corresponding dry season data were recorded for individual transects over five-day periods in March 2004, using two data loggers per transect. The percent canopy cover was determined during the rainy season in August 2003 at four sections of each transect, using a spherical densitometer (Lemmon Forest Densiometer, Model-C) as described in Lemmon (1957). During the dry season in March 2004, cover was estimated from the same sections again. However, this was done visually because a densiometer was no longer available. The basal tree cover (m^2 ha^{-1}), a proxy for woody biomass, was estimated for each transect in March 2004 by measuring all standing woody vegetation on the transect with $\geq$ 5 cm basal diameter. On the same occasion, the dry season leaf litter biomass (g dry weight m^{-2}) was calculated by collecting, oven-drying and weighing all leaf litter from 0.5 m × 0.5 m quadrats placed in each of four transect sections.

2.5. Data analysis

Belt transect surveys generate two kinds of data, species richness and the number of termite encounters. Encounter numbers have been considered as a surrogate for relative abundance (Davies, 2002). Because they refer to a definite, three-dimensional stratum, we use encounter numbers not as surrogates but as true estimates of relative abundance.

The frequency distribution of termite encounters in different forest compartments (microsites) of the two forest ecosystems was analysed with a *G*-test (Zar, 1999). Acceptance of the null-hypothesis here would mean that termite microhabitat structure is similar among forests.

Differences in species richness among forest types were analysed using one-way analysis of variance (ANOVA) (SPSS 12.0). For two factor levels only, ANOVA yields the same results as a two-sample *t*-test. ANOVAs were also performed to compare encounters of individual termite species or higher taxonomic groupings (total termite assemblage, family and subfamily). In these analyses, encounters were transformed using a double square root transformation (Clarke and Green, 1988), which proved best for removing variance heterogeneity. Otherwise, we used Mann-Whitney two-sample test as a non-parametric alternative. In this paper, we report all nominal *P*-values for individual analyses but also indicate corrected levels resulting from sequential Bonferroni adjustments for multiple testing.

Individual species accumulation curves and first-order jackknife estimates of the total number of species were calculated for each transect using PC-ORD 4.17 (McCune and Mefford, 1999). For the graphical presentation, we calculated the mean of the four accumulation curves of each forest type.

Based on a new feeding group classification developed by Donovan et al. (2001), we calculated a weighted humification score (HS) for each termite assemblage:

$$HS = [\sum (n_i \times f_i)] / N$$

where n_i is the number of termite encounters in the *i*th feeding group, f_i the corresponding feeding group score, ranging from $f = 1$ for wood and grass feeders (group I) to $f = 4$ for true soil-feeders (group IV), and N the total number of encounters per transect. The HS depicts the position of termite species along a gradient of increasing humification of their food substrate (Donovan et al., 2001; Davies et al., 2003), and the weighted HS the position of whole termite assemblages along this gradient. Note that our weighting procedure differs from the one of Davies et al. (2003) in that we weighted by numbers of encounters rather than by numbers of species. We expected humification scores to be higher in semi-deciduous forest than in teak plantations because termite assemblages in equatorial forests usually have a higher proportion of species representing feeding groups III–IV (mainly soil-feeders) than open habitats (Eggleton et al., 1995; Davies et al., 2003,). We used one-way ANOVA to compare weighted HS among forest types.

Environmental data were also analysed with one-way ANOVA. Because spatially or temporally repeated measurements from individual transects represented pseudoreplicates, we used the mean or median of these measurements as entry data. Thus, each replicate site contributed a single datum, with similar degrees of freedoms for all analyses (forest type: d.f. = 1; residual: d.f. = 6).

We combined principal components analysis (PCA) and multiple regression to analyse the relationship between termite assemblages and environmental variables (Manly, 1994; Scott and Clark, 2000). The PCA was conducted using PC-ORD 4.27. All termite species were included as variables in this analysis. Unstandardized data (i.e., the covariance matrix) were used to derive principle components. This places emphasis on those species whose abundance is most variable. The first principal component was regressed on subsets of the environmental variables. A selection of variables was necessary because their number was higher than the number of data points (ordination scores), and because of their different scale and precision. We therefore included only measured, continuous variables with substantial differences among forest types. These variables were expected to be the most important predictors of termite assemblages. Stepwise multiple regression was performed using backward selection and a default removal probability of $P \geq 0.1$ (SPSS 12.0). Model assumptions were inspected visually by plotting standardized residuals for the first principal component against the fitted value predicted form the regression equation.

3. Results

3.1. Microsites

The total number of termite encounters was 1,282 (all transects pooled). The proportion of samples including the soldier caste was 76.7%. Fifty percent of all termites were sampled from wood (stumps, wood litter, sheetings or galleries on dead or live wood, etc.) and 43.6% from soil. The majority (67.8%) of soil-dwelling termites were found in subterranean fungus combs. Another 5.2% of all termites were encountered at the soil-humus interface and 1.2% in mounds or carton nests. The frequency distribution of termite microsites was significantly different between forests ($G = 76.0$, d.f. = 3, $P < 0.001$). In natural forest, about 65% of all encounters were made in the wood sphere, and about 33% in the soil sphere (Fig. 2). Corresponding values for teak plantations were 42% and 49%, respectively. The high proportion of soil encounters in teak was mirrored in a high density of fungus combs, totalling 299 (21.6 combs m^{-2}), compared to 80 (5.8 combs m^{-2}) only in natural forest (replicate transects pooled).

3.2. Termite assemblages

Termite assemblages in Lama forest were remarkably species-poor, with only 19 species encountered on the eight transects (Table 1). All dry wood termites (Kalotermitidae), one species of the fungus growing Macrotermitinae (*Odontotermes* sp. 2) and two species of the *Termitinae* (*Amitermes evuncifer* and *Microcerotermes* sp. 2) occurred only in semi-deciduous forest, whereas *Macrotermes bellicosus* and *Odontotermes* sp. 3 (Macrotermitinae) were found exclusively in teak plantations. Seventeen species belonged to feeding groups I and II (wood and/or litter-feeders) and only two species to group III (Termitidae feeding in the upper soil layers). Surprisingly, we found no representatives of feeding group IV (true soil-feeders), which was also reflected by the complete absence of Apicotermitinae.

Species richness was significantly higher in natural forest (9.5 ± 0.6; mean ± SE) than in teak plantations (6.5 ± 0.5; $F_{1,6} = 13.5$, $P = 0.01$). First-order jackknife estimates of the total number of species were low, ranging between 10.9–15.7 for semi-deciduous forest and between 5.0–8.9 for teak plantations and indicating that the observed species richness was close to the estimated true species richness. This is also evident from the species accumulation curves which are both approaching the asymptote (Fig. 3).

Contrary to species richness, the mean number of termite encounters per transect was significantly lower in natural forest (96 ± 13) than in teak plantations (219 ± 24; $F_{1,6} = 20.3$, $P = 0.004$), equivalent to 0.43 and 1.09 encounters m^{-2}, respectively. A more detailed inspection on family and subfamily level (Fig. 4) revealed significant differences in termite encounters among forests for Kalotermitidae (only present in natural forest) and Macrotermitinae (far more abundant in teak plantations). The predominance of fungus-growers in teak plantations was due mainly to the abundance of *Ancistrotermes* sp., a species about tenfold more often encountered in teak than in natural forest (Table 1). Other fungus-growers were also more abundant, but these differences were not significant after Bonferroni adjustment.

3.3. Humification score

The weighted humification score was only 1.914 ± 0.030 (mean ± SE) in natural forest but 1.996 ± 0.006 in teak plantations ($F_{1,6} = 7.3$; $P = 0.036$). The difference reflects a dissimilar feeding group structure of the two termite assemblages. Natural forest had a substantial proportion of group I feeders whereas teak plantations almost exclusively comprised group II feeders (Table 1).

3.4. Environmental variables

Differences in microclimatic conditions among forest types showed a strong seasonal effect, with a tendency towards greater dry season amplitudes in teak plantations (Table 2). For example, maximum temperatures in teak plantations were similar to those in natural forest during the rainy season (29.8 ± 0.03 vs. 28.0 ± 0.02 °C) but more than 7°C higher during the dry season (41.2 ± 0.06 vs. 33.7 ± 0.04 °C) when teak plantations shed most of their leaves, as reflected in a low canopy cover (17.7 ± 0.8 vs. 66.2 ± 2.4% in natural forest). Differences in soil water content and relative humidity were also more pronounced during the dry season. Basal tree cover was similar among forests, whereas (dry season) leaf litter biomass was higher in teak plantations. No litter biomass data were available from the rainy season, but it was known from a previous study that leaf litter cover (hence biomass) in teak plantations was higher during the rainy season too (Attignon et al., 2004).

3.5. Relationship between environmental variables and termite assemblages

The first principal component of the PCA accounted for 72% of the total variance (Fig. 5). Of the environmental variables listed in Table 2, five were included in the multiple regression of the first principal component, (1) dry season soil water content, (2) dry season maximum temperature, (3) dry season minimum relative humidity, (4) leaf litter biomass and (5) basal tree cover. Regression analysis with backward selection lead to the elimination of variables two, three and five. The resulting regression model was:

$$\mathrm{PCA}_1 = 154.3 + 0.233\ \mathrm{LB} - 16.6\ \mathrm{SW}$$

$$(R^2 = 0.961, P = 0.002)$$

where PCA_1 is the first principle component, LB = litter biomass and SW = soil water content. t-Values for the two regression coefficients in the model were $t = 5.5$ ($P = 0.003$) for LB and $t = -2.8$ ($P = 0.039$) for SW, indicating that litter biomass was the more important predictor of termite assemblages. Termite assemblages in teak plantations (dominated by fungus-growers) showed high values of LB and low values of SW, and those in semi-deciduous forest (with several species of dry wood termites) low values of LB and high values of SW (Fig. 5).

4. Discussion

4.1. Species richness and functional diversity

Species richness and functional diversity of termite assemblages in Lama forest transects differed considerably from the ones reported in the literature (Davies et al., 2003). First, overall species richness was lower than in any other lowland forest transect in the African region, comparable only to sub-montane and dry evergreen forest transects in Madagascar (4–10 species; Davies et al., 2003) or a high altitude juniper forest transect in Malawi (2 species; Donovan et al., 2002). Second, species belonging to feeding groups III–IV (soil-feeders of the soil/humus interface and true soil-feeders) were either rare (group III) or absent (group IV). Taxonomically, the termite fauna was characterised by the rarity of Termitinae and absence of Apicotermitinae in both types of forest, the dominance of Macrotermitinae in teak plantations, and a relatively high number of Kalotermitidae in semi-deciduous forest. Notably, the number of Kalotermitidae species per transect in semi-deciduous forest was higher (2–3 species) than the number observed in other African transects (0–1), and again very similar to the one in Malagasy transects (2–4; Davies et al., 2003). Finally, resulting from the predominance of group I–II feeders in both assemblages, humification scores were low not only in teak plantations but even more so in natural forest.

While it is known that tropical termite assemblages are vulnerable to disturbances such as deforestation, logging, habitat fragmentation or conversion of forest into tree plantations (de Souza and Brown 1994; Davies, 2002; Davies et al., 2003), resulting in reduced species richness and changes in functional diversity, it was surprising that termite assemblages in Lama forest were depauperate even in natural, undisturbed forest, albeit significantly less than in teak plantations. This suggests that a local factor accounts for the overall low termite diversity. Comparing our transects to those run elsewhere in the African region (Davies et al., 2003), environmental conditions differ with respect to rainfall and altitude (lower in Lama forest), but these differences are small compared to the range encountered among African or even global transects. We therefore assume that the low species richness, in particular the absence of soil-feeders, was due mainly to soil type.

Vertisols are compact, hydromorphic clay soils with strong seasonal swelling and shrinking cycles. These conditions appear to be unsuitable for group III–IV feeders. This is supported by observations that termites are absent from semi-permanently flooded areas and certain deeply cracking vertisols (Wood, 1988). Likewise, the decline of the soft-bodied soil-feeders in disturbed tropical forests has been partly attributed to soil compaction (Eggleton et al., 1997). Another possible explanation for the scarcity of soil-feeders in Lama forest would be an insufficient soil organic matter content. However, organic carbon and nitrogen contents of the vertisols of Lama forest (Attignon et al., 2004) were similar to those reported for forest sites supporting high soil-feeder species richness (Eggleton et al., 1996, 1997). This confirms that physical rather than chemical soil properties restrict soil-feeder species richness and abundance in tropical forests. In contrast, some fungus-growers proved to be well adapted to the vertisols (see below), as evidenced by high densities of fungus combs in the surface soil. Similarly, other soil-dwelling detritivores such as diplopods and earthworms also displayed high activity and/or abundance in the vertisols of Lama forest (Attignon et al., 2004).

Even though the world-wide study of Davies et al. (2003) gives no details on the soils of the 87 transects studied, it can be inferred from the workability of the standard protocol on all of these transects, and from some of the original work cited in Davies et al. (2003) that no vert sols were included. Vertisols rarely cover large areas but are widely distributed in Africa (FAO/UNESCO, 1977) and other tropical regions. Because of their high fertility, they are often used for agriculture as well as for silviculture, if the drainage permits. Therefore, the pedological situation encountered in Lama forest, though specific, is not exceptional, and it is important to understand the interaction between soil characteristics and anthropogenic disturbances when interpreting the functional diversity of tropical forest termite assemblages.

4.2. Response of termite assemblages to disturbance

Responses to habitat disturbance of termite assemblages in tropical forests show typical p terns. Soil-feeders are usually more vulnerable to disturbances than litter and wood-litter feeders (de Souza and Brown, 1994). The latter may even be more abundant and species-rich in disturbed conditions, at least temporarily, because forest disturbances such as habitat fragmentation, logging or the conversion into forest plantations often lead to an increase in feeding resources due to the accumulation of litter and increased die-off of trees (de Souza and Brown, 1994; Eggleton et al., 1995; Davies, 2002). The disturbance regime in Lama forest follows a somewhat different trajectory.

First, the humification score, which denotes the trophic state of termite assemblages, was slightly but significantly lower in natural forest than in teak plantations. This resulted from the presence of group I feeders in semi-deciduous forest and their absence in teak, and the near absence of group III–IV feeders in both forest types. In most situations, disturbances would diminish rather than enhance the humification score, due to the “attenuation of termite assemblage penetration down the humification gradient of organic matter decomposition” (Davies, 2002). In view of this, the humification score can only be used as a measurement endpoint in termite monitoring studies if calibrated on the site-specific trophic structure in undisturbed conditions.

Second, overall species richness was consistently lower in teak plantations, due to the absence of dry wood termites. Therefore, Kalotermitidae were the most vulnerable group in terms of species loss. This is related to the absence of non-teak stumps and logs in teak plantations where termite-resistant teak logs are the only type of dry wood available, and even then only at low densities because logs and wood-litter are collected by foresters and the local population. The situation might be different in mature (> 40 years) teak stands which, in Lama forest, often have dense understorey vegetation (Lachat et al., 2004). Dead wood volume there amounted to 2–7 m^3 ha^{-1}, corresponding to about one seventh of the volume in natural forest but three times the volume in fuelwood plantations (Lachat, unpublished data; no data are available for the 15-year old teak plantations of this study). Notably, mature teak forests support a high diversity of detritivorous and xylophagous arthropods (Lachat et al., 2004).

The third aspect relates to the predominance and high abundance of litter and wood-litter feeders in teak plantations, most of them Macrotermitinae. Multiple regression analysis established a positive relationship between leaf-litter biomass and termite assemblages, with higher values of the first principal component being associated with termites dominating in teak plantations. These findings confirm those from other studies that fungus-growers respond positively to an increase in litter or dead wood biomass (Eggleton et al., 1995; Davies et al., 1999; Korb and Linsenmair, 2001a), and that leaf-litter may be a seasonally limited resource competed for by different fungus-growers (Korb and Linsenmair, 2001b). In teak plantations of Lama forest, leaf-litter provides a year-round available food resource. This may explain the high density of *Ancistrotermes* sp., the species accounting for most of the increase in Macrotermitinae encounters. It was usually found in small fungus combs at 5–10 cm below the soil surface, i.e., just below the litter layer. *Macrotermes* spp. are also known to feed on leaf-litter (Eggleton et al., 1995; Korb and Linsenmair, 2001b; Eggleton et al., 2002). *M. bellicosus* has a wide distribution in West African savannahs and gallery forests. It is also common in the cropland adjacent to Lama forest. Its presence in teak plantations can be interpreted as a response to the drier microclimate (compared to the *Noyau central*) and the availability of leaf-litter.

A special feature of our study is that species richness in teak plantations was significantly lower than in natural forest, while the number of encounters was significantly higher. Moreover, whereas the termite fauna of Lama forest may be considered as depauperate in terms of species richness, it is certainly not depauperate in terms of termite encounters. Unfortunately, only few published studies report encounter data that can be referred to for comparison. An exception is a study conducted in Sabah (Eggleton et al., 1999) which found 1,269 termite encounters in combined quadrates and belt transects covering a total surface of 1,920 m^2 in three different forest types, corresponding to an encounter density of 0.7 encounters m^{-2}. Overall encounter density in Lama forest (forests pooled) was very close to this value (0.8 encounters m^{-2}), despite a lower sampling effort and the rarity of soil-feeders.

Disturbances may affect termite assemblages directly by changing their resource base or indirectly via food-web perturbations. Davies (2002) supposed that disturbance-induced changes in the structure and abundance of ant assemblages might reduce the predation pressure on termites, resulting in increased termite densities. Likewise, studies in West Africa have shown that army ants frequently eliminate *M. bellicosus* colonies from entire areas (Korb and Linsenmair, 2001b). In Lama forest, with average termite encounter densities of 0.48 m^{-2} in natural forest versus 1.09 m^{-2} in teak plantations, we found supporting evidence for the predator-release hypothesis. The abundance of epigeal ants in semi-deciduous forest was about twice as high as in teak plantations (Attignon et al., 2004). These results were confirmed in an independent baiting study (Attignon, unpublished). Other indications of relatively high ant densities in natural forest are our personal observation of a raid of army ants against *Odontotermes* sp. 3 on one of our belt transects, and the abundance of myrmecophilous birds in the *Noyau central* (M. van den Akker, IUCN, personal communication). To conclude, it is well possible that a reduced predation pressure by ants, along with the better litter resource base contributed to the high termite encounter density in teak plantations.

4.3. Methodological considerations

Studies on the effect of disturbances on forest termite assemblages using belt transect surveys usually focus on species richness. However, species richness alone does not always depict the often gradual changes in termite assemblages brought about by anthropogenic disturbances of forest ecosystems (Eggleton et al., 1995, 1999, 2002; Davies, 2002), unless on the extreme end of complete clearance (Eggleton et al., 1995; Davies et al., 1999). Even though encounter data have been included as a “surrogate for abundance” (Davies, 2002; Eggleton et al., 2002) in multivariate analyses of termite assemblage structure, they are rarely reported or analysed individually. Yet our results show that encounter numbers are valuable and reliable data that can be exploited to analyse shifts in termite assemblage structure and abundance. In fact, encounter numbers in Lama forest were very consistent among replicate transects, as indicated by low standard errors. In previous studies, we used encounter data (binary or presence/absence data) effectively to monitor the relative abundance of other insects (Peveling et al., 1999; Langewald et al., 2003). We therefore propose to use and report encounter numbers not as surrogates but as abundance estimates of their own right.

In the present study we had to modify the standardised protocol in order to make up for the extra time needed to take the soil samples. The time spent on the remaining microhabitats was arbitrarily set to 40 min. Practice has shown that this time period was adequate to search an entire section, and we do not believe that our modification hampers comparison of results across studies because the same strata were searched. However, as with most sampling methods employing human effort, there is a risk that sampling effort is not evenly allocated to different substrata, or that it differs among studies, depending on observer performance, accessibility of microsites and searching reward (in terms of encounters). This would affect both species richness and encounter numbers. A note of caution on this issue has been given by Davies (2002) who supposed that encounters in dead wood might be biased towards smaller, more accessible items. In fact, it is striking that the most species-poor transects in the African region (our own and the Malagasy ones) were the richest for Kalotermitidae, giving the impression that more effort was devoted to searching dry wood termite habitats than in other transects. The modified sampling protocol adopted in Lama forest provided enough time to search all microhabitats, including the interior of logs or stumps, which were cut open with machetes and axes. This may be difficult if other strata yield high numbers of encounters already and consume most of the available searching time. Certainly, a possible sampling bias towards more easily accessible and species-rich (hence more rewarding) microsites must be taken into account when adopting the standard protocol and interpreting termite assemblage data.

5. Conclusions

The overall species richness of termite assemblages in Lama forest was low due to the near absence of soil-feeding species. Nevertheless, we found clear differences among forest types. The conversion of semi-deciduous forest into teak plantations was characterised by a significant decline in species richness and a shift in termite assemblage structure towards litter-feeding Macrotermitinae. Moreover, the density of Macrotermitinae (in terms of encounter numbers) increased dramatically. Termite-mediated processes such as nutrient cycling, carbon flux and soil formation are largely dependant on the composition of termite assemblages (Davies, 2002). Considering the drastic changes in density and functional diversity of termite assemblages, such processes would be expected to play an important role in Lama forest. In fact, a significant decrease of soil carbon and nitrogen has already been noted in young teak plantations (Attignon et al., 2004). This might be explained by the translocation of litter decomposition processes into termite nests (Jones, 1990). In view of our findings and observations in other tropical forest plantations (Lavelle et al., 1997), there is an elevated risk of soil degradation in Lama forest, with possible consequences for teak production. We therefore recommend to examine this issue in follow-up studies, and to conduct complete inventories of the termite fauna of Lama forest.

Acknowledgments

This study was conducted as part of the *BioLama* project, a research partnership between NLU-Biogeography, University of Basel, and the *Faculté des Sciences Agronomiques*, University of Abomey-Calavi. The Swiss National Science Foundation and the Swiss Agency for Development and Cooperation are acknowledged for their financial support. We are also grateful to the *Office National du Bois* und the International Institute of Tropical Agriculture (IITA) for logistical and technical support. C. Houngbédji and B. Kola (Benin) are acknowledged for their field assistance, and T.G. Myles (Canada) and J. Korb (Germany) for their help in termite identification.

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Table 1. Termite assemblages in semi-deciduous (natural) forest and teak plantations.

		Mean # of encounters / transect (SE)		Nominal	
	F	Natural forest	Teak plantation	*P*–value	
Kalotermitidae					
Cryptotermes sp. 1	1	3.7 (2.2)	0 (0)	0.047	
Cryptotermes sp. 2	1	0.2 (0.2)	0 (0)	n.a.	
indet.	1	0.2 (0.2)	0 (0)	n.a.	
Kalotermes sp.	1	1.0 (0.7)	0 (0)	n.a.	
Glyptotermes sp. 1	1	0.5 (0.3)	0 (0)	n.a.	
Glyptotermes sp. 2	1	0.2 (0.2)	0 (0)	n.a.	
Rhinotermitidae					
Coptotermes sp.	1	3.5 (2.0)	1.5 (1.2)	0.466	
Termitidae, Macrotermitinae					
Macrotermes bellicosus	2	0 (0)	9.7 (6.9)	0.039	
Ancistrotermes sp.	2	11.0 (7.0)	105.0 (12.7)	0.001	*
Microtermes sp.	2	20.2 (4.2)	21.2 (5.9)	0.907	
Odontotermes sp. 1	2	10.5 (8.2)	15.5 (15.5)	0.335	
Odontotermes sp. 2	2	0 (0)	18.0 (10.8)	0.047	
Odontotermes sp. 3	2	0.2 (0.2)	0 (0)	n.a.	
Termitidae, Nasutitermitinae					
Nasutitermes latifrons	2	3.2 (2.9)	15.0 (5.8)	0.263	
Termitidae, Termitinae					
Amitermes evuncifer	2	9.2 (9.2)	0 (0)	n.a.	
Termes hospi	3	0.5 (0.3)	0.2 (0.2)	0.537	
Termes sp.	3	0.2 (0.2)	0.2 (0.2)	n.a.	
Microcerotermes sp. 1	2	28.5 (6.0)	36.2 (6.1)	0.411	
Microcerotermes sp. 2	2	3.0 (1.8)	0 (0)	n.a.	

* Significant at $P < 0.05$ after sequential Bonferroni adjustment for $n = 10$ comparisons

n.a. = not assessed (no ANOVA performed because of low frequency of occurrence)

Table 2. Environmental conditions in semi-deciduous natural forest and teak plantations.

	Mean (SE)		Nominal
	Natural forest	Teak plantation	*P*–value
Soil water content (%)			
Rainy season [a]	26.6 (0.9)	25.9 (1.1)	0.617
Dry season	17.4 (0.6)	15.6 (0.4)	0.078
Temperature (°C)			
Rainy season min. [b]	22.7 (0.2)	22.5 (0.1)	0.286
Rainy season max. [b]	28.0 (0.2)	29.8 (0.3)	< 0.001 *
Dry season min.	23.2 (0.8)	23.3 (0.9)	0.984
Dry season max.	33.7 (0.4)	41.2 (0.6)	< 0.001 *
Relative humidity (%)			
Rainy season min. [b]	90.4 (1.2)	83.1 (1.8)	< 0.001 *
Rainy season max. [b]	100.0 (0.1)	99.5 (0.1)	< 0.001 *
Dry season min.	47.1 (2.8)	26.1 (2.2)	< 0.001 *
Dry season max.	99.4 (0.9)	98.9 (1.4)	0.791
Canopy cover (%)			
Rainy season [c]	78.8 (3.9)	69.1 (6.9)	0.271
Dry season	66.2 (2.4)	17.7 (0.8)	< 0.001 *
Leaf litter (g dry weight m^{-2})	376.4 (32.2)	599.1 (66.2)	0.021
Basal tree cover (m^2 ha^{-2})	40.9 (5.9)	37.6 (5.6)	0.702

[a] Measured at nearby sites in May 2004 (*n* = 8)

[b] Measured at one site each in natural forest and teak plantations over a 30-d period (*n* = 30) in June 2002

[c] Measured with a spherical densiometer

[*] Significant at $P < 0.05$ after sequential Bonferroni adjustment for *n* = 14 comparisons

Legends

Fig. 1. Map of Lama forest and location of belt transects. S: settlement; triangle: natural forest; circle: teak plantations.

Fig. 2. Frequency distribution of main termite microsites. Differences among forests are significant at $P < 0.001$.

Fig. 3. Species accumulation curves for termite assemblages in natural forest and teak plantations. Values are means of four replicate curves per forest type.

Fig. 4. Mean number (± standard error) of termite encounters for different families and subfamilies sampled in Lama forest. *P*-values are nominal significance levels for individual ANOVAs. Differences are also significant after Bonferroni adjustment at $* = P < 0.05$ and $** = P < 0.01$.

Fig. 5. Ordination biplot of the PCA. Lines are linear correlations of the two environmental variables soil water content (Water) and leaf-litter biomass (Litter) that were statistically significant predictors of PCA_1 (Axis 1) site scores in the multiple regression analysis. PCA_1 accounts for 72% of the total variance. Open triangle: natural forest; filled triangle: teak plantations; scores for species calculated by weighted averaging; Kalotermitidae: Cryp1,2: *Cryptotermes* sp. 1,2; Kalo: *Kalotermes* sp.; Glyp1,2: *Glyptotermes* sp. 1,2; K_ind: Kalotermitidae indet.; Rhinotermitidae: Copt: *Coptotermes* sp.; Macrotermitinae: Macr: *Macrotermes bellicosus*; Anci; *Ancistrotermes* sp., Micr: *Microtermes* sp.; Odon1,2,3: *Odontotermes* sp. 1,2,3; Nasutitermitinae: Nasu: *Nasutitermes latifrons*; Termitinae: Amit: *Amitermes evuncifer*, Term1,2: *Termes* sp. 1,2; Mcer1,2: *Microcerotermes* sp. 1,2 (K_ind, Cryp1 and Odon3 only shown as points to avoid overlapping labels).

Fig. 1.

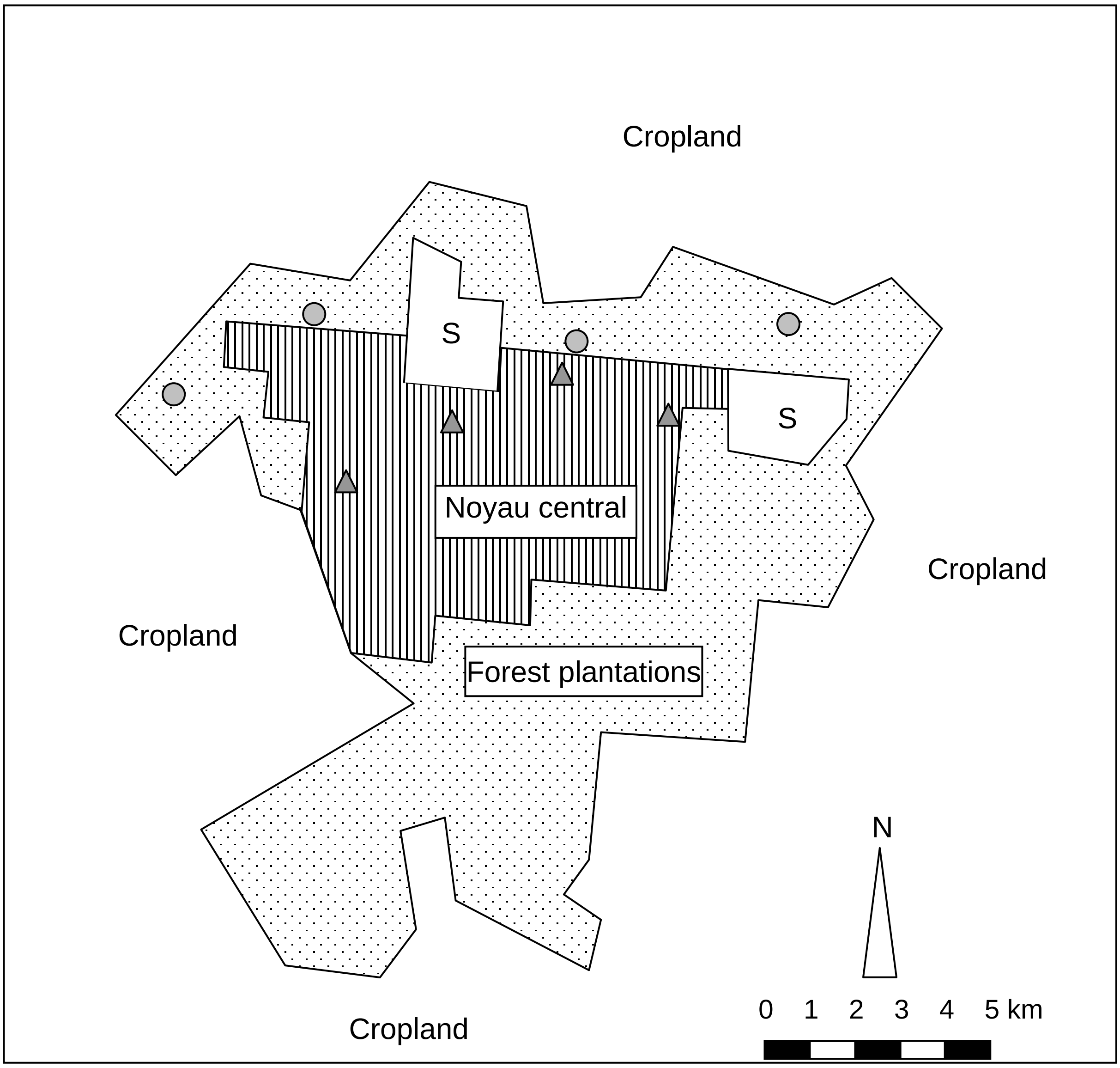

Cropland
S
S
Noyau central
Cropland
Cropland
Forest plantations
N
0 1 2 3 4 5 km
Cropland

Fig. 2.

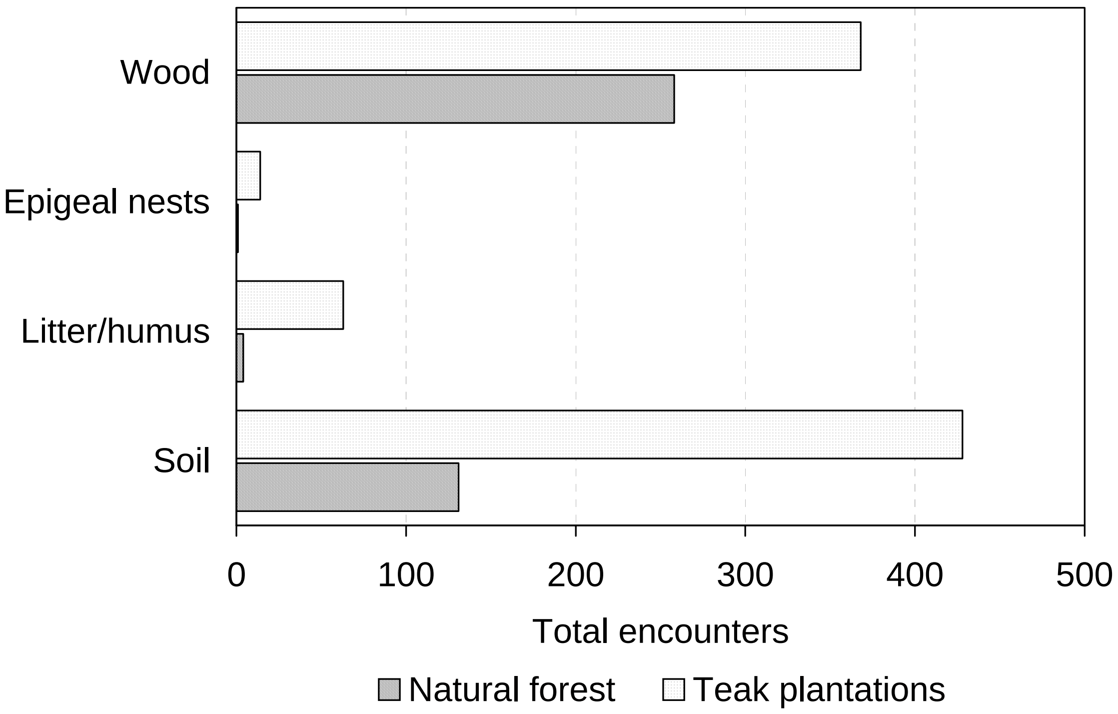
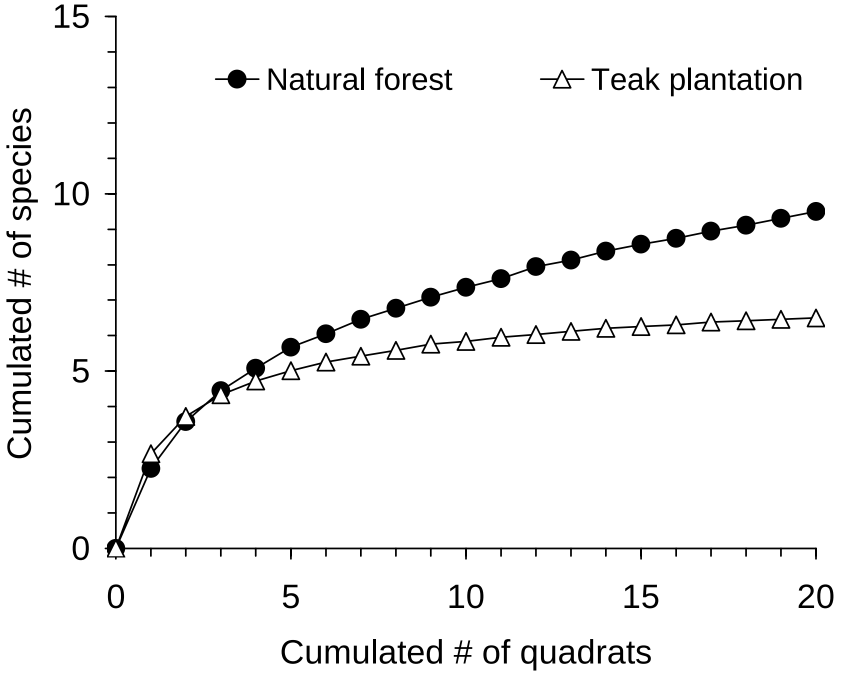

Wood
Epigeal nests
Litter/humus
Soil
0
100
200
300
400
500
Total encounters
Natural forest
Teak plantations

Fig. 3.


15
10
5
0
Cumulated # of species
Natural forest
Teak plantation
0
5
10
15
20
Cumulated # of quadrats

.

Fig. 4.

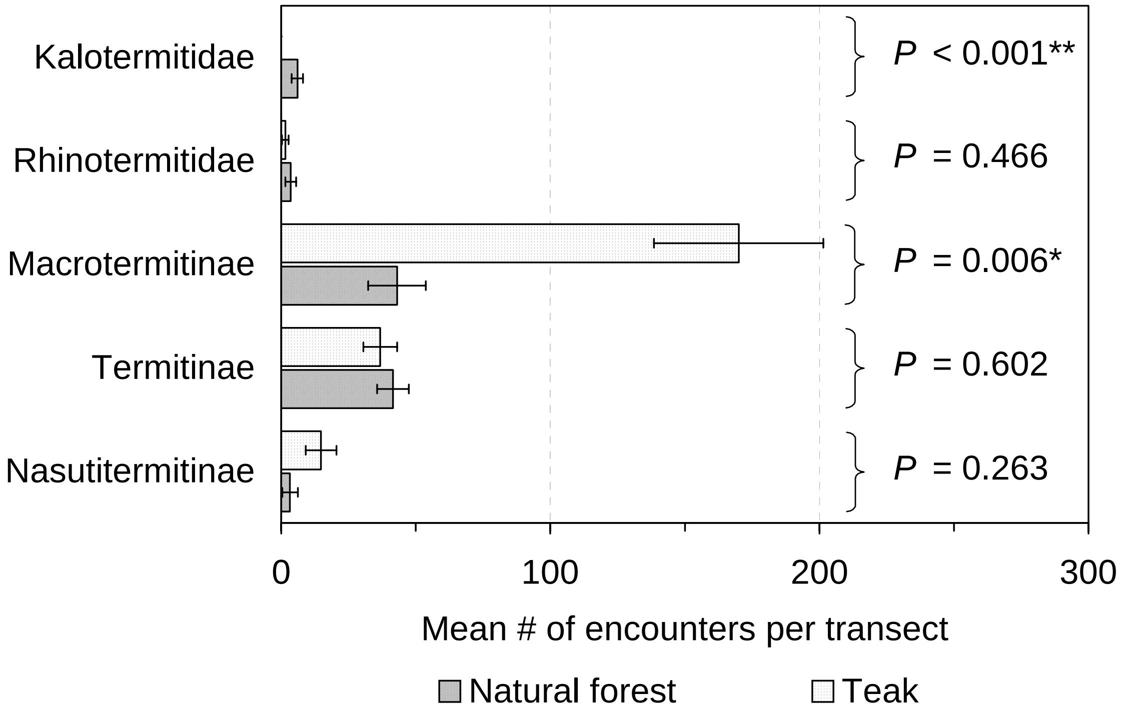
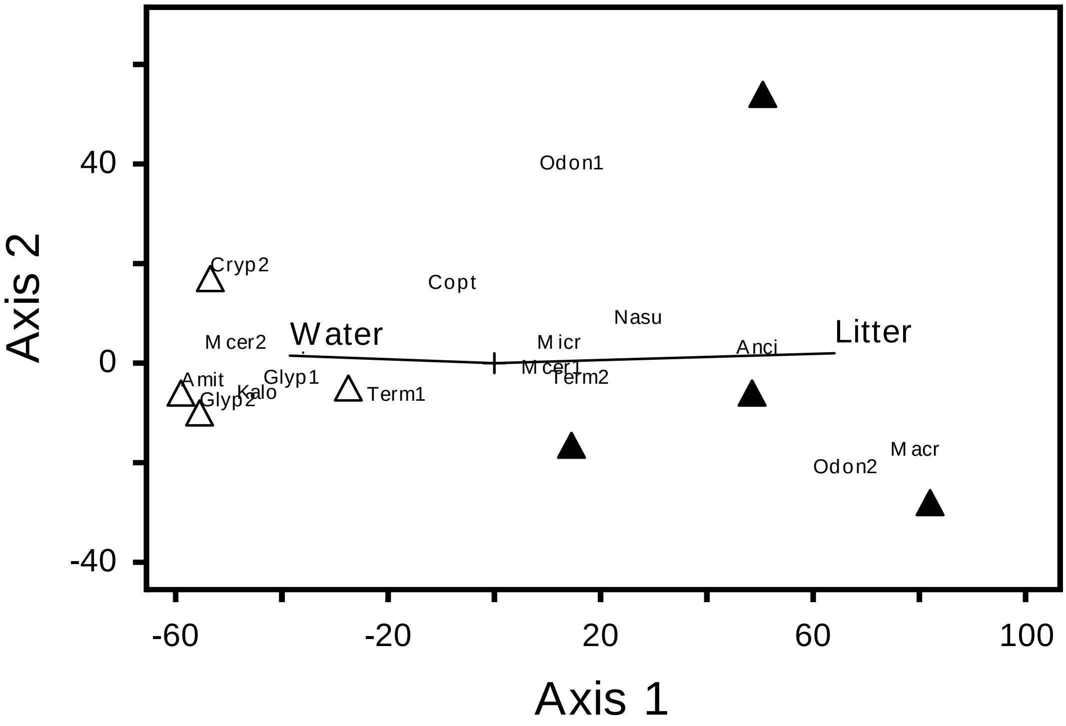

Kalotermitidae
Rhinotermitidae
Macrotermitinae
Termitinae
Nasutitermitinae
P < 0.001**
P = 0.466
P = 0.006*
P = 0.602
P = 0.263
0
100
200
300
Mean # of encounters per transect
Natural forest
Teak

Fig. 5.


Axis 2
Axis 1
40
0
-40
-60
-20
20
60
100
Odon1
Cryp2
Copt
Nasu
Mcer2
Water
Micr
Anci
Litter
Mcer1
Term2
Amit
Glyp1
Kalo
Glyp2
Term1
Macr
Odon2

Chapter 4

Activity of Termites and other Epigeal and Hypogeal Invertebrates in Natural Semi-deciduous Forest and Plantation Forests in Benin

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Abstract

Soil invertebrates represent an important base of terrestrial food chains and play an important role in maintaining the soil fertility and productivity of forest ecosystems. We examined the activity of termites and other soil- and litter-dwelling invertebrates in natural semi-deciduous forest, teak plantations of different age and firewood plantations of the Lama forest reserve, Benin, using a cardboard baiting method. The frequency of occurrence of individual invertebrates attracted to the baits was measured from May 2002 to April 2004, covering two rainy and two dry seasons. Twenty-one different invertebrate groups were sampled. The overall frequency of occurrence of invertebrates differed among forest types. It was significantly higher in natural forest (476) than in young teak (377) and old teak plantations (338). No significant differences were found among firewood plantations (412) and the other forest types. Analyses of individual taxa showed that Isopoda, Hymenoptera and Araneae dominated in natural forest, with frequencies of occurrence of 94, 25 and 27, respectively. Collembola dominated in firewood plantations (127), whereas Isopteran and Diplopod were more active in old teak plantations, with frequencies of occurrence of 65 and 49, respectively. Overall, Collembola, Isopoda, Isopteran, Diplopod, Araneae and Hymenoptera (ants) were the most frequent soil invertebrates of Lama forest. Repeated measures analyses showed significant differences in the frequency of occurrence among seasons for all majors invertebrate groups, as well as significant differences among forest types for all these groups except Diplopoda and Araneae. The activity of soil invertebrates was usually lowest during the long dry season. Moreover, termites were more active in old teak plantations (ferralsol soils) than in the other forest types (vertisol soils).

Keywords: Semi-deciduous tropical forest; teak and firewood plantations; termites; soil invertebrates; seasonality; cardboard-baiting.

1. Introduction

Invertebrates are by far the most abundant and most diverse animals in tropical forests. They are an essential component of nutrient- and energy-processing ability of the soil and play a key role in soil fertility and the productivity of forest ecosystems by taking part in nutrient turnover (Crossley, 1977; Coleman et al., 1996). Moreover, soil invertebrates represent an important base of terrestrial food chains and are vital to the survival of many forest wildlife species (Kremen et al., 1993). For example, soil invertebrates are essential to the process of decomposition. In tropical forests, in general, biological activity is concentrated in litter and a few upper centimetres of soil (Barros et al., 2002), and many studies provided evidence that soil fauna communities are very sensitive to the management of soil and plant cover (Lavelle et al., 1992; Stork and Eggleton, 1992). Despite the importance of soil invertebrates, there are no studies on the impact of land use changes on soil invertebrates in southern Benin. Understanding the impact of land use change on soil fauna is essential to achieve sustainable forest management and conservation of biodiversity. The Lama forest reserve comprises some of the last vestiges of semi-deciduous lowland forest within the Dahomey Gap in southern Benin (Nagel, 1987; Ern, 1988; Sokpon, 1995; Ballouche et al., 2000). It is an important refuge for several endangered wildlife species and rare plants (Sinsin et al, 2002). Part of the former natural forest has been converted to plantations for timber (teak) and firewood production. Thus, the reserve offers the opportunity to compare different forest ecosystems and has become of primary interest for biodiversity studies and conservation in Benin. However, except for a preliminary list of insects (Boppré, 1994; Tchibozo, 1995; Emrich et al., 1999) and a butterfly inventory (Fermon et al., 2001), invertebrates have not been studied as yet.

In the present study we examine the activity of termites and other soil- and litter-dwelling invertebrates, in particular detritivores, in different forest types of the Lama forest reserve. The goal was to study the effect of forest system (natural versus plantation forests) and season (dry versus rainy seasons) on the activity of soil invertebrate assemblages.

2. Materials and methods

2.1 Study area and experimental sites

The Lama forest reserve is situated in the so-called Dahomey gap, a discontinuity of the West African rainforest belt (Jenik, 1994). The reserve (*forêt classée*) lies in the Lama depression, about 80 km north of Cotonou (between 6°55.8–58.8’N and 2°4.2–10.8’E), covering 16,250 ha (Fig. 1). The study was conducted from May 2002 to April 2004 and focused on four different forest ecosystems: (I) Remnants of semi-deciduous forest (Adjanohoun et al., 1989) are scattered within the *Noyau Central* (NC), the inner, now fully protected part of the reserve (4,800 ha) which is composed of a mosaic of natural forest (1’900 ha), secondary forest, *Chromolaena odorata* thickets and enrichment plantings (Specht, 2002). Dominant tree species of the semi-deciduous forest are *Afzelia africana, Albizia zygia, Anogeissus leiocar-*

pus, Ceiba pentandra, Dialium guineense and *Diospyros mespiliformis.* (II) Young teak plantations, *Tectona grandis*, were planted between 1985–1995. They enclose the NC nearly entirely, forming a buffer zone that separates the NC from surrounding cropland. In this study, we only included stands planted between 1988–1991. (III) Old teak plantations are contiguous to young teak plantations, representing northerly and southerly extensions. They were established between 1963–1965. Old and young teak plantations cover about 10,000 hectares. (IV) Firewood plantations (2,400 ha) are located in the south-western part of Lama forest. They are composed of *Senna siamea* mixed with teak (ratio 3:1). These plantations were planted between 1988–1996, of which we studied stands from 1990–1992.

Four replicate linear transects, each about 40 m long, were selected within each forest type (Fig. 1). The sites were selected according to soil type, vegetation and – in case of plantations – tree age. The distance among replicate transects within forest types varied between 0.5 and 19.0 km, and the minimum distance between sites and forest edges was 50 meters.

2.2 Climate

The climate in Lama forest is subequatorial with a mean annual precipitation of 1,100 mm. Precipitation follows a bimodal pattern, with four distinct seasons, (1) a long rainy season from March to mid-July, (2) a short dry season from mid-July to August, (3) a short rainy season from September to October, and (4) a long dry season from November to February. The annual precipitation deficit is about 200 mm, but relative humidity is always high. Average annual temperatures vary between 25–29°C. The median of monthly rainfall data from three stations in the vicinity of our study sites is shown in Figure 2.

2.3 Soil

Lama (‘mud’ in Portuguese) forest is poorly drained, and during the long rainy season a substantial part of the forest is temporarily flooded (Paradis and Hougnon, 1977). Granulometric analyses of Lama forest soils conducted by Emrich et al. (1999) showed a relatively homogenous particle size of < 2 µm (50% of all particles) in the 20–30 cm soil layer, and the soils were classified as vertisols. Only towards the borders of the reserve (old teak plantations) are vertisols gradually replaced by sandy ferralsols (Specht, 2002). An overview of soil and other site characteristics recorded on transects of the study sites is presented in Table 1. Differences in carbon content, canopy cover and the number of tree species were substantial. The number of tree species was obviously highest in semi-deciduous natural forest, whereas litter biomass and litter cover recorded during the long dry season was highest in teak plantations. Litter cover and basal tree cover were relatively similar.

2.4 Litter availability

In the four forest types, litter biomass was measured between April 2002 and July 2003. Litter fall was measured by collecting leaf litter from four 1 m^2 plots per site (Djego, unpublished). The leaf litter in these plots was collected periodically. In the present study, we used six-weekly litter fall data. The litter collected was oven-dried to constant weight and weighed. Figure 3 presents data for each forest type and for different seasons, showing that overall litter fall differed among forest types as well as seasons.

2.5 Sampling of soil invertebrates

We examined the activity of soil invertebrates using a cardboard baiting technique. Baits were composed of three 10.0 × 2.5 cm cardboard pieces placed in 50 ml polypropylene centrifugation tubes (Sarstedt, Germany). The tubes had a diameter of 2.8 cm and a length of 11.5 cm. Each tube had twelve entry holes (0.8 cm diameter) for soil or litter invertebrates, plus the opening on the top. The total number of baits (sub-samples) per sampling site was 20. The baits were half dug into the soil in a horizontal position (i.e., at the soil-litter interface). Thus, half of the diameter of the tube was buried and the other half exposed. This was done to attract both epigeal and hypogeal termites and other invertebrates. The inter-bait distance was ≈ 2 m along a linear transect, covering a total distance of 40 m. The baits were installed with the red lid placed next to them for easy recognition. Between May 2002 and April 2004, baits were exposed every six weeks for a period of seven days. The total number of samples was 17, with six samples each from the short rainy and long dry season, three samples from the short rainy season and two from the short dry season.

Upon collecting the baits, the tubes were closed with the lid, transferred into individual plastic bags and taken to the field research station for sorting. The presence of all invertebrates was recorded. Termites were identified to genus and the other taxa on higher taxonomic levels. Termite specimens were stored in 80% alcohol, and the other invertebrates in 70% alcohol.

Termite attraction to the bait was indicated either by the presence of termites or by the presence of galleries, sheetings or tunnels in the cardboard (Abensperg-Traun and Milewski, 1995; Nash et al., 1999; Dawes-Gromadzki, 2003). In some cases, baits were entirely consumed by detritivorous invertebrates.

2.6 Data analysis

Parametric analysis of variance (ANOVA) and Sidak multiple comparison tests (Zar, 1999) were conducted to compare invertebrate baiting effects among forest types (main factor), using the cumulative frequency of occurrence as a measure of invertebrate activity.

ANOVAs and Sidak *post hoc* tests were also used to compare individual frequencies of occurrence of certain taxonomic groups. For termites, these analyses were done on species or morphospecies level. In case of heterogeneous variances, data were $\log_{10}(x+1)$-transformed to achieve homogeneity of variances. Alternatively, we switched to non-parametric Kruskal-Wallis analyses, followed by Nemenyi multiple range tests. The experiment-wise error was set at $\alpha = 0.05$.

Reciprocal averaging (RA), also known as correspondence analysis (CA), a multivariate method based on χ^2-distance (Hill, 1973; Greenacre, 1984), was performed for invertebrate groups, using PC-ORD (McCune and Mefford, 1999). Reciprocal averaging yields both normal and transposed ordinations automatically and gives a simultaneous projection of samples and variables on the same graph. Variable-points located within a certain group of sample-points are typical for this group. For a better perceptibility, we present separate graphs for the ordination of sites and invertebrates. Frequencies of occurrence of invertebrate groups rarer than F_{max} /5 (where F_{max} is the frequency of the most common species) were down-weighted in proportion to their frequency**.**

The seasonality of the activity of the most frequent invertebrate taxa – those representing more than 3% of the total frequency of occurrence – was analysed using repeated measures analysis (SPSS 12.0). For this purpose, we first calculated the median frequency of occurrence of the respective invertebrate taxon per season. These median frequency data were entered as dependent variables and were examined with regard to differences between forest type (between-subject factor) and season (within-subject factor). Sequential Bonferroni adjustments were made to account for multiple-testing.

The rate of bait emptiness (R), i.e., the number of baits that had been fully consumed, was calculated according to:

$R = (N_{empty}/N)*100$,

where N_{empty} is the number of empty baits and N the total number of baits.

Differences in R among forest types and seasons were also tested using repeated measures analysis.

3. Results

3.1. Invertebrate assemblages

3.1.1 Overall frequency of occurrence of invertebrates

The overall mean frequency of occurrence of invertebrates differed significantly among forest types (ANOVA: $F_{3/12} = 8.2$, $P = 0.03$), increasing in the following order: old teak plantations (338.0) < young teak plantations (376.7) < firewood plantations (411.7) < natural forest (476.2) (Fig. 4). Table 2 summarises frequencies of occurrence in different forest types for individual invertebrate taxa. Natural forest had the highest values for Annelida, Isopoda, Araneae, Acari, Pseudoscorpiones, Dermaptera, Blattodea, Coleoptera and Hymenoptera (only Formicidae). Firewood plantations had the highest values for Chilopoda, Diplura, Collembola, Zygentoma, Orthoptera, Homoptera, Heteroptera and Diptera. Young teak plantation had the highest values for Gastropoda and Psocoptera, and old teak plantation only for Isoptera.

Parametric analyses of variance or non-parametric Kruskal Wallis tests showed significant differences among forest types only for Gastropoda (young > old teak), Diplura (firewood > natural forest), Blattodea (natural forest > young teak), Isopoda (old teak > all other forests), Heteroptera (firewood > old teak) and Hymenoptera (natural forest > young teak) (Table 2).

Reciprocal averaging was performed for all sites and invertebrate groups (Fig. 5). Axes 1 to 3 account for 34.0, 31.2 and 14.0% of the total variance, respectively. Axis 1 is strongly polarized towards old teak plantations which had the lowest soil carbon content, the lowest soil water content, as well as the lowest total frequency of occurrence of invertebrates. This axis reflects a soil type gradient, with all old teak plantation sites and one firewood plantation site having sandy ferralsols, whereas all other sites had vertisols. However, one old teak site is an outlier in that it plots at the same position (axis 1 score) as young teak and natural forest. Axis 2 shows a strong grouping of natural forest sites. Natural forest had the highest frequency of occurrence of invertebrates compared to forest plantation sites. Thus, axis 2 reflects a land use (or disturbance) gradient.

3.1.2 Seasonal activity patterns

A total of 21 invertebrate taxa were sampled during the study. Of these, all but one (Homoptera) were present in all forest types. Six taxa occurred at > 3% of the total frequency of occurrence. These most frequent taxa were, in decreasing order, Collembola, Isopoda, Isoptera, Diplopoda, Araneae and Hymenoptera (Formicidae). Table 3 presents the result of the repeated measures analyses for these most frequent invertebrates. We found significant effects of both forest type and season, as well as an interaction among these factors, for Isopoda, Collembola and Isoptera. Season was also significant for Diplopoda and Araneae, while Hymenoptera showed a significant effect for both main factors but not interaction.

Collembolans showed similar activity in all forest types (Fig. 6a), but their activity differed significantly between seasons. A significantly higher frequency of occurrence was noted during the short rainy and dry seasons, compared to the long seasons (Fig. 6b). The significant forest × season interaction (c.f., Tab. 3) is depicted in Fig. 7a which shows that the seasonal pattern was dissimilar across forest types.

Isopods were more abundant in natural than in plantation forests, but only between natural forest and old teak plantations was this difference significant (Fig. 6c). Isopods were less active during the long dry season but significantly more so during the short rainy and the short dry season (Fig. 6d). The significant forest × season interaction is due to the fact that isopods were most frequent in natural forest during all but one season (short rainy season) when they were more frequent in firewood plantations (Fig. 7b).

Termites were significantly more active in old teak plantations than in natural forest and teak, but similar to firewood plantations (Fig. 6e). The peak activity was during the long rainy season and the lowest activity during the short dry season (Fig. 6f). The significant interaction between the two factors (c.f., Tab. 3) was related to an unproportionally high increase in activity in old teak plantations during the short rainy season (Fig. 7c).

The frequency of occurrence of diplopods was not significantly different among forest types (Fig. 6g). However, we noted a significant difference among seasons. They were most active during the long rainy season and least active during the long dry season (Fig. 6h).

No significant differences among forest types were found for spiders (Fig. 6i). However, their frequency of occurrence was highest during the long dry season and lowest during the short dry season, with intermediate levels during the rainy seasons (Fig. 6j).

Ants were most active in natural forest, but the difference was only significant compared to young teak plantations (Fig. 6k). They were active during all seasons but showed a significant low activity during the long dry season (Fig. 6l).

3.2 Termite assemblages

A total of 5,440 baits were exposed over the entire study period. Of these, the majority (98.6%) was recovered. Of the total number of baits, 774 (14.4%) were attacked by termites, and 660 termite samples were collected, comprising nine species in seven genera. Six species were fungus-growers (Macrotermitinae) and one species each wood/litter-feeders of the Termitinae, Nasutitermitinae and Rhinotermitidae, respectively.

The frequency of occurrence of termites differed greatly among species. The dominant species was *Ancistrotermes* sp., accounting for 64% of all records, followed by *Microtermes? pusillus?* (19%) and two species of *Odontotermes* (5% each). The remaining species comprised < 2% of the total number. Several species were not recorded in all forest types. *Pseudacanthotermes* sp. was found only in old teak plantations, *Nasutitermes* sp. in natural forest and teak plantations, and *Coptotermes* sp. in old teak and firewood plantations. *Microcertermes? pusillus?* was found only in firewood and young teak plantations, while *Macrotermes bellicosus* was found in all forests except for young teak plantations. Despite large nominal differences in termite occurrence frequencies among forest types, we found only one that was significant in terms of frequency of occurrence. *Microcertermes? pusillus?* was significantly more frequent in old than in young teak plantations (Table 4).

3.3 Rate of full bait consumption

A total of 130 baits (2.4%) were completely consumed by detritivores. However, the rate of full bait consumption was not significantly different among forest types (Fig. 8a), nor did we find significant differences among seasons (Fig. 8b).

4. Discussion

4.1 Invertebrate assemblages

The overall frequency of occurrence of invertebrates was highest in natural forest, intermediate in firewood plantations and lowest in teak plantations. In a study of litter breakdown in Lama forest, Attignon et al. (2004) found the highest invertebrate abundance in natural forest, but the lowest in firewood plantations. Contrary to the present study, the litter breakdown study was conducted during one long rainy season only, and the method differed from the one in the present study. Even though natural forest and firewood plantations represent completely different land use classes, the soil invertebrates sampled showed similar invertebrate activity patterns.

Correspondence analysis clearly separated old teak plantations from other forest types. These plantations showed a greater activity of termites and diplopods, which may be due to the type of soil (sandy ferralsol) and an increase of macronutrients in the soil via the large production of litter. The ordination also clearly separated natural forest sites from plantations, due to a much higher biological activity of invertebrates.

4. 2 Activity of the most frequent taxa

Our results showed that there was no significant difference in the frequency of occurrence of springtails in different forest types. In contrast, Quang and Nguyen (2000) found higher Collembola species richness in cultivated land than in a subtropical evergreen forest.

Isopods were more abundant in natural forest than in old teak plantations. However, there was no difference in occurrence frequencies among the other forest types. The difference in soil type may explain the difference observed, indicating that isopods are more active in vertisols than in ferralsols. A related explanation is the high humidity in natural forest. Terrestrial isopods are among the few land-living groups of crustaceans, and many species prefer humid microclimates. Similar to some millipedes, they are saprophagous, hypogeal or epigeal animals. Isopods are responsible for the primary fragmentation of leaf litter, but due to their feeding on invertebrate faeces, they are also considered as secondary decomposers.

Isoptera showed significantly higher activity in old teak plantations than in the other types of forest (c.f., Fig. 6e). Our results confirm those of Attignon et al. (2004) who found significantly higher termite frequencies of occurrence in leaf litter bags placed in old teak plantations than in other forest types. This clearly indicates that termites are more active in old teak plantations. We relate this to the more favourable physical soil conditions in ferralsols compared to vertisols. Lee and Wood (1971) reported that due to the strong shrinking and swelling, termitaria construction may be difficult in vertisol.

Diplopoda were active in all forest types and showed no significant differences among forests. This may be explained by the generalist feeding behaviour of most diplopods (Hoffman, 1986). Their main role is one of comminution of plant material, i.e., they break up dead plant material into small pieces, thereby increasing the surface area and providing microhabitats for the bacterial and fungal decomposition of organic matter.

Ants showed significantly higher frequencies of occurrence in natural forest than in young teak plantations, indicating that this group benefited from the forest environment. Basu (1997) found more leaf litter ant species in closed canopy forest than in treefall gaps in the Western Ghats in India. In contrast, Belshaw and Bolton (1993) surveyed the leaf litter ant fauna in primary forest, secondary forest and cacao plantations in Ghana and concluded that forest clearance and establishment of cacao farms had little effect on the leaf-litter ant fauna. Among the 91 bird species recorded in the Lama forest, 60% represent forest interior species (Emrich et al., 1999), and among them are numerous insectivores relying on ants as food or to flush insect prey. The abundance of myrmecophagous birds in semi-deciduous forest might be linked to higher activity and/or abundance of ants. However, more studies are needed to examine the effect of forest type and management system on the interaction between birds and ants in Lama forest.

4.3 Seasonal activity patterns

The most frequent taxa showed distinct and highly significant seasonal activity patterns. Collembolans, the most frequently encountered group, had their highest activity during the short rainy and the short dry season. In contrast, significantly lower activities were observed during the long seasons (dry and rainy). The long dry season showed the lowest activity of collembolans, probably because of the dry microclimate. As a matter of fact, sufficient humidity is important for many invertebrates, especially those who breathe through their integument (Athias, 1974; Joosse, 1979; Verhoef and Van Slem, 1983).

Isopods showed similar seasonal patterns as collembolans. Although these animals are sensitive to dry conditions, very high rainfall is also not favourable to their development, which may explain the low activity of these two taxa during the long rainy season.

Termites were active during all seasons, with higher frequencies of occurrence during the rainy season, but diplopods were not active during the dry season. Korb and Linsenmair (2001) found that termites in a West African savannah gallery forest were active all year round, with a peak during the rainy season when diplopods and earthworms were also active. Finally, ants were most active between the long and the short rainy season but far less during the long dry season.

The general seasonal pattern drawn from this study is that most invertebrate taxa are least active during the long dry season. During this season, the soil water content is drastically reduced, and the compact and dry cracking vertisols becoming unfavourable to soil-dwelling animals. Definite conclusions, however, are difficult to draw. In this study, we provided external food (cardboard) in different forest types, and the attraction to invertebrates can be explained in different ways. First, the presence of invertebrates in the baiting tubes might be a function of abundance. In this case, higher frequencies of occurrence would indicate higher invertebrate abundance or biomass. Alternatively, attraction may also result from the scarcity of natural food. This means that baits are more attractive during food shortages, and high encounter rates might reflect this shortage rather than the abundance or biomass of detritivores. Our results showed that during the long dry season, litter biomass is high due to the litter fall (Figure 3), and soil invertebrates, especially detritivores, may not be attracted to the baits. However, comparison of the rate of baits that were entirely consumed did not reveal consistent results.

4.4 Termite assemblages

Nine species of termites were recorded from the baits. Of these, *Ancitrotermes* and *Microtermes* species comprised more than 80% of all samples. The same dominant species were found in a study on the density and functional diversity of termite assemblages in semi-deciduous forest and young teak plantations (Attignon et al., 2004). Only few species were found in the present study because the baits attracted mainly wood- and litter-feeders. The frequency of occurrence of only one species (*Microtermes? pusillus?*) differed significantly among forest types. This species was more frequent in old teak than in young teak plantations. A possible explanation for this is the more favourable soil type in old teak. Ferralsol seems to be a more suitable soil type for termites than vertisol. More studies are needed to examine the effect of soil type on the composition and biomass of termite assemblages.

5. Conclusions

This study examined the effect of forest use on the activity of epigeal and hypogeal termites and other invertebrates in a tropical semi-deciduous forest in southern Benin. It indicates that although few taxonomic groups showed significant differences among forest types, the biological activity of soil invertebrates was mostly higher in natural forest than in plantation forest. Collembolans, Isopods, Isoptera and Diplopoda were found to be the most frequent invertebrates attracted to cardboard bait. Our results showed that most soil invertebrates were less active during the long dry season. This was related to the dry microclimate. Termites were an exception as they were found to be active during all seasons.

Acknowledgements.

This study was conducted within the scope of *BioLama*, a research partnership between *NLU-Biogeographie* and the *Faculté des Sciences Agronomiques*. The Swiss National Science Foundation and the Swiss Agency for Development and Cooperation are acknowledged for their financial support. A number of people provided assistance and advice in this study. We would like to thank C. Houngbédji, M. Guedegbé, L. Konetche, K. Bankolé M. Boukari (*BioLama*) L. Houéssou and N. Worou (Laboratoire d'Ecologie Appliquée) and P. Houayé, R. Akossou, D. Honfozo, H. Hodonou, V. N'velin (*Office National du Bois*).

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Table 1. Characteristics of the forest types in Lama forest. Values are means of replicate sites (*n* = 4; ± standard error)

Character	Forest type: Natural forest		Young teak plantations		Old teak plantations		Firewood plantations	
Soil[a]								
Type	Vertisol		Vertisol		Sandy ferralsol		Vertisol	
pH mean[c]	4,5	(0,5)	4,5	(0,5)	4,8	(0,6)	5,0	(0,6)
C (%)[c]	4,1	(0,3)	2,5	(0,3)	1,4	(0,3)	3,2	(0,4)
Soil water content (%)[b]	17,3	(0,3)	17,6	(0,3)	8,6	(0,5)	17,6	(0,4)
Litter biomass (g/m^2)[b]	368,8	(33,2)	528,0	(46,3)	591,0	(45,1)	353,5	(40,0)
Canopy cover (%)[b]	69,4	(1,2)	21,2	(1,5)	40,7	(5,0)	45,6	(2,9)
Dead wood cover (%)[b]	7,6	(0,9)	8,1	(1,9)	3,6	(1,5)	20,5	(1,7)
Litter depht (%)[b]	4,9	(0,2)	19,0	(0,4)	16,1	(1,9)	3,9	(0,5)
Litter cover (%)[b]	89,1	(1,2)	92,9	(0,3)	76,9	(9,9)	83,0	(0,4)
Basal cover (m^2/ha)[b]	17,8	(4,3)	18,6	(3,0)	18,1	(6,4)	15,1	(3,1)
Number of tree species[b]	7,0	(1,1)	1,3	(0,2)	1,0	0,0	1,0	0,0

[a] topsoil; [b] assessment conducted in March 2004; [c] after Weibel 2003

Table 2. Mean frequency of occurrence (*n* = 4; ± standard error) of invertebrate groups in different forest types of Lama forest. Means in rows with different letters are significantly different at *P* < 0.05, those with similar or without letters are not statistically significant. Capital letters indicate parametric, small letters non-parametric analyses.

	Mean Frequency of occurrence (n =4;± Standart error)											
Taxon/Type of forest	Natural forest			Young teak			Old teak			Firewood		
Diplopoda	46.4	(3.1)		28.4	(3.7)		49.5	(13.8)		20.4	(9.9)	
Isopoda	94.5	(5.2)	A	66.4	(7.2)	A	34.2	(9.8)	B	77.3	(8.8)	A
Gastropoda	14.2	(1.5)		28.9	(4.4)	a	4.6	(2.2)	b	7.5	(0.9)	
Aranea	27.0	(1.5)		18.7	(3.4)		23.1	(2.3)		23.7	(2.9)	
Pseudoscorpiones	15.5	(4.3)		7.9	(1.0)		7.4	(1.0)		8.0	(1.2)	
Acari	14.0	(3.9)		8.4	(2.2)		6.4	(2.1)		8.5	(4.9)	
Collembola	126.4	(5.3)		121.2	(5.6)		103.0	(8.5)		129.8	(7.9)	
Isoptera	37.1	(6.7)		40.5	(4.1)		64.8	(12.1)		51.0	(10.1)	
Blattodea	27.0	(2.3)	A	1.0	(0.4)	B	5.1	(3.0)		7.7	(2.0)	
Zygentoma	2.7	(1.5)		12.8	(4.4)		4.7	(1.4)		15.0	(4.7)	
Hymenoptera	25.1	(3.6)	A	10.1	(1.6)	B	12.8	(2.0)		14.2	(2.9)	
Chilopoda	3.4	(0.5)		1.5	(0.3)		2.2	(0.5)		7.0	(5.0)	
Annelida	5.9	(3.1)		2.7	(0.2)		2.2	(0.6)		2.5	(1.0)	
Heteroptera	1.0	0.0		0.5	(0.2)		0.2	(0.2)	a	3.7	(1.1)	b
Coleoptera	3.9	(1.2)		2.5	(0.9)		1.5	(0.9)		2.5	(0.6)	
Diptera	0.7	(0.2)		0.5	(0.2)		0.2	(0.2)		1.0	(0.4)	
Dermaptera	15.2	(8.8)		6.9	(2.0)		2.2	(1.6)		6.2	(1.1)	
Orthoptera	4.4	(0.6)		3.0	(1.1)		2.7	(0.5)		8.2	(4.2)	
Diplura	2.9	(0.9)	a	8.9	(0.4)		3.9	(1.9)		14.5	(4.0)	b
Psocoptera	0.2	(0.2)		1.2	(1.2)		1.0	0.0		1.0	(0.4)	
Homoptera	0.0	0.0		0.0	0.0		0.2	(0.2)		0.7	(0.4)	
Total	**476.2**	**(14.4)**	**A**	**376.7**	**(21.6)**	**B**	**338.0**	**(23.9)**	**B**	**411.7**	**(20.7)**	

Table 3. Results of repeated measure analyses of frequencies of occurrence of major invertebrate taxa attracted to cardboard bait. Significant results are shown in bold face.

	Frequency of occurence		
Factor	df	F	P
Collembola			
Forest	03:36	**3.6**	**0.048**
Season	03:36	**71.6**	**< 0,001**
Forest*Season	03:36	**2.9**	**0.010**
Isopoda			
Forest	03:36	**6.5**	**0.008**
Season	03:36	**61.0**	**< 0,001**
Forest*Season	03:36	**2.5**	**0.026**
Diplopoda			
Forest	03:36	2.0	0.163
Season	03:36	**20.2**	**< 0,001**
Forest*Season	03:36	1.5	0.169
Isoptera			
Forest	03:36	**4.0**	**0.035**
Season	03:36	**22.1**	**< 0,001**
Forest*Season	03:36	**3.7**	**0.002**
Aranea			
Forest	03:36	0.6	0.642
Season	03:36	**20.9**	**< 0,001**
Forest*Season	03:36	1.0	0.439
Hymenoptera			
Forest	03:36	**4.6**	**0.022**
Season	03:36	9.1	< 0,001
Forest*Season	03:36	0.7	0.687

Table 4. Mean frequency of occurrence (*n* = 4; ± standard error) of termite species in different forests types of the Lama forest. Means in rows with different letters are significantly different at $P < 0.005$, those with similar or without letters are not statistically significant. Capital letters indicate parametric, small letters non-parametric analyses.

	Mean Frequency of occurrence (n =4;± Standart error)											
Taxon/Type of forest	Natural forest			Young teak			Old teak			Firewood		
Macrotermitinae												
Odontotermes ? schmitzi ?	2.5	(1.5)		1.5	(0.9)		2.4	(1.8)			(1.7)	
Odontotermes ? akengeensis ?	2.0	(0.4)		1.2	(0.7)		2.2	(0.8)			(14.0)	
Ancitrotermes sp.	14.5	(5.5)		28.1	(1.0)		34.8	(9.0)		28.1	(6.1)	
Microtermes ? pusillus ?	8.8	(2.0)	AB	2.4	(1.5)	A	12.8	(3.8)	B	7.5	(1.9)	AB
Macrotermes bellicosus	0.5	(0.5)		0.0			1.0	(0.7)		1.2	(0.9)	
Pseudacanthotermes sp.	0.0			0.0			2.2	(1.4)		0.0		
Termitinae												
Microcerotermes sp1	0.0			0.5	(0.3)		0.0			0.0	(0.4)	
Nasutitermitinae	1.2	(0.6)		0.0			1.7	(1.4)		1.2	(0.6)	
Nasutitermes latifrons (Sjöstedt)	1.7	(1.4)		0.0			1.7	(0.6)		0.0		
Rhinotermitidae												
Coptotermes sp.	0.2	(0.2)		0.0			0.0			0.5	(0.3)	

Legends

Fig. 1. Map of the Lama forest reserve and location of sampling sites (after Specht, 2002); NC = noyau central, T = teak plantations, S = settlement areas, F = firewood plantations; diamond = semi-deciduous forest, open circle = young teak plantations, filled circle = old teak plantations, triangle = firewood plantations.

Fig. 2. Rainfall in Lama forest during the study period.

Fig 3. Litter biomass in different forests during different seasons.

Fig.4. Mean frequency of occurrence ($n = 4$; ± standard error) of invertebrates in different forest types. Means marked with different letters are significantly different at $P < 0.05$ or lower.

Fig. 5. Correspondence analysis (CA) on all sampled invertebrate groups. Projection of forest type (a) and taxa (b) in the plane of axes 1 and 2. I: Natural forest; II: Young teak plantations; III: Old teak plantations; IV: Firewood plantations; aranea: Araneae; blattode: Blattodea; chilo: Chilopoda; coleopte: Coleoptera; collembo: Collembola; dermapte: Dermaptera; diplopod: Diplopoda; diplure: Diplura; heteropt: Heteroptera; gastropod: Gastropoda; homopter: Homoptera; hymenopt: Hymenoptera; orthopte: Orthoptera; pseudosc: Pseudoscorpiones and zygentom: Zygentoma.

Fig. 6. Mean frequency of occurrence ($n = 4$; ± standard error) of the most frequent invertebrate groups in different types of forest and during different seasons. Means marked with different letters are significantly different at $P < 0.05$ or lower

Fig. 7. Mean frequency of occurrence ($n = 4$; ± standard error) of the most frequent invertebrate groups by forest type and season.

Fig. 8. Rate of full bait consumption by forest type and season

Fig. 1.

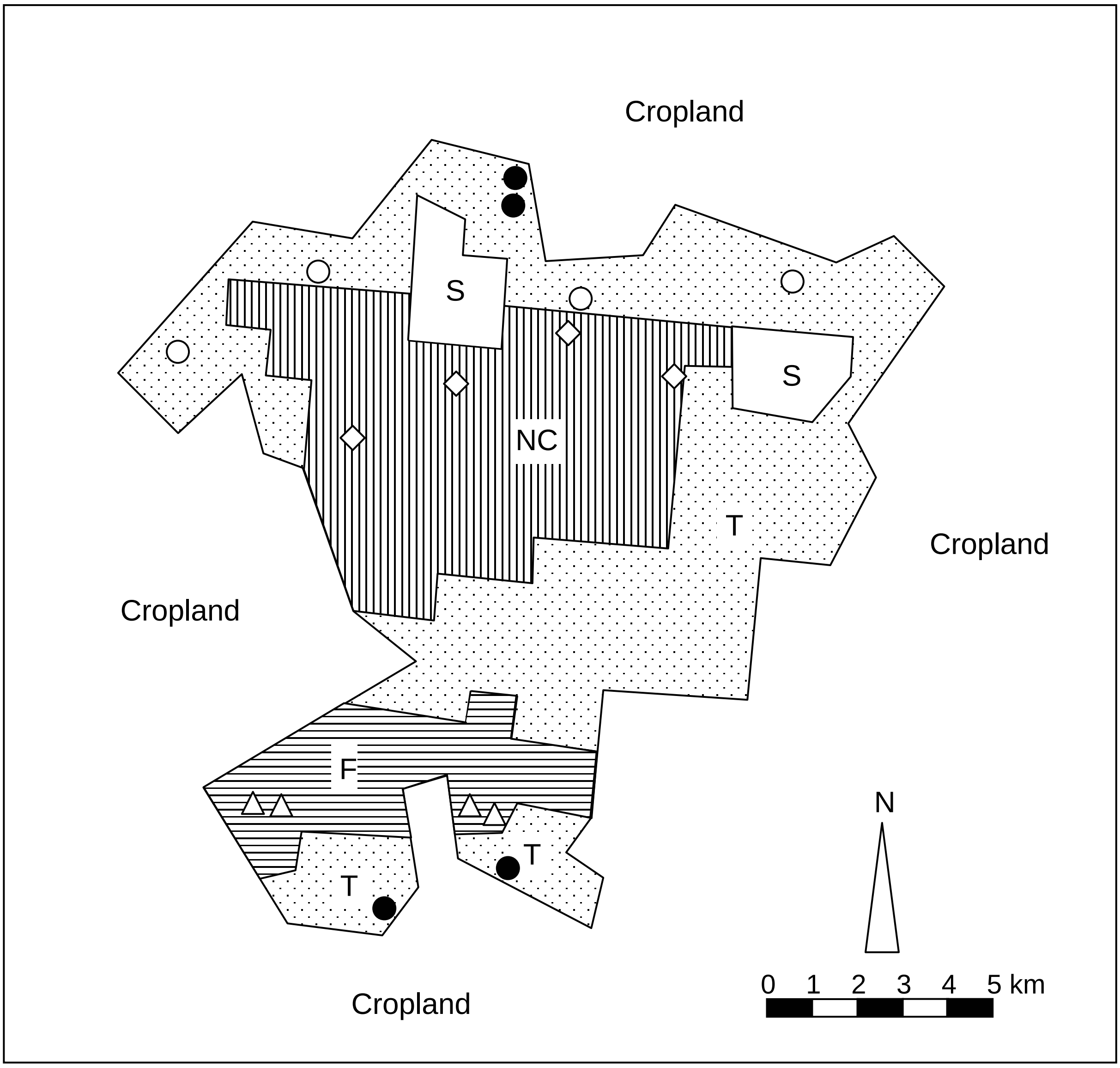


Fig. 2.

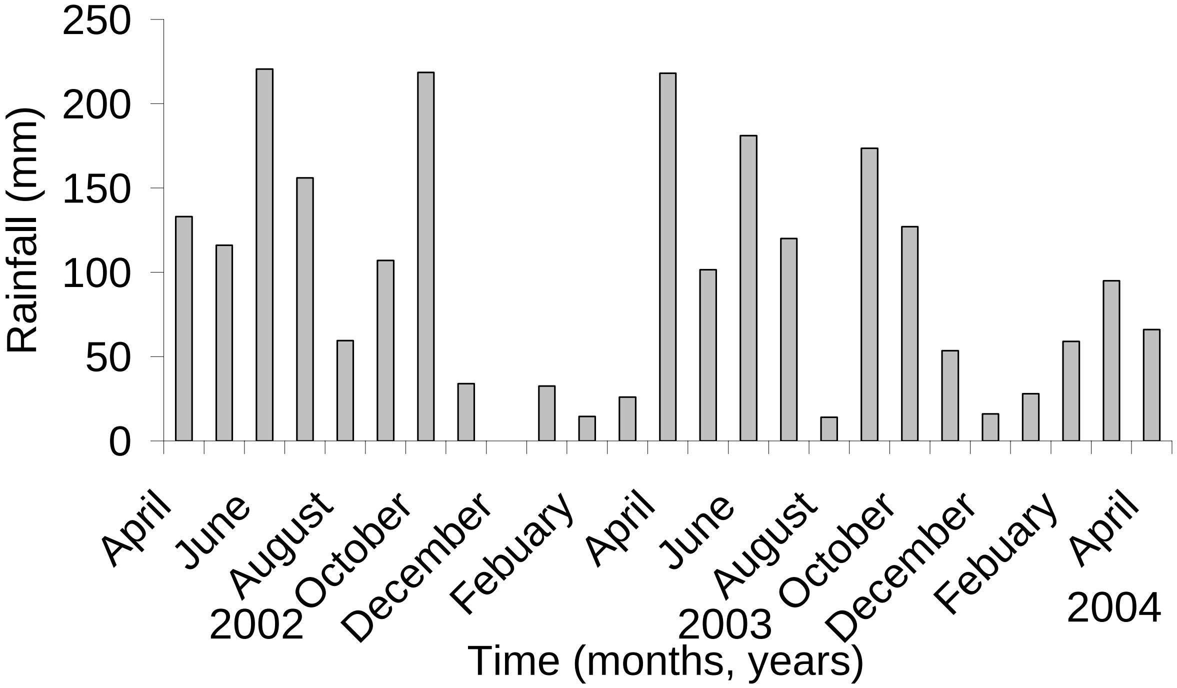

250
200
150
100
50
0
Rainfall (mm)
April
June
August
October
December
Febuary
April
June
August
October
December
Febuary
April
2002
2003
2004
Time (months, years)

Fig 3.

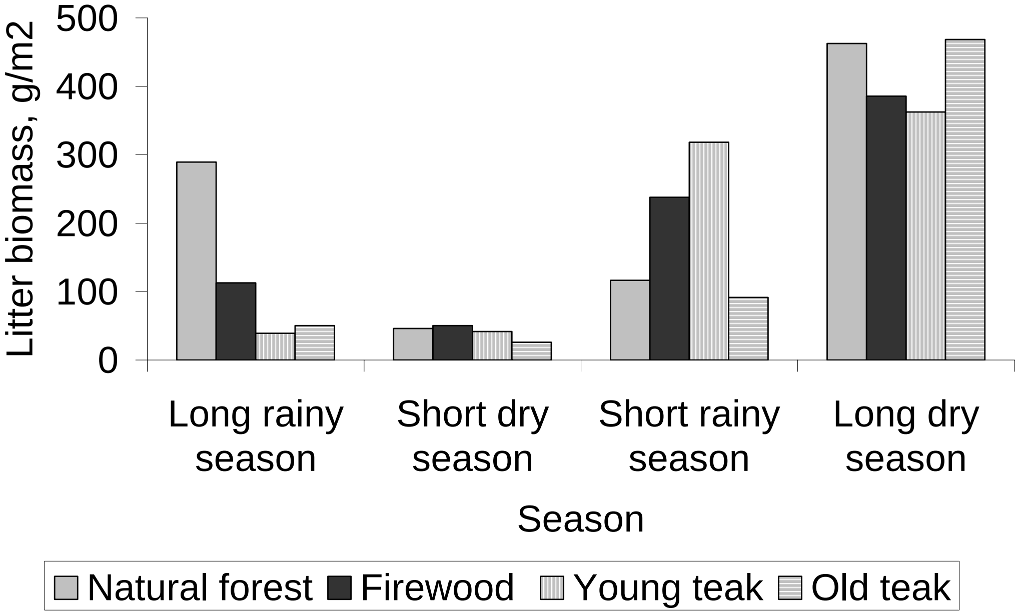

Litter biomass, g/m2
500
400
300
200
100
0
Long rainy season
Short dry season
Short rainy season
Long dry season
Season
Natural forest
Firewood
Young teak
Old teak

Fig.4.

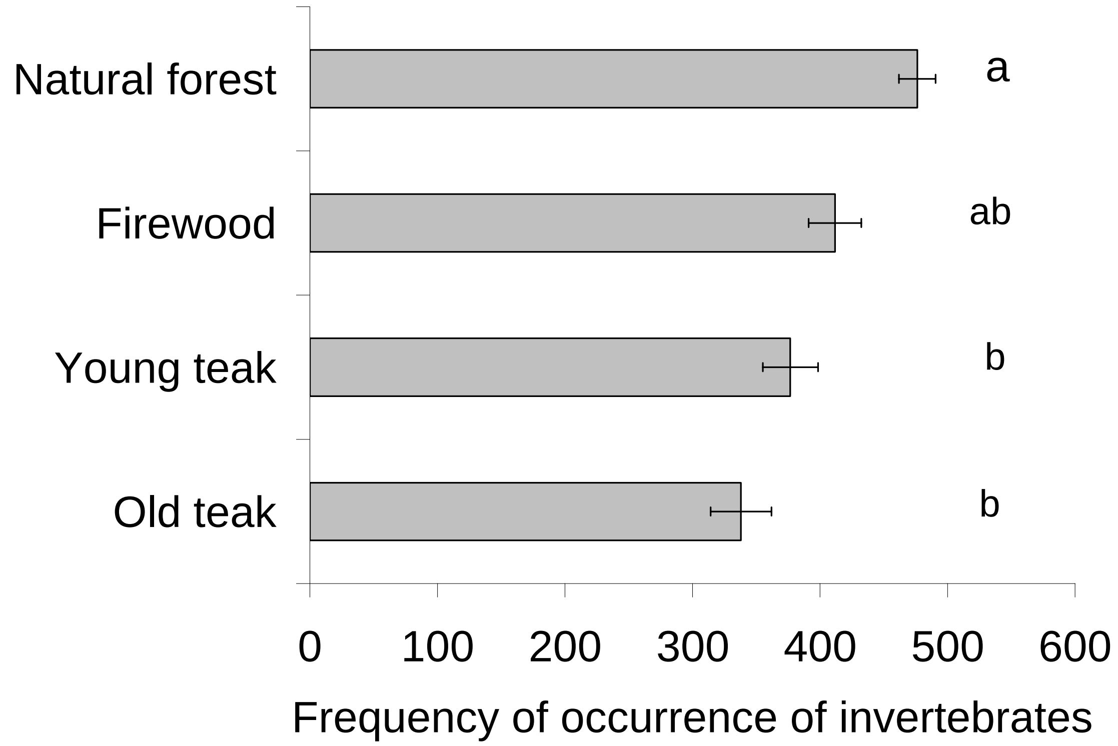

Natural forest
Firewood
Young teak
Old teak
a
ab
b
b
0
100
200
300
400
500
600
Frequency of occurrence of invertebrates

Fig. 5.

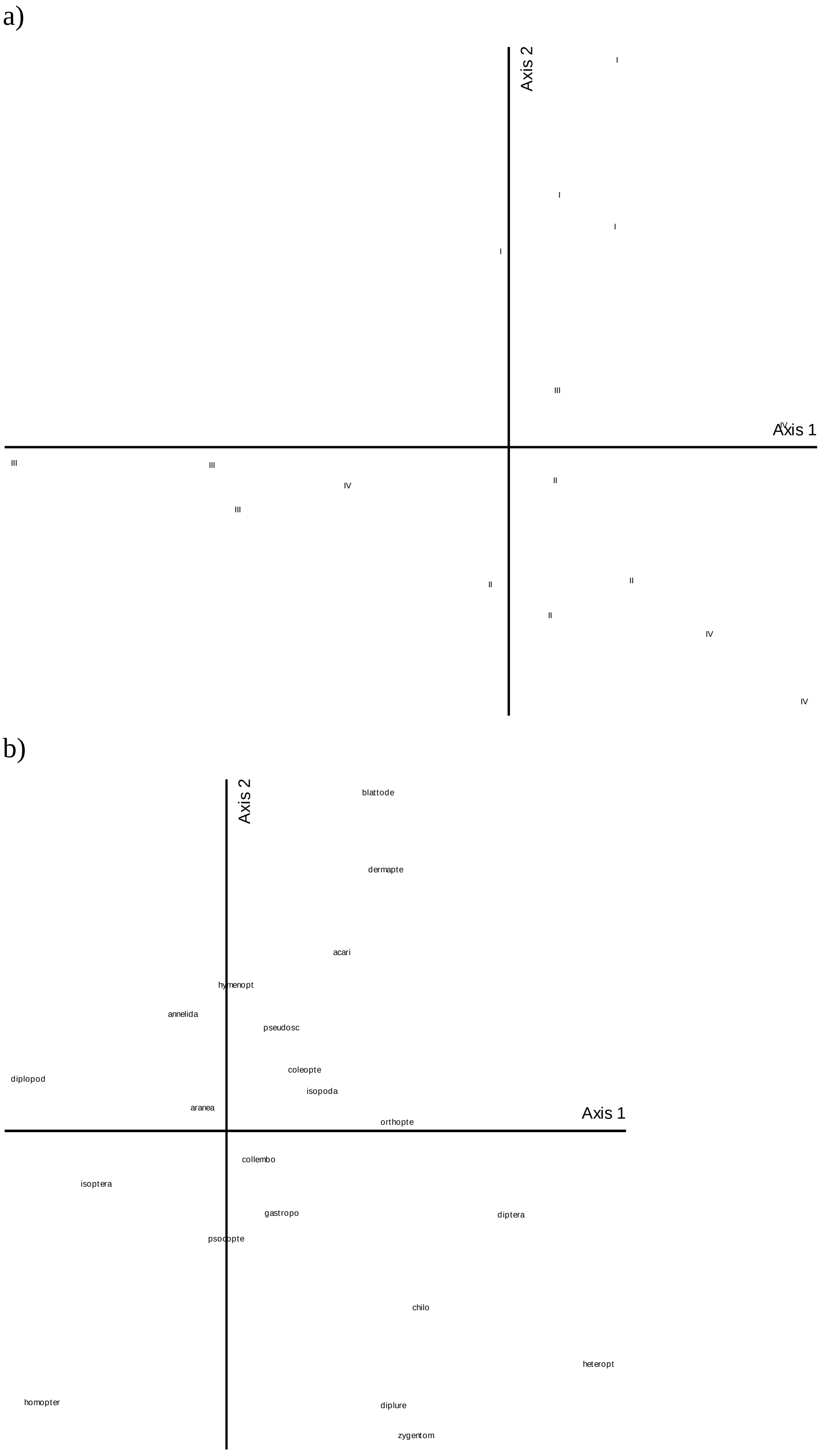

a)
Axis 2
I
I
I
I
III
IV
Axis 1
III
III
IV
II
III
II
II
II
IV
IV
b)
Axis 2
blattode
dermapte
acari
hymenopt
annelida
pseudosc
coleopte
diplopod
isopoda
aranea
Axis 1
orthopte
collembo
isoptera
gastropo
diptera
psocopte
chilo
heteropt
homopter
diplure
zygentom

Fig. 6.

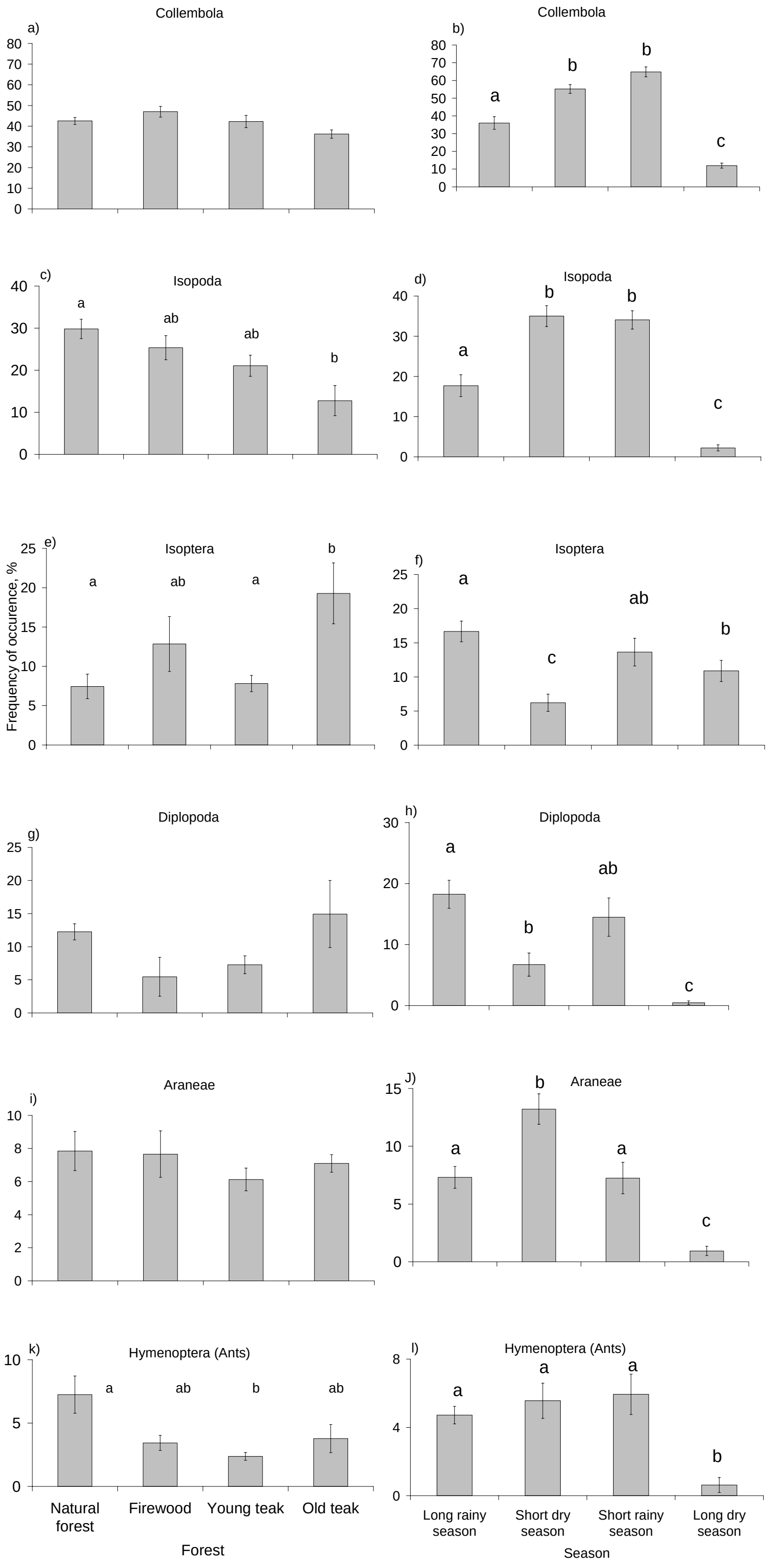

a)
Collembola
0
10
20
30
40
50
60
70
80
b)
Collembola
0
10
20
30
40
50
60
70
80
a
b
b
c
c)
Isopoda
0
10
20
30
40
a
ab
ab
b
d)
Isopoda
0
10
20
30
40
a
b
b
c
e)
Isoptera
Frequency of occurence, %
0
5
10
15
20
25
a
ab
a
b
f)
Isoptera
0
5
10
15
20
25
a
c
ab
b
g)
Diplopoda
0
5
10
15
20
25
h)
Diplopoda
0
10
20
30
a
b
ab
c
i)
Araneae
0
2
4
6
8
10
J)
Araneae
0
5
10
15
a
b
a
c
k)
Hymenoptera (Ants)
0
5
10
a
ab
b
ab
l)
Hymenoptera (Ants)
0
4
8
a
a
a
b
Natural forest
Firewood
Young teak
Old teak
Forest
Long rainy season
Short dry season
Short rainy season
Long dry season
Season

Fig. 7.

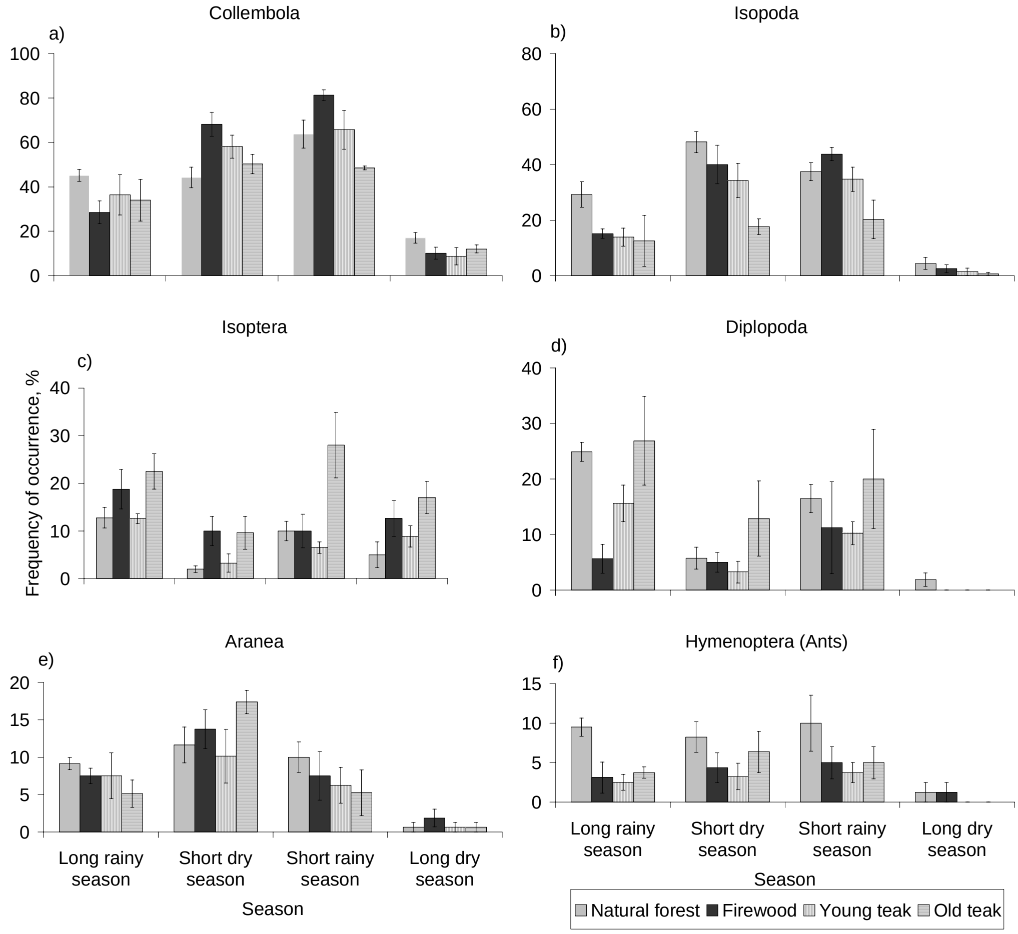
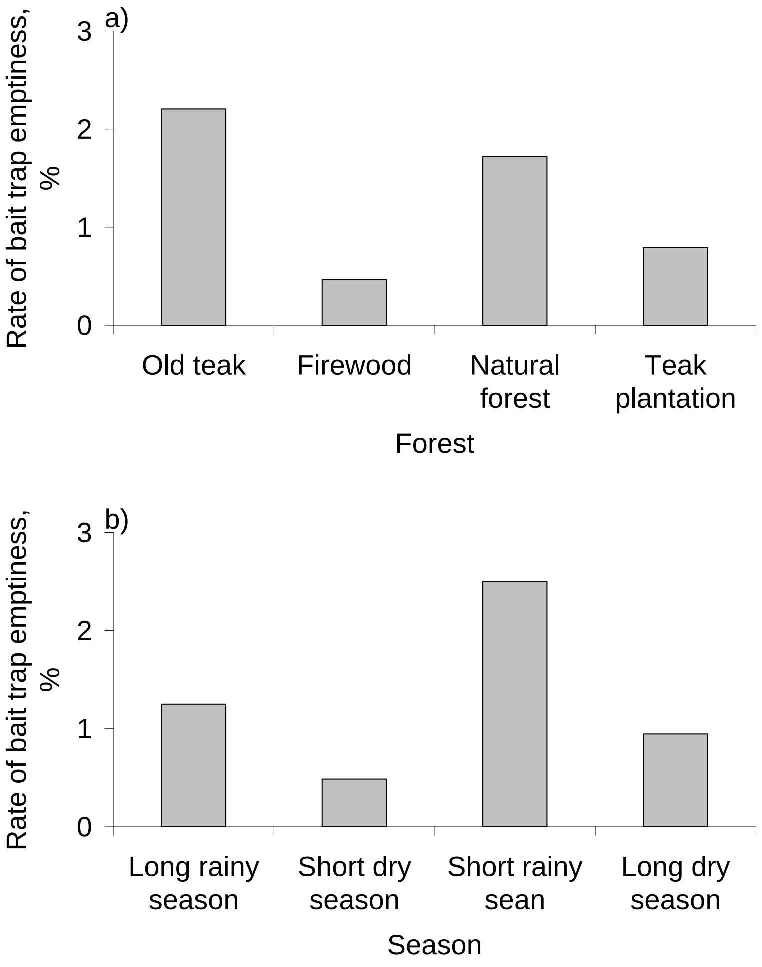

Collembola
a)
100
80
60
40
20
0
Isopoda
b)
80
60
40
20
0
Isoptera
c)
40
30
20
10
0
Frequency of occurrence, %
Diplopoda
d)
40
30
20
10
0
Aranea
e)
20
15
10
5
0
Long rainy season
Short dry season
Short rainy season
Long dry season
Season
Hymenoptera (Ants)
f)
15
10
5
0
Long rainy season
Short dry season
Short rainy season
Long dry season
Season
▨ Natural forest ■ Firewood □ Young teak ▤ Old teak

Fig. 8.


a)
Rate of bait trap emptiness, %
3
2
1
0
Old teak
Firewood
Natural forest
Teak plantation
Forest
b)
Rate of bait trap emptiness, %
3
2
1
0
Long rainy season
Short dry season
Short rainy sean
Long dry season
Season

Chapter 5

Stemmiulus (Diopsiulus) lama n. sp., a New Millipede from Benin (Myriapoda, Diplopoda, Stemmiulidae)

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Manuscript

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Abstract

This short note describes the new species, *Stemmiulus lama* n. sp., collected in Lama forest reserve (Benin). Although 34 species of the subgenus *Diopsiulus* are known from Cameroun to Senegal, it is the first record of a stemmiulid millipede in Benin.

Keywords: *Stemmiulus lama* n. sp.; Diplopoda; Lama forest; Benin.

Introduction

The millipedes of the small order Stemmiulidae, with it's about 100 described species, comprise an assemblage of obviously very specialised organisms with a fragmented, relictual distribution. 49 species have been described from West Africa to East Africa, all belonging to the genus *Stemmiulus* and divided in three subgenera (*Stemmiulus, Diopsiulus* and *Nethoiulus*). The subgenus *Diopsiulus* comprises 34 species confined to West Africa from Cameroon to Senegal. They are characterized by a simple gonopod without any lateral projection on the angiocoxite (Mauries, 1989).

Among the diplopods collected by S. Attignon in Lama forest occurs a new species of the subgenus *Diopsiulus* which is described in the present note. It is the first record of a Stemmiulidae from Benin.

Abbreviations are: MP, Microscopic Preparation; MRAC, Musée Royal d'Afrique Centale; ♂, Male; ♀, Female.

***Stemmiulus (Diopsiulus) lama* n. sp. (**Figures 1 to 9)

Material studied

Type material- Holotype: 1♂, Benin, Lama forest, Cardboard baiting technique, June 2003, S. Attignon. (MRAC)

Paratypes: 1♂ (MP), 1♂ (missing head and the 3 first body rings), 18 ♀♀, S. Attignon. (MRAC), funnel pitfall traps, May 2001-April 2002 and Cardboard baiting technique, June 2003

Diagnosis

A species of *Stemmiulus* characterised by the occurrence on each body ring of a row of macrosetae on the posterior part of metazonite and a simple gonopod with the distal part of the angiocoxite forming a kind of corolla.

Description

Holotype – Adult male, ca. 12 mm in length, 0.8 mm in maximum diameter, body with 40 rings. Head and collum dark brown, other body rings dark brown with a light median dorsal stripe, legs almost colourless.

Head of typical form, set with numerous simple macroseate (fig. 1); ocelli 2-2, the anterior slightly smaller, antennae long and setose. Gnathochilarium concave, stipes densely and uniformly porose.

Collum surrounded by a row of macrosatae.

Body rings circular (height/width ratio of midbody rings ca. 1.14), 1 legless body ring in front of the telson. Prozonite smooth, metazonite with a row of macrosetae along the margin (fig.2)

First pair of legs unmodified, tarsal segment with a fringe of setae on basal two thirds of ventral surface forming a kind of comb; femur, postfemur and tibia each with a prominently enlarged ventral macroseta and several smaller setae in compact cluster, no plumose or spatulate setae presents (fig. 3).

Second pair of legs with coxa enlarged, setose on entire anterior surface, glabrous on posterior except on apical lateral corner on which occurs a cluster of prominently enlarged ventral macrosetae; telopodite bisegmented, the distal segment long and slender, curved mesad and distally plumose (figs 5,6).

Third pair of legs unmodified, similar to those following, without specialised setae.

Gonopods (figs: 7-9) of the structure typical of the subgenus, angiocoxite simple with a terminal corolla-shaped part bearing several long setae. Apex of colpocoxite with a flat lobe surrounding the flagella. The later largely overtops the apex of the colpocoxite (fig.8).

Paragonopods small and trisegmented, distal segment conical, without setae (fig.4)

Relationships - The simplicity of the gonopods relates *S. lama* to several species from West Africa (*S. verus* Silvestri 1916 –Ghana-, *S. regressus* Silv.1916 –Guinea-, *S. tremblayi* and *S. keoulentanus* Demange & Mauries 1975 –Mont Nimba-) but the external morphology of the new species strongly reminds of the species *S. giffardii* Silv. 1916 (Ghana coast) which also shows a row of long setae on the margin of each segment. Nevertheless, the males of the two species can easily be distinguished by the structure of the gonopods.

Etymology – The species name refers to the Portuguese word “lama” (mud), alludes to the characteristic of the local soil type (vertisol) of Lama forest in southern Benin.

Distribution - Known only from Lama forest reserve. The Lama forest is a semi-deciduous forest situated in the so-called Dahomey Gap, a discontinuity of West African rainforest belt (Jenik, 1994). The reserve lies in the Lama depression, about 80 km north of Cotonou (between 6°55.8–58.8’N and 2°4.2–10.8’E), covering 16,250 ha (Sinsin et al., 2003). *Stemmiulus lama* n. sp. was collected in most habitats of the reserve, including natural forest, degraded forest and teak plantations. Funnel pitfall traps and cardboard baiting technique served to collect the specimens of *S. lama* n. sp.

The funnel pitfall trap consist of collecting jar in a plastic sleeve; funnel 11 cm (top) and 3 cm (exit tube) in diameter, roofed with a transparent plastic sheet 20 cm in diameter (Southwood, 1978).

Cardboard baits were composed of three 10 x 2.5 cm cardboards pieces placed in 50 ml polypropylene centrifugation tube (Sarstedt, Germany). Tubes had a twelve entry (0.8 cm diameter) for soil invertebrates, plus the opening of the top and baits were buried at the soil-litter-interface (Attignon, unpublished).

Acknowledgments - Thanks are due to Nadine VanNoppen for the drawings

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Legends

Figs. 1 to 9: *Stemmiulus (Diopsiulus) lama.*n. sp.

Fig. 1. Drawing of the head showing the disposition of the macrosetae.

Fig. 2. First pair of leg aboral aspect.

Fig. 3. 10th segment, lateral view.

Fig. 4. Paragonopods, ventral aspect.

Figs. 5 & 6: Second pair of leg (5) aboral aspect, (6) oral aspect.

Fig. 7. Gonopods, aboral aspect, C, colpocoxite; A, angiocoxite.

Fig.8. Apex of colpocoxite; F, flagella.

Fig. 9. Gonopods, oral aspect, C, colpocoxite; A, angiocoxite.

Fig.1

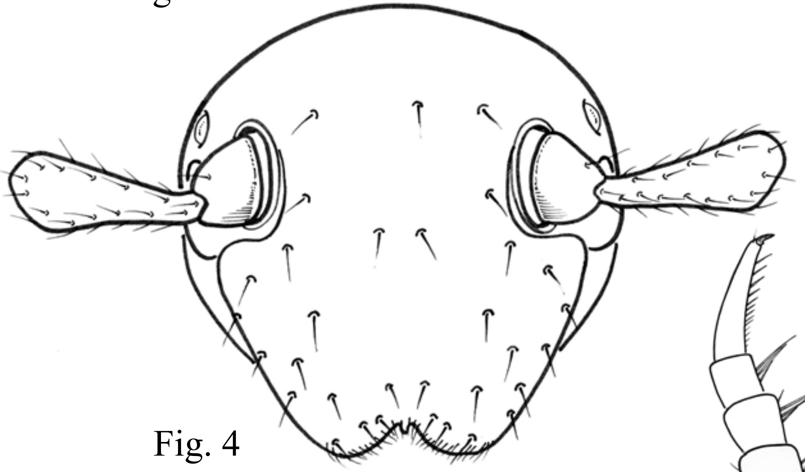


Fig. 2

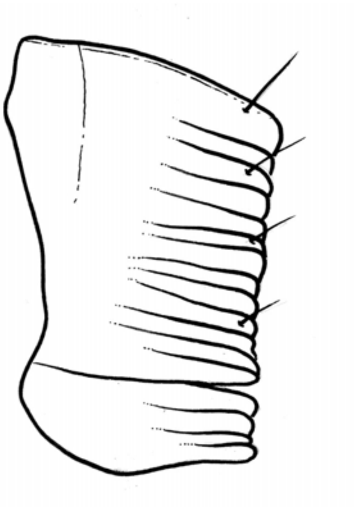


Fig. 3

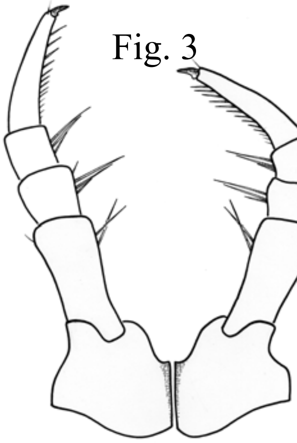


Fig. 4

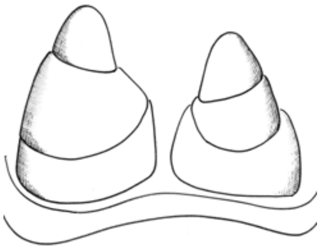


Fig. 5

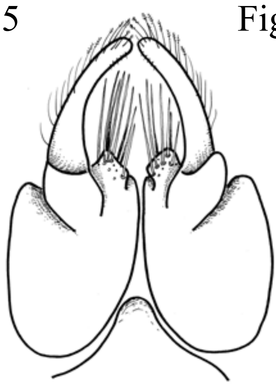


Fig. 6

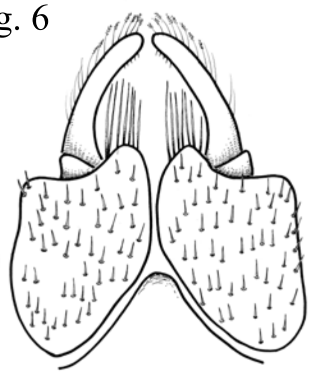


Fig. 8

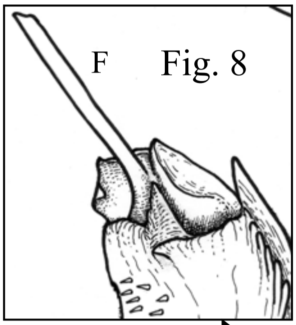


Fig. 7

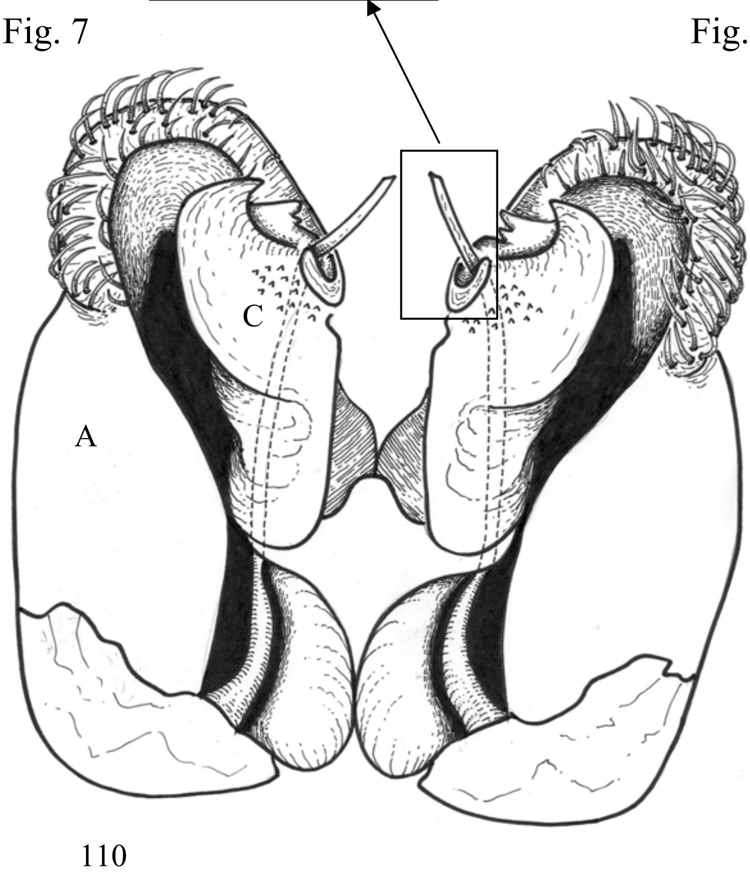
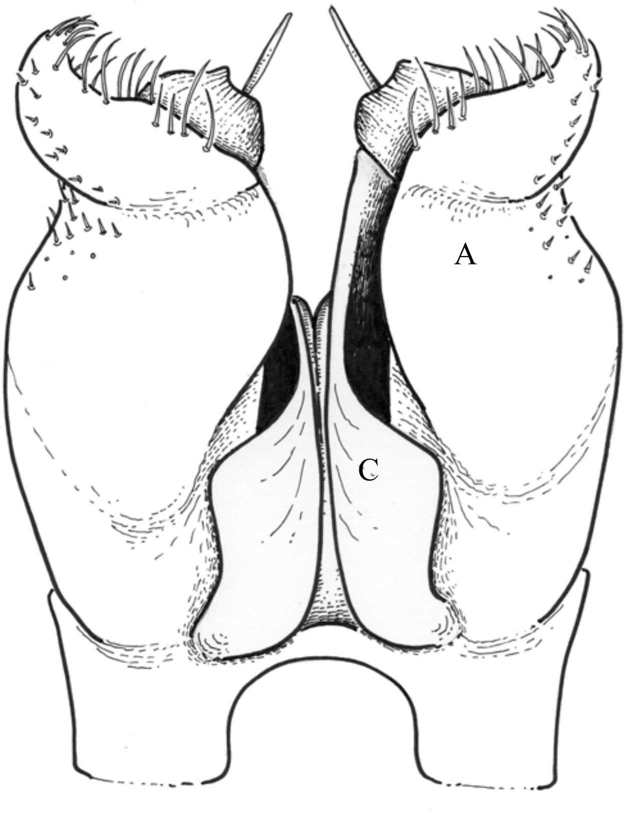


Fig. 9



Chapter 6

Diversity of True Bugs (Heteroptera) in Various Habitats of the Lama Forest Reserve in Southern Benin.

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Manuscript

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Abstract

The effect of forest use on the diversity and community structure of Heteroptera was investigated in the Lama forest reserve in southern Benin. Bugs were collected using funnel pitfall traps, ground photo-eclectors, Malaise traps, flight traps and sweep-nets. In each of the following nine habitats, four replicate sites were monitored over a 12-month period: semi-deciduous forest, lowland forest, dry forest, abandoned settlements, *Chromolaena odorata* thicket, young teak plantations, old teak plantations, firewood plantations and isolated forest fragments. The 893 Heteroptera collected represented 104 species in 16 families. Four families (Reduviidae, Lygaeidae, Pentatomidae and Coreidae) constituted 74.0 % of all species collected while 80.4% of all specimens were from the families Alydidae, Lygaeidae, Reduviidae and Pentatomidae. The total number of specimens collected from different habitats ranged from 48 in young teak plantations to 290 in lowland forest, and the total of number of species from 21 species in semi-deciduous forest to 48 in isolated forest fragments. Overall no significant differences in species richness among habitats were documented. Shannon-Wiener diversity indices were highly variable among forest types, ranging from 0.90 in lowland forest to 3.41 in isolated forest fragments. Evenness ranged from 0.27 in lowland forest to 0.94 in young teak plantations. We found a significant positive correlation between the age of forest and the Heteroptera abundance as well as Berger-Parker dominance, but evenness was negatively correlated with the age of forest. Although we found no significant differences in species richness among forest individual habitats, species richness, Shannon index and Berger-Parker dominance differed significantly among disturbed and undisturbed forest within the *Noyau Central*. Finally two indicator species were documented for two of the disturbed habitats.

Keyword: natural forest; degraded forest; forest plantation; Heteroptera; diversity; indicator species.

1. Introduction

The true bugs (Heteroptera) are an ecologically very diverse group, including phytophagous, saprophagous and predatory species (Dolling, 1991). Both larval stages and adults live in similar habitats and respond sensitively to environmental changes (Otto, 1996). Some species are generalists while others are specialists. Studies in agricultural landscapes have shown that bug diversity correlates strongly with total insect diversity. Therefore, bugs have been used as highly representative indicators in previous biodiversity assessments (Duelli and Obrist, 1998; Duelli et al., 1999; Giulio et al., 2001). However, no studies have investigated the diversity of Heteroptera in tropical forest ecosystems.

There is plentiful ecological information about true bugs, yet its relevance is highly variable. Many papers deal with individual species of economic importance (pests or beneficials), and only few studies provide a wider overview of global bug assemblages (Fauvel, 1999). Many studies show that insect communities are most species-rich in closed forest (Morse et al., 1988; Barlow and Woiwod, 1989), but it is not sure whether this also holds for true bugs assemblages.

In this paper we study the diversity of Heteroptera in natural forest, degraded forest, teak plantations, firewood plantations (*Senna siamea*) and isolated forest fragments of the Lama forest reserve, and identify species that can be used as indicators of specific forest habitats. We also study the relationship between true bug diversity and habitat characteristics (environmental variables).

2. Materials and Methods

2.1 Study area

The study was conducted in the Lama forest reserve (southern Benin), one of the last remaining forests located in the so-called “Dahomey Gap”. Lama forest lies between 6^o 55.8’ to 6^o 58.8’ N and 2^o 4.2’ to 2^o 10.8’ E (Fig. 1). The soils are mainly vertisols, but towards the borders of the reserve (old teak plantations and forest fragments) the vertisols are gradually replaced by sandy ferralsols (Specht, 2002). The climate is relatively dry, with an annual precipitation of 1,100 mm. Two rainy seasons and two dry seasons can be distinguished. The natural vegetation is a semi-deciduous forest belonging to the drier peripheral semi-evergreen Guineo-Congolian rain forest system (White, 1983; Adjanohoun, 1989).

Nine habitats, representing all major vegetation formations within the reserve boundary, and a few forest remnants outside the reserve were included for this study. Each was replicated four times, giving a total of 36 study sites. Five of these forest types were located in the *Noyau central* (NC) and four outside.

1. Semi-deciduous forest (SF, 1,937 ha) with *Afzelia africana, Ceiba pentandra, Dialium guineense, Diospyros mespiliformis, Drypetes floribunda, Celtis brownii* and *Mimusops andongensis* as dominant tree species.
2. *Cynometra megalophylla* lowland forest (LF, part of SF), area flooded in the rainy season.

3. *Anogeissus leiocarpus* dry forest (DF, 1,222 ha), a secondary forest with trees reaching 20 m in height.
4. Abandoned settlements (AS, 166 ha) of the Holli population, characterized by the presence of oil palm (*Elaeis guineensis*), guajava (*Psidium guajava*) and secondary regrowth.
5. Perennial *Chromolaena odorata* thicket (CT, 1452 ha), growing on former farmland. *C. odorata* is an invasive species encroaching open canopy patches, forest clearings as well as fallow land.
6. Young teak plantations (YT, 7,200 ha), planted between 1985 and 1995 on vertisol around the NC.
7. Old teak plantations (OT, 2,200 ha), planted between 1955 and 1965 on ferralsol.
8. Firewood plantations (FP, 2,400 ha), planted between 1990 and 1992. These forests are composed of fast growing firewood species such as *Senna siamea* and *Acacia auriculiformis* to satisfy the firewood demand and to avoid deforestation.
9. Isolated forest fragments (IF) are isolated patches of forest (< 1 ha) situated outside the Lama forest reserve. They are surrounded by farmland or degraded savannah and are considered as sacred groves by people practicing the voodoo cult.

2.2 Sampling methods

A similar combination of collecting methods was used in each site to sample Heteroptera. The sampling devices included one Malaise traps, about three quarters the size of Townes' model (Townes, 1972), three funnel pitfall traps (collecting jar in plastic sleeves, funnel 11 cm (top) and 3 cm (exit tube) in diameter), roofed with a transparent plastic sheet 20 cm in diameter (Southwood, 1978), one 0.75 m^2 rectangular ground photo-elector equipped with one pitfall trap (Mühlenberg, 1993), one flight trap intercepting insects between 1.0 and 1.5 meter above the ground (top and bottom funnels 50 cm in diameter, black netting as intercepting surfaces) (Wilkening et al., 1981). The traps were placed on transects oriented north-south, using the same design at all sites. Distances between sites of the same forest type ranged from 0.3 km to 19.0 km. A minimum distance of 20 m (small patches) or 50 m (large patches) was maintained between sampling sites and patch borders. The sampling started in May 2001 and finished in April 2002. The collection vials were filled with 0.5% formaldehyde as preservative, with a few droplets of detergent to lower the surface tension. Heteroptera were collected once monthly for one week. An exception was the sampling period in May 2001 which lasted two weeks. In addition to traps we also used sweep nets to collect Heteroptera. Samples were taken twice at a height of 0-3 m from the vegetation adjacent to the stationary traps (≈ 3 m), once during the dry season (October to December 2002) and once during the rainy season (April to June 2003). Around each trap, 20 sweeps were made, totalling 120 sweeps per site. The net was emptied after a series of 10 sweeps. All adult Heteroptera were sorted to morphospecies, using general keys for preliminary identification to the family level. They were later identified to species at the International Institute of Tropical Agriculture (IITA) in Benin. Voucher specimens were deposited at the IITA Biodiversity Center. The analysis was done on morphospecies level if species identification was difficult (e.g., some Lygaeidae).

The vegetation composition and cover was analyzed between July and September 2001 and again between December and January 2002, using the Braun-Blanquet method (unpublished data). Moreover data were collected on the canopy cover, and the undergrowth vegetation cover. Canopy cover was estimated using a spherical densitometer (Forest Densiometer Model-C, Lemmon), a hand-held, concave mirror with gridlines, held at 1 m from the ground. Openings in the canopy were manually counted within the grid, and a conversion factor yielded the canopy cover value. Four measurements were made to the North, South, West and East of each site, and the mean was calculated (Lemmon, 1957).

The age of each forest type was assessed according to its known history. Semi-deciduous forest, lowland forest and isolated forest fragments were considered to be more than 100 years old. The age of the plantations were exactly known and the age of degraded forest habitats was assessed according to resettlement of people from the forest.

2.3 Data analysis

Arthropod assemblages are often compared using similarity and/or diversity indices. Many different diversity and richness indices exist, each with its own strengths and weaknesses. No single index encompasses all characteristics of an ideal index, i.e., high discriminant ability, low sensitivity to sample size, and ease in calculation (Marguran, 1988). This is why we decided to combine different indices reflecting species richness, dominance and diversity heterogeneity. These indices provide a basis to interpret differences in Heteroptera diversity among forest types. We chose some of the most commonly used and most often recommended indices (e.g., Samways, 1983; Southwood, 1987; Margurran, 1988; Krebs, 1989; Roth et al., 1994): species richness (S), Shannon index (H), Berger-Parker index (D), and evenness (E). A brief explanation of each index follows:

S: Species richness is simply the total number of species in a community. It provides a great deal of information about the community and represents an instantly comprehensible expression of diversity (Margurran, 1988). As an index, S is easily conceptualized and comparable across habitats.

H: Shannon's index of diversity (Price, 1997) reflects both evenness and richness (Colwell and Huston, 1991) and is commonly used in diversity studies (Krebs, 1989). It is calculated according to:

$$H = -\sum P_i \ln P_i;\ i = 1 - n$$

where n is the number of species and P_i is the proportion of the *i*th species in the total. Samples having high species richness and similar abundance between species will generate high H values.

D: The Berger-Parker dominance measure expresses the proportional importance of the most abundant species (Margurran, 1988). The Berger-Parker index or $P_{i(\max)}$ is the proportion of the most abundant species.

E: Evenness indicates the degree of homogeneity in abundance between species and is based on the Shannon index of diversity. Both the Berger-Parker dominance index and Evenness index are important measures of heterogeneity. Shannon evenness is calculated according to:

$$E = H / H_{\max} = H/\ln S,$$

where H is the Shannon diversity index and S the number of species in the community. Evenness ranges from 0 to 1.

In addition to these indices, we also used a similarity index for a closer examination of the species composition in different forest types. The percent similarity (P) shows the proportion of species in common between sites (Krebs, 1989). The index is relatively insensitive to sample size and species diversity and is calculated by the equation:

$$P = \sum \text{minimum } (P_{1i}, P_{2i}) \times 100$$

where P is the percentage similarity between sites 1 and 2, P_{1i} is the proportion of species *i* in community sample one and P_{2i} is the proportion of species *i* in community sample two.

One way analysis of variance (ANOVA) was used to compare diversity and richness indices and the environmental variables canopy cover: undergrowth vegetation cover, tree species richness, undergrowth plant species richness and tree height among forest types. Parametric tests were used when the data were normally distributed, followed by Student Newman-Keuls multiple comparison of means if the ANOVA revealed significance. Data transformations were made for all diversity indices, using the natural logarithm. However, normalisation of the data was only achieved for species richness.

For the remaining indices, we used non-parametric Kruskal-Wallis analysis of variance followed by the Nemenyi *post hoc* test. Non-parametric analysis were necessary because the data presented high variance heterogeneity.

We pooled data of all disturbed forest habitats (*A. leiocarpus* dry forest, abandoned settlements and *C. odorata* thicket) and all undisturbed forest habitats (semi-deciduous forest and *C. megalophylla* lowland forest) from within the *Noyau Central* and compare Heteroptera species richness, Shannon diversity index and Berger-Parker dominance, using unbalanced one way analysis of variance (ANOVA).

Simple correlations between habitat characteristics and Heteroptera abundance and diversity indices were determined using the SPSS 11.0 software. These analyses allowed testing for the effect of abiotic factors on diversity.

When the same data were used repeatedly the errors was adjusted using Bonferroni adjustment.

Indicator species include species restricted to a particular type of forest and those more widely distributed yet especially abundant in a particular type of forest. We used the method of Dufrêne and Legendre (1997) to determine Heteroptera indicator species for the different habitats. This method combines data on the concentration of species abundance in a particular group of sites (habitats) and the faithfulness of occurrence of species in a particular group. Indicator species analysis was performed as described by Lachat et al. (2004). The significance of indicator values was tested using Monte Carlo randomisation (1,000 runs). The threshold level was set to 25% and the significance level to $P \leq 0.01$, as proposed by Dufrêne and Legendre (1997).

3. Results

3.1 Composition of bug assemblages

A total of 893 adult specimens comprising 104 species were recorded in the nine habitats (Tables 1 & 2). These species belong to 16 families of which Alydidae made up the largest proportion of the total catch (35.9%), followed by Lygaeidae (21.3%), Reduviidae (16.2%), Pentatomidae (6.9%), Pyrrhocoridae (4%), Coreidae (3.9%), Plataspidae (3.8%), Cydnidae (3.4%) and Largidae (2.9%). The greatest number of species was found in the Reduviidae family (26), followed by Lygaeidae (19), Pentatomidae (19), Coreidae (13), Plataspidae (6) and Alydidae (5). Thirty four percent of all Heteroptera specimens were singletons (Table 2).

Both species richness (*n* = 49) and the number of families (*n* = 14) were highest in isolated forest fragments (Table 3). Species richness was lowest in semi-deciduous forest (*n* = 21), whereas the lowest number of families was found in young teak plantations (*n* = 8). Bug abundance was highest in lowland forest, with a total of 290 adult bugs, and lowest in young teak plantations (48 adult bugs). Each habitat had at least one unique species. Fifteen species were restricted to isolated forest fragments, six species to *Anogeissus leiocarpus* dry forest, six species to abandoned settlements and four species to *Chromolaena odorata* thicket. Old teak plantations, *Cynometra megalophylla* lowland forest and firewood plantations had three unique species each, and young teak plantations and semi-deciduous forest two and one species, respectively (Table 4).

The most abundant species was *Stenocoris southwoodi* Ahmad, comprising 304 individuals (34%). The second most abundant species was Lygaeidae sp. 12 (*n* = 51, 5.7%), followed by Pyrrhocoridae sp. 1 (*n* = 35, 3.9%), Lygaeidae sp. 11 (*n* = 32, 3.6%), Cydnidae sp. 1 (*n* = 29, 3.2%), *Lisarda crudelis* (*n* = 27, 3%), Largidae sp. 1 (*n* = 26, 2.9%), Lygaeidae sp. 14 (*n* = 24, 2.7%), Lygaeidae sp. 6 (*n* = 18, 2%) and *Oncocephalus* sp. 1 (*n* = 16, 1.8%) (Table 5). Only one species (Lygaeidae sp. 12) occurred in all nine forest types. Another four species occurred in eight forest types. *Stenocoris southwoodi* Ahmad and Cydnidae sp. 1 were found in all forest types except in *Chromolaena* thicket and young teak plantations respectively, and *Lisarda crudelis* and Largidae sp. 1 were only absent in firewood plantations. Fifty species (48.1%) collected in this study were identified to morphospecies only, and some species are probably new to Benin.

3.2 Diversity of Heteroptera

Species richness was highest in isolated forest fragments, *A. leiocarpus* dry forest and abandoned settlement, with 15.7 ± 0.8, 13.2 ± 2.8 and 12.0 ± 2.0 (mean ± standard error) species, respectively, and lowest in semi-deciduous forest (8.0 ± 0.9), young teak plantations (8.2 ± 1.4) and firewood plantations (8.7 ± 0.7). The remaining habitats had intermediate levels of species richness, ranging from 9.0 ± 0.6 in lowland forest to 11.2 ± 4.1 in old teak plantations. However, differences in species richness among forest types were not statistically significant (ANOVA: $F_{8,27} = 1.6$, $P = 0.168$).

The highest Shannon diversity was found in isolated forest fragments (2.5 ± 0.1) and the smallest Berger-Parker index too (0.17 ± 0.03) (least dominance by a single species), followed by *A. leiocarpus* dry forest, abandoned settlement and *C. odorata* thicket. These habitats had similar evenness (0.9).

Although the nine habitats did not differ significantly in species richness (see above) and evenness (Kruskal-Wallis: $\chi^2 = 10.5$, d.f. = 8, $P = 0.231$), some differences in abundance (Kruskal-Wallis: $\chi^2 = 17.5$, d.f. = 8, $P = 0.025$), Shannon diversity (Kruskal-Wallis: $\chi^2 = 19.2$, d.f. = 8, $P = 0.014$) and Berger-Parker dominance (Kruskal-Wallis: $\chi^2 = 10.5$, d.f. = 8, $P = 0.017$) were found (Fig. 2). All normally significant indices are significant at $P < 0.05$ after Bonferroni adjustment.

The Nemenyi-tests revealed four significant differences. The Shannon index was significantly higher in isolated forest fragments than in *C. megalophylla* lowland forest, and the mean number of individuals of Heteroptera was significantly higher in *C. megalophylla* lowland forest than in young teak plantations. The Berger-Parker dominance index was significantly higher in *C. megalophylla* lowland forest than in isolated forest fragments and abandoned settlements (Fig. 2.).

Comparison between disturbed and undisturbed forest within the *Noyau Central* showed that differences in species richness, Shannon index and Berger-Parker index among forest types were statistically significant (ANOVA: $F_{1,18} = 4.8$, $P = 0.0426$; $F_{1,18} = 17.9$, $P = 0.0005$ and $F_{1,18} = 16.5$, $P = 0.0007$ respectively. Disturbed forest had higher species richness and Shannon diversity but lower Berger-Parker dominance than undisturbed forest (Fig. 3).

The similarity of Heteroptera assemblages varied among habitats. The highest similarity was observed between *Anogeissus leiocarpus* dry forest and *Chromolaena odorata* thicket (45%), semi-deciduous forest and abandoned settlements (43%), semi-deciduous forest and old teak plantations (41%), and *Anogeissus leiocarpus* dry forest and isolated forest fragments (38%) (Table 6).

Two indicator species were identified for two forest types. *Stenocoris southwoodi* Ahmad (Alydidae) was an indicator for *C. megalophylla* lowland forest and Lygaeidae sp. 11 for *A. leiocarpus* dry forest. However, we found no indicator species for the remaining forest habitats.

3.3 Difference in habitat characteristics and correlation with bug diversity

Canopy cover and undergrowth vegetation cover were significantly different between habitats (ANOVA: $F_{8,27} = 8.9$, $P < 0.001$ and $F_{8,27} = 3.3$, $P = 0.009$, respectively), as were tree species richness and tree height (Kruskal-Wallis: $\chi^2 = 24.6$, d.f. = 8, $P = 0.002$ and $\chi^2 = 16.8$, d.f. = 8, $P = 0.032$, respectively). But undergrowth plants species richness was not significantly different (ANOVA: $F_{8,27} = 2.1$, $P = 0.070$).

Student Newman Keuls tests showed that canopy cover was significantly lower in *Chromolaena odorata* thicket than in the others habitats. In contrast, in young teak plantations the undergrowth vegetation cover was significantly lower than in the other habitats, but did not differ significantly from old teak plantations (Table 7).

Non-parametric Nemenyi post hoc tests showed that tree species richness was significantly higher in isolated forest fragments than in the old teak plantations, and that tree height was significantly higher in old teak plantations than abandoned settlements (Table 7).

Age of the forest habitats was the only parameter significantly correlated with Heteroptera community diversity and/or structure. The correlations were significant for Heteroptera abundance ($r = 0.410$, $P = 0.013$), Berger-Parker dominance, ($r = 0.436$, $P = 0.008$) and Shannon evenness ($r = -0.452$, $P = 0.006$) (Table 8).

4. Discussion

4.1 Heteroptera assemblages

This is the first study on the diversity of Heteroptera assemblages in natural and plantation forests in Benin. The study yields an understanding of how bug community structure varies with various types of habitat and forest use. Our data demonstrate no difference in Heteroptera species richness between natural, degraded and plantation forests of the Lama forest reserve. These results confirm those of Kalif et al. (2001) who found similar species richness yet different composition of ant assemblages in degraded (logged) and natural forest in eastern Amazonia. However, we found that Shannon diversity was significantly higher in isolated forest fragments than lowland forest. This seems to be due to the low species richness and uneven distribution of dominant bugs in lowland forest, where a single species, *Stenocoris southwoodi* Ahmad, represented 84.9% of all specimens, but only 8.9% in isolated forest fragments. Roedel and Braendle (1995) reported that *Stenocoris elegans*, the second most common species of this genus, occurred in island and riverine forest of the Comoe National Park in Côte d'Ivoire. They also observed aggregations of millions of individuals. *Stenocoris southwoodi* is found in high number in most forests in Benin, independent of their size (Goeorgen, personal communication). Species in isolated forest fragment were more evenly distributed (E = 0.90) than in *C. megalophylla* lowland forest (E = 0.27). Shannon diversity decreased in lowland forest, an area which may be heavily flooded during the long rainy season. In addition, the decrease in bug species corresponds to increased domination by one species in the community (*Stenocoris southwoodi* Ahmad). This phenomenon has been previously observed by Samways (1983) in a study of ant community structure in a series of habitats associated with citrus.

Isolated forest fragments, *A. leiocarpus* dry forest and abandoned settlement had higher levels of dominant species (Berger-Parker dominance index) than lowland forest. Higher diversity of Heteroptera in isolated forest fragments can be attributed to higher habitat diversity and heterogeneity. Most isolated forest fragments are located outside of the Lama forest reserve, and are bordering to open degraded savannah or farmland. Based on results of this study, we assume that the proximity to colonizing sources may be important. Paoletti (1999) found that true bugs are distinct indicators of farmland. This could explain the high species richness found in isolated forest fragments. *A. leiocarpus* dry forest and abandoned settlements are secondary forests in degraded areas of the *Noyau central* and showed higher Heteroptera diversity compared to undisturbed natural forest (semi-deciduous and lowland forest).

Even though differences among the various forest types within the *Noyau central* were not significant (probably due to insufficient statistical power), the high diversity in disturbed forest may indicate the important role of secondary forest as a habitat for heteropterans. Dunn (2004) reviewed studies on the recovery of animal species in tropical forest and found that secondary forest may play an important role in biodiversity conservation. Our result confirms common knowledge that Heteroptera diversity is high in open landscapes.

Heteroptera are distinct indicators in farmland (Paoletti, 1999). In agricultural landscapes, their diversity has been found to correlate closely with total insect diversity. Yet we found only two indicator species for forest habitats. Our results suggest that Heteroptera may be inappropriate indicators in tropical forests. However, more data need to be collected to improve the understanding of Heteropteran diversity in tropical forest ecosystems before drawing such strong conclusions.

4.2 Similarity between habitats

Even though α-diversity was similar across habitats in the Lama forest reserve, similarity was highest between *Anogeissus leiocarpus* dry forest and *Chromolaena odorata* thicket, between *A. leiocarpus* dry forest and isolated forest fragments and between semi-deciduous forest and abandoned settlements. *C. odorata* thicket shared 45% of the species with *A. leiocarpus* dry forest but only 8.6% with *C. megalophylla* lowland forest, although these habitats are closer to each other. In contrast old teak plantations shared most species with semi-deciduous forest, despite of lying far from each other. Open forest with low canopy cover and isolated forest surrounded by farmland showed a high similarity in Heteroptera communities. It is difficult to explain the similarity between semi-deciduous forest and abandoned settlements as both of these two habitats exhibit a high number of unique species (5 to 13). Degraded habitats such as *Chromolaena odorata* thicket have significantly lower canopy cover due to low tree species densities. However, canopy cover and plant diversity that have been demonstrated to affect the diversity of insects in previous studies (Levings, 1983, Lynch et al., 1988) were not correlated to Heteroptera diversity in our study. This may be explained by the strong spatial heterogeneity of habitats within the *Noyau central* of Lama forest, which forms a small-scale mosaic of natural and degraded forest. Even though, our results showed that the abundance, evenness and Berger-Parker dominance structure of Heteroptera assemblages were strongly related to the successional stage (age) of the forest habitats. This suggests that the abundance and dominance of individual bug species increase as the forests mature, whereas species richness would be expected to decrease.

5. Conclusions

This paper assessed the diversity and community structure of true bugs in various habitats of the Lama forest reserve in Benin. The bug fauna consisted of 16 families of which the Reduviidae, Lygaeidae, Pentatomidae and Coreidae were the most species-rich. We found few differences in species richness and diversity of Heteroptera. However, lowland forest was characterized by the lowest species richness and diversity whereas isolated forest presented the highest species richness and diversity, but the lowest dominance of individual species. We found significant difference between disturbed and undisturbed forest within the *Noyau central* and this reflects common knowledge that Heteroptera diversity is high in open landscapes. The total abundance of Heteroptera was a function of habitat age, but habitat characteristics such as canopy cover, undergrowth vegetation cover and plant species richness did not influence species richness and diversity of bug assemblages in Lama forest reserve. Our study suggests that contrary to agricultural landscapes true bugs may not be suitable bioindicators for tropical forest habitats. However, we are aware that our study is only a first approach and that it is limited in scale and sampling effort, so more studies have to be conducted before final conclusions can be drawn.

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Table 1. Heteroptera collected in the Lama forest reserve in Benin.

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Alydidae										
Stenocoris southwoodi Ahmad	16	246	3	5		1	23	1	9	304
? Tupalus maculatus Distant		1								1
Sjostedtina sp.			2	1						3
Riptortus dentipes Fabricius	1			4				6		11
Daclera punctata Signoret				1			1			2
Totals										321
Aradidae										
Meriza sp.					1					1
Aradus flavicornis Dalman									1	1
Totals										2
Berytidae										
Berytidae sp. 1									1	1
Totals										1
Coreidae										
Acanthocoris collarti Schouteden			2							2
Coreidae sp. 1				1			1		1	3
Coreidae sp 2		1							2	3
Anoplocnemis curvipes Fabricius	4						3		2	9
Clavigralla curvipes Stål		1								1
Cletus pronus Berger			1							1
Anoplocnemis curvipes Fabricius						1			1	2
Hydara tenuicornis Westwood									2	2
Phyllogonia biloba Signoret			1							1
Coreidae sp. 3							1			1
Coreidae sp. 4	1		1						1	3
Coreidae sp. 5							1	2		3
Homoeocerus pallens Fabricius							1	2	1	4
Totals										35
Cydnidae										
Cydnidae sp. 1	5	5	1	1	1		1	2	13	29
Cydnidae sp. 2	1								1	2
Totals										31
Dinidoridae										
Coridius remipes Stål		1			1					2
Totals										2
Largidae										
Largidae sp. 1	2	4	4	4	2	4	3		3	26
Totals										26
Lygaeidae										
Lygaeidae sp. 1	1		1			1	1		3	7
Lygaeidae sp. 2		1			2	2		1		6
Lygaeidae sp. 3		1					1	5	1	8
Lygaeidae sp. 4		1				1			1	3
Lygaeidae sp. 5		1		2			2			5
Lygaeidae sp. 6		1	3	3		2	5	1	3	18
Lygaeidae sp. 7					1					1
Lygaeidae sp. 8					1					1
Lygaeidae sp. 9							1			1
Lygaeidae sp. 10								1		1

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Aspilocoryphus fasciativentris Stål			2	1				1	1	5
Lygaeidae sp. 11	4	1	17	6	2				2	32
Lygaeidae sp. 12	7	1	12	8	9	3	1	9	1	51
Lygaeidae sp. 13				1						1
Lygaeidae sp. 14			5	9	3	4	1		2	24
Lygaeidae sp. 15		1	1				3			5
Lygaeidae sp. 16		1		1		2	4	1		9
Lygaeidae sp. 17		1	3			1	1		1	7
Lygaeidae sp. 18	1	1	3							5
Totals										190
Miridae										
Miridae sp. 1									1	1
Miridae sp. 2									1	1
Miridae sp. 3				1						1
Totals										3
Nabidae										
Nabidae sp. 1						1		1		2
Totals										2
Pentatomidae										
Pentatomidae sp. 1	1									1
Durmia haedula Stål				1						1
Aspavia hastator Fabricius	4			3	3		2	1		13
Stenozygum alienatum Fabricius						1				1
Carbula sp.			1							1
Pentatomidae sp. 2									2	2
Aspavia accuminata							8	4	1	13
Aspavia brunnea Signoret									1	1
Lerida punctata (Palisot de Beauvois)							2		1	3
Sepontia misella Stål								2	1	3
Leptolobus murrayi Signoret				3						3
Aspavia sp.			1							1
Pentatomidae sp. 3									1	1
Pentatomidae sp. 4						3			2	5
Pentatomidae sp. 5				1					4	5
Macrorhaphis acuta Dallas									1	1
Pentatomidae sp. 6									1	1
Nezara viridula Linnaeus		1					2		1	4
Acrosternum rinapsis Dallas							2			2
Totals										62
Plataspidae										
Plataspidae sp. 1	1	1				1	1	2	2	8
Plataspidae sp. 2				1			1	1		3
Plataspidae sp. 3					2			2	1	5
Plataspidae sp. 4		4		1	3		1	2		11
Plataspidae sp. 5			1		2		1			4
Coptosoma nigriceps Signoret					1		2			3
Totals										34
Pyrrhocoridae										
Pyrrhocoridae sp. 1	1	1	17	1	4		1		10	35
Probergrothius sexpunctatus Laporte									1	1
Totals										36

Taxon	Forest types									
	SF	LF	DF	AS	CT	YT	OT	FP	IF	Totals
Reduviidae										
Ectmetacanthus annulipes Reuter				1						1
Petalocheirus (Platychiria) murrayi Signoret	4	2			1				1	8
Oncocephalus pilicornis Herrich-Schaeffer		1						1		2
Vestula lineaticeps Signoret		1			1					2
Peirates (Cleptocoris) sp.		3				3				6
Cleptria (Cleptriola) togoana Schouteden			4		2				4	10
Sphedanolestes lamottei Villiers				1				2	1	4
Rhynocoris bicolor Fabricius					1					1
Peprius nodulipes Signoret			3	1	1	3	5		2	15
Santosia dahomeyana Villiers		2								2
Tribelocephala tristis Breddin						1				1
Haematochares obsuripennis discalis Schouteden									1	1
Reduviidae sp. 1	1			1						2
Pisilus tipuliformis Fabricius				1						1
Nagusta praecatoria Fabricius									1	1
Reduviidae sp. 2						1	1			2
Lisarda crudelis	4	1	6	6	2	4	1		3	27
Microcarenus clarus Bergroth			3							3
Oncocephalus sp.1			4		1			11		16
Lisarda vandenplasi Schouteden	1	3			3			1		8
Ectomocoris cruciger Fabricius			1	3	2			1		7
Reduviidae sp. 3	1				1	6	1			9
Ectrichodia lucida Lepeletier & Audinet-Serville					1	1	3	1		6
Sphedanolestes sp.								1		1
Rhynocoris crudellis Stål			3	1	1				1	6
Microstemma atrocyanea Signoret	1				1	1				3
Totals										145
Rhopalidae										
Leptocoris sp.								1		1
Peliochrous nigromaculatus Stål									1	1
Totals										2
Tingidae										
Tingidae sp. 1									1	1
Totals										1

Table 2. Species richness and abundance of Heteroptera.

Family	Species richness	Abundance	Singletons
Reduviidae	26	145	7
Lygaeidae	19	190	5
Pentatomidae	19	62	9
Coreidae	13	35	3
Plataspidae	6	34	0
Alydidae	5	321	1
Miridae	3	3	3
Aradidae	2	2	2
Cydnidae	2	31	0
Pyrrhocoridae	2	36	1
Rhopalidae	2	2	2
Berytidae	1	1	1
Dinidoridae	1	2	0
Largidae	1	26	0
Nabidae	1	2	0
Tingidae	1	1	1
Total	104	893	35

Table 3. Richness, abundance and diversity indices of various forest habitats of the Lama forest reserve.

Forest type	Species richness	Family richness	Abundance	Unique species	Shannon index	Berger Parker index	Evenness
SF	21	9	62	1	2.59	0.26	0.85
LF	29	10	290	3	0.90	0.85	0.27
DF	28	9	106	6	2.88	0.16	0.86
AS	31	10	75	6	3.10	0.12	0.90
CT	29	9	56	4	3.14	0.16	0.93
YT	23	8	48	2	2.94	0.13	0.94
OT	34	9	88	3	2.98	0.26	0.84
FP	28	10	67	3	2.94	0.16	0.88
IF	49	14	101	15	3.50	0.13	0.90

Table 4. List of Heteroptera species found exclusively in specific habitats.

Species per habitat	Number of unique species per habitat
Semi-deciduous forest	1
Pentatomidae sp1	
***Cynometra megalophylla* lowland forest**	
? Tupalus maculatus Distant	3
Clavigralla curvipes Stål	
Santosia dahomeyana Villiers	
***Anogeissus leiocarpus* dry forest**	6
Cletus pronus Berger	
Phyllogonia biloba Signoret	
Microcarenus clarus Bergroth	
Acanthocoris collarti Schouteden	
Carbula sp.	
Aspavia sp.	
Abandoned settlement	6
Miridae sp. 3	
Durmia haedula Stål	
Leptolobus murrayi Signoret	
Ectmetacanthus annulipes Reuter	
Pisilus tipuliformis Fabricius	
Lygaeidae sp. 3	
***Chromolaena odorata* thickets**	4
Meriza sp.	
Lygaeidae sp. 7	
Lygaeidae sp. 8	
Rhynocoris bicolor Fabricius	
Young teak plantation	2
Stenozygum alienatum Fabricius	
Tribelocephala tristis Breddin	
Old teak plantation	3
Coreidae sp. 3	
Lygaeidae sp. 9	
Acrosternum rinapsis Dallas	
Firewood plantation	3
Lygaeidae sp. 10	
Sphedanolestes sp.	
Leptocoris sp.	
Isolated forest fragment	15
Hydara tenuicornis Westwood	
Miridae sp. 1	
Miridae sp. 2	
Aspavia brunnea Signoret	
Pentatomidae sp. 4	
Macrorhaphis acuta Dallas	
Pentatomidae sp.7	
Probergrothius sexpunctatus Laporte	
Haematochares obsuripennis discalis Schouteden	
Nagusta praecatoria Fabricius	
Peliochrous nigromaculatus Stål	
Tingidae sp. 1	
Pentatomidae sp. 2	
Aradus flavicornis Dalman	
Berytidae sp. 1	

Table 5. List of the most abundant heteropterans.

			Number of individuals per habitat								
Species	Abundance	Percentage	SF	LF	DF	AS	CT	YT	OT	FP	IF
Stenocoris southwoodi Ahmad	304	34.0	16	246	3	5		1	23	1	9
Lygaeidae sp. 12	51	5.7	7	1	12	8	9	3	1	9	1
Pyrrhocoridae sp. 1	35	3.9	1	1	17	1	4		1		10
Lygaeidae sp.11	32	3.6	4	1	17	6	2				2
Cydnidae sp. 1	29	3.2	5	5	1	1	1		1	2	13
Lisarda crudelis	27	3.0	4	1	6	6	2	4	1		3
Largidae sp. 1	26	2.9	2	4	4	4	2	4	3		3
Lygaeidae sp. 14	24	2.7			5	9	3	4	1		2
Lygaeidae sp. 7	18	2.0		1	3	3		2	5	1	3
Oncocephalus sp.1	16	1.8			4		1			11	
Peprius nodulipes Signoret	15	1.7			3	1	1	3	5		2
Aspavia hastator Fabricius	13	1.5	4			3	3		2	1	
Aspavia accuminata	13	1.5							8	4	1
Riptortus dentipes Fabricius	11	1.2	1			4				6	
Plataspidae sp. 4	11	1.2		4		1	3		1	2	
Cleptria (Cleptriola) togoana Schouteden	10	1.1			4		2				4

Table 6. Percent similarity of Heteroptera assemblages among forest habitats.

	SF	LF	DF	AS	CT	YT	OT	FP	IF
SF		32.70	34.92	43.08	37.04	24.46	41.53	21.98	35.68
LF			7.81	13.13	8.62	7.26	33.24	8.04	16.50
DF					45.13	30.60	19.88	20.99	37.67
AS					40.98	36.67	30.38	29.97	29.82
CT						29.46	18.99	31.93	28.15
YT							29.55	17.29	24.96
OT								21.39	31.57
FP									15.87

Table 7. Site characteristics of the different habitat types studied. Values are means ± standard errors (*n* = 4). Means in columns not sharing the same letter are significantly different at $P < 0.05$. All remaining differences are not significant. Asterisks denote levels of significance following Bonferroni adjustment: * $P < 0.05$ and ** = $P < 0.01$. Capital letters indicate parametric, small letters non-parametric post hoc test.

Habitat	Age (year)	Canopy cover (%)	**	Undergrowth vegetation cover (%)	*	Tree species richness	**	Undergrowth plant species richness	Tree height (m)	*
SF	> 100	56.7 (3.6)	A	74.0 (12.8)	A	7.0 (0.4)		37.7 (5.1)	18.0 (1.1)	
LF	> 100	71.0 (3.3)	A	66.7 (4.4)	A	7.0 (1.8)		41.7 (4.0)	21.0 (0.8)	
DF	25	58.2 (4.2)	A	67.2 (13.2)	A	7.7 (1.0)		41.5 (5.9)	17.7 (0.9)	
AS	15	60.5 (5.5)	A	67.2 (7.7)	A	7.7 (0.9)		36.7 (3.2)	17.0 (0.9)	b
CT	15	18.2 (9.7)	B	69.0 (17.8)	A	9.0 (2.3)		25.2 (6.0)	18.2 (4.2)	
YT	15	76.7 (4.4)	A	19.5 (6.1)	B	2.2 (0.3)		37.7 (5.6)	17.7 (1.7)	
OT	40	63.2 (5.9)	A	43.0 (10.8)		1.2 (0.3)	a	35.5 (0.6)	24.0 (0.9)	a
FP	10	61.7 (2.4)	A	61.7 (5.7)	A	2.7 (0.8)		32.7 (5.5)	15.0 (1.8)	
IF	>100	55.5 (6.8)	A	83.0 (6.6)	A	9.2 (0.6)	b	50.7 (4.6)	23.7 (2.1)	

Table 8. Correlations between habitat characteristics and Heteroptera diversity and dominance indices; N = number of individuals, S = species richness, H = Shannon diversity , E = evenness, D = Berger-Parker dominance. Note that, due to a high number of comparisons, correlations which are normally significant are only significant at $P < 0.15$ after Bonferroni adjustment.

Habitat's characterisrics	Diversity indices				
	N	S	H	E	D
Age					
Pearson correlation	0.41	0.067	-0.284	-0.452	0.436
Significance	0.013	0.698	0.094	0.006	0.008
n	36	36	36	36	36
Canopy cover					
Pearson correlation	0.198	-0.16	-0.251	-0.18	0.258
Significance	0.248	0.353	0.139	0.293	0.128
n	36	36	36	36	36
Undergrowth vegetation cover					
Pearson correlation	0.141	0.24	0.109	-0.113	0.047
Significance	0.413	0.159	0.527	0.511	0.783
n	36	36	36	36	36
Tree species richness					
Pearson correlation	-0.065	0.253	0.29	0.128	-0.149
Significance	0.707	0.137	0.086	0.457	0.384
n	36	36	36	36	36
Undergrowth plant species richness					
Pearson correlation	0.177	0.209	0.06	-0.082	0.072
Significance	0.307	0.22	0.727	0.634	0.676
n	36	36	36	36	36
Tree height					
Pearson correlation	0.203	0.184	-0.014	-0.155	0.161
Significance	0.234	0.284	0.933	0.368	0.35
n	36	36	36	36	36

Legends

Fig. 1. Map of the Lama forest reserve. NC = *Noyau central*, T = teak plantation, FP = firewood plantation, S = settlement, IF = (not to scale) isolated forest fragment.

Fig. 2. Mean number of individuals, Shannon diversity and Berger-Parker dominance ($n = 4$; ± standard error) for nine different forest habitats. Means not sharing the same letter are significantly different at $P < 0.05$, all remaining differences are not significant.

Fig. 3. Mean species richness, Shannon diversity and Berger-Parker dominance for undisturbed forest of the *Noyau Central* ($n = 4$; ± standard error) and disturbed forest ($n = 12$; ± standard error). Mean species richness is significant at $P < 0.05$, and Shannon diversity and Berger-Parker dominance $P < 0.01$ after Bonferroni adjustment.

Fig. 1.

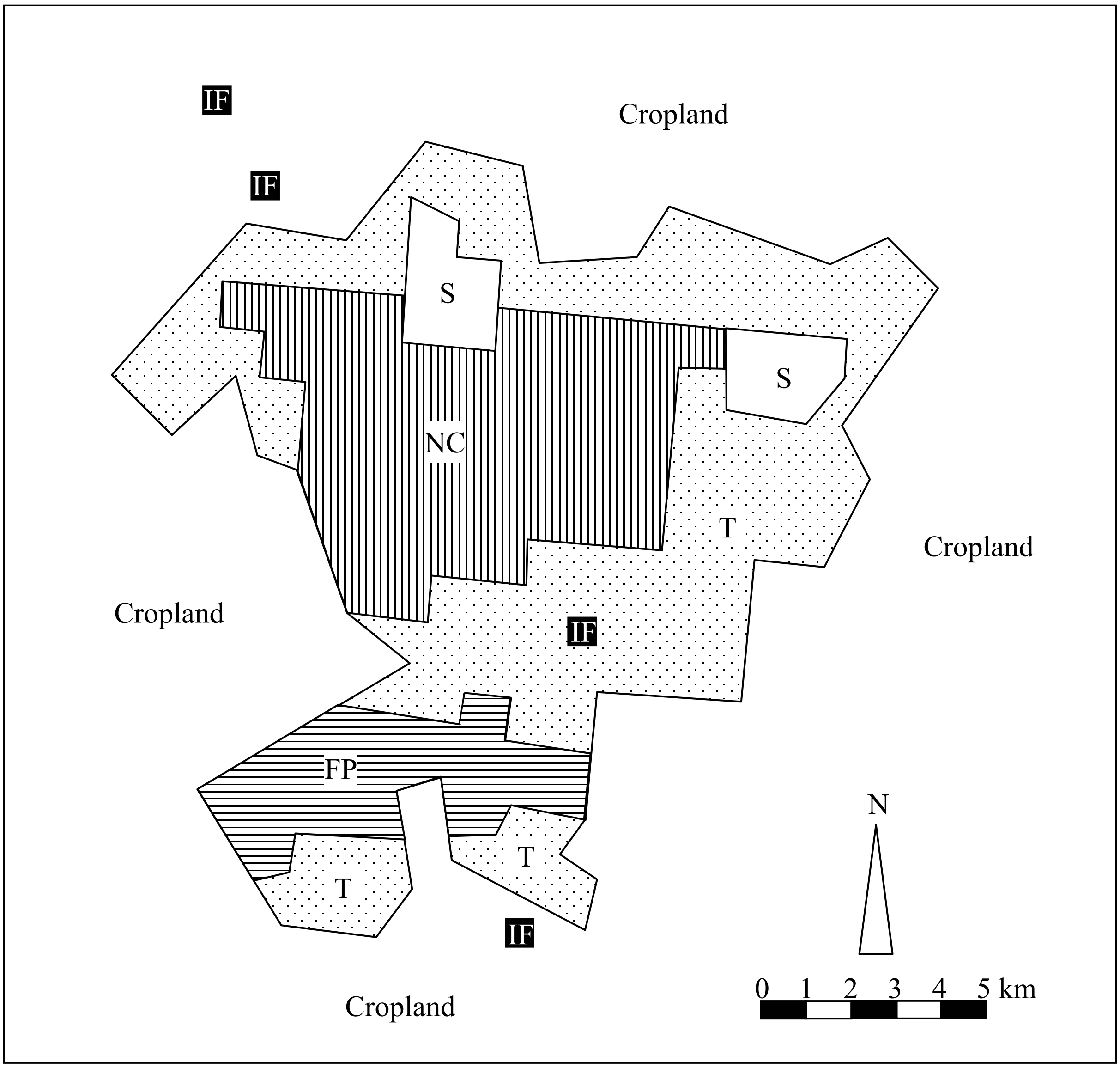

IF
IF
Cropland
S
S
NC
T
Cropland
Cropland
IF
FP
T
T
IF
N
0 1 2 3 4 5 km
Cropland

Fig. 2.

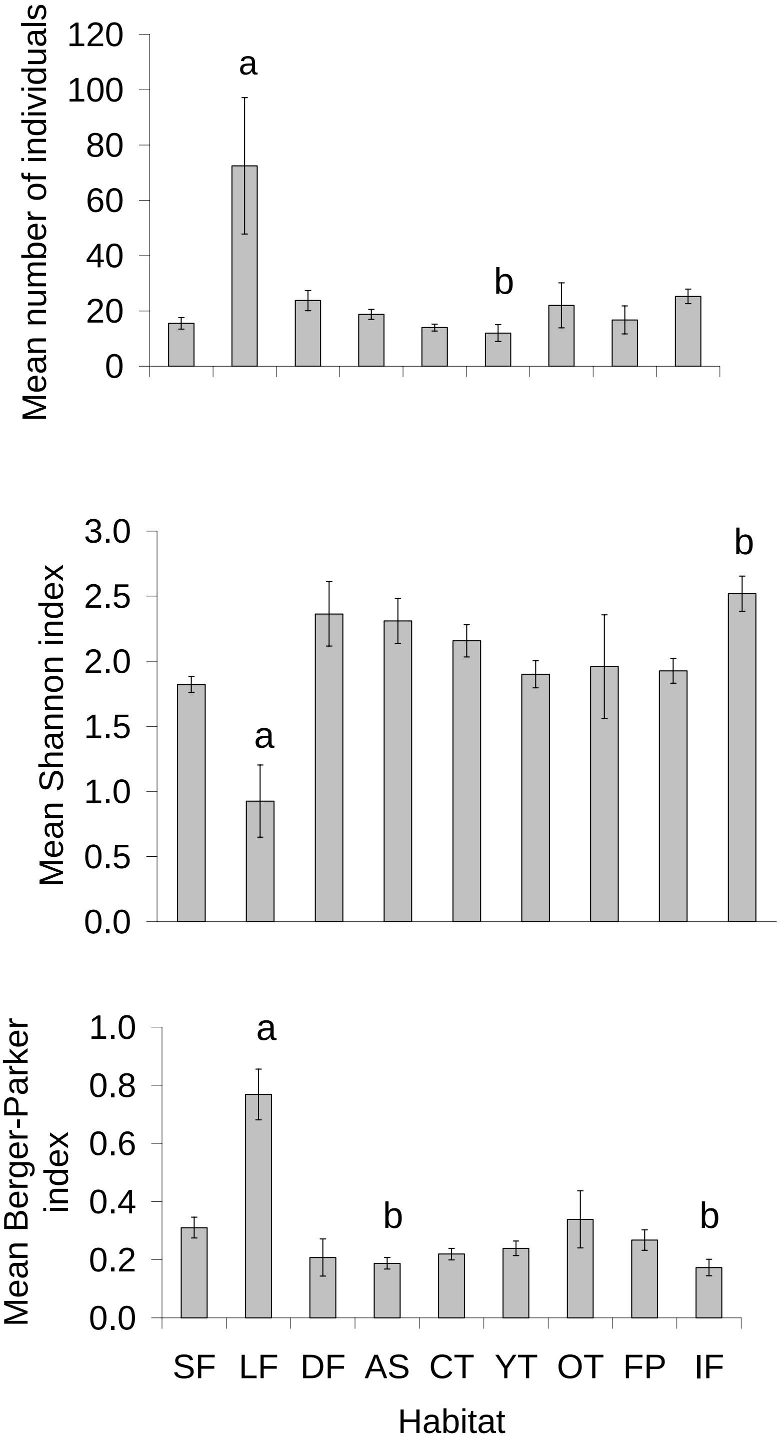
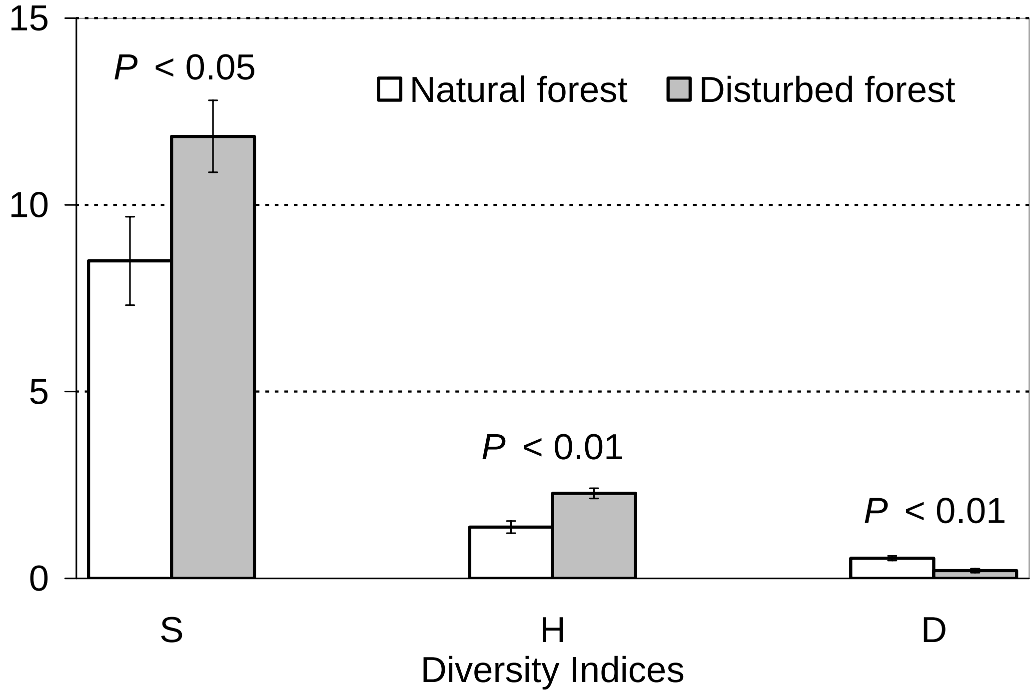

Mean number of individuals
0
20
40
60
80
100
120
a
b
Mean Shannon index
0.0
0.5
1.0
1.5
2.0
2.5
3.0
a
b
Mean Berger-Parker index
0.0
0.2
0.4
0.6
0.8
1.0
a
b
b
SF
LF
DF
AS
CT
YT
OT
FP
IF
Habitat

Fig. 3.


15
10
5
0
P < 0.05
Natural forest
Disturbed forest
P < 0.01
P < 0.01
S
H
D
Diversity Indices

Chapter 7

Summary and General Conclusions

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Summary and General Conclusions

The aim of this thesis was to investigate the diversity of invertebrates in natural semi-deciduous forest and plantation forests of the Lama forest reserve in Benin. Litter decomposition, being a key ecosystem process, was studied, and the importance of decomposer assemblages was investigated. An inventory of termite assemblages in semi-deciduous forest and teak plantations was conducted, and the effects of different forest types and seasons on the activity of termites and soil- and litter-dwelling invertebrates investigated. Furthermore, a new diplopod species, *Stemmiulus lama* n. sp. (Diplopoda: Stemmiulidae), the first record of Stemmiulidae for Benin, was described. Finally the diversity of true bugs (Heteroptera) in different habitats of the Lama forest was investigated.

Leaf litter decomposition is influenced by litter quality, climatic factors and soil biota. In **Chapter 2** ("Leaf litter breakdown in natural and plantation forests of the Lama forest reserve in Benin"), we used the litterbag technique to examine the breakdown of leaf litter from two indigenous (*Afzelia africana* and *Ceiba pentandra*) and two exotic tree species (*Tectona grandis* and *Senna siamea*), and investigated the relationship between litter breakdown and relative abundance of litter-dwelling invertebrates. The study focused on semi-deciduous forest, teak plantations and firewood plantations. We showed that litter species and forest type had significant effects on litter breakdown. We found that decay rates were highest for *Afzelia africana* in natural forest ($k = 4.7$) and lowest for *Tectona grandis* in firewood plantations ($k = 1.3$). We also found a significant litter × forest interaction, indicating dissimilar changes in litter breakdown across forest types. We observed higher frequencies of occurrence of invertebrates in indigenous than in exotic litter, and litter bags in natural forest attracted more invertebrates than those in plantations.

Our results indicate that litter breakdown is strongly influenced by litter type, forest type and the activity of litter-dwelling invertebrates. Therefore, management practices should aim to enhance biological activity of decomposer communities to avoid soil degradation and maintain productivity.

Conversion of natural semi-deciduous forest to teak plantations may influence termite species richness and composition. In **Chapter 3** ("Termite assemblages in a West-African semi-deciduous forest and teak plantations"), we used a modified standardised transect method to establish the first termite inventory in the Lama forest reserve. Overall termite diversity turned out to be surprisingly low (19 species), irrespective of forest type. This was due to the soil conditions which were unfavourable for soil feeders, the most species-rich termite group in African forests. Nevertheless, termite species richness was significantly higher in natural forest than in teak plantations. Termite assemblages were characterised by Kalotermitidae in natural forest, whereas fungus-growers (Macrotermitinae) dominated in teak plantations. Termite relative abundance (= encounter density) was higher in teak plantations than in natural forest. The difference in termite assemblages was due to differences in two environmental variables, litter biomass and soil water content.

Forest type and season can influence the activity of termites and soil invertebrates. In **Chapter 4** ("Activity of termites and other epigeal and hypogeal invertebrates in natural semi-deciduous forest and plantation forests in Benin"), we used a cardboard baiting method to monitor the activity of termites and soil and litter-dwelling invertebrates in semi-deciduous and plantation forest. The overall frequency of occurrence of invertebrates was highest in semi-deciduous forest, followed by firewood plantations, young teak and old teak plantations. Collembola, Isopoda, Isoptera, Diplopoda, Araneae and Hymenoptera (ants) were the most common soil invertebrates. We found that the activity of the most abundant taxa varied among forest types (except for Diplopoda and Araneae), with a higher activity in natural forest. We observed a significant effect of season on the frequency of occurrence of soil- and litter-dwelling invertebrates, the lowest value being recorded during the long dry season. The frequency of occurrence of termites was higher in old teak plantations than in the other forests, but only one species, *Microtermes? pusillus?*, showed a significant difference.

Many invertebrate species occurring in tropical ecosystems are unknown to science. In **Chapter 5** ("*Stemmiulus (Diopsiulus) lama* n. sp., a new millipede from Benin (Myriapoda, Diplopoda, Stemmiulidae)"), we describe a new species, *Stemmiulus lama* n. sp., from the Lama forest. This species is the first record of a stemmiulid millipede in Benin.

Forest use may influence the diversity and community structure of true bugs (Heteroptera).
In **Chapter 6** ("Diversity of true bugs (Heteroptera) in various habitats of the Lama forest reserve in southern Benin"), we compare Heteroptera assemblages in relation to forest use in different habitats, including natural forests, degraded forest, plantations and isolated forest fragments. We sampled 893 Heteroptera over a 12-month period, representing 104 species in 16 families. We found no significant effect of habitat type on species richness and evenness.

However significant differences in abundance, Shannon-Wiener diversity and Berger-Parker dominance were found. In isolated forest fragments, Shannon-Wiener diversity was significantly higher than in lowland forest, and the abundance of Heteroptera was higher in lowland forest than in young teak plantations. We also found that the Berger-Parker dominance index was lower in isolated forest fragments than in lowland forest. Species richness and Shannon-Wiener diversity were significantly higher, and Berger-Parker dominance lower in disturbed than in undisturbed forest patches within the *Noyau central*, a now fully protected part of the reserve. We identified two indicator species for two forest types, one for lowland forest (*Stenocoris southwoodi* Ahmad) and one for dry forest (Lygaeidae sp.11). We found that Heteroptera community diversity was mainly a function of habitat age, while other habitat characteristics had no influence on the diversity of true bugs.

To sum up, the present thesis provides baseline data on the diversity of invertebrates in the Lama forest reserve in Benin and gives ample evidence of the ecological significance of decomposer assemblages in natural as well as plantation forests. It shows that management practices should aim to enhance decomposer communities in order to safeguard the productivity and sustainable use of the Lama forest reserve.

Acknowledgements

This study was conducted within the scope of BioLama project, a research partnership between the Institute of Environmental Sciences (*NLU)* – Biogeography of the University of Basel, Switzerland and the Faculty of Agronomy (*FSA)* of the University of Abomey-Calavi, Benin. The Swiss National Science Foundation and the Swiss Agency for Development and Cooperation are acknowledged for their financial support.

Many people and institutions in different manner contributed to the realization of this work.

I am greatly indebted to my supervisor and project coordinator PD. Dr. Ralf Peveling for giving me the great opportunity to realize my PhD thesis. He is gratefully acknowledged for his excellent advice and guidance during the whole study.

Special thanks go to Prof. Dr. Peter Nagel (project director, Switzerland) and to Prof. Dr. Brice Sinsin (project director, Benin) for their guidance and for integrating me easily in their working teams.

My gratitude goes to the team of BioLama project in Benin for their collaboration and constant help during the project. Special thanks to Thibault Lachat, Julien Djego, Daniel Weibel, Camille Houngbédji, Mathurin Guèdègbé, Lamidi Konetché, Isabelle Specht, Ottmar Joos, Klaus Ullenbruch, Kola Bankolé, Mohamed Boukari and Toussaint Yadelin. Many thanks to the numerous students, trainees and workers, whose names are not mentioned here.

I am very grateful to Dr. Georg Goergen (IITA) for his reliable collaboration and for identifying insect specimens.

I wish to thank all the staff of the *Office National du Bois* (ONAB) in Benin, for authorizing me to conduct my research in the Lama forest reserve, especially to Dr. Pierre Houayé, Raphael Akossou, Daniel Honfozo, Hodonou Houndonougbo and to Victorin N’velin.

Special thanks to my colleagues of the Laboratory of Applied Ecology in Cotonou, Benin: Claire Delvaux, Etotépé Sogbohossou, Sylvain Gbohayida, Sévérin Tchibozo, Georges Nobime, Pierre Agbani, Adi Mama, Barthelemy Kassa and Yvonne Cakpo.

My gratitude goes to all my colleagues of NLU of the University of Basel for the nice working atmosphere and their help during my stays in Basel and the final stage of my thesis: Clarah Andriamalala, Vreny Wey, Petra Meyer, Gwendoline Altherr, Nathalie Baumann, Dr. Brigitte Baltes, Dr. Michelle Glasstetter, Prof. Cesar Boroni Urbani, Roland Mühlethaler, Dr. Roland Molenda, Andreas Kaup, Dr. Henryk Luka, Sonia Rodriguez and Ruth, Bächli.

Special thanks to all scientists of the International Institute of Tropical Agriculture in Benin for their collaboration and useful advice, in particular to Dr. Chris Lomer, Dr. Jürgen Langewald, Dr. Hugo. De Groote, O.K Douro-Kpindou, Dr. Ousman Coulibaly, Dr. Andy Cherry, Dr. Christian Koyman, Peter Neuenschwander, Si Abdoul Azis, Gounou Saka and Dr. Alexi Honzo.

Thanks to Dr. Christophe Chrysostome, Dr. Seibou Toleba Soumanou, Dr. Appolinaire Mensah, Dr. Marcel Winato and Dr. Armand Natta of the University of Abomey-Calavi and Georges Agbahungba of Institut National des Recherches Agricoles du Bénin (INRAB) who encourage me during the whole study period.

I would like to thank Dr. J. Korb (Germany) and Dr. T. Myles (Canada) for helping in identification of termite specimens and Dr. D. VanderSpiegel (Belgium) for identification of diplopoda and for describing the new millipede species from the Lama forest.

Many thanks to Doris, Edgard, Daniel and Matthias Weibel for taking care of me during my stays in Basel.

Thanks go to all my friends in Switzerland: Yvonne Steiner, Judith Ladner, Urs Draeger, Christina Frischknecht, Issa Barry and Souleye Bodiang.

I would like to thank my friends Conforte Mensah and Claude Houssou for their moral support and encouragement.

Thanks to Dr. Frederic Dohou, Minister of Culture, Craft Industry and Tourism of Benin for his moral support during my study.

Thanks to my father-in-law, Serge Lima and my mother-in-law, Valerie Lima for their encouragements.

Special thanks to my mother Jeannette for praying God every day, to my father Samson and to my brothers and sisters: Alain, Rose, Nina and Karl for their unfailing support and encouragement to achieve my goal.

Last but not least big special thanks to my beloved wife Nicole, to my daughters Salimatou and Charlène, and to my son Ryan, for their never-ending support.

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PhD thesis title:	Invertebrate Diversity and the Ecological Role of Decomposer Assemblages in Natural Forest and Plantation Forest in Southern Benin

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