Soil Macrofauna Community Structure along a Gradient of Land Use Intensification in the Humid Forest Zone of Southern Cameroon

Madong à Birang

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Proefschrift

Dedicated to my parents Marie and Etienne Madong à Bebom

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Introduction

Introduction

The biodiversity of the planet has varied tremendously over the past 600 years during which there have been around five major extinction events. We are currently in the middle of a sixth wave of extinction, and continue to lose species rapidly at all spatial scales as a result of human economic activity and associated habitat destruction. Over the past decade, topics relating to biodiversity have shot to the top of international and national research agendas. A key question has been how the loss of species affects the provision of ecosystem goods and services necessary for our survival (Wardle, 1999)

Soil macrofauna as a component of the ecosystem

The humid forest zone has a large and diverse soil-associated fauna that strongly influence soil properties and development. This fauna has been little studied, particularly in Africa. It has been said that we know more about the 2 kilograms of bird tissue flying over each hectare than about the 200 kilograms of earthworms working the soil of each hectare (Bouché, 1977). In recent years some progress has been made in describing the taxonomic diversity of certain groups. But little is known of community structures and the functional roles of the soil fauna in ecosystem processes. This constitutes a major challenge for soil science and biology. Soil fauna is commonly classified according to body width into microfauna (<100 μm), mesofauna (100-2000 μm) and macrofauna (>2000μm) (Swift et al., 1979). Soil macrofauna are the most conspicuous soil animals with the greatest potential for direct effects on soil properties in the tropics. In their review, Lavelle et al. (1997) presented a model showing the interactions between plants, animal and microbial components of the soil biota. Their model allocated a pivotal functional role to the large, abundant invertebrates, which ingest or manipulate both organic and mineral material, forming long-lasting microstructures. These invertebrates are designated soil ecosystem engineers and Lavelle et al. (1997) argued, using data on numerical and biomass abundances, geographical distribution and known functional roles, that earthworms, termites and ants are the most important engineers in terrestrial ecosystems. Evidence was presented that they may exert influence on the diversity and activity of biota subordinate trophic levels. They have also been considered keystone species whose removal from the ecosystem would significantly alter the functioning of that ecosystem, and many other organisms would be impacted negatively.

Earthworm, termite and ant diversity

Earthworms (Annelida: Oligochaeta) are an important but much neglected component of ecosystems. James (2000) estimates about 4 300 species known worldwide, and many more may await description, including some in the Congo basin, where lies the humid forest zone of southern Cameroon. Three main ecological categories of earthworms are widely recognized: epigeic, anecic and endogeic (Bouché, 1977). It is in general considered that two groups of macro-arthropods, termites and ants, dominate tropical rainforests in abundance, biomass and ecological impact. Termites (Insecta: Isoptera) are important as decomposers by virtue of their numerical dominance of the belowground arthropod community (Eggleton et al., 1995, 1996). Termites belong to the most abundant arthropods in the savannas and forests of the humid tropics. Estimates of 1995 indicate approximately 2 750 species identified in 285 genera worldwide (Dibog et al., 1998). In contrast, the arthropod community of tropical forest canopies is dominated numerically by ants (Loren and Linsenmaier, 1997; Watt et al., 2002). Ants (Hymenoptera: Formicidae) are abundant among the soil fauna of tropical forests. Ants are perhaps the most successful of all extant insects. There are approximately 8 800 described species of ants worldwide (Holldöbler and Wilson, 1990).

Importance of the soil macrofauna in ecosystems

Soil fauna is known to play a critical role in the biological turnover and nutrient release from plant residues by fragmenting them, resulting in enhanced microbial activity and grazing of microflora. A number of ecological studies have been carried out on soil invertebrates in the humid tropics and the importance of soil fauna in sustaining soil fertility and crop production has been stressed (Brussaard et al., 1992, 1993). Critchley et al. (1979) found that earthworms are the most abundant invertebrate macrofauna in soil under native semi-deciduous rainforest in South-western Nigeria. It appears, however, that the relative importance of earthworms improving soil physical and nutritional properties under different management systems is depending on soil characteristics. While on high base saturation Alfisols earthworms may turn over up to 80 Mg ha^{-1} of soil (Hauser and Asawalam, 1998), their impact on acid Ultisos may be as little as 2 Mg ha^{-1} (Norgrove et al., 1998) or less (Henrot and Brussaard, 1996). Along with the reduction of earthworm importance goes an increase in the importance of termites in acid soils in forested areas. They may contribute to nutrient acquisition, as some wood feeding species have the ability to fix nitrogen in their guts (Martius, 1997). A review by Lal (1988) summarises the influence of earthworms, termites and ants on physical, chemical and biological properties. They influence rates of soil turnover, mineralization and humification of soil organic

matter, soil texture and consistency, total porosity and macroporosity, infiltration rate and soil water retention. Biologically worked soil often has more organic matter and more plant-available nutrients and water reserves than the adjacent soil.

Earthworm, termite and ant activities affect soil structure through: i) the selective ingestion of mineral and organic particles; ii) their egestion as faecal pellets and organomineral aggregates at some distance from the ingestion; iii) digestion processes that may modify the colloidal properties of organic matter; iv) building of long lasting galleries, chambers and mounds (Lavelle, 1997; Lavelle et al. 1997; Gijsman, 1992; Wood, 1996). In moist savannas of Ivory Coast the overall dry mass of soil ingested by earthworms often reaches 500 to 1000 Mg $ha^{-1}yr^{-1}$ (Lavelle, 1988). In these systems humivorous termites ingest 45 Mg dry soil $ha^{-1}yr^{-1}$ and significant amounts of soil are also incorporated in mounds and surface sheetings produced by termites of other functional groups (Mboukou, 1997; Tondoh, 1998). The estimated annual soil turnover by ants in an *Atriplex vesicaria* shrubland in the semi-arid region of Australia was 350-420 kg ha^{-1} yr^{-1}(De Bruyn and Conacher, 1990). In a humid savanna environment, de Bruyn and Conacher (1994) estimated that one ant species, *Paltothyreus tarsatus*, transported approximately 30 $g.m^{-2}yr^{-1}$ of sand particles and soil aggregates. This ant species increased the concentrations of clay, carbon, iron oxides, and coarse sand in the A-horizon.

Galleries are common products of activities of 'ecosystem engineers'. Gallery networks made by earthworms may be extremely dense: in a large survey in several regions of France, Lopes-Assad (1987) examined 24 different soil profiles and found 60-290 active (i.e., open to the surface) galleries m^{-2}; their total length ranged from 6.2 to 66.6 m m^{-3} and they comprised approximately 0.6% of the total volume of soil. In east African savannas, termites built 15 km of galleries and 90 000 storage chambers ha^{-1} which occupy approximately 0.4% of the soil volume down to 20 cm deep (Wood, 1988). At Lamto (Ivory Coast), Lepage (unpbl. data) estimated the volume of galleries and chambers created by fungus growing termites to be 0.37-0.59 m^3 ha^{-1}, and the volume of modified soil that surrounds these structures was 4.32 m^3. In Western Australia, ant community on gray soil were estimated to turnover 46.5 kg $ha^{-1}yr^{-1}$ and on yellow soils, the soil-nesting ant community was estimated to turn over 22.3 kg ha^{-1} yr^{-1} (De Bruyn et al., 1994). Earthworms, termites and ants generally contribute to the maintenance of a relatively high porosity by digging galleries. Deposition of earthworm casts at the soil surface is a mechanism that regulates soil porosity, as a volume of voids equivalent to that of casts is created inside the soil. Colonization of new soils by earthworms always results in a significant increase of porosity, which may be doubled (Elhers, 1975; Chan and Heenan, 1993; Hoogerkamp et al., 1983).

Gas diffusion is affected in the same way as water infiltration, although diffusion around galleries is more important than direct diffusion along the burrows (Kretzschmar, 1989). Similar effects have been observed with termites and their exclusion from the soil of a North-American desert significantly increased the bulk density of the soil and erosion, while water infiltration was decreased (Elkins et al., 1986). Whitford (2002) reported that the macropores constructed by ants affect rates of infiltration and rates of percolation. Ant biopores were found to transmit water down the soil profile only when the soil was saturated. Termite and ant galleries and earthworm burrows have a significant effect on water infiltration despite their low contribution (<1%) to soil volume. Lavelle (1997) quotes results of experiments by Urbanek and Dolezal (1992), Casenave and Valentin (1989) in West Africa. They claim that when ploughing is substituted for direct drilling, anecic earthworms are favored and as a result of their enhanced activity, hydraulic conductivity at the interface between A and B horizons may double in arable land. A significant relationship was also found between the presence of earthworm casts and termite sheetings and water infiltration rate: infiltration increased with percentage of soil covered by earthworm casts and termite sheetings and maximum values were obtained when more than 20% and 30% of the soil surface was covered with earthworm casts and termite sheetings, respectively. It was concluded that earthworms could diminish surface crusting. The increase of infiltration stems mainly from water retention owing to an increase of surface roughness and the presence of macropores and galleries below surface structures. Similar effects have been mentioned by several authors (Mando, 1997b; Mando et al., 1996; Lal, 1988).

Earthworms contribute to soil aggregation mainly through the production of casts; almost all macroaggregates in tropical moist savannas are earthworm casts (Blanchart et al., 1993). Earthworm burrows can also contribute to aggregate stability, since they are often lined with oriented clays and humic materials, which can form a stable structure (Jeanson (1964) cited by Edwards and Bohlen, 1996). Many workers agree that earthworm casts contain more water-stable aggregates than the surrounding soil (Marinissen and Dexter, 1990; Guild, 1955; Lee, 1985). Faecal pellets of some termites are organomineral micro-aggregates which form the walls of termite mounds and even surface soil horizons of some tropical soils (Garnier-Sillam et al., 1987; Wielemaker, 1984; Eschenbrenner, 1986).

Earthworms, termites and ants may therefore be significant determinants of pedogenetic processes in the upper 30-60 cm of soils (Lee and Wood, 1971). Vermic soils with high earthworm activity have been recognized as a separate entity in the USDA '7th approximation'. Pop and Postolache (1987) in Lavelle (1997) state that: 'by definition, a normally developed soil must be vermic when defining mull'. Kubiena (1955) states 'Practically all aggregates are

earthworm casts or residues of them'. There is also evidence that termites may influence pedogenesis in deeper soil strata (Wielemaker, 1984; Eschenbrenner, 1986; Jones, 1990).

Effects of soil invertebrates on soil organic matter (SOM) dynamics and nutrient release

The role of soil invertebrates on SOM has been extensively studied by Lavelle (1997), Lavelle et al. (1997), Brussaard and Juma (1996), Martius (1997) and Ohiagu and Wood (1979). Earthworms are known to increase the decomposition rates of surface-applied litter and the release of nutrients (Tian et al., 1995; Parmelee et al., 1998).The ability of earthworms to release mineral N and P from resources with high C:N and C:P ratios is a result of : (1) their high efficiency at digesting compounds - that they excrete as intestinal and cutaneous mucus - which leaves nutrients in excess; (2) the rapid turnover of nitrogen in biomass (Ferrière and Bouché, 1985; Barois et al., 1987) and (3) the continuation of mineralization for some hours in freshly deposited casts resulting from enhanced microbial activity. Estimates of the overall release of assimilable N range from 25 to 150 kg mineral N ha^{-1} in tropical grasslands. The amount of mineral P released was estimated to 50 kg ha^{-1} in a Vertisol in Martinique (Lopez-Hernandez, 1993; Brossard, 1996, Barois et al., 1987; Lavelle, 1992; quoted in Lavelle (1997)). Gilot (1997) reported on the effects of earthworms on yam production and soil characteristics in Africa. Earthworms altered soil structure by decreasing the percentage of small aggregates and increasing the percentage of the larger ones. These larger aggregates, primarily ageing casts, may even contribute to the protection of soil C, as indicated by a decrease of only 5% in C mineralization after three years. Using the CENTURY carbon model, Lavelle et al. (1997) considered that earthworms can promote stabilization of soil organic matter and maintain the organic pool and soil structure in the long term (10-50 years). Nutting (1985) reported that the termite species *Heterotermes aureus* and *Gnathamitermes perplexus* are dominant factors in soil turnover, litter decomposition and nutrient cycling in the Sonoran desert below 1200 m. Together, they move 744 kg ha^{-1} year^{-1} of soil to the surface. They increase the clay content of surface soil by 21 kg ha^{-1} year^{-1} by selectively bringing up soil richer in clay. They alter the pH from slightly acid to basic, mainly by bringing lime to the surface. They enrich the soil with organic C, total N, Ca, Mg, K and Na as a result of digesting plant material and decomposing faeces and/or saliva in their workings at the surface.

Wood (1996) reported in his review of termite food, foraging and food utilization that with few exceptions, food consumed by termites is low in nitrogen and contains a high proportion of plant structural polysaccharides. Nitrogen in the diet is supplemented by fixation of atmospheric N, digestion of symbionts and recycling of microbial and faecal wastes.

Considerable quantities of food are consumed and processed by a combination of the termites' digestive enzymes and enzymes produced by endosymbiotic gut protozoa and/or bacteria, or in the case of Macrotermitinae, exosymbiotic fungi belonging to the genus *Termitomyces*. Faeces are re-ingested within the colony and some are used in nest construction. The net result is degradation of cellulose (74-99%), hemicellulose (65-87%) and lignin (0.3-83%) in addition to digestion of soluble carbohydrates.

Effects of soil invertebrates on soil fertility and plant growth

Macro-invertebrates may affect soil fertility at different scales of time and space. Experiments have been carried out to test the effect of inoculation of earthworms in tropical soils from Mexico, Peru, and Ivory Coast, submitted to slash and burn low-input agriculture (Barois et al. 1999; Gilot, 1994; Pashanasi et al., 1996). Soils under that type of management generally have few earthworm species, due to lack of adaptable populations. Recently, experiments to evaluate the effects of earthworms on plant growth in 6 tropical countries, involving 14 plant species, 6 major groups of soils, and at least 11 species of earthworms were undertaken (Brown et al., 2000). Additional data were taken from the literature (Blakemore, 1995; Senapati et al. 2000), totalling over 240 data points, on the percent increase in plant growth in the presence of over 30 earthworm species. The overall average increase obtained was $63 \pm 11\%$ (SE), significant at $P < 0.07$, and the greatest increases were observed in soils with high sand content, poor in organic matter and with a moderately acid pH. Under the conditions of these experiments, the effect on plant growth was proportional to the earthworm biomass; significant effects started to appear at biomass values ≥ 30 g fm (fresh mass). Grain production increased more than stover and root production. Not all earthworm species had the same impact, and not all the plant species responded positively. In his review, Lavelle (1997) quoted Swift (1986), van Noordwijk and De Willigen (1986) and Tomati and al. (1988) to summarize the probable mechanisms whereby earthworms stimulate plant growth as: (i) mobilization of nutrient pools that normally are not available (e.g., adsorbed phosphorus and nutrients in resistant organic fractions); (ii) favorable changes in water and oxygen supply to roots; (iii) more efficient use of nutrients based on an improved synchronization and juxtaposition of nutrient release and nutrient uptake by plants; (iv) and 'hormone-like' effects of earthworms. In Nigeria, Tian et al. (1992) compared the effect of various types of prunings on soil faunal activity and crop yield. They found that microclimatic conditions of the soil with a mulch layer were more favorable for soil fauna than unmulched plots, due to the decrease in soil temperature and increase in soil water content. Prunings of low nutritional quality, which decomposed slowly and, consequently, had a more

durable effect on microclimate, were found to promote the abundance of termites. Highly nutritious prunings attracted earthworms and ants. Crop yields had increased by 40 to 70 % in plots mulched with *Leucaena* prunings compared to the unmulched control. Mulching at a rate of 5 Mg *Leucaena* prunings per ha in combination with an N-dose of 45 kg ha^{-1} resulted in higher crop yields than application of 135 kg N ha^{-1} without adding prunings. This difference may stem from an improved soil physical condition due to increased soil faunal activity, combined with release of nutrients from decomposed prunings.

Termites can enhance plant growth as well as impede it. In reviewing this topic, Lee and Wood (1971) summarized the complex and interacting factors responsible for enhanced growth as: (i) protection from burning allowing survival of seedlings that would otherwise be destroyed by fire; (ii) better drainage compared with surrounding soil in seasonally waterlogged areas; (iii) accumulation of greater depth of soils in areas with shallow, stony soils; (iv) provision of moist soil by enhanced water retention due to addition of clay brought from deeper horizons; (v) chemically altered soil, principally of higher base status; (vi) resistance to termite attack by plant species growing on the mounds; (vii) possible response of plants to substances produced by the termites.

Ant effects on plant growth can be indirectly evaluated through the effects of ants on soil and their interactions with the plants. Associations between plants and ants range from facultative and opportunistic to obligate for one or both partners. Literature on the direct effects of ants on plant growth is scarce.

Evidence of co-evolution between plants and ants is provided by many plant structural adaptations that facilitate feeding by ants, offer them shelter or promote transport of seed. Although parasitic ant species can predominate on some ant-plants (Yu and Pierce, 1998), many studies have shown that in exchange for living space and food, common ant inhabitants either protect their host plants against herbivores, encroaching vines, and competing plants, or supply nutrients essential for growth, or both (Fiala et al., 1995; Vasconcelos, 1991).

Soil fauna - vegetation diversity interactions

Tropical rainforests are among the most complex and species-rich ecosystems of the world (Wilson, 1995). According to Gillison (2000), the tropical lowland agroforested landscapes of Cameroon contain 50-100 vascular plant species per 40 x 5 m plot while in the Western Amazon basin there were 70-100 per plot and more than 150 species per plot of the same size in Sumatra. He argued that density patterns appear to vary with disturbance history and type

of manipulation. Zapfack et al. (2002) conducted floristic surveys in different land use systems in the humid forest zone of southern Cameroon (primary and secondary forests, fallow of different ages, cocoa plantations and crop fields). They found that the forest, which represents the historic biodiversity of the region, preserved the greatest species richness (160 species in primary forest and 171 in secondary forest) and the crop field the lowest (64), where only weeds and crops contributed to plant biodiversity. They concluded that secondary forests might constitute refuge areas for primary forest species that function as a starting point for possible regeneration of original biodiversity. It is often assumed the invertebrate communities are dependent upon the species composition and structure of the plant community and that management practices to maintain the vegetation should therefore be of equal benefit to invertebrate communities (Panzer and Schwartz, 1998). There is, however, remarkably little evidence for this statement

Effects of deforestation and disturbance on soil ecosystem engineers

The effects of deforestation on the soil fauna can be divided in direct and indirect effects (Gijsman, 1992). The direct effects result from the damage done to soil faunal habitats by soil disturbance during the clearing process itself. This damage concerns, e.g., soil compaction, scraping off of topsoil, mixing of soil layers and heating up of the soil during burning. The indirect effects result from the change in micro-environmental conditions after removal of the forest cover. These effects concern, e.g., the change in micro- and meso-climate (temperature, air/water stress) in the soil and the decline in organic matter input and change in its chemical composition. The subsequent use of the cleared land for cultivation may lead to further disturbance of the soil and thus may enhance the degeneration of the soil habitat. Lavelle and Pashanasi (1989) performed a principal component analysis of their data on soil faunal populations under various land use practices. They found two major differentiating factors between land uses. The first and most important factor was the type of vegetation, which differentiated forests from pastures, whereas cultivated land and fallow took intermediate position. On the forest side of the differentiating vector, a high population density but a low biomass, due to the importance of termites and various litter-dwelling epigeics, characterized the macrofauna community. On the pasture side of the vector, the macrofauna community was strongly dominated by the earthworm *Pontoscolex corethrurus*, resulting in a low population density but a high biomass. The second factor represented the physical protection of soil by vegetation, which shows that in conditions of a high exposure to weather influences, the surface

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dwelling fauna (termites and ants) tend to disappear and fauna are restricted to deeper layers. This factor separated crops with a poor cover from forest and improved pasture, the latter two having a dense cover. It may be hypothised that the effect of vegetation combines degree of soil disturbance due to land cultivation, and amount and type of organic matter input, since they are the major differences among land use types.

Burning is a central component in shifting cultivation or slash and burn agriculture. This can lead to a drastic heating up of soil, killing soil fauna and destroying soil organic matter. The effect of burning depends on its intensity and frequency. Raison (1979) reported a partial sterilization of the soil down to a depth of 20 cm after burning. The increase in maximum soil temperature and the lower moisture content of the top layer after deforestation force animals which cannot withstand dry conditions to die or to move to deeper soil layers. Drought-resistant animals will then become dominant in the top layer. There seems to be an inverse relationship between the size of soil invertebrates and their individual resistance to temporarily unfavorable conditions of soil temperature and moisture. Under forest, therefore, macrofauna tend to dominate, whereas under the more extreme conditions of a cleared plot micro- and mesofauna mostly prevail. Hauser (1992) showed that exclusion of rain from a site cleared from a 4-year old bush in Nigeria resulted in an immediate suspension of earthworm activity, which even was not resumed when the rain was allowed to enter dry plots again. Janssen and Wienk (1990) compared the litter fauna of a recently cleared plot under various crops. They found that under cassava, being an open crop offering little protection to environmental extremes, drought-resistant taxa such as centipedes and certain beetle families dominated, whereas these were hardly found in *Pueraria* litter, having a higher moisture content and less extreme maximum temperature. On the other hand, more sensitive animals such as earthworms were encountered under *Pueraria*, but seldom under cassava.

The effect of soil compaction on soil fauna during or after clearing arises from an alteration of (i) the air/water balance of the soil due to changes in porosity; (ii) the temperature regime in the soil; (iii) penetration resistance of the soil for burrowing animals, which depends on the combined effects of bulk density and matric potential of the soil, reflected in the soil strength. Brussaard and van Faassen (1990) reviewed some of the literature on the effect of soil compaction on various soil inhabiting animals. They cited research of Dexter (1978) and McKenzie and Dexter (1988) on the axial and radial pressures exerted by earthworm species in soil. It was found that better ability to overcome high values of soil strength occurred with species of the endogeic type. Studying termites in Kenya, Kooyman and Onck (1987) observed that species richness and population densities decreased with increasing intensity of cultivation.

Especially those species, which live in the upper few centimetres of the soil, and thus are more susceptible to tillage operations, disappeared after cultivation of the land.

Slash and burn agriculture and soil biodiversity

The traditional food production systems in the humid forest zone of southern Cameroon are shifting cultivation or slash and burn agriculture. It involves the manual clearing of a small area of natural vegetation (forest, bush, woody savanna or grassland) and leaving the area fallow for an extended period after a few harvests to allow the natural vegetation to regenerate. Figure 1 presents the formation of different agricultural production systems after conversion of natural forest by slash-and-burn in southern Cameroon.

The increasing food demand of a rapidly growing population has led to an intensification of agricultural land use. As compared to the traditional system of slash and burn, the current systems do not permit long fallow periods for a full recovery of soil fertility and the return to the original community structure of the soil biota. Cropping phases have become longer and fallow phases shorter. Living conditions for at least some soil macrofauna are worsened to the extent that they cannot persist. Agricultural intensity is defined as a set of patterns of land use change with the common feature of increased use of the same resources for agricultural production, usually as a result of switch from intermittent to continuous cultivation of the same area of land. Associated trends are specialization in crop or livestock species utilized, increased management intervention and greater reliance on markets. The common endpoint of intensification is substitution of labor with mechanization and of organic and biological inputs and controls by chemical and mechanical inputs. The transitions from internally to externally regulated systems, and from sustainable to degraded systems may occur progressively or abruptly (Giller, 1997; Ruthenberg, 1980; Izac et al, 1996; Van Noordwijt, 2002). Deforestation and increased land use intensity are likely to change species composition in all groups of soil fauna. Furthermore, the rate of intensification of agriculture in the tropics is greater than in other regions of the world, so that ecosystems are under particular threat of major changes or loss (Izac et al., 1996). As certain macrofauna make major contributions to ecosystem functioning, their disappearance might lead to accelerated degradation (Lavelle et al., 1997). If land use does not encompass some techniques or measures to maintain a minimum of factors that contribute to soil regeneration in fallow phases (and particularly in shortened phases), further soil degradation and forest conversion is expected. Soil fertility is built and maintained by a complex of factors and processes in which soil macrofauna play a part. It is

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hypothesized that a great diversity of soil macrofauna will more likely maintain all ecosystem functions than a system low in diversity. It is however recognized that the complexity of the system will require focusing on so called 'keystone species', known to be mediators of, or contributing at disproportionate rates to important ecosystem processes. Land use systems and changes reducing soil macrofauna diversity and density are more likely to lead to soil degradation than systems and changes that maintain soil macrofauna diversity and density. Grime (1977) made the distinction between long-term stress and short-term perturbations or disturbance. Whilst a single cultivation such as ploughing (short-term disturbance or low land use intensity) will result in a dramatic disruption of soil structure, repeated ploughing (long-term stress or high land use intensity) will have further effects by enhancing the rate of soil organic matter turnover which will gradually lead to a reduction in organic substrates. Short term, periodic disturbance may cause disruption in the relative abundance of particular organisms but not extinction, whereas long-term stresses are more likely to lead to gradual elimination of some species. Slash-and-burn agriculture combines deforestation and burning, two factors known to result in the decline of soil faunal populations directly or indirectly. In Cameroon, over 85% of deforestation is attributed to smallholder agriculture; thus the rural population density plays a significant role in determining the extent of closed canopy forest and the stock of woody biomass (Kotto-Same et al., 2000). It is therefore important to quantify the level of soil macrofauna diversity and density under these conditions in order to provide options for the introduction of management techniques to farmers that will maintain soil macrofauna diversity for ecosystem functioning.

Scope of the thesis

Soil is the habitat of plant roots and a diverse array of organisms (bacteria, fungi, protozoa and invertebrate animals) that contribute to the maintenance and productivity of agroecosystems. As intensification occurs, the regulation of function through biodiversity is progressively replaced by regulation through chemical inputs. However, the causal relationship between (1) composition, species richness and abundance of soil organisms and (2) sustained fertility are unclear. Swift and Anderson (1993) recognized that the functional importance of biodiversity for the maintenance of soil fertility remains one of the main fundamental gaps in current understanding of terrestrial ecosystems. Anyhow, there is a popular assumption that land use intensification results in the loss of biodiversity; and it is hypothesized that loss of the soil macrofauna may impair the functioning of the soil in terms of hydraulic conductivity, soil

structure, decomposition of organic matter and nutrient cycling. Furthermore, in tropical agricultural systems undergoing intensification, farmers have limited access to inputs and rely mainly on biological processes and therefore the maintenance and enhancement of soil biodiversity may be particularly relevant to such farmers (Giller et al., 1997).

Hence, the objectives of the thesis are:

1- To determine the perception and appreciation by land users of soil fauna and their effect on soil fertility and crop performance

2- To describe the community structure of earthworms, termites and ants along a gradient of land use intensification

3- To determine the relationships between both soil properties and vegetation and soil fauna community structure, i.e. aboveground-belowground biodiversity relationships, in relation to the main land use systems of the humid forest zone of southern Cameroon

4- To evaluate the impact of land management on soil macrofauna activity through monitoring earthworm surface casting

Description of the research area

The project was implemented in the Forest Margins Benchmark Area (FMBA) of southern Cameroon (Kotto-Same et al., 2000). The Cameroon benchmark encompasses a gradient in resource use intensity. The range of socio-economic and biophysical conditions in the benchmark permit the study and targeting of short, medium and long fallow agricultural systems over areas with population densities ranging from 5 to 100 persons km^{-2} (Figure 1).

At the southern end of the resource use intensity is the Ebolowa block, with a low population density (around 5 people km^{-2}) and large tracts of intact primary forest (59% of land cover). There is still significant reliance on natural resource-based activities, e.g. bushmeat hunting and gathering of non-timber forest products. Local agricultural markets are comparatively small, agricultural input markets are underdeveloped, and road infrastructure is poor and not maintained.
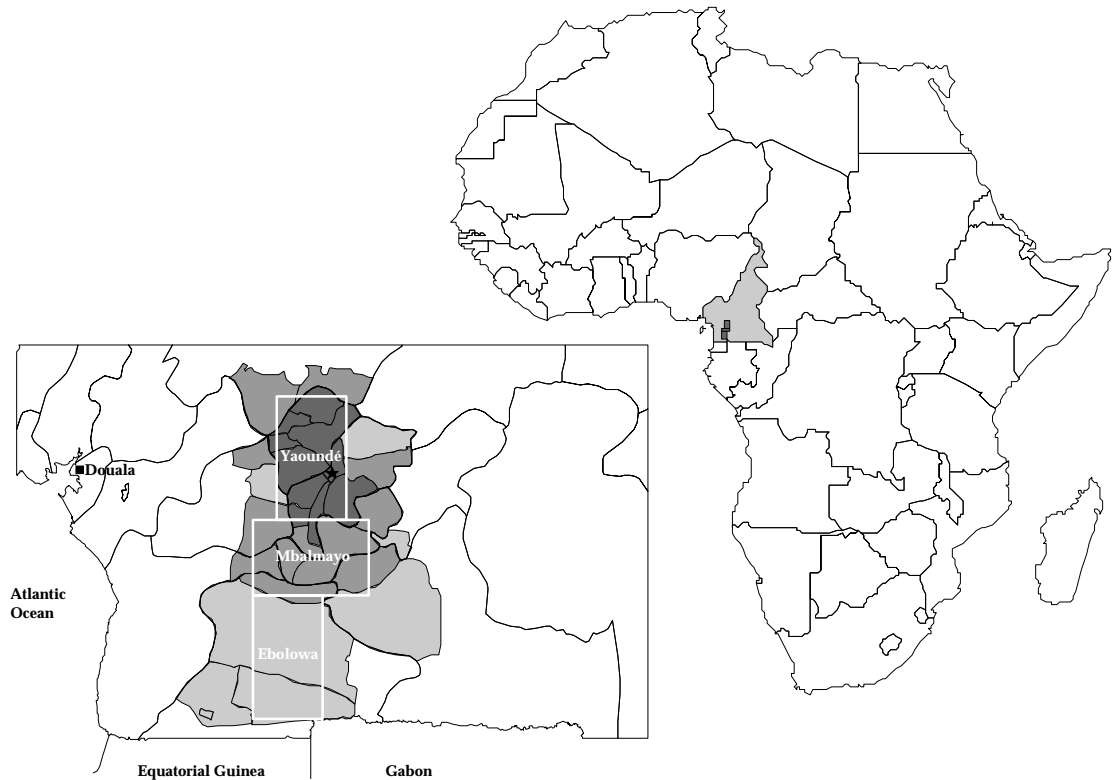
Figure 1. Map of southern Cameroon and the three land use intensification blocks within the forest margins benchmark

At the northern end of the resource use gradient is the Yaoundé block, with an average population density of around 80 persons km^{-2} and most of the land in some phase of an agricultural cycle; only 4% of land remains covered by primary forest. Land constraints at the household level result in shorter fallow periods. Proximity to the Yaoundé market, better-developed market institutions, and rural infrastructure has led to a process of agricultural intensification, diversification and commercialization. At the same time, the stock of forest resources has been seriously degraded (declines in carbon stocks, biodiversity and watershed functions).

The southern and northern parts of the benchmark area represent distinct resource use domains, shaped by significant differences in farmer, village and regional circumstances, with great variation in the opportunities for and constraints to environmental protection and income generation. The Mbalmayo block represents a medium resource use area with a population density of 15 people km^{-2}. Although logging is intensive, there still remains a considerable area of primary forest. In each block, the study was implemented in 2 villages (Table 1).

The red and red-yellow soils in the benchmark area mainly fall into the broad FAO soil class of Orthic Ferrasols. Annual rainfall in the area is bimodal and ranges from 1350 to

1900 mm. Rains start in mid-March and end in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November.

Land use systems incorporated in the research were (Figure 2):

(1)   Secondary forest: long-fallow regrowth after cropping ca. 30 years previously, surrounded by food crop fields and short fallows.

(2)   Traditional cocoa plantations established under retained forest shade trees for over 30 years; the cocoa shade canopy includes productive fruit trees

(3)   Old fallow in transition to young secondary forest of about 10 years

(4)   Young *Chromolaena odorata* fallow of at least two to three years; *Chromolaena odorata* is an invasive weed that dominates all young fallows

(5)   Mixed food crop fields planted in a short *C. odorata* fallow

These land use systems represent a sequence of increasing levels of disturbance and at the same time they represent the most common situations in agricultural land use in the region.

Outline of the thesis

Chapter 2 describes the perceptions of the farmers on the effects of earthworms on soil fertility and crop performance. There is a traditional indigenous knowledge of the value of some components of the soil biological resources. Farmers being the main actors of forest conversion, it is important to know their level of awareness in terms of what soil faunal species do; how they value it will dictate how they manage it. This can give a framework for the development of management technologies, which might be easily adopted by them.

In chapter 3, the impact of the type of farming system on soil biota activity is examined through the study of earthworm surface cast deposition in different land use systems.

Chapters 4, 5 and 6 examine the community structure of earthworms, termites and ants, respectively, along a gradient of land use intensity. These soil organisms have different functions and activities; they partially inhabit different niches and differ in their feeding habits and peak seasons of activity. The spatial gradient of land use intensity is used as a substitute for long term changes in macrofaunal diversity and composition that would be seen in a chronosequence of land degradation.

Table 1. Characterization of the 6 villages under study in southern Cameroon.

Block and population density	Level of deforestation and LUI*	Village	Distance from Yaoundé	Geo-references	Soil type	Land under forest cover (%)	Land under fallow (%)	Land under crop (%)
Yaoundé >80 km^{-2}	High	Nkometou (Nk)	40 km North	11°35'E, 4°05'N	Rhodic Kandiudult			
		Minkoameyos (Mi)	15 km West	11°27'E, 3°51'N		25	29	27
Mbalmayo 15 km^{-2}	Medium	Mbalmayo (Mb)	50 km South	11°28'E, 3°27'N	Typic Kandiudult			
		Metet (Me)	90 km South	11°45'E, 3°25'N		40	16	19
Ebolowa <5 km^{-2}	Low	Akok (Ak)	150 km South	11°14'E, 2°44'N	Typic Kandiudox	57	10	13
		Ngoungoumou (Ng)	130 South	12°01'E, 3°18'N				

*Land Use Intensity
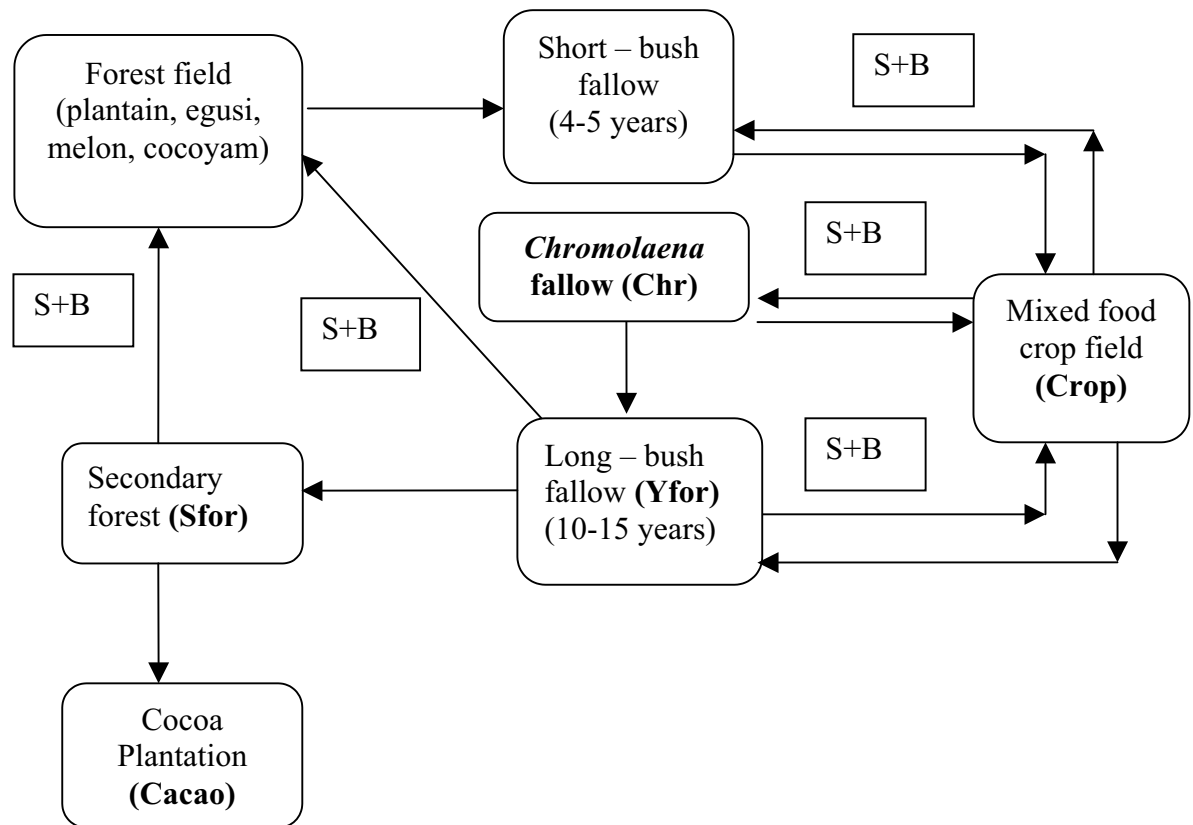
Figure 2. Model of the formation of different forest types and agricultural production systems in the humid forest zone of southern Cameroon (adapted from Weise and Tchamou, 1999). S+B = slash-and-burn. The five LUSs on which this thesis focuses are indicated in bold.

In chapter 7, relationships between the fauna and the environment in which they live are investigated, including aboveground-belowground biodiversity relationships. What are the key environmental determinants of faunal diversity that may help to make predictions on their fate and to identify management techniques to be developed to conserve and promote it?

In chapter 8, the main findings of the thesis are discussed and some directions for future research are suggested.

Farmers' perception the effects of earthworms on soil fertility and crop performance in southern Cameroon

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Summary

The knowledge and perception of the effects of earthworms on soil fertility and crop performance was surveyed in the humid forest zone of southern Cameroon. A total of 215 farmers were interviewed in seven villages: two villages were near the capital Yaoundé, severely deforested with a high land use intensity, three villages were 60-100km south of Yaoundé, moderately deforested, with a medium land use intensity and two villages were 130-200km south of Yaoundé, mainly forested with a low land use intensity.

To assess if the fallow phase has attained sufficiently high levels of fertility, the status of soil macrofauna was used by 42% of the farmers as an indicator. The presence of earthworm casts was used by 35% of farmers to determine if the land was ready for cropping.

Earthworms were not believed to have any effect on soil fertility (98.6 %) and only 0.7% of farmers believed that earthworms either increased or decreased soil fertility. Across all crops, 71.6% of the farmers reported that earthworms have no effect on crop yields. Any positive effects on yield were regarded as crop specific: 30.1% of the farmers believed that groundnut (*Arachis hypogaea*) and cassava (*Manihot esculentus*) yields increased if earthworms were present. For maize (*Zea mays*), plantain (*Musa* spp.), cocoyam (*Xanthosoma sagittifolium*) and cacao (*Theobroma cacao*), between 27.7 and 19.2% of farmers believed that earthworms created yield increases. Few respondents (mean across crops 1.8%) believed that earthworms decreased crop yields, with the greatest proportion of these related to plantain (3.8%). Farmers' perception of earthworms effects on cassava and groundnut yields was highly dependent on location and related to the levels of surface casting.

Key words: Crop yield response, earthworm casts, slash and burn agriculture

Introduction

With the recently increased interest in the role of soil macrofauna in ecological processes and the maintenance of soil properties, a large volume of knowledge on the effects of environmental conditions on earthworms has been acquired. Key roles of earthworms in agricultural land use systems have been elucidated and their positive effects on soil physical and chemical properties have been widely documented. In pot experiments (Makumbi-Kidza 1995; Norgrove & Hauser 1999) and in field experiments in which either earthworms (Gilot 1997) or casts (Asawalam 1997) were applied, positive effects on crop yields were reported. While there is scientific knowledge and appreciation of the role of earthworms in low input agricultural systems, we know little about the knowledge and perception of farmers of earthworms in their different land use systems. Agricultural production in southern Cameroon and the Congo basin relies on 'slash and burn' techniques for a wide range of fallow ages and types. Burning is the most frequently used practice to remove biomass, and external inputs are virtually absent (Büttner 1996). Tillage is usually crop-specific and only groundnut (*Arachis hypogaea*) fields are hand- tilled. Mulching is not a common practice and if used at all, is limited to the piling of weeds around long term crops such as cassava (*Manihot esculentus*). Thus, the cropping practices are characterized by several factors known to be detrimental to earthworms (Hauser 1993; Hauser & Asawalam 1998)**.** It does not appear that any land use system or management practice has been developed to promote the activity of earthworms specifically to exploit any positive effects on sustained and increased crop growth and production. Global environmental and local production-related concerns of long-term effects of slash-and-burn agriculture have triggered research on alternative systems to slash-and-burn. Some of these potential systems, such as leguminous cover crops or alley cropping, rely on planted fallows with species providing superior conditions for earthworms (Hauser 1993; Hauser & Asawalam 1998). Earthworm abundances and surface casting increased in such systems. If implemented in farmers' fields, similar effects can be expected and thus it will be an advantage to elucidate what farmers' perceptions of earthworms are. This would be of particular importance if earthworms are perceived as pests. Furthermore, if a modular approach is taken to step-wise transform slash-and-burn agriculture into forms with less negative environmental, biological and agronomic effects, it may be helpful to support the introduction of such steps with information on the components in the systems which are promoted and will contribute to increased production. Earthworms are a group of soil fauna, which can both benefit from alternative systems to slash-and-burn and contribute to yield increases. A survey was designed to evaluate: (1) farmers'

awareness of presence and activity of earthworms, (2) the use of presence or activity of earthworms as indicators of soil fertility, and (3) farmers' perception of earthworms effects on soil fertility and crop production.

Materials and methods

Survey sites

The survey was conducted in seven villages in southern Cameroon, within a benchmark area characterized by the level of deforestation, population density and level of agricultural intensification (Thenkabail 1999). The villages Nkometou and Nkolfoulou are near (< 50 km) the capital Yaoundé. According to Nolte et al. (2001) the area around and north of Younde, where Nkolfoulou and Nkometou are located, is severely deforested with a high land use intensity and population densities of up to 80 persons km^{-2}; 24.9% of land is under forest, 28.5% under fallow and 26.7% is cropped. The villages Metet, Awae and Mvoutessi are 60 - 100 km south of Yaoundé in a moderately deforested area with medium land use intensity and population densities of around 30 km^{-2}; 39.5% of the land is under forest, 15.8% under fallow and 19.9 is cropped. The villages Akok and Ngoungoumou are 130 - 200 km south of Yaoundé in a largely forested area with 56.8% of land under forest, 10.2% under fallow and 12.6% currently being cropped, thus with a low land use intensity and population densities ranging from 20 to 4 persons km^{-2} (Kotto-Same et al. 2000).

The principal ethnic group in southern Cameroon is the Beti with sub-groups of Ewondo, Bane and Eton dominating near Yaounde, and Fong, Bulu, Ngoumba, Maka, being the main tribes in Akok and Ngoungoumou. The history of agriculture of this area could be traced back to the pre-colonial era when division of labor was based on gender, age, and social status with specialization in art, performance, rhetoric and hunting (Diaw 1997).

Survey approach

The survey was conducted in three steps. The first step was an interview of 20 farmers in Nkometou and Akok in March 1999 to develop the questionnaire which, was used in the second stage during April and May 1999. Forty farmers per village were expected to respond individually. This target was only reached at Nkometou (Table 1). Farmers were questioned at their homes. After the compilation of answers, in a third step, two workshops were held with 24 farmers from Ngoungoumou, Metet, Mvoutessi and Akok and 24 farmers from Awae, Nkolfoulou and Nkometou to validate the responses (Table 1).

Table 1. Number of farmers interviewed from different villages

Distance from Yaounde	up to 50 km		60 to 120 km			130 to 200 km		Total
Village name	Nkometou	Nkolfoulou	Mvoutessi	Awae	Metet	Akok	Ngoungoumou	
Farmers interviewed	41	31	35	36	27	16	29	215
Farmers at the workshops	9	9	6	6	6	6	6	48

Statistical analysis

The FREQ procedure of SAS release 8 was used to calculate frequency distributions of responses. Differences between the distributions of responses were determined by the Chi-square test. Differences with P values <0.05 are regarded as statistically significant, yet P values are reported up to P <0.1.

Results

Demographic information

All of the 215 questioned farmers practiced slash-and-burn agriculture based on fallow / crop rotation. The age of the respondents ranged from 19 to 82 years. The gender distribution of the respondents was 51.9% female and 48.1% male which is close to the southern Cameroonian average (Anonymus 2000).

Indigenous knowledge about earthworms in southern Cameroon

Almost all farmers (99.1 %) reported that surface casts were deposited by earthworms, that casting occurs mainly in the early morning hours and is restricted to the rainy season.

Individual farmers distinguished up to 5 'types' of earthworms. An approximate total of 12 perceived 'types' was compiled across villages. Length, color and habitat were the main characteristics used to differentiate between 'types'. Not all types had common local names.

Mucus linings and, at certain times in the year, surface casts were noticed as indicating the presence of earthworms. In a few cases farmers claimed that wilting plants are indicating the activity of earthworms.

Table 2. Relative distribution (%) of farmers perceived abundance of earthworms in different land use systems in the forest zone of southern Cameroon

Land use system	Abundance of earthworms				
	Absent	Few	Moderate	Many	No opinion
Forest	10.2	10.6	17.6	25.1	36.5
Crop after forest	7.4	11.6	24.5	21.3	35.2
Valley fringe	7.4	4.2	11.6	33.8	43.0
Young fallow	12.0	15.3	16.6	19.5	36.6
Crop after young fallow	8.3	19.5	26.4	7.4	38.4
Cacao plantation	5.1	18.5	17.1	11.1	48.2

The perceived abundance of earthworms was reported to be land use system specific (Table 2). In the valleys and forests 33.4% and 24.7% of farmers, respectively, reported that earthworm abundance was higher than in any other land use system. The reasons given were: good structured soil (40.9% of farmers), soil humidity (31.6%) and a high soil fertility status (2.3%). A clear reduction in earthworm abundance was reported from cropped fields after short bush fallow of 3-7 years.

Earthworms as indicators of soil fertility

Farmers use several indicators to assess if the soil under fallow has attained sufficiently high levels of fertility to be ready for cropping. Next to fallow age and vegetation composition, signs of presence or activity of soil macrofauna was used by 42.1% of farmers as an indicator of sufficient soil fertility to crop. The presence of earthworm casts was the best indicator for 38.9% of farmers. Another 3.2% of farmers believed that termites, ants and other soil animals are the best indicators of soil fertility.

Perception of earthworm' effects on soil fertility

Most farmers (98.6%) believed that earthworms had no effect on soil fertility, and only 0.7% of farmers believed that earthworms either increased or decreased soil fertility. The remaining 0.7% of farmers did not express an opinion. Farmers made no distinction between different crops or fallows with respect to earthworms effect on soil fertility.

Perception of earthworms' effects on crop production

Across all crops, 71.2% of the farmers (range 68.0 - 80.3%) reported that earthworms have no effect on crop yields (Table 3). Positive effects were regarded as crop specific: 30.1% of the farmers believed in yield increases of groundnut (*Arachis hypogaea*) and cassava (*Manihot esculentus*), due to the presence of earthworms. For maize (*Zea mays*), plantain (*Musa* spp.), cocoyam (*Xanthosoma sagittifolium*) and cacao (*Theobroma cacao*), 27.7, 26.4, 26.3 and 19.2% of the farmers believed in yield increases. Across crops only 1.8% of the farmers (range 0.5 - 3.8%) believed that earthworms reduced crop yields, with the highest proportion in plantain (3.8%).

Between villages, there were significant differences in frequency distributions of answers on the yield response of crops to earthworms. For groundnut and cassava these differences are reported in tables 4 and 5. A highly significant differences were found between the villages Awae and Metet compared with the more southern villages of Akok and

Table 3. Relative distribution (%) of farmers' responses on effects of earthworms on crop yields

Crops	Yield increases	Yield decreases	No effect
Groundnut	30.1	1.9	68.0
Plantain	26.4	3.8	69.8
Cassava	30.1	1.4	68.5
Maize	27.7	2.4	69.9
Cacao	19.2	0.5	80.3
Cocoyam	26.3	0.5	73.2
Mean	26.6	1.8	71.6

Ngoungoumou as well as Mvoutessi and Nkolfoulou. Farmers at Awae and Metet were convinced strongly that positive effects were caused by the presence of earthworms. At Nkometou about one quarter of the respondents believed in positive yield effects due to earthworms. In all other villages, the majority believed that earthworms had no effect on yields of either cassava or groundnut yields. For other crops a similar comparison was not possible because there were not enough farmers in all villages who had sufficient experience with all other crops.

Gender differences were insignificant, yet it is noteworthy to mention that female farmers appear to be less convinced of any yield effects caused by earthworms (73.6% no effects) than male farmers (62.2% no effects). Of the male farmers, 35.9% believed in yield increases of cassava and groundnut.

Discussion

Virtually all southern Cameroonian farmers are aware of earthworms and their activities. Many of the basic features of earthworm ecology are well known and farmers' reports on the abundance of earthworms in different land use systems reflect or can be explained by the results of the few investigations conducted in southern Cameroon. The absence of a common set of names for the most frequently encountered earthworms may, however, indicate that the interest in the animals is limited. This contrasts strongly with the level of resolution in knowledge of the local names of trees and weeds, which is often to species level. An indigenous system of earthworm taxonomy was reported from south-east Mexico (Ortiz et al. 1999), which, however, did not tally with the scientific classification because farmers grouped different species under the same name.

Table 4. Relative distribution (%) of farmers' perception by village of the effect of earthworms on groundnut production

Village	Increase (%)	Decrease (%)	No effect (%)	Levels of significance of differences between villages, determined by Chi-square test.					
				versus Metet	versus Nkometou	versus Akok	versus Ngoungoumou	versus Mvoutessi	versus Nkolfoulou
Awae	91.5	0.0	8.5	0.06	<0.001	<0.001	<0.001	<0.001	<0.001
Metet	74.1	0.0	25.9		<0.001	<0.001	<0.001	<0.001	<0.001
Nkometou	21.9	0.0	78.1			ns	0.03	0.04	0.01
Akok	6.3	6.2	87.5				ns	ns	ns
Ngoungoumou	3.7	0.0	96.3					ns	ns
Mvoutessi	2.9	5.7	91.4						ns
Nkolfoulou	0.0	3.1	96.9						

Table 5. Relative distribution (%) of farmers' perception by village of the effect of earthworms on cassava production

Village	Increase (%)	Decrease (%)	No effect (%)	Levels of significance of differences between villages, determined by Chi-square test.					
				versus Metet	versus Nkometou	versus Akok	versus Ngoungoumou	versus Mvoutessi	versus Nkolfoulou
Awae	85.7	0.0	14.3	ns	<0.001	<0.001	<0.001	<0.001	<0.001
Metet	77.8	0.0	22.2		<0.001	<0.001	<0.001	<0.001	<0.001
Nkometou	24.4	4.9	70.7			ns	0.03	0.02	0.003
Akok	6.3	0.0	93.7				ns	ns	ns
Ngoungoumou	3.7	0.0	96.3					ns	ns
Mvoutessi	2.9	2.8	94.3						ns
Nkolfoulou	0.0	0.0	100.0						

The abundance, species richness and surface casting activity is different in the villages surveyed (chapters 3 and 4). It has to be assumed that farmers' accuracy in observing earthworms, their activity and effects is related to their abundance and the level of surface casting activity. Metet and Awae are villages reporting a high level of surface casting, particularly when compared to the villages of Nkometou and Ngoungoumou (chapter 3). High levels of surface casting were usually associated with a strong belief in positive yield effects from earthworms, which may result from farmers observing that casting and abundance were reduced in short fallow fields, which are often perceived as less productive after a number of fallow / crop cycles. Hauser & Asawalam (1998) and Norgrove et al. (1998) showed that surface casting is drastically reduced in slash and burn systems after short fallows of 2 - 4 years. Short fallow fields are not capable to support the production of certain crops such as plantain which is usually planted after forest clearing (Hauser 2000). Perceived differences in earthworm abundance between forest and fields which are usually planted to plantain are small (Table 2), indicating that, in these probably more fertile soils, earthworms can persist after forest clearing. Norgrove & Hauser (2000) showed that casting reduction in plantain fields after plantation forest clearing was less than in fields cleared from short fallow (Norgrove et al. 1998).

Earthworms are considered to be indicators of soil fertility by more than one third of farmers. Traditionally, 4 criteria are used to recognize fertile soil: (1) fallow length (fertility status positively correlated to fallow age), (2) soil color (the darker the soil the more fertile), (3) type of vegetation (locally differentiated, yet, mainly through the absence of certain species, usually weeds of the cropping phase in short fallow systems) and (4) presence of macrofauna. The relative importance of earthworms as indicators of a fertile soil stands in strong contrast to farmers not believing that earthworms increase soil fertility. Farmers apparently believe that earthworms are the consequence rather than the creators of the fertile soil. This belief contrasts with results from southern Cameroon, which show that earthworms concentrate plant nutrients in the surface casts (Norgrove & Hauser 2000), which are usually richer than the top-soil. The factor by which casts are enriched increases with decreasing soil nutrient concentration. Thus, the poorer the soil the more important the contribution of earthworms to nutrient accumulation at the soil surface. Here, it appears that raising farmers' awareness of earthworms effects on soil fertility could lead to a better understanding of the role of earthworms in crop production, which may help to introduce alternative farming techniques to slash-and-burn, which, in turn, may maintain larger earthworm populations and

levels of activity. An average of 26.6% of the farmers that believe in positive yield responses of crops in the presence of earthworms is thus rather encouraging.

However, the belief of the farmers that earthworms reduce crop yields needs to be addressed. For groundnut, maize, cocoyam, cacao and cassava the number of farmers believing in earthworms causing crop damage was low and no specific reasons were given. In the case of damage to plantain, farmers reported that they could see the earthworms (feeding) in the rotten pseudostems and corms. Therefore they believed that the earthworms had caused the death of the plantain. A similar reason was given to using wilting plants as indicators of earthworm activity: earthworms can often be found (feeding) on the dead root system of wilting plants.

Conclusion

Because many causal agents of crop damage are not visible (nematodes, fungi, bacteria, viruses), there is sometimes a misconception that earthworms are pests. This is most likely due to their feeding on dead or damaged plant tissue. However, the appreciation of earthworms as soil fertility indicators and the predominant belief that they have positive effects on crop yields, is a good basis for the introduction of alternative technologies, such as slash-and-mulch and green manure cover crop systems without prior burning; such approaches may maintain diverse earthworm communities.

Acknowledgments

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Earthworm surface-casting activity on slash-and-burn cropped land and in undisturbed *Chromolaena odorata* and young forest fallow in southern Cameroon

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Summary

The effect of slash-and-burn agriculture on earthworm surface-cast deposition was assessed in 4-5 year old *Chromolaena odorata* (CHR) and young forest (YFOR) fallow (12-15 years) in the humid forest zone of southern Cameroon. In the villages Ngoungoumou (56.8% forest cover), Metet (39.5% forest cover), and Nkometou (24.9% forest cover), plots were established in both fallow types and half were slashed, burned, and cropped in 2000, the rest were maintained as undisturbed controls. In 2001, cropped plots were split, one half abandoned to fallow, the other cropped a second time as in 2000. Casts were collected weekly from April to December in 2000 and 2001.

In 2000, surface-cast deposition was different between villages, in both fallow types and land uses. At Nkometou casting was lowest and no effects of fallow type or land use were found. At Metet and Ngoungoumou, more casts were deposited in undisturbed fallow (22.5 and 3.0 Mg ha^{-1}) than in the cropped treatment (7.1 and 0.6 Mg ha^{-1}). Cropping reduced cast deposition in both fallow types, yet more so in CHR than in YFOR.

In 2001, as in 2000, no differences were found at Nkometou. At Metet and Ngoungoumou, more casts were deposited in undisturbed controls than in the other treatments. Cast deposition was higher in plots in the first year of fallow after cropping than in double-cropped plots, indicating an immediate recovery after cropping. Cast production was not correlated with soil chemical properties across villages. Earthworm species assemblages were different between villages, with large-bodied, endogeic and anecic species most abundant at Metet. Earthworm species assemblage is likely to be the main factor determining surface-cast deposition and thus differences between villages.

Key words: Congo basin, land use intensification, slash-and-burn agriculture, southern Cameroon

Introduction

Tropical smallholder farming systems rely largely on biological processes of soil fertility maintenance and restoration. Earthworms can contribute to nutrient cycling and accumulation by casting at the soil surface. Earthworm casts can positively affect plant growth in the tropics (Spain et al. 1992; Pashanasi et al. 1996, Asawalam & Hauser 2001), most likely due to higher nutrient concentrations in casts than in the soil (Lal & De Vleeschauwer 1982). Norgrove & Hauser (1999) showed that nutrients from casts were more available to a maize crop than those from the soil. Hauser & Asawalam (1998) and Norgrove & Hauser (2000) showed that with decreasing soil nutrient concentration the factor by which earthworms enriched the casts increased, indicating the increasing importance of earthworm surface-casting with decreasing soil fertility. Thus, a high earthworm surface-casting activity is desirable in low input agricultural systems to concentrate nutrients at the soil surface.

Total cast production is an indicator of burrowing and soil turnover, because 99.9% of ingested material is egested as casts (Lavelle 1974). Norgrove & Hauser (1998) did not find sub-surface-casts while sampling to 2 m depth in pits near Mbalmayo, a location not far from the villages reported upon here. Thus, it appears that surface-casting alone can serve as a direct indicator of earthworm activity. Cast deposition at the surface is a viable indicator of earthworm biomass (Dash & Patra 1979).

Food crop production in smallholder systems is largely by slash-and-burn agriculture. Slashing, burning and cropping reduce earthworm density, diversity and activity (Critchley et al. 1979; Lavelle & Pashanasi 1989). In southern Cameroon and larger parts of the Congo basin, farmers maintain a mosaic of fallow types and age classes for their different crop fields. The most commonly established food crop field in southern Cameroon is a groundnut / maize / cassava intercrop, for which either 4 to 5 years old fallow, dominated by *Chromolaena odorata* or young secondary forest of 12 to 15 years is slashed and burned (Büttner 1996).

It has been shown in planted fallow systems and other researcher-managed trials, that earthworms are strongly affected by the type of fallow, the biomass management system (Hauser & Asawalam 1998) and the crop cover (Norgrove et al. 1998). Little information is available on the effects on earthworm surface-cast deposition, in slash-and-burn agriculture in farmers' fields of different fallow age in the Congo basin.

We hypothesize that (1) cast deposition is higher in young forest than *Chromolaena odorata* fallow, (2) clearing young forest leads to more severe reductions in surface-cast deposition than clearing *C. odorata* fallow, (3) during a first-year fallow, casting is higher

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than in a field cropped for a second year and (4) there is no effect on cast deposition of the location of the village within which these land use changes are imposed.

Materials and Methods

Location

The experiment was established at Ngoungoumou (12°01' E, 3°18' N, Typic Kandiudox), Metet (11°45' E, 3°25' N, Typic Kandiudult) and Nkometou (11°35' E, 4°05' N, Rhodic Kandiudult), three villages in southern Cameroon, representing increasing levels of deforestation and land use intensification (Thenkabail 1999). According to Nolte et al. (2001) in the area north of Yaounde (Yaounde block), where Nkometou is located, 24.9% of the land is under forest, 28.5% under fallow and 26.7% is cropped. Around Mbalmayo (Mbalmayo block), where Metet is located, 39.5% of land is under forest, 15.8% under fallow and 19.1% is cropped. Ngoungoumou is represented by the southern part (Ebolowa block) of the area investigated by Nolte et al. (2001) with 56.8% of land under forest, 10.2% under fallow and 12.6% currently being cropped. Due to the large number of plant species in fallows and forests it is not possible to include a botanical description of the fallow types. For details, refer to Zapfack et al. (2002), who characterized the vegetation in several villages in these three blocks. Annual rainfall in the area is bimodal. Rains start in mid-March and end in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November. In 2000 and 2001 rainfall totals were respectively 1347 mm and 1114 mm in Nkometou, 1495 and 1265 in Metet and 1456 mm and 1167 mm in Ngoungoumou.

Experimental set-up

In each village, a 4-5 year old *Chromolaena odorata* fallow (CHR) and a 10-12 year old young forest (YFOR) were identified. Sites were selected on the basis of: size, as they were required to be at least 100 m x 25 m large; proximity of the two vegetation types; and, that the previous land use prior to vegetation succession to CHR or YFOR, was in all cases a mixed food crop field dominated by groundnut, maize and cassava. Each site was divided into 6 plots, 15 m x 15 m, located in the centre of the site and thus leaving borders up to 5 m with the bordering vegetation. Three plots were cleared and burned and 3 served as undisturbed controls. In February 2000, the CHR sites and the understorey of the YFOR were slashed. In the YFOR sites all trees were felled manually. The biomass was left to dry and burned by the end of March 2000. In both fallow types, unburned materials were piled and burned again. The 3 cropped and

the 3 undisturbed plots in each site served as replicates, thus, a total of 18 cropped and 18 undisturbed control plots were established.

An intercrop of groundnut (*Arachis hypogaea* L.) local cultivar, maize (*Zea mays* L.) cultivar CMS 8704 and cassava (*Manihot esculenta* Crantz) cultivar 8017 was planted in both fallow types. First, groundnuts were seeded at approximately 20 seeds m^{-2}, by tilling the grains into the soil with hand hoes. Cassava was planted at 1.5 by 1.5 m inter- and intra-row distance. Two, approximately 30 cm long, cassava sticks were planted in each hole. Two pockets of two maize seeds were planted between cassava pockets at 0.5 m distance between cassava pockets, yet only in one direction of the lines. Seeding was in the second and third week of April in 2000 and the third and fourth week of April in 2001.

Measurement of earthworm surface-casting

Surface-casts were collected in 0.75 m x 0.75 m frames. Six frames were placed at random in each plot. All surface-casts were collected from the frame once a week, beginning in April of each year. Casting stopped in December. Casts were oven-dried at 65°C for 48 hours after each sampling and the dry weight per frame was recorded. Cast material was pooled by plot at the end of each year for analyses of texture and chemical properties.

Earthworm sampling and identification

Between May and August 1999, prior to establishing the cropped plots, five soil monoliths of 50 x 50 x 30cm (L x W x D) were dug out in each fallow. Earthworms were hand-sorted immediately; specimens were killed in ethanol and preserved in 4% formaldehyde solution. At about 2 m distance from each monolith, 10 liters of 0.004% formaldehyde solution were gently poured into a PVC ring of 50 cm diameter and 10 cm height. Ten minutes were allowed for the solution to infiltrate, and then worms were collected from the surface. Samples were identified at Systematic Zoology Research Group of the Hungarian Academy of Sciences at ELTE University, Budapest, Hungary. Both sample types were used to compile the species assemblage.

Soil sampling

Soil was sampled in 2001, at groundnut and maize harvest in July. Next to each of the cast sampling frames three samples of the 0-10 cm soil layer were taken and bulked. Samples were oven dried at 65°C, then ground to pass through a 0.5 mm mesh size sieve and analyzed for pH, total N, organic C, available P and exchangeable Ca, Mg and K. Soil pH was determined

in a water suspension at a 2:5 soil/water ratio. Exchangeable Ca^{2+}, Mg^{2+}, K^+ and available P were extracted by the Mehlich-3 procedure (Mehlich 1984). Cations were determined by atomic absorption spectrophotometry and P by the malachite green colorimetric procedure (Motomizu et al. 1983). Organic C was determined by chromic acid digestion and spectrophotometry (Heanes 1984). Total N was determined using the Kjeldahl method for digestion and ammonium electrode determination (Bremner 1982; Bremner & Tabatabai 1972).

Design and statistical analysis

Analyses of variance were conducted using the General Linear Model (GLM) procedure of SAS version 8. Data were analyzed in a 3-factorial design: (1) village at 3 levels, (2) fallow type at 2 levels (*Chromolaena odorata* dominated fallow 4-5 years, and young forest of 10-12 years), (3) land use at 2 levels in 2000 (undisturbed control and cropped) and 3 levels in 2001 (undisturbed control, first year fallow, and second year crop). Replicates were treated as nested within fallow type. Data were log (n+1) transformed prior to analysis. All treatment interactions were included in the model. Years were analyzed separately. Where a factor was significant, pairwise comparison of least square means of selected treatments was performed using the Pdiff option. Procedure REG was used to conduct simple and stepwise regressions between amounts of casts and soil chemical parameters.

Results

Cast production

In 2000, the factors village and land use and all two-way interactions were significant (Table 1). All three villages were significantly different from each other in casting in the two fallow types and in cropped and undisturbed land. In Nkometou, cast production was generally very low and no effects of treatments were detected. At Metet cast production was the highest, with no difference between fallow types. At Ngoungoumou casting was significantly higher in YFOR (2.090 Mg ha^{-1}) than in CHR (1.566 Mg ha^{-1}, P=0.024). Across villages, there were no differences in cast production between undisturbed CHR and undisturbed YFOR. However, at Metet and Ngoungoumou cropping reduced casting significantly (P<0.001). Within each fallow type, cropping reduced casting significantly with greater absolute and relative reductions in CHR than in YFOR. In CHR casting in the undisturbed control was higher than in YFOR, while when cropped, casting was higher in CHR than YFOR (P=0.03).

Table 1. Cumulative earthworm casts (Mg ha^{-1} dry matter) deposited in three villages and cropped fields versus undisturbed controls in *Chromolaena odorata* dominated and young forest fallow, in southern Cameroon, in 2000. P values values based on log-transformed data for tables 1-3.

Fallow	Village			P values		
	Metet	Ngoungoumou	Nkometou	Metet vs. Ngoungoumou	Metet vs. Nkometou	Nkometou vs. Ngoungoumou
Chromolaena	17.789	1.566	0.019	<0.001	<0.001	<0.001
Young forest	11.841	2.090	0.046	<0.001	<0.001	<0.001

Land use	Metet	Ngoungoumou	Nkometou	Metet vs. Ngoungoumou	Metet vs. Nkometou	Nkometou vs. Ngoungoumou
Undisturbed	22.488	2.970	0.035	<0.001	<0.001	<0.001
Cropped	7.146	0.648	0.030	<0.001	<0.001	0.004

Fallow	Undisturbed	Cropped	P values
Chromolaena	10.584	2.332	<0.001
Young forest	6.409	2.909	<0.001

Table 2. Cumulative amount of earthworm casts (Mg ha^{-1} dry matter) deposited in three villages and first year fallow, second time cropped fields and undisturbed controls in southern Cameroon, in 2001 (mean of *Chromolaena odorata* dominated and young forest fallow).

Land Use	Village			P between villages		
	Metet	Ngoungoumou	Nkometou	Metet vs. Ngoungoumou	Metet vs Nkometou	Nkometou vs Ngoungoumou
Undisturbed	18.839	1.851	0.224	<0.001	<0.001	<0.001
1. year fallow	7.702	0.684	0.134	<0.001	<0.001	ns
2. time cropping	5.422	0.112	0.103	<0.001	<0.001	ns

Fallow type	Metet	Ngoungoumou	Nkometou	Metet vs. Ngoungoumou	Metet vs Nkometou	Nkometou vs. Ngoungoumou
Chromolaena	11.435	0.594	0.198	<0.001	<0.001	ns
Young forest	9.873	1.171	0.109	<0.001	<0.001	<0.001

CHR = Chromolaena, YFOR = young forest, ns = not significant

Table 3. ANOVA results of soil chemical properties in three villages (village) and cropped fields versus undisturbed controls (land use) in *Chromolaena odorata* dominated and young forest fallow (fallow), in southern Cameroon, in 2001. org.=organic, av.=available, exch.=exchangeable

	pH	Total N	org. C	av. P	exch. Ca	exch. Mg	exch. K
land use	<0.001	ns	ns	ns	<0.017	<0.050	ns
fallow	<0.008	ns	ns	ns	ns	ns	<0.017
Village	<0.001	ns	ns	<0.001	<0.009	<0.001	<0.034
fallow * village	ns	<0.045	ns	ns	ns	ns	ns
village * fallow * land use	ns	ns	<0.047	ns	ns	<0.021	<0.015

ns = not significant

In 2001, the factors village and land use and the village x fallow and village x land use interactions were significant. The undisturbed controls were different between all three villages (Table 2). At Metet, significantly more casts were deposited in all three land uses than at Ngoungoumou and Nkometou. Again, at Nkometou casting was lowest and no significant treatment effects were detected. At Ngoungoumou and Metet, cast production was greater in the undisturbed control plots than in the plots cropped for a second time (P<0.001) and those in the first year of fallow after cropping (P<0.003) and a significant recovery of casting occurred in the plots fallowed after cropping compared to those that were double cropped (P<0.048). Fallow type had no effect at Metet, while in Ngoungoumou, more casts were deposited in YFOR than in CHR fallow (P=0.004).

The change in casting caused by cropping compared to the undisturbed control depended on both the fallow type and the village. At Nkometou, no reduction in casting was found in the CHR fallow, yet the largest decrease in casting in the YFOR fallow (-87.5%) compared to the other two villages (Metet -70.1% in CHR and -55.5% in YFOR, Ngoungoumou -98.6% in CHR and -47.6% in Yfor). The increase in casting in the CHR fallow (+7.5%) at Nkometou was significantly different from all the other treatments.

Relationships between soil chemical properties and cast production

Soil pH, available P, exchangeable Ca, Mg and K were different between villages (Table 3). Nkometou had higher pH (6.60), available P (8.63 mg kg^{-1}), and exchangeable Ca (4.36 cmol[+]kg^{-1}) and Mg (1.06 cmol[+]kg^{-1}) concentrations than the other two villages. Ngoungoumou had the lowest pH (5.17), available P (5.31 mg kg^{-1}), and exchangeable Ca (2.17 cmol[+]kg^{-1}) and Mg (0.68 cmol[+]kg^{-1}) concentrations. Soil properties at Metet were somewhat intermediary with the exception of exchangeable K (0.107 cmol[+]kg^{-1}) which was lower than at Nkometou (0.140 cmol[+]kg^{-1}) and Ngoungoumou (0.146 cmol[+]kg^{-1}). Total N had a village x fallow interaction, organic C had a significant village x fallow x land use interaction.

Across villages, cast production was not correlated to any of the soil chemical properties (all r^2 < 0.018, all P > 0.33). Within Nkometou, no correlations between cast production and soil chemical properties were found. Within Metet, cast production was weakly positively correlated with exchangeable K (Cast = 81.6 K + 1.95 , r^2 = 0.286, P = 0.022). Within Ngoungoumou, cast production was weakly, positively correlated with total N (Cast =36.1 N - 5.97, r^2 = 0.302, P = 0.018).

Earthworm species assemblages

A total of 21 species was found in the two fallow types in all three villages (Table 4). Of these, 6 are undescribed, including one new genus. Fourteen species were found at Metet and 7 species at both Ngoungoumou and Nkometou. The number of species found in YFOR CHR were similar (14 and 15 respectively). The number of species found exclusively in one village, was 9 at Metet, 4 at Ngoungoumou and 2 at Nkometou. Thus 15 out of 21 species were site-specific. On the other hand, species that occurred in only one fallow type were 7 in CHR and 6 in YFOR

Table 4. Earthworm species assemblages in three villages and two land use systems in southern Cameroon.

Species	Chromolaena fallow	Young forest	Species found in only one village	Species found in only one fallow
Acanthodrilidae				
Dichogaster annae	M		M	CHR
Dichogaster bolaui	K	M		
Dichogaster ehrhardti	K G			CHR
Dichogaster gracilis		M	M	YFOR
Dichogaster kungulunensis	G		G	CHR
Dichogaster modiglianii		M K		YFOR
Dichogaster sp. nov. 1		M	M	YFOR
Eudrilidae				
Eudrilidae gen. nov.	K		K	CHR
Buettneriodrilus sp. nov. 1		G	G	YFOR
Legonodrilus sp. nov. 2.	G		G	CHR
Legonodrilus sp. nov. 3.	M	G		
Malodrilus buarensis	M	M K		
Malodrilus camerunensis		M	M	YFOR
Rosadrilus camerunensis	M	M	M	
Scolecillus tantillus		M	M	YFOR
Ocnerodrilidae				
Gordiodrilus sp. 1	G	G	G	
Ilyogenia sp.	M	M	M	
Nematogenia lacuum	M		M	CHR
Nematogenia panamaensis	M		M	CHR
Xibaro lavellei	K	K	K	
Xibaro sp. nov. 1	M K G	M K G		
TOTALS	8 M 5 G 5 K	10 M 4 G 4 K	9 M 4 G 2 K	7 CHR, 6 YFOR

M = Metet, G = Ngoungoumou, K = Nkometou

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Discussion

Earthworm surface-cast production was strongly affected by the site, yet, could not be explained by soil chemical properties across sites or within sites. Hypothesis 4 has thus to be rejected. The level of deforestation was apparently not related to the levels of cast deposition. No information on earthworm surface-cast production at different levels of disturbance from different sites in the humid tropics could be found. Within one site, Hauser & Asawalam (1998) reported no effects of soil chemical properties on cast production on an Alfisol in south-western Nigeria. Here, the remarkable aspect is that at Nkometou, on soil well endowed with N, P, C and basic cations and a relatively high pH, casting was the lowest, while in the two less fertile sites casting was higher than at Nkometou.

As in all three sites the same fallow type was used and the same intercrop was planted, it can be assumed that substrate (food) quality and availability were the same. Rainfall and its distribution did not differ profoundly between the villages. Thus, differences other than climatic and chemical conditions caused the differences in cast production. Earthworm population densities were higher at Nkometou, yet the species assemblages were not the same in all villages (chapter 4). Large-bodied, endogeic and anecic species were most abundant at Metet. *Rosadrilus camerunensis*, a large-bodied, probably anecic species and *Scolecillus tantillus,* an endogeic species, were abundant at Metet, yet were not found in the other villages. Probably all *Dichogaster* spp. found here are epigeics, thus not likely to contribute large surface-casts. The species of the Ocnerodrilidae are all small-bodied endogeics (6 species), of which 4 were present at Metet (three exclusively so). Although little is known about their ecology, these differences in species assemblages may be the main reason for the large differences in surface-cast deposition between villages. However, it remains to be investigated which factors are responsible for the presence or absence of certain species in certain sites.

Higher cast deposition in YFOR than CHR was only found at Ngoungoumou, thus hypothesis 1 cannot generally be accepted. Slash and burn agriculture has multiple effects on the soil and soil fauna, many of which are dependent on the scale and intensity of disturbance. Detrimental effects of slash and burn agriculture on earthworm casting were reported by Badhauria & Ramakrishnan (1989), Hauser & Asawalam (1998) and Norgrove et al. (1998). Here the effect of slash and burn on the amounts of casts was only significant under the medium and high casting conditions at Ngoungoumou and Metet. Considering the low casting level at Nkometou, our results do not contradict previous results. Asawalam (1997) found

highly variable responses in cast production after slash and burn on an Alfisol in south-western Nigeria. Norgrove et al. (this issue) showed that surface-cast deposition after slashing *C. odorata* dominated fallow was significantly affected by biomass management (burning and mulching), yet in all cases lower than in the undisturbed control.

The more severe reductions in casting in cropped CHR than in YFOR indicate that either edaphic conditions in YFOR are maintained more favorably for earthworms survival and continued activity or the YFOR assemblages are more resilient. Hypothesis 2 was based on the expectation that in land more often cropped and with shorter phases of recovery between slash-and-burn cropping, assemblages are better adapted to the sudden change imposed. This is apparently not the case and hypothesis 2 has to be rejected.

The recovery of cast deposition during first-year fallow after cropping indicates resilience of the assemblages, as soil properties usually do not recover quickly. However, the magnitude of recovery, expressed as a percentage of the difference between undisturbed control and second year cropping was only 16% and 17% at Metet and Nkometou, respectively and 31% at Ngoungoumou. Hypothesis 3 can thus be accepted, yet information on the time required to reach casting levels as in the undisturbed control is not available from investigations in realtime-series.

Where casting levels are moderate to high such as in Ngoungoumou and Metet, slash-and-burn agriculture has a negative effect on earthworm surface-casting and thus nutrient cycling. However, as this effect was dependent on the fallow type and as recovery started immediately after cropping, long-term effects cannot be assessed. Thus further research on individual factors affecting surface-casting and its recovery during fallow phases is required.

Acknowledgements

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Earthworm community structure along a gradient of land use intensification in the humid forest zone of southern Cameroon

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Abstract

This study describes the community structure of earthworms along a gradient of land use intensity (LUI) in the forest margin zone of southern Cameroon. High LUI (Nkometou and Minkoameyos villages) is highly deforested (25% forest cover); medium LUI (Mbalmayo and Metet villages) is moderately deforested (40% forest cover) and low LUI (Akok and Ngoungoumou) is largely forested (57% forest cover) with low population density. In each village, earthworms were collected during the rainy season in 5 land use systems (LUSs) of different levels of disturbance by hand- sorting 5 monoliths (50 x 50 x 30 cm). The sampled LUSs were: secondary forest 30 years old (Sfor), shaded cacao plantation (Cacao), young forest of 12-15 years (Yfor), 4-5 year old *Chromolaena odorata* (Chr) and a groundnut/maize/cassava intercrop (Crop).

A total of 36 earthworm species were found of which 1 new genus and 17 undescribed species, belonging to 3 families: Acanthodrilidae, Eudrilidae and Ocnerodrilidae. Abundance ranged from 64 to 236 individuals m^{-2}. Biomass ranged from 2 g m^{-2} to 16 g m^{-2}. Low LUI harbored more species (24) than medium (21) and high (18) LUI but these differences were not significant. Epigeic earthworms in Yfor in the medium LUI were 3 times more abundant than endogeic earthworms and this LUS significantly outnumbered all the other LUSs in earthworm abundance and biomass. Diversity was low but evenness high in all 3 LUIs. LUI had a significant effect on the diversity indices of all the LUSs based on species data. There was a significant effect of LUI (F=4.31, P=0.033) and a highly significant effect of LUS (F=7.35, P=0.0003) on Simpson's diversity index on a biomass basis. PCA and CA on species data clearly separated the high LUI block from the other two but no difference was found between low and medium LUIs. High LUI harbored a completely different earthworm assemblage while low and medium LUI had a lot of species in common. Intensification is likely to be the factor determining this difference in community structures between LUIs.

Key words: Earthworm, community structure, land use intensity, land use system, disturbance, south Cameroon.

Introduction

The importance of earthworms in soil processes and their potential use in agriculture are currently of wide interest. Many studies have evidenced that earthworms are powerful regulators of soil processes, contributing to the maintenance of soil structure and the regulation of soil organic matter dynamics (Lavelle, 1997; Brussaard, 1998). They produce physical structures (casts, burrows) that are specific sites of regulation for macroscale soil processes. Their casts are organo-mineral aggregates that, after drying, generally are more stable than bulk soil aggregates (Blanchart et al., 1997). Mineralization of organic matter is enhanced in fresh casts, while diminished or even inhibited in dry casts (Martin, 1991; Lavelle et al., 1998). The positive impact of earthworms on plant growth was first recognized by Darwin (1881) and has been confirmed in recent studies, although negative and null effects have also been described (Brown et al., 1999). However, although their importance is well documented, their species diversity remains largely unknown, especially in the tropics. The most recent account of earthworm diversity (Edwards, 1998) is 3627 species described worldwide, with an average annual addition of 70 (Reynolds, 1994; Edwards and Bohlen, 1996). The overall species number is expected to be at least twice the current number of described species, with the majority of undescribed species living in the tropics. Of the few studies published on earthworm communities in the Congo Basin, no references were found on their distribution in the different land use systems. Within a larger program on the effects of land use change on soil macrofauna, earthworms were considered an important group of soil animals, contributing to soil property maintenance (Hauser and Asawalam, 1998; Norgrove and Hauser, 2000), yet susceptible to land use change (Norgrove et al. 1998). The increasing food demand of a rapidly growing population has led to an intensification of agricultural land use. As compared to the traditional system of slash and burn, the current systems do not permit long fallow periods for a full recovery of soil fertility: cropping phases are longer and fallow phases are shorter. Living conditions for at least some soil macrofauna are worsened to the extent that they cannot persist. Agricultural intensity is defined as a set of patterns of land use change with the common feature of increased use of the same resources for agricultural production, usually as a result of switch from intermittent to continuous cultivation f the same area of land. Associated trends are specialization in crop or livestock species utilized, increased management intervention and greater reliance on markets. The common endpoint of intensification is substitution of labor with mechanization and of organic and biological inputs and controls by chemical and mechanical inputs. The transitions from internally to externally

regulated systems, and from sustainable to degraded systems, may occur progressively or abruptly (Giller, 1997; Ruthenberg, 1980; Izac, 1996; Van Noordwijt, 2002). Deforestation and increased land use intensity are likely to change species composition in all groups of soil fauna. Furthermore, the rate of intensification of agriculture in the tropics is greater than in other regions of the world, so that ecosystems are under particular threat of major changes or loss (Izac et al., 1996). Little is known about such changes in earthworm communities in the Congo basin.

This study presents preliminary data on earthworm diversity and abundance in southern Cameroon at different levels of deforestation and land use intensity. Earthworms were sampled and differences in communities examined in five common land use systems representing different levels of ecosystem disturbance.

Materials and Methods

Study sites

The study was conducted in six villages in southern Cameroon classified into three blocks representing increasing levels of deforestation and land use intensity (LUI) within the benchmark established by ASB, IRAD and IITA (Thenkabail, 1999) known as: (1) Yaoundé block (high), (2) Mbalmayo block (medium) and (3) Ebolowa block (low) (Figure 1 and Table 1). Annual rainfall in southern Cameroon is bimodal. Rains start in mid-March and ends in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November. In 1999, annual rainfall was 1500 mm.

The commonest 5 land use systems (LUS) of the region presenting a gradient of disturbance from low to high were selected such that the ages and plot histories of the LUSs of the same type in the different villages were approximately the same: a secondary forest (>30 years, Sfor), a shaded cacao plantation (Cacao), young forest fallow (12-15 years, Yfor), 4-5 year old *Chromolaena odorata* fallow (Chr), and a groundnut / maize / cassava intercrop field (Crop). For details on vegetation, see Zapfack et al. (2002) who characterized the vegetation in several villages of these three blocks.

Earthworm sampling, counting and identification

In each LUS five soil monoliths of 50 x 50 x 30 cm (L x W x D) were dug along a 100 m transect at 20-m intervals in the rainy season between May and July 1999. Earthworms were hand-sorted immediately and specimens preserved in 4% formaldehyde (Anderson and

Ingram, 1993), then identified by the Systematic Zoology Research Group of the Hungarian Academy of Sciences ELTE University, Budapest, Hungary, then classified into ecological groups (main ecological categories, i.e., epigeic, anecic and endogeic species according to Bouché (1977)). Biomass was determined on preserved specimens after 2 years of storage. Individual worms were cleaned from formaldehyde with blotting paper, and weighed with a Mettler AE 200 digital. Data were pooled for all the individuals of a transect and expressed in g m^{-2}. We computed the ratio of epigeic/endogeic to assess the dominance of one group over the other since this can give an indication of the type of the dominant ecosystem roles fulfilled in a particular habitat.
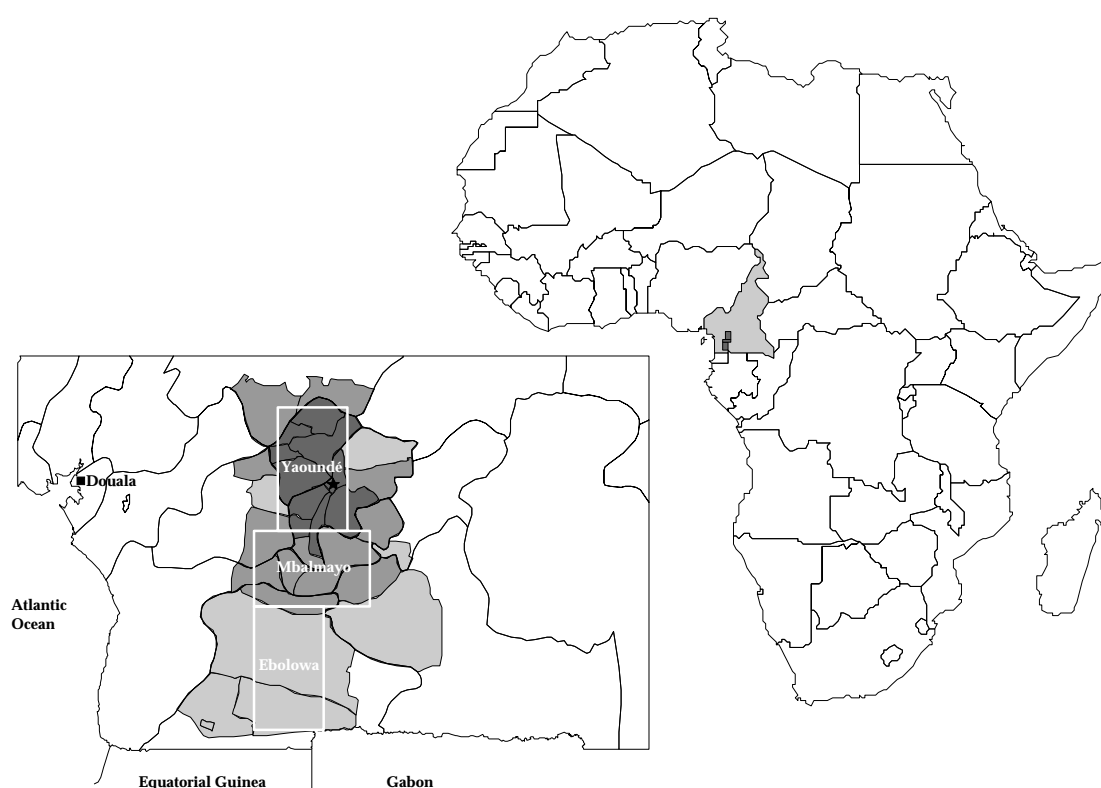
Figure 1. Map of southern Cameroon and the three land use intensification blocks within the forest margins benchmark

Diversity indices

Shannon diversity index (H') and evenness (E) were calculated based on species abundance and weight. The Simpson's index of diversity (D) was used on the same data to reduce the bias that may rise from the interpretation of a single diversity index (Magurran, 1988). D = 1- $\sum n_i(n_i-1)/N(N-1)$ where n_i = number of individuals in the ith species, and N = the total number of individuals (Magurran,1988). Steinhaus' coefficient (Legendre and Legendre, 1983) was

Table 1. Characterization of the 6 villages under study in southern Cameroon.

Block	Level of deforestation and LUI	Village	Distance from Yaounde	Geo references	Soil class	% land under forest cover	% land under fallow	% land under crop
Yaounde	High (**HL**)	Nkometou (Nk)	40 km North	11°35'E, 4°05'N				
		Minkoameyos (Mi)	15 km West	11°27'E, 3°51'N	Rhodic Kandiudult	25	29	27
Mbalmayo	Medium (**ML**)	Mbalmayo (Mb)	50 km South	11°28'E, 3°27'N				
		Metet (Me)	90 km South	11°45'E, 3°25'N	Typic Kandiudult	40	16	19
Ebolowa	Low (**LL**)	Akok (Ak)	150 km South	11°14'E, 2°44'N	Typic Kandiudox	57	10	13
		Ngoungoumou (Ng)	130 South	12°01'E, 3°18'N				

used to look at the similarity of pairs of land use systems within each village on the basis of abundance: $S_A= 2W/ (A+B)$ where W=sum of the lower of the two abundances of each species and A and B are the sums of abundances of each community.

Statistical analyses

Because juveniles could not be identified to species, only data on adults and pre-adults were used for statistical analyses at the species level. Data obtained were first subjected to simple descriptive statistics (totals, means and standard deviation, max and min, range) using villages as replicates in each LUI level. Where deemed necessary for variance homogeneity, data were subjected to log or arcsin transformation before the analyses. For analyses of variance (ANOVA), the data were treated as a nested experimental design where land-use systems were nested within intensification levels using PROC GLM of SAS version 8 (1999). Pairwise comparison of least square means of selected treatments was performed using the Pdiff option. PCA and CA multivariate analysis and co-inertia analyses on species data were performed using CANOCO for windows 4.5 (ter Braak and Smilauer, 2002) in order to assess affinities among species and between species and land use.

Results

Earthworm community

A total of 36 species (Table 2) was found, belonging to 3 families: Acanthodrilidae were represented with 12 species (4 undescribed), Eudrilidae with a new genus and 16 species (8 undescribed) and Ocnerodrilidae represented with 8 species (5 undescribed).The low LUI block had 24 species, followed by medium and high LUI blocks with 21 and 18 species, respectively. Across LUI, 8 species were found in all 3 LUI blocks and they may be considered as the basic earthworm fauna of the zone, 11 in 2 and 17 in only 1 LUI block (Table 2). Fourteen of the 36 species can be considered as characteristic for the various LUI blocks; they predominantly appear in one LUI; there were 5 such species in the high LUI block (*D. bolaui, D. modiglianii, E. kisantuanus, Lybiodrilus sp1 and X. lavellei*). The 5 species characteristic for the medium LUI were: *E. lamani, Legonodrilus sp1, Legonodrilus sp3, Rosadrilus camerounensis* and *Malodrilus buarensis*. Four species only occurred in the low LUI block: *Buettneriodrilus sp1, Gordiodrilus sp2, Gordiodrilus sp2 and Xibaro sp2*. All the other species are found in at least 2 different LUI blocks (Table 2).

Table 2. Earthworm species and number of time found per LUS, village and LUI[@]

Species	Ecologic group	Sfor	Cacao	Yfor	Chr	Crop	Ng	Ak	Mb	Me	Nk	Mi	LL	ML	HL
Acanthodrilidae															
Dichogaster (D.) ehrhardti **(Dehr)**	epigeic	1	1	1	2	0	1	0	2	1	1	0	1	3	1
Dichogaster sp. nov.1 **(Dsp1)**	epigeic	4	1	1	0	0	1	1	2	2	0	0	2	4	0
Dichogaster sp. nov. 2 **(Dsp2)**	epigeic	1	2	0	1	0	0	0	1	0	0	3	0	1	3
Dichogaster sp. nov. 3 **(Dsp3)**	epigeic	0	0	1	0	0	0	1	0	0	0	0	1	0	0
D. (Dt.) adjelana **(Dadj)**	epigeic	0	0	0	0	1	1	0	0	0	0	0	1	0	0
D. (Dt.) annae **(Dann)**	epigeic	1	1	0	1	0	0	0	2	1	0	0	0	3	0
D. (Dt.) bolaui **(Dbol)**	epigeic	2	2	1	2	2	0	0	0	3	3	3	0	3	6
D. (Dt.) gracilis **(Dgra)**	epigeic	1	0	2	1	0	0	2	1	1	0	0	2	2	0
D. (Dt.) kangulunensis **(Dkun)**	epigeic	1	0	1	1	0	2	0	0	0	0	1	2	0	1
D. (Dt.) modglianii **(Dmod)**	epigeic	2	2	3	0	2	0	1	1	2	3	2	1	3	5
D. (Dt.) terricola **(Dterr)**	epigeic	1	0	1	0	0	0	1	0	0	0	1	1	0	1
Wegeneriella sp. nov. 1 **(Wsp1)**	epigeic	1	0	0	0	0	0	1	0	0	0	0	1	0	0
Eudrilidae															
Buettneriodrilus sp. nov. 1 **(Bsp1)**	endogeic	1	1	1	0	0	1	2	0	0	0	0	3	0	0
Eminoscolex kisantuanus **(Ekis)**	epigeic	1	1	0	1	1	0	0	0	0	3	1	0	0	4
Eminsocolex lamani **(Elam)**	epigeic	2	1	1	1	2	1	1	3	1	0	1	2	4	1
Eminoscolex sp. nov. 1 **(Esp1)**	epigeic	2	0	1	0	0	0	0	1	0	0	2	0	1	2
Eminoscolex steindachneri **(Este)**	epigeic	0	1	1	0	0	1	1	0	0	0	0	2	0	0
Eudrilidae gen. nov. 1 **(Eusp1)**	endogeic	1	2	1	1	0	1	0	0	0	2	2	1	0	4
Legonodrilus sp. nov 1 **(Lsp1)**	endogeic	2	1	2	2	2	0	3	5	0	0	1	3	5	1
Legonodrilus sp. nov 2 **(Lsp2)**	endogeic	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Legonodrilus sp. nov. 3 **(Lsp3)**	endogeic	2	2	1	1	2	4	0	0	4	0	0	4	4	0
Legonodrilus sp. nov. 4 **(Lsp4)**	endogeic	1	1	0	0	0	0	0	0	2	0	0	0	2	0
Lybiodrilus sp. nov. 1 **(Lysp1)**	endogeic	0	1	0	1	1	0	0	0	0	0	3	0	0	3
Rosadrilus camerunensis **(Rcam)**	anecic	2	1	3	1	0	0	2	2	3	0	0	2	5	0

Taxon		C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14
Schubotziella mildbreadi (**Scmil**)	epigeic	1	0	0	0	0	0	0	0	0	0	1	0	0	1
Scolecillus tantillus (**Sctan**)	endogeic	1	0	1	0	0	0	0	0	2	0	0	0	2	0
Malodrilus buarensis (**Mbua**)	epigeic	2	1	3	1	0	0	0	3	3	1	0	0	6	1
M. camerunensis (**Mcam**)	endogeic	0	0	1	0	0	0	0	0	1	0	0	0	1	0
Ocnerodrilidae															
Gordiodrilus sp. nov. 1 (**Gsp1**)	endogeic	0	0	1	1	1	3	0	0	0	0	0	3	0	0
Gordiodrilus sp. nov. 2 (**Gsp2**)	endogeic	1	0	0	1	0	0	2	0	0	0	0	2	0	0
Ilyogenia sp. (**Ilsp1**)	endogeic	3	2	3	4	4	1	5	2	4	0	4	6	6	4
Nematogenia lacuum (**Nlac**)	endogeic	2	2	2	3	1	0	4	0	1	0	5	4	1	5
N. panamaensis (**Npan**)	endogeic	2	2	2	2	3	0	4	3	4	0	0	4	7	0
Xibaro lavellei (**Xlav**)	endogeic	2	2	1	2	2	0	0	2	0	5	2	0	2	7
Xibaro sp. nov. 1 (**Xsp1**)	endogeic	3	3	5	4	5	4	4	0	4	5	3	8	4	8
Xibaro sp. nov. 2 (**Xsp2**)	endogeic	0	0	1	1	1	1	2	0	0	0	0	3	0	0

@ For meaning of abbreviations in column headings see Table 1 and Materials en Methods section

Species richness, abundance and biomass per LUI

a) <u>Richness</u>

Species richness varied from 4 in the Cacao in the low LUI to 10 in Sfor in the medium LUI. No significant differences were found between and within LUI levels (Tables 3a, b, c).

b) <u>Abundance</u>

Earthworm abundance ranged between 236 in Cacao in the high LUI to 64 in Cacao in the low LUI. Although no significant effects of LUI and LUS within LUI were found, pair-wise comparison of least square means revealed a significant difference between Chr and Cacao (P=0.049) within the low LUI block (Table 3a).

Table 3a.Characteristics of earthworms in different land use systems at low LUI in southern Cameroon[#]

	Sfor	Cacao	Yfor	Chr	Crop
Number of species	7,5	3,5	6	7	6
Abundance (ind m^{-2}) (Abun)	124^{ab}	64^{b}	118^{ab}	240^{a}	112^{ab}
Biomass (g m^{-2}) (Biom)	16^{a}	2^{b}	3^{ab}	5^{ab}	2^{b}
H'abundance (Hab)	1,32^{a}	1,02^{a}	1,19^{a}	1,69^{a}	1,62^{a}
H' biomass (Hb)	0,95^{b}	0,85^{b}	1,25^{ab}	1,56^{a}	1,32^{a}
E abundance (Eab)	0,70^{b}	0,82^{ab}	0,67^{b}	0,90^{a}	0,91^{a}
E biomass (Eb)	0,55^{b}	0,69^{ab}	0,72^{ab}	0,81^{a}	0,75^{ab}
D abundance (Db)	0,63^{ab}	0,61^{ab}	0,58^{b}	0,82^{a}	0,82^{a}
D biomass (Db)	0,49^{b}	0,49^{b}	0,65^{a}	0,75^{a}	0,68^{a}
Epigeic:Endogeicabundance (Ep/Enab)	0,33^{a}	0,07^{a}	0,03^{a}	0,44^{a}	0,16^{a}
Epigeic:Endogeicbiomass (Ep/Enb)	2,72^{a}	1.05^{a}	0,20^{a}	1.15^{a}	1.79^{a}

Table 3b. Characteristics of earthworms in different land use systems at medium LUI in southern Cameroon

	Sfor	Cacao	Yfor	Chr	Crop
Number of species	9,5	7,5	8,5	5	4
Abundance (ind m^{-2})	184	128	66	84	132
Biomass (g m^{-2})	5	5	15	7	3
H'abundance	1,46^{ab}	1,71^{ab}	1,95^{b}	1,00^{a}	0,98^{a}
H' biomass	1,85^{a}	1,58^{a}	0,85^{b}	0,72^{b}	0,78^{b}
E abundance	0,65^{c}	0,86^{ab}	0,93^{a}	0,75^{bc}	0,73^{bc}
E biomass	0,82^{a}	0,83^{a}	0,40^{b}	0,62^{ab}	0,59^{ab}
D abundance	0,64^{b}	0,79^{ab}	0,91^{a}	0,58^{b}	0,58^{b}
D biomass	0,80^{a}	0,75^{a}	0,39^{b}	0,39^{b}	0,44^{b}
Epigeic:Endogeicabundance (Ep/Enab)	0,25^{b}	0,95^{b}	3.68^{a}	0,05^{b}	0,03^{b}
Epigeic:Endogeicbiomass (Ep/Enb)	1,03^{b}	3.97^{b}	32,84^{a}	0,08^{b}	0,01^{b}

Table 3c. Characteristics of earthworms in different land use systems at high LUI in southern Cameroon

	Sfor	Cacao	Yfor	Chr	Crop
Number of species	6	5,5	6,5	6	5
Abundance (ind m^{-2})	96	236	76	96	98
Biomass (g m^{-2})	5	10	3	3	3
H'abundance	1,31	1,41	1,40	1,46	1,20
H' biomass	1,29	1,21	1,25	1,51	1,04
E abundance	0,74	0,83	0,78	0,82	0,76
E biomass	0,72	0,71	0,71	0,85	0,66
D abundance	0,66	0,73	0,72	0,73	0,64
D biomass	0,67^{ab}	0,64^{ab}	0,65^{ab}	0,74^{a}	0,55^{b}
Epi:Endnum	0,33	0,67	0,29	0,37	0,84
Epi:Endbio	1,19	0,68	0,63	0,50	1,86

 # in a row, means followed by the same superscript are not significantly different at P= 0.05

c) <u>Biomass</u>

Biomasses ranged from 2 g m^{-2} in Crop and Cacao to 16 g m^{-2} in Sfor in the low LUI where significant differences were found between Sfor and Cacao (P=0.0083) and between Sfor and Crop (P=0.05) (Table 3a). No other significant differences were found.

Ecological groups distribution per LUI

On an abundance basis, the ratio epigeic:endogeic earthworms ranged from 0.03 in table 3a in Yfor in the low LUI to 3.68 in table 3b in Yfor in the medium LUI. Although no significant overall effect of LUI was found, specific significant differences were observed for Yfor between medium and high LUI blocks (P=0.0035) and between medium and low LUI blocks (P=0.013) (Figure 2a). Similar significant differences were found for this ratio on a biomass basis (Figure 2b).

Species diversity indices and evenness per LUI

a) <u>Diversity</u>

Shannon species diversity indices based on abundance data ranged from 1.95 in Yfor in the medium LUI block to 0.98 in Crop in the same LUI (Table 3b). Thus, this LUI had the largest range (0.97) between the highest and lowest index values; this indicates a greater variability among LUSs in this block compared to the others; the lowest range (0.26) was found in the high LUI block between Chr and Crop. The only significant differences were found in the medium LUI block between Chr and Yfor (P=0.025) and between Crop and Yfor (P=0.023) (Table 3b).

There was a significant effect of LUS (within LUI) on the Shannon index based on biomass (F=4.68, P=0.0031). LUI had a significant effect on the diversity index of all the LUSs but Yfor (Figure 3b); within LUI, significant differences were found in low and medium but none in high LUI (Table 3a,b). The highest range was also found in the medium LUI (1.13) with the highest diversity found in Sfor and the lowest in Chr.

There was a significant effect of LUI (F=4.31, P=0.033) and a highly significant effect of LUS within LUI on Simpson's diversity index (F=7.35, P=0.0003). Simpson's indices confirmed the patterns obtained with Shannon's index on both abundance and weight basis with many more significant differences between and within LUI (Figure 4a,b).
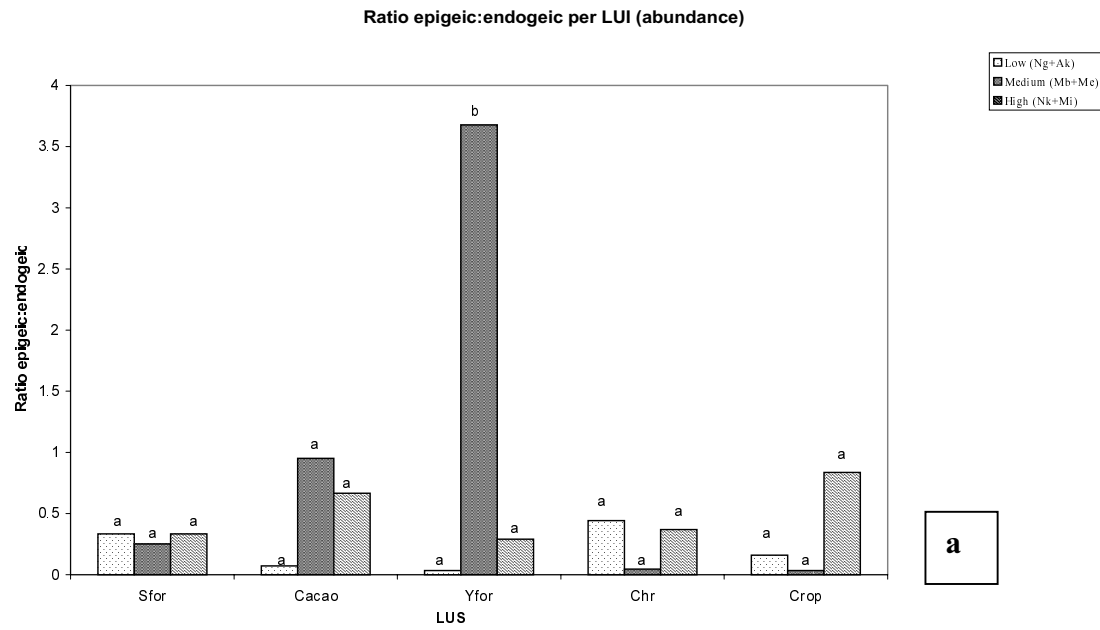
Ratio epigeic:endogeic per LUI (abundance)

Ration epigeic:endogeic per LUI (biomass)
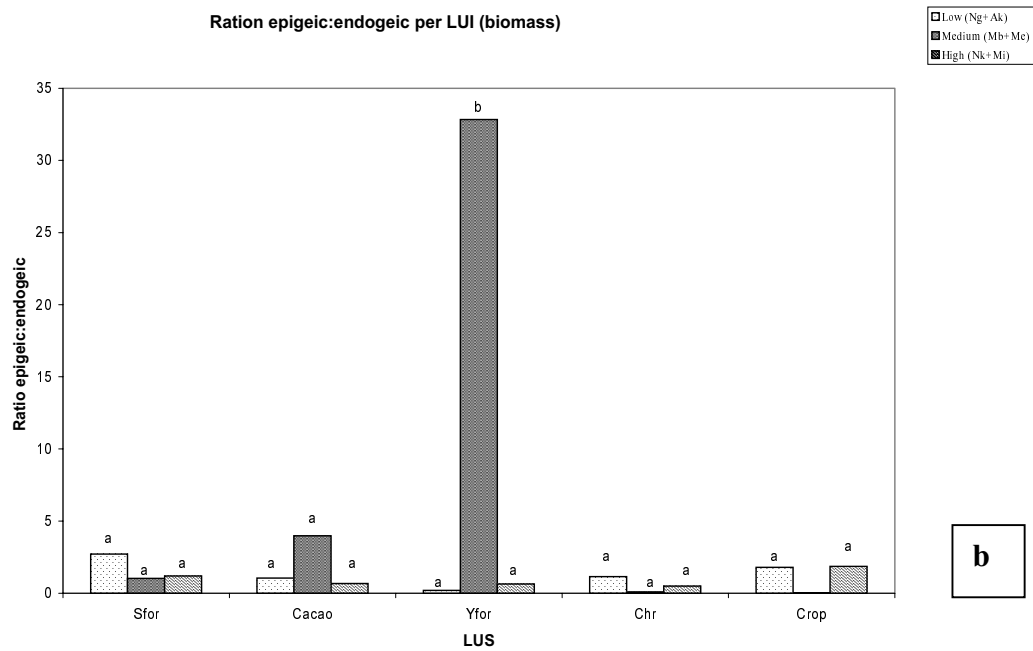
Figure 2. Effect of LUI on earthworm ecological groups
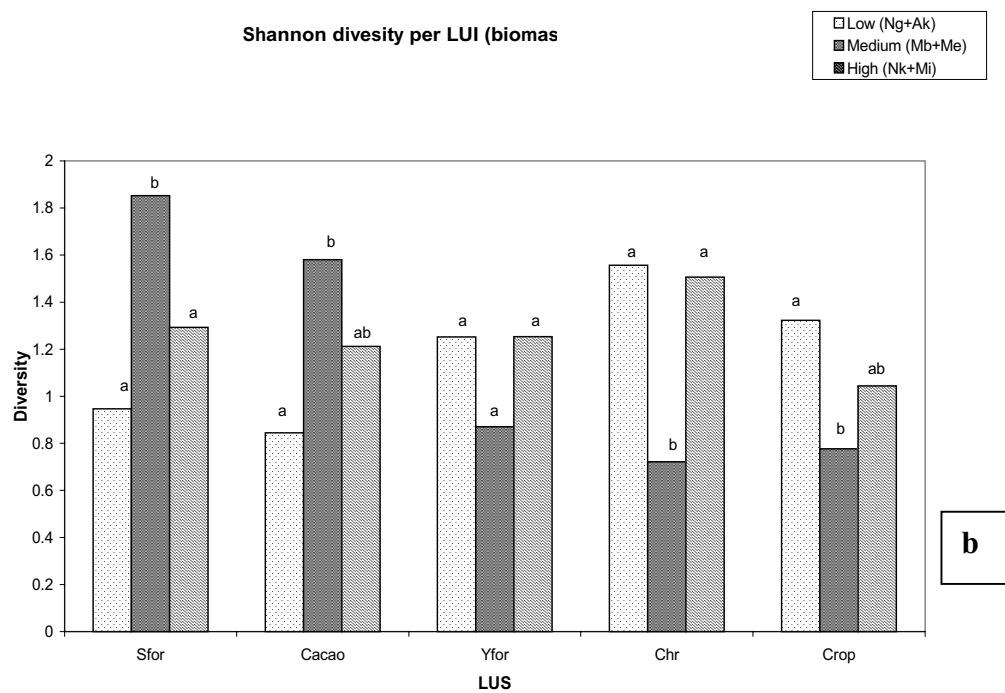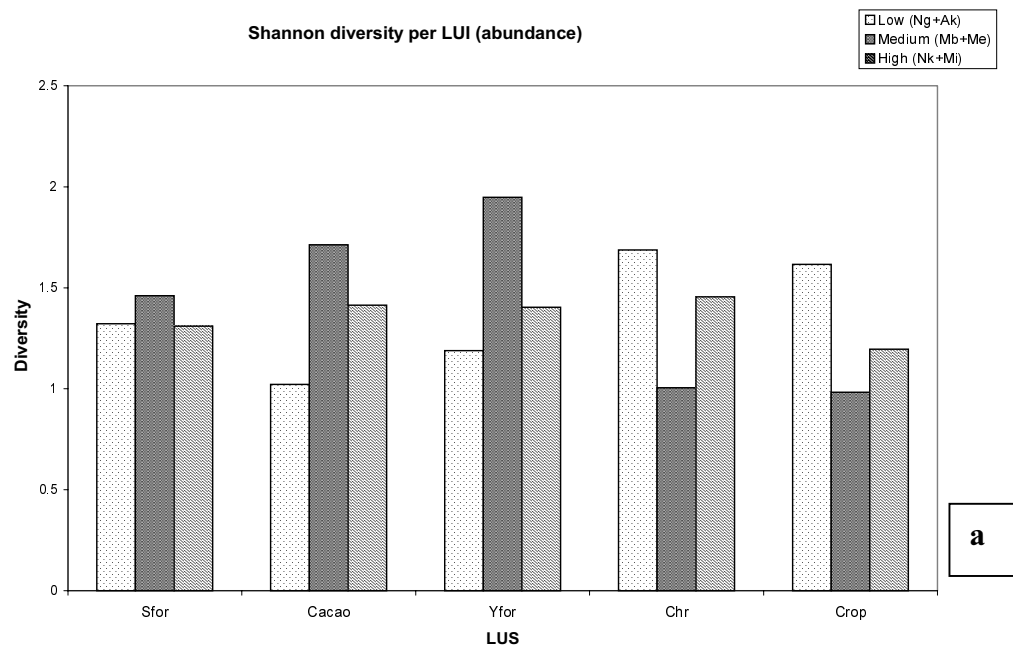a: based on species abundance; b: based on species biomass

Figure 3. Effect of LUI on the Shannon index
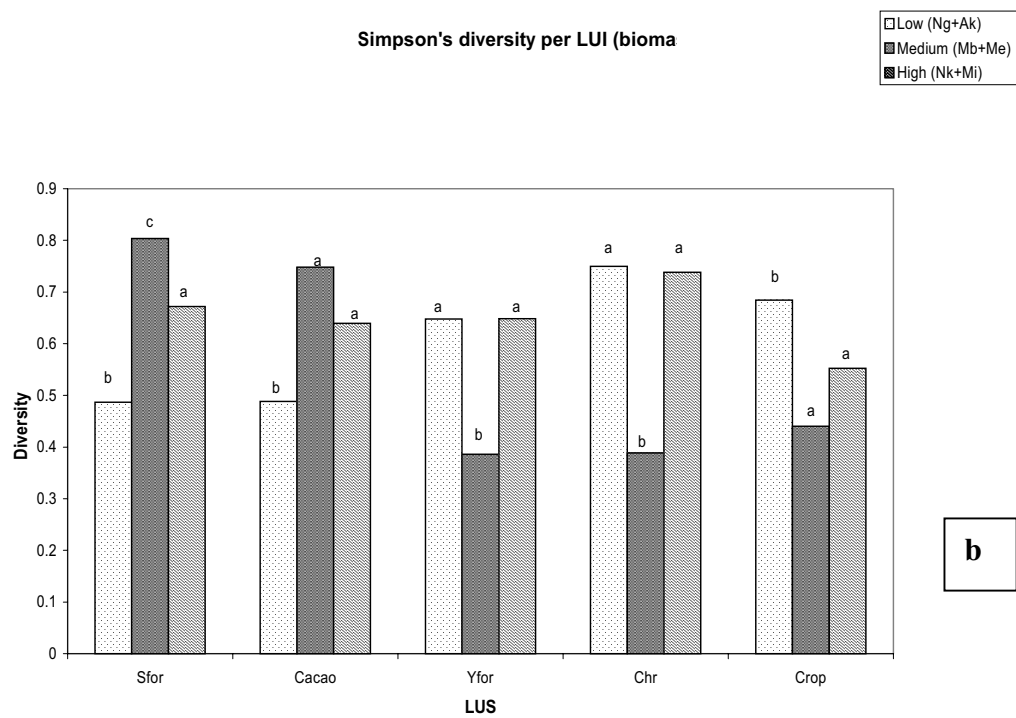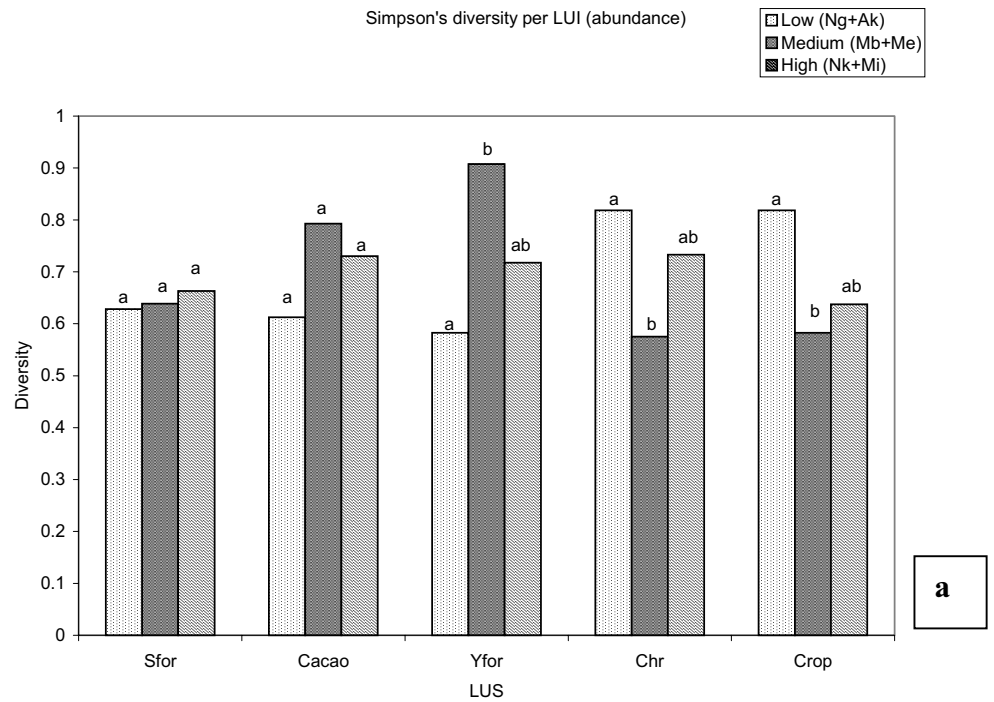a: based on earthworm abundance; b: based on earthworm biomass

Figure 4. Effect of LUI on Simpson's diversity index
a: based on eartworm abundance; b: based on earthworm biomass

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b) Evenness

Based on species abundance, evenness was high in general and ranged from 0.65 in Sfor to 0.93 in Yfor in the medium LUI block (Table 3a,b,c). There were no significant effects of LUI and LUS on evenness. Pair-wise means comparisons revealed some significant differences; for Yfor, the medium LUI block had higher E than the low LUI block (P=0.0062) and for Crop the reverse was the case (P=0.0446) (Figure 5a). In the low LUI, Chr and Crop had significantly higher E than both Sfor and Yfor, respectively (P=0.028 and 0.014 for Chr and P=0.021 and 0.01 for Crop) (Table 3a); in the medium LUI block, Yfor exhibited significantly higher E than Chr (P=0.047), Crop (P=0.026) and Sfor (P=0.0042). In addition Cacao had higher E than Sfor (P=0.026) (Table 3b).

On a biomass basis, evenness varied from 0.40 in Yfor to 0.83 in the medium LUI block. Except this lowest value, evenness was above 0.55 within LUSs across all the LUIs. Although values of evenness were somewhat lower on a biomass basis, the reverse pattern was found for Yfor where the medium LUI block had lower E than both low LUI (P=0.019) and high LUI (P=0.021) blocks. For Sfor, the medium LUI block had higher E than the low LUI block (P=0.038) (Figure 5b). Within the low LUI block, Chr showed a higher E than Sfor (Table 3a). In the medium LUI block, Sfor and Cacao had higher E than Yfor (P=0.0033 and P=0.0029, respectively, Table 3b). No significant difference was found between LUSs in the high LUI block.

c) Similarity

Steinhaus similarities (Legendre and Legendre, 1983), based on abundance, ranged from 0.22 (Cacao-Chr) to 0.57 (Cacao-Yfor) within the low LUI block, from 0.20 (Yfor-Crop) to 0.70 (Sfor-Crop) in the medium LUI block and from 0.24 (Cacao-Yfor) to 0.76 (Chr-Crop) in the high LUI block. On average, mean similarities between LUSs were lower in the low LUI block (0.39) than in the medium LUI (0.45) and the high LUI block (0.47) (Table 5).

On the basis of biomass, Steinhaus similarities showed generally the same pattern.

Multivariate analysis

Principal Component Analysis (PCA) and correspondence analysis (CA) were based on species data combining village and LUS. The first four PCA factors explained 61% of variance with respective contributions of 20.3%, 19.2%, 11.8% and 9.5%. For CA, the first four unconstrained factors explained 46% of the total variance. Both analyses clearly distinguished 3 groups of samples. The first group was composed of samples from the high

LUI. The low and medium LUI were further separated by the second axis but no delineation can be drawn since villages of the 2 blocks are shuffled (Figure 6a, b) forming the 2 other groups.
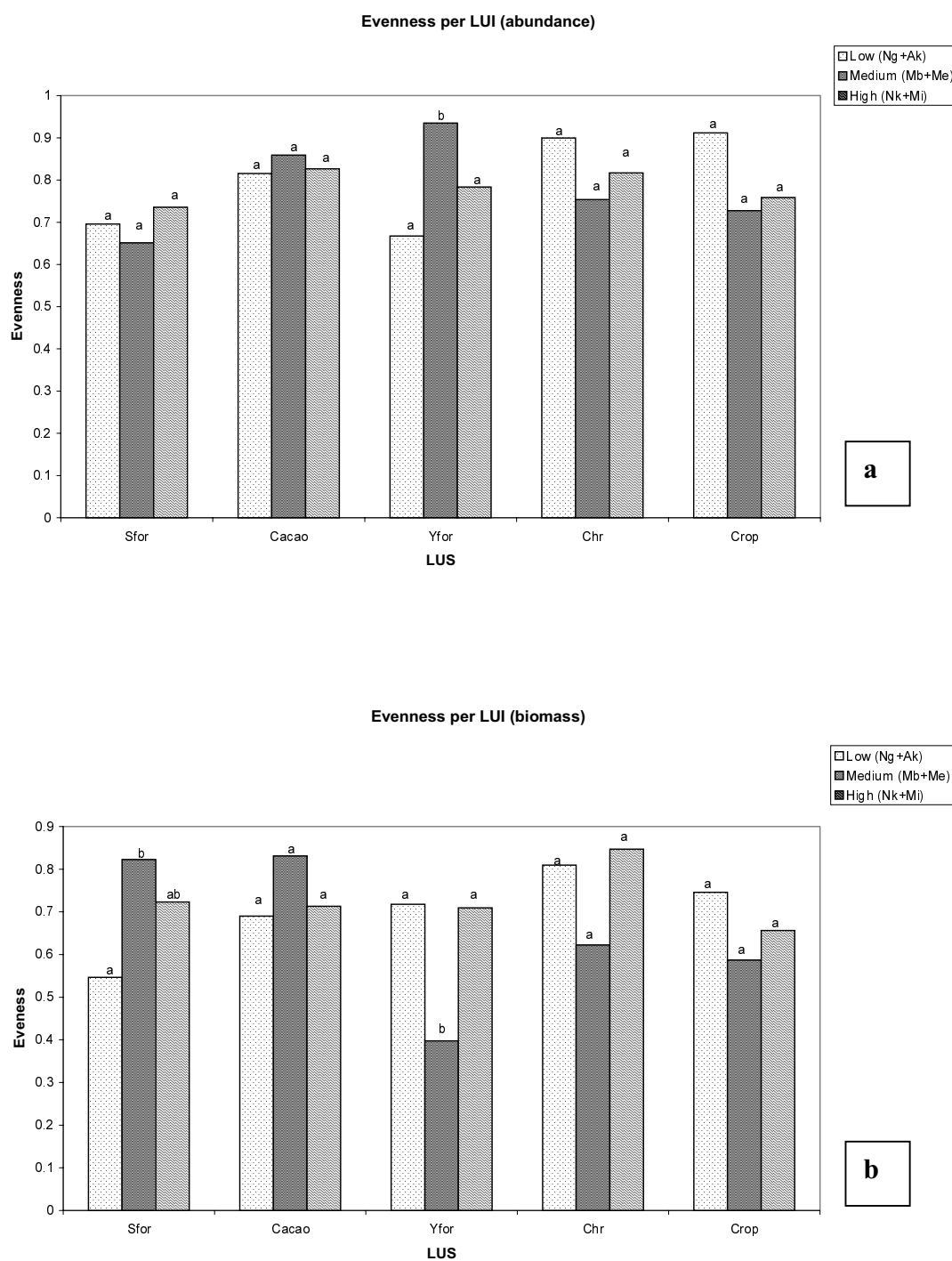
Evenness per LUI (abundance)

Evenness per LUI (biomass)

Figure 5. Effect of LUI on earthworm evenness
a: based on earthworm abundance; b: based on earthworm biomass

Table 4. Ranges between maximum and minimum values of different earthworm characteristics[$]

	Specie	Abund	Biom	H'ab	H'b	Eab	Eb	Dab	Db	Ep/Enab	Ep/Enb
Low	4	176	14	0.67	0.71	0.24	0.26	0.24	0.26	0.24	2.23
Med	6	118	12	0.97	1.13	0.28	0.43	0.33	0.42	0.67	4.12
High	2	160	8	0.26	0.46	0.09	0.19	0.10	0.19	0.27	1.41

$ For the different column titles see Table 3a for meaning

Table 5. Average similarities per village and LUI, based on abundance

	Low LUI		Medium LUI		High LUI	
	Ng	Ak	Mb	Me	Nk	Mi
S_A	0.36	0.33	0.30	0.41	0.45	0.41
$S_{A\ LUI}$	0.39		0.45		0.47	
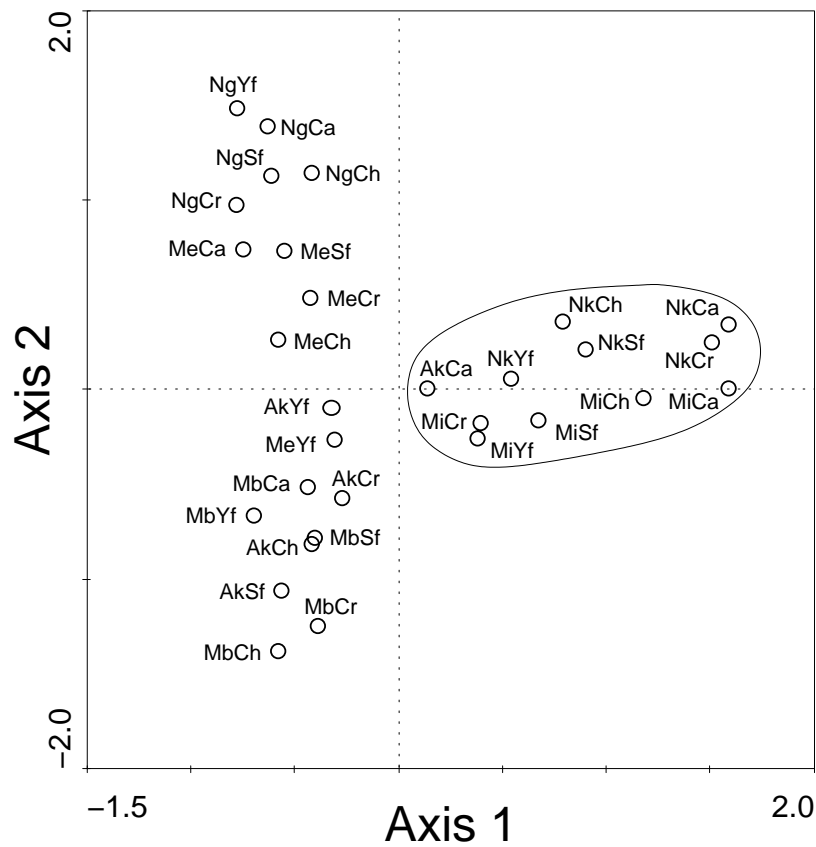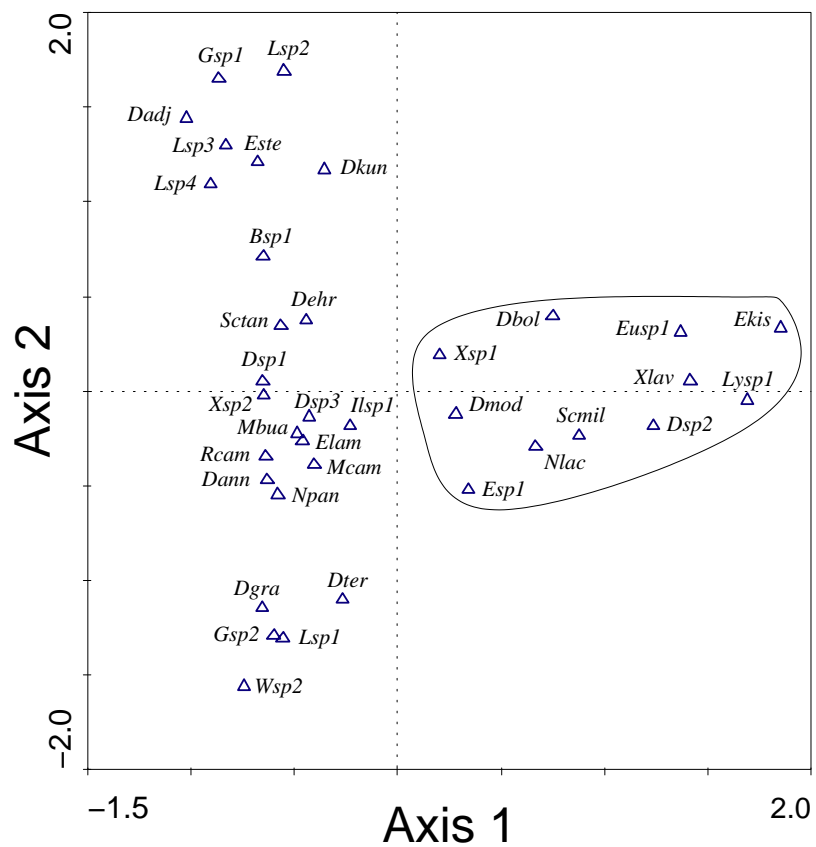
Figure 6. Ordination plot of species abundance (axes 1 and 2) based on Correspondence Analysis. For earthworm species labels see Table 2 and for site labels see text; site is a combination of village and LUS.

a: Species, grouped according to the composition of the assemblage of each site.

b.: Sites, grouped according to their earthworm assemblage.

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Discussion

From the 3 families of earthworms collected in southern Cameroon, 15 genera and 36 species were found with probably 1 new genus and 12 new species. These figures are quite high for the single sampling exercise as compared to findings reported in other tropical and subtropical regions. Borges and Alfaro (1997) found 8 species in the Banos de Oro region in Venezuela; Fragoso and Lavelle (1987) reported 17 species at Chajul (Chiapas, Mexico). In south India, Blanchart and Julka (1997) identified 28 species, 3 new genera and 16 new species out of 5326 earthworms collected; Römbke et al. (1999) found approximately 8 species and mainly Glossoscolecidae in Central Amazonian primary and secondary forests and a polyculture plantation after 8 sampling dates. Results of our study confirm that the region may be considered as one of the richest in biodiversity in the world (Eggleton et al., 1995). Species of the Ocnerodrilidae (living in the deeper soil layer) seem to thrive in southern Cameroon; they occurred in at least 3 LUSs and the only species found in 5 out of the 6 villages belongs to this family. Furthermore, the species of this family are more abundant in the most disturbed LUSs (Crop and Chr) than in the less disturbed (Table 2) and as such constitute a reservoir from which they may colonize Sfor, Yfor and Cacao.

Species richness did in general not differ throughout the land use intensity blocks (Tables 3a,b,c). This suggests that the entire pool of earthworm fauna of the southern Cameroon may still be present. This still needs to be confirmed and the definition of an index of intensification taking into account the conditions of the area would be a necessary tool for this evaluation. However, in an absolute sense, the trend may already be set for species loss since the high level of intensification harbored a lower species number (18) than the medium (21) and low (24) ones, and in general, less disturbed land use systems in the gradient within blocks conserved more species than the most disturbed ones. Many authors have reached the same conclusions (Dacaens and Jimenez ,2002; Cortet at al., 2002; Barros et al., 2002; Smeaton et al., 2003; Sinha et al., 2003).

Abundance and biomass were in most of the cases positively correlated. Land use intensification affected earthworm communities in different ways. The medium LUI exhibited the highest range in values, the high LUI the lowest and the low LUI block was between the two extremes (Table 4). This suggests that in the medium LUI block, there is more differentiation between LUSs and it provided a better environment for earthworm development, probably in terms of food quality and availability.

Biomass figures seemed low on average for this survey compared to many studies in temperate and tropical ecosystems. This may be due on one hand to the fact that earthworm biomass was based on earthworm preserved mass recorded after 2 years which is less than living or fresh mass generally used in such studies. Moreover, only adult weights were used and the numerous juvenile earthworms were not considered for biomass purposes as they cannot be identified to species and ecological groups. Probably anecic species were under-sampled since monolith hand-sorting is not the most efficient method of assessing their populations. Jimenez (1999) and Decaens and Jimenez (2002) contended that larger-bodied anecics escape into deep layers when using classic hand-sorting and even formaldehyde methods, due to their large size and the deep semi-vertical burrows they dig. They proposed methods such as direct correlation between the number of individuals and the number of fresh casts present at the soil surface as more efficient.

Each LUI block under study harboured at least 4 characteristic earthworm species. Diversity indices were not high but evenness was above 55% throughout the zone which suggests an absence of truly dominant species. Correspondence analysis (Figure 6a,b) clearly presented the high LUI block as having species that are largely different from those present in the other blocks, while the low and high LUI blocks harbor several species in common. Long-term deforestation and high pressure put on land due to increasing population and subsequent shortened fallow phases (80 inhabitants km^{-2} on average, highest frequency of fallow/cropped cycles in the same land) may have created conditions leading to the elimination of original species and favoring the migration of new species well adapted to the high LUI. This is evidenced by a fauna rich in peregrine species (50% at Nkometou and only 13% at Ngoungoumou) and the higher abundance of endogeics (Table 2). It may also be that this block has reached a low resilience, mainly evidenced by the lack of significant differences in the gradient of LUS disturbance (Table 3c) and the high similarity indices found between LUSs.

Grime (1977) made the distinction between long-term stress and short-term perturbations or disturbance. E.g., whilst a single cultivation such as ploughing (short-term disturbance) will result in a dramatic disruption of soil structure, repeated ploughing (long-term stress) will have further effects by enhancing the rate of soil organic matter turnover which will gradually lead to a reduction in organic substrates. Short-term, periodic disturbance may cause disruption in the relative abundance of particular organisms but not extinction, whereas long-term stresses are more likely to lead to gradual elimination of some species. In this study, the high LUI block seems to show this. Zaller and Arnone (1998) found

that the elimination of plant species to which earthworms are particularly attracted because of palatability of their litter or because of the plant species'effect on stand microclimate, may be responsible for the disappearance of some species. However, in a further study, Birang et al. (2003) showed that, although soil fertility status was higher at Nkometou (in the high LUI block) than at the other villages (Ngoungoumou in low and Metet in medium LUI blocks), earthworm cast deposition was lowest suggesting that probably species composition was the main factor responsible for the casting activity.

Conclusions

The survey of earthworm species along a gradient of LUI in southern Cameroon revealed the following:

1) Undescribed species occur in all the LUI and LUS under study

2) Species richness does not drastically change along the LUI gradient and each LUI block harbours characteristic species

3) The high LUI possesses a completely different earthworm community structure than the medium and low LUI blocks

4) Medium LUI block presents most suitable conditions for earthworm development

5) There is no clear delineation between low LUI and medium LUI

6) Within LUI, highly disturbed LUS have less earthworm abundance and biomass than less disturbed ones.

Information from this study can be used for the development of management systems that are conducive to the growth and development of earthworms. The large number of undescribed species calls for a more intensive survey of the area for it may be a hot spot of earthworm endemism. Moreover, characteristic earthworm species may serve as indicators of land use intensity.

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Termite community structure along a gradient of land use intensification in the forest zone of southern Cameroon

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Abstract

Termites were surveyed in two villages in three blocks differing in level of land use intensity (LUI) in southern Cameroon. In each of 6 villages, 5 land use systems (LUSs) of different levels of disturbance were sampled. The sampled LUSs were: secondary forest of 30 year old (Sfor), shaded cocoa plantation (Cacao), young forest of 12-15 year old (Yfor), 4-5 year old Chromolaena odorata (Chr) and a groundnut/maize/cassava intercrop (Crop). Termites were sampled in a belt transect, combined with hand-sorting soil monoliths. A total of 223 species were recorded of which 43% (91) were undescribed and 6.25% (14) were new genera; 80% were soil-inhabiting species and 13% were potential pests to agricultural crops. There was no significant effect of LUI but a strong effect of LUS on termite species richness and abundance. Overall termite richness declined with intensity of disturbance from Sfor to Crop. Soil-feeding species numerically dominated except in Crop in the high LUI block. Ordination analysis clustered together LUSs of similar canopy cover.

Key words. Termites, land use intensity, land use system, disturbance, southern Cameroon

Introduction

Rates of habitat conversion, especially of forests, are higher in tropical regions than elsewhere on earth (FAO, 1993; Whitmore, 1997). Tropical deforestation proceeds at a rate of 154 000 km2 year-1 (Aldhous, 1993). The present forest of southern Cameroon, although for a considerable part consisting of primary vegetation, is a mosaic of land uses: patches of secondary forest and fallow fields, crop fields, some tree plantations and agroforestry and remnants of primary vegetation. The traditional food production system is shifting cultivation (slash and burn). The traditional shifting cultivation system has been practiced for millennia throughout the tropics. It involves the manual clearing of a small area of natural vegetation (forest, bush, woody savannah or grassland) and leaving the area fallow for an extended period after a few harvests to allow the natural vegetation to regenerate soil fertility (ASB, 2002).

Soil fauna are known to play a critical role in the biological turnover and nutrient release from plant residues by fragmentation, incorporation into the soil, and enhancement of microbial activity. A number of ecological studies have been carried out on soil invertebrates in the humid tropics and the importance of soil fauna in sustaining soil fertility and crop production has been well established (Brussaard et al. 1992, 1993; Lavelle et al., 1994; Wood, 1996). In African forest biomes, these fauna are pre-eminently termites.

Termites are active diggers and exert an important influence on physical and chemical soil characteristics (Lee & Wood 1971, Lobry de Bruyn & Conacher, 1990; Mando et al., 1996), generally inducing an increase in aggregate stability, porosity, aeration and water storage capacity of soils. Termites can contribute to a thorough mixing of different soil strata. Termites are important "ecosystem engineers"; their nests represent structural elements which affect plant growth and influence diversity and composition of plant and animal communities (Martius, 1994; Kooman and Onck, 1987; Lavelle et al., 1997). Termites are also notable pests of crops and of human artifacts (Wood, 1996), an undesirable effect of their search for cellulose as a basic diet. In fact, the abundance of some termite pest species conceals the fact that many termite species are potentially threatened by extinction due to the drastic anthropogenic habitat modifications, which occur in the tropics. In recent papers, Eggleton et al. (1995, 1996, 1997, and 2002) presented termite assemblage data from sites subjected to varying degrees of forest disturbance and their conclusions were that complete clearance had

a very strong impact on termite diversity. Conversion to secondary forest had little effect on termite species richness but had clear effects on termite community structure.

In southern Cameroon, increasing socioeconomic changes including population growth and declines in urban employment opportunities have led to gradual intensification of agricultural practices in an effort to assure reasonable land productivity. Intensification is a combination of a number of factors such as (1) the fraction of time land is used for crop production; for instance, fallow length is becoming shorter and fallows of as little as 4 years are increasingly common (Dibog et al., 1999; Eggleton et al., 2002), (2) the fraction of total biomass harvested, (3) the amounts of fertilizer, irrigation water and pesticides used, as well as (4) the amount of (fossil) energy used in soil tillage and mechanized farm operations (Giller et al., 1997).

In general, the parameters of intensification most detrimental to soil fauna and the services that they provide are tillage, poor soil cover by annual plants, and pesticides. In general, larger scale determinants as the time elapsed since the first use of the soil after clearing, or since the last fallow period, are significant long-term determinants of biodiversity, as well as the proportion of the landscape that is submitted to agricultural practice (Lavelle, 1997). Living conditions for at least some soil macrofauna are worsened by intensification to the extent that they cannot persist. As certain macrofauna make major contributions to ecosystem functioning, their disappearance might lead to accelerated degradation (Lavelle et al., 1997).

While differences in forest type, climate, soil structure and biogeographical history are important determinants of termite assemblages, changes in the composition and functional characteristics of termite assemblages are likely to have major influences on soil properties (Eggleton et al., 1996, 2002). In view of their key role and the increasing human pressure on the forest zone of southern Cameroon, more profound studies are urgently needed. It is therefore appropriate to continue to investigate the causes that determine the fate of termite communities in a wide range of conditions when forests are converted. Our study aimed at assessing the impact that land use (intensification) may have on termite community structure.

Materials and Methods

Study area and treatments

The study was conducted in six villages in southern Cameroon classified into three blocks representing increasing levels of deforestation and land use intensity (LUI) within the benchmark established by ASB, IRAD and IITA (Thenkabail, 1999) known as: (1) Yaoundé block (high), (2) Mbalmayo block (medium) and (3) Ebolowa block (low) (Figure 1 and Table 1). Annual rainfall in southern Cameroon is bimodal. Rains start in mid-March and end in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November. In 1999, average annual rainfall across the region was 1500 mm.

The commonest 5 land use systems (LUSs) of the region representing a gradient of disturbance from low to high were selected such that the ages of the LUSs of the same type in the different villages were approximately the same: a secondary forest (>30 years, Sfor), a shaded cacao plantation (Cacao), young forest fallow (12-15 years, Yfor), 4-5 years old Chromolaena odorata fallow (Chr), and a groundnut / maize / cassava intercrop field (Crop). For details on vegetation, see Zapfack et al. (2002) who characterized the vegetation in several villages of these three blocks.

The methods followed closely those of Anderson and Ingram (1993).

Qualitative assessment

Transect sampling was used for a rapid biodiversity assessment from July to August 1999 during the short dry season. The sampling was performed along a 100 m belt transect of two meter width, divided into 20 sections of five meter long each. Each section was sampled (hand-picking) by two trained persons for 30 minutes. The investigated microhabitats were as follows:

- soil samples at ground surface and topsoil of at least five centimeters depth

- litter and humus on the soil surface, at the base of trees, and between buttress roots, if any soil within and beneath rotten logs

- runways on trees and arboreal nests up to accessible height

- epigeal termite mounds on the ground surface and at the base of trees

- the inside of dead wood and logs, tree stumps, branches and twigs, damp and dead trees.

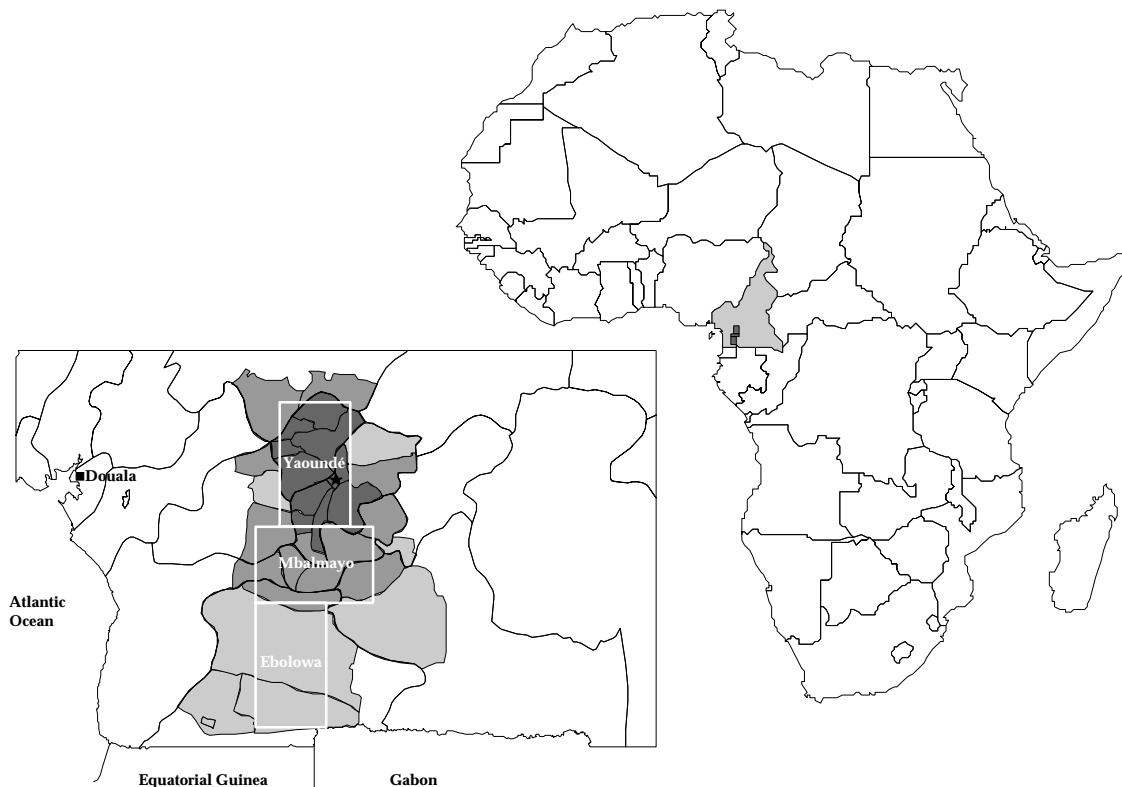The methods followed closely those of Anderson and Ingram (1993).

Figure 1. Map of southern Cameroon and the three land use intensification blocks within the forest margins benchmark *Termite sampling methods and identification*

Table 1. Characterization of the 3 blocks under study in southern Cameroon.

Block	Level of deforestation and LUI	Village	Distance from Yaoundé	Geo-references	Soil class	land under forest cover (%)	land under fallow (%)	land under crop (%)
Yaoundé	High	Nkometou (Nk)	40 km North	11°35'E, 4°05'N	Rhodic Kandiudult	25	29	27
		Minkoameyos (Mi)	15 km West	11°27'E, 3°51'N				
Mbalmayo	Medium	Mbalmayo (Mb)	50 km South	11°28'E, 3°27'N	Typic Kandiudult	40	16	19
		Metet (Me)	90 km South	11°45'E, 3°25'N				
Ebolowa	Low	Akok (Ak)	150 km South	11°14'E, 2°44'N	Typic Kandiudox	57	10	13
		Ngoungoumou (Ng)	130 km South	12°01'E, 3°18'N				

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- the inside of dead wood and logs, tree stumps, branches and twigs, damp and dead trees.

Quantitative assessment

In each LUS five soil monoliths of 50x50x30 cm (LxWxD) were dug along a 100 m transect at 20-m intervals and termites were hand sorted and preserved in 70% ethyl alcohol.

Identification and classification into trophic groups

All termites that were considered for identification were soldiers and workers. Termites collected were identified at The Laboratory of Entomology of IRAD, Yaoundé,Cameroon in collaboration with The Natural History Museum, London, UK. Specimens are kept at IRAD and The Natural History Museum. The termite taxonomy followed the traditional clading procedure of naming organisms in application of the technique described by Sands (pers. comm.) taking into account previous numbered morphospecies of earlier work in the zone (Eggleton et al.,1995, 1996; Davies et al., 1999; Dibog, 1998; Dibog et al., 1999). Results from transectsand monoliths were combined to establish species richness in each land use system and further in each village and intensification block,but statistical analyses were based on monolith data only.

An understanding of termite functional groups is a prerequisite to assess the role of termites in ecosystem function. Definitions of termite functional groups incorporate a wide range of characteristics to include inquilines and arboreal species. Donovan et al. (2001) and Eggleton et al. (2002) recognized four termite-feeding groups namely:

- Feeding group1: wood, litter and grass feeders (lower termites)

- Feeding group 2: wood, litter and grass feeders (some higher termites)

- Feeding group 3: very decayed wood or high organic content soil (all higher termites)

- Feeding group 4: low organic content soil (true soil feeders—all higher termites)

For analysis purposes, we placed termites into two broad putative trophic groups: wood feeders (group 1 to 3) andsoil feeders (group 4).

Diversity and Similarity

Shannon diversity index (H') and evenness (E) were calculated based on the monolith data. Simpson's index of diversity (D) was calculated for the same data to reduce the bias that may arise from the interpretation of a single diversity index measure (Magurran, 1988). These data are presented at LUS level but were analyzed at monolith level.

Steinhaus' coefficient (Legendre and Legendre, 1983) was used to determine the similarity of pairs of land use systems within each village and LUI on the basis of abundance: SA= 2W/ (A+B), where W = sum of the lower of the two abundances of each species and A and B is the sum of abundances of each community, respectively.

Design and statistical analyses

Differences in species richness between the LUSs in each village were examined by constructing species accumulation curves following the method used by Eggleton et al. (1995). Each 5 m section of the transect was treated as an independent sample. Ten random sequences of sections were generated for each transect. The cumulative number of species was calculated for the first section, then the second section, then the third and so on up to twenty. The mean of the 10 sets was then calculated for each section of each set, and species accumulation curves drawn. An estimate of the actual number of species in each LUS was

obtained by using a Bootstrap estimator with Specpool fuction of the Vegan package in R 1.5.1 (Oksanen, 2003). The sections were assumed to be randomly sampled although, as they form successive parts of a transect, this assumption may not strictly hold. Further, polar ordination based on the Sørensen dissimilarity matrix was performed on the basis of species presence/absence using the Mva package in R1. 5.1.

Quantitative data recorded or calculated from hand-sorting soil monoliths were analyzed as a nested design with two factors: (1) LUI with 3 levels (low, medium and high) and LUS nested within LUI with 5 levels (Sfor, Cacao, Yfor, Chr and Crop). Analyses of variance were carried out on log-transformed data using the General Linear Model (GLM) procedure of SAS version 8 (SAS, 1999). Pair-wise comparison of least square means of selected treatments was performed using the PDIFF option. The tested variables were:

(1)   termite species number: the number of species per monolith

(2)   termite abundance: the number of termite individuals m^{-2}. The abundances of termites were log-transformed to normalize the distribution before the statistical analysis. The same transformation was applied to soil and wood feeder abundance

(3)   Trophic groups: soil and wood feeders; proportions of trophic group species abundance were arc sines transformed

(4)   Shannon and Simpson's diversity indices and

(5)   Evenness index

Results

Overall species incidence and richness (transects and monoliths combined)

In the 30 transects sampled in the 6 villages involved in the study, a total of 223 species were recorded from two families (Appendix 1): the Rhinotermitidae with 2 species and the Termitidae with 223 species. In the latter family, Apicotermitinae were the most abundant with 130 species, followed by the Termitinae (60 spp.), the Macrotermitinae (18 ssp.) and the Nasutitermitinae (13 spp.) respectively. Of these 223 species, 43% (91) were undescribed, 6.25% (14) were new genera; 80% were soil-inhabiting species and 13% were potential pests to agricultural crops.

The observed and estimated species richness of all five LUSs in each village are shown in Table 2, while the species accumulation curves are in Appendix 2. Across LUI blocks (Figure 2), on average Sfor harbored the highest species numbers, followed by Yfor and Cacao; Chr and Crop had the lowest species numbers. At the LUI level, species numbers were similar.

In the low LUI block, 4 species (Apilitermes longiceps, Astalotermes sp 10, Astalotermes sp 3 and Ondotermes sp 2) occurred more often than all the others and in the medium LUI block, 3 such species were recorded (Adaiphrotermes sp 2, Anenteotermes polyscolus and Pseudacanthotermes spiniger). No characteristic species was found in the high LUI block (Appendix 1).

Table 2. Observed and extrapolated species number for each LUS in the different villages surveyed . Extrapolations derived from Appendix 2.

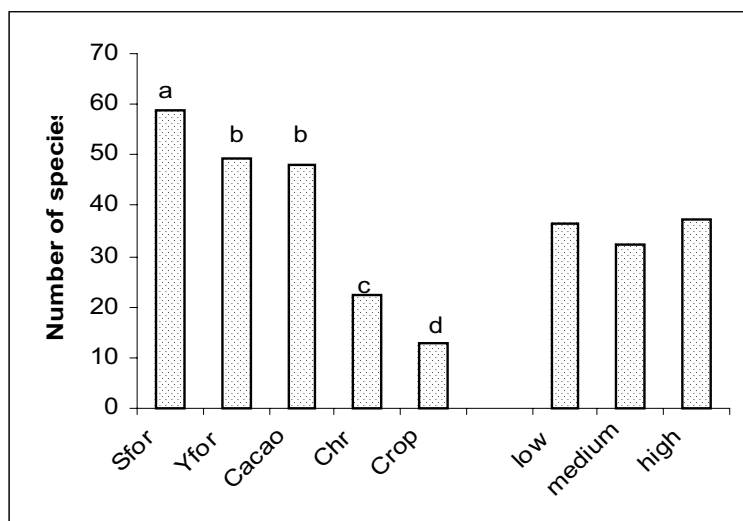|	Sfor		Yfor		Cacao		Chr		Crop	
	Observed	*Extrapolated*	Observed	*Extrapolated*	Observed	*Extrapolated*	Observed	*Extrapolated*	Observed	*Extrapolated*
Ng	58	*71*	48	*59*	41	*49*	12	*14*	19	*23*
Ak	45	*56*	70	*84*	28	*39*	33	*40*	13	*16*
Mb	31	*39*	21	*26*	43	*51*	20	*25*	6	*7*
Me	52	*64*	19	*23*	36	*45*	24	*29*	14	*16*
Nk	43	*51*	44	*54*	55	*67*	16	*19*	5	*5*
Mi	60	*72*	42	*50*	31	*38*	6	*7*	9	*11*

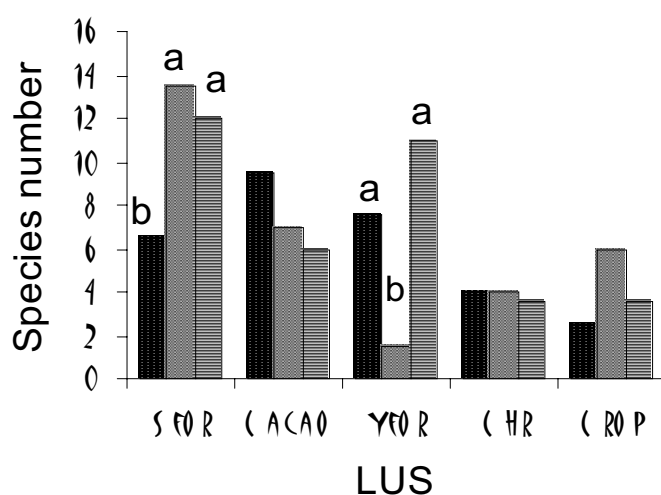**Figure 2.** Overall potential mean species richness across LUIs and per LUI**.**

Figure 3. Termite species richness per land use intensity

Bars with the same or no letter in a LUS are not significantly different at P<0.05

Species richness, incidence and abundance (individuals m-2) from monolith data

<u>Species richness</u>

Species richness ranged from less than 2 in Yfor to14 in Sfor in the medium LUI block (Table 3). There were no significant effects of LUI but rather a significant effect of LUS on termite species richness (Table 4). However there were significant differences in species richness between intensification blocks for Sfor and Yfor (Figure 3). Medium and high LUI blocks harbored more termite species than the low LUI block for Sfor (P=0.039 and P=0.029, respectively). For Yfor, high and low LUI blocks had more termite species than the medium

LUI block (P=0.0039 and P<0.0001, respectivily) (Table 3). In each block, there was a significant effect of LUS (Table 3). Within each block, Chr and Crop had significantly less termites species than the 3 more undisturbed LUSs except in the medium LUI block where Yfor had the lowest number of species.

Table 3. Termite community as affected by LUI and LUS based on monolith data#

Mean species number per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	6.50^a	9.50^a	7.50^a	4.00^b	2.50^b
Medium (Mb+Me)	13.50^a	7.00^a	1.50^b	4.00^b	6.00^b
High (Nk+Mi)	12.00^a	6.00^a	11.00^a	3.50^b	3.50^b
Mean abundance per m^2 per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	259.60^{ab}	184.80^b	604.80^a	466.40^a	39.60^c
Medium (Mb+Me)	325.20^a	192.00^{ab}	14.40^c	187.60^{ab}	71.20^b
High (Nk+Mi)	220.80^a	88.00^b	447.20^a	32.40^b	102.40^b
Shannon's diversity per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	1.40^a	1.24^a	1.07^a	0.67^b	0.48^c
Medium (Mb+Me)	1.42^a	1.19^b	0.32^c	0.94^b	1.19^b
High (Nk+Mi)	1.65^a	1.19^{ab}	1.39^a	0.77^b	0.49^b
Simpson's diversity per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	0.79^a	0.73^a	0.73^a	0.51^b	0.61^b
Medium (Mb+Me)	0.80^a	0.78^a	0.31^b	0.52^b	$0.72a^b$
High (Nk+Mi)	0.77^a	0.78^a	0.69^b	0.53^b	0.35^c
Evenness per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	0.79	0.57	0.55	0.49	0.60
Medium (Mb+Me)	0.55	0.62	0.79	0.70	0.67
High (Nk+Mi)	0.70^a	0.87^a	0.60^{ab}	0.65^{ab}	0.39^c

#In a row, means followed by the same superscript are not significantly
different at P=0.05

Table 4. ANOVA results of the effect of LUI and LUS(LUI) on termite'
characteristics in southern Cameroon

Parameter	LUI		LUS (LUI)	
	$F_{[2, 14]}$	P	$F_{[12, 14]}$	P
Species richness	0.13	0.88	5.28	<0.0001
Abundance	1.50	0.22	5.01	<0.0001
Soil feeder abundance	1.38	0.25	4.77	<0.0001
Wood feeder abundance	0.62	0.53	3.17	0.0005
Shannon (H')	0.92	0.39	3.42	0.0002
Evenness (E)	3.66	0.028	1.45	0.15
Simpson (D)	1.61	0.20	12.83	<0.0001

Table 5. Abundance per m^2 of termite trophic groups per land-use intensity block as affected by LUS[@].

Soil feeders per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	218[a]	199[a]	311[a]	565[a]	40[a]
Medium (Mb+Me)	315[a]	173[ab]	16[b]	134[a]	50[a]
High (Nk+Mi)	247[a]	80[b]	508[a]	31[b]	2[b]
Wood feeders per land-use intensity					
	Sfor	Cacao	Yfor	Chr	Crop
Low (Ng+Ak)	96[a]	30[a]	242[a]	16[b]	8[b]
Medium (Mb+Me)	89[a]	60[a]	2[b]	72[a]	26[b]
High (Nk+Mi)	28[a]	29[a]	38[a]	8[b]	108[a]

@ In a column, means followed by the same superscript are not significantly different at P<0.05
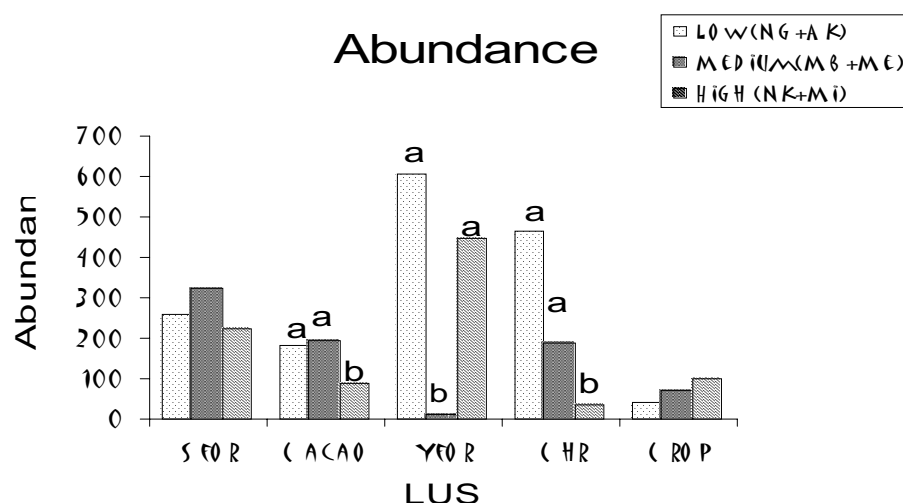
Figure 4. Termite abundance (ind m^{-2}) per land-use intensity

Bars with the same or no letter in a LUS are not significantly different at P<0.05

Abundance

Termite abundance ranged from less than 15 individuals m-2 in Yfor in the medium LUI block to more than 600 in the same LUS in the low LUI block (Table 3). Across blocks, there were no significant effects of LUI on termite abundance (Table 4). However, significant differences between LUSs of the same type were found between blocks for Cacao, Chr and Yfor (Figure 4). Differences due to the effect of LUS disturbance were significant within each LUI block (Table 3). In the low LUI block, Crop had significantly less termites than all the

other LUSs. In the medium LUI block, Yfor harbored significantly less termites than all the other LUSs and Sfor significantly outnumbered Crop. Within the high LUI block, Sfor and Yfor had significantly more termites than the other 3 LUSs.

Trophic groups abundance and distribution per LUI

Soil feeder abundance ranged from 2 m-2 in Crop of the high LUI block to 565 m-2 in Chr in the low LUI block across LUSs. LUI had no significant effect on soil feeder abundance (Table 5). However, Cacao, and Chr in the low LUI block had significantly more soil feeders than their counterparts in the high LUI block (P values were 0.018 and 0.03, respectively). For Yfor, the low and high LUI blocks contained more soil feeders than the medium LUI block (P=0.0078 and 0.007 respectively).

Wood feeder abundance ranged from less than 2 in Yfor in the medium LUI block to 242 m-2 in the same LUS in the low LUI block (Table 5). The medium LUI block had more species than the low and high LUI blocks (P=0.018 and 0.0048) for Chr and the reverse was the case for Yfor (P<0.0001 and 0.01, respectively).

Within individual LUSs in each block, soil feeders significantly outnumbered wood feeders except in Crop in the high LUI block and in Yfor in the medium LUI block (Table 5 and Figure 5). But proportionally (Figure 5), these differences were significant only in Cacao and Chr in the low LUI block (89 and 96% soil feeders respectively), in Sfor (78%) in the medium LUI block and in the high LUI block, in Sfor (78%), Yfor (89%) and conversely in Crop (74% for wood feeders).
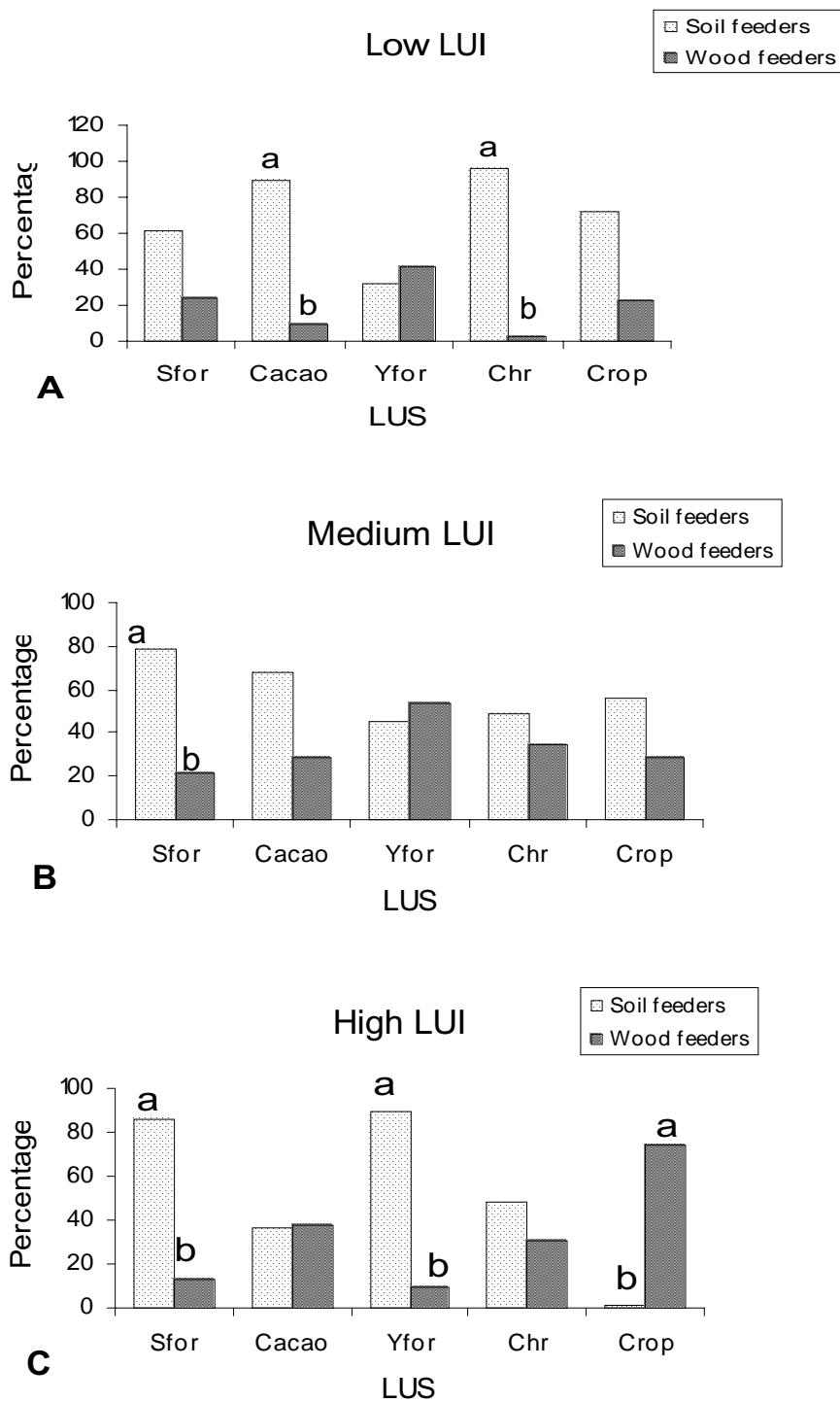
Figure 5. Proportion of species in each termite trophic group per land-use intensity block. A= low LUI; B= medium LUI; C= high LUI.
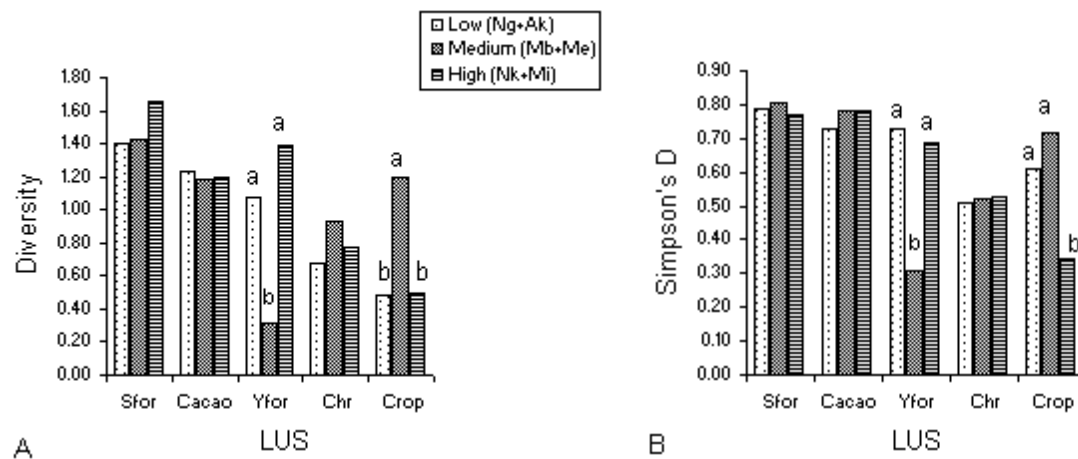Bars with the same or no letter in a LUS are not significantly different at P<0.05

Figure 6. Termite diversity indices per land-use intensity

H'= Shannon diversity index D= Simpson's diversity index
Bars with the same or no letter in a LUS are not significantly different at P<0.05

Diversity indices and evenness per LUI

Diversity

Shannon diversity indices ranged from 0.32 in Yfor in the medium LUI block to 1.65 in Sfor in the high LUI block. Simpson's diversity ranged from 0.80 in Sfor in the medium LUI block to 0.31 in Yfor in the same LUI block (Table 3). There were no significant effects of LUI on Shannon or on Simpson's diversity indices whereas significant effects of LUS were found (Table 4). Significant differences were found on both H' and D for Yfor and Crop (Figure 6).

Differences between LUSs are given in Table 3.Within the high LUI block, Sfor, Yfor and Cacao had higher H' and D than Chr and Crop. Within the medium LUI block, Sfor exhibited a higher H' and D than all the other LUSs except Cacao; in addition, H'in Yfor was higher than in both Cacao and Crop. Cacao had a higher D than all the other LUSs except Sfor. Within the low LUI block, all three more undisturbed LUSs had higher H' and D than Chr and Crop (the most disturbed LUSs).
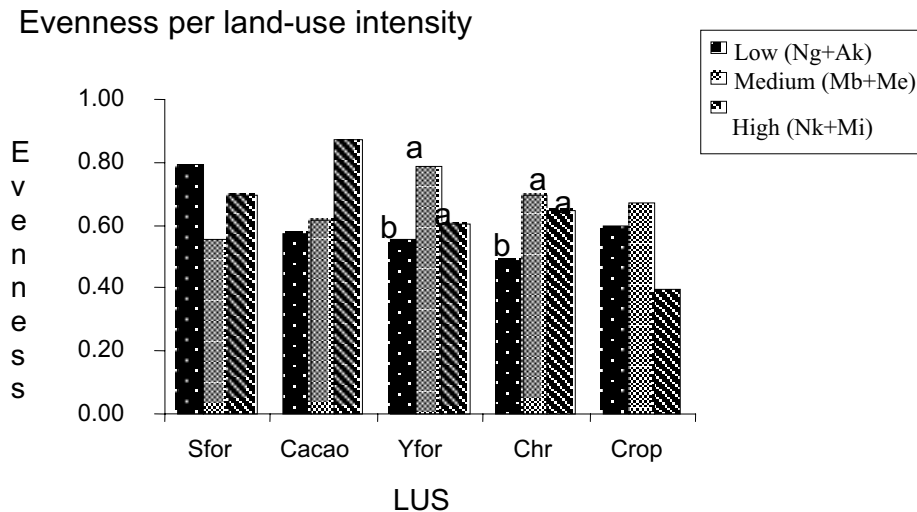
86

Figure 7. Termite evenness per land-use intensity.

Bars with the same or no letter in a LUS are not significantly different at P=0.05.

Evenness

Evenness ranged from 0.39 in Crop to 0.87 in Cacao both in the high LUI block. Ranges within blocks were low (0.30, 0.24 and 0.48, for low, medium and high LUI blocks, respectively) which suggests that distributions are patchy within blocks across LUSs. There was a significant effect of LUI on evenness; on average the medium LUI had significantly higher evenness than the high LUI block (P=0.01). Significant differences were found between LUIs for Chr and Yfor where high and medium LUI blocks had higher evenness coefficients than the low LUI block (Figure 7). On average there were no significant effects of LUS on overall termite species evenness (Table 4) but a significant pair-wise difference was found within the high LUI block where Crop had a significantly lower evenness than Sfor and Cacao (Table 3).

Similarity

Steinhaus similarities SA based on termite species presence/absence ranged from 0.00 (Sfor-Yfor) to 0.18 (Cacao-Chr) in the medium LUI block (Table 6). Similarity coefficients were very low across and within blocks suggesting a high differentiation both between blocks and between LUSs for the species composition of the termite communities.

Table 6. Steinhaus similarity coefficients of pairs of LUSs per LUI

Low land-use intensity		Cacao	Yfor	Chr	Crop	Average
	Sfor	0.05	0.02	0.01	0.03	0.02
	Cacao		0.01	0.01	0.04	
	Yfor			0.03	0.02	
	Chr				0.02	
Medium land-use intensity		Cacao	Yfor	Chr	Crop	Average
	Sfor	0.06	0.00	0.05	0.04	0.06
	Cacao		0.01	0.18	0.09	
	Yfor			0.01	0.02	
	Chr				0.09	
High land-use intensity		Cacao	Yfor	Chr	Crop	Average
	Sfor	0.09	0.03	0.09	0.05	0.05
	Cacao		0.07	0.01	0.12	
	Yfor			0.02	0.05	
	Chr				0.01	
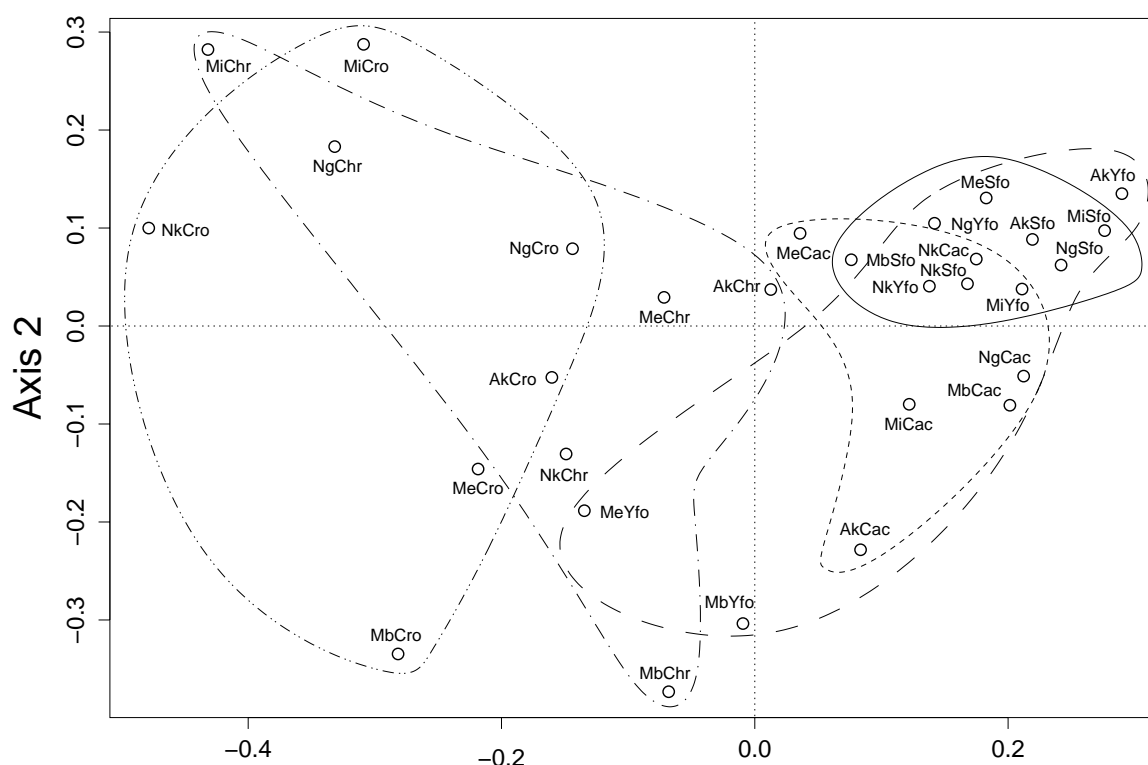
Figure 8. Ordination plot of LUSs (axes 1 and 2) based on termite dissimilarity index . The eigenvalues of the first six axes are 1.402, 0.792, 0.666, 0.507, 0.450 and 0.403, respectively.

Multivariate analysis

Ordination of LUSs was based on the species dissimilarity matrix (presence/absence). Total eigenvalue for the first six axes was 4.222. The ordering of LUSs along the first two vectors revealed that LUSs of similar canopy cover tend to aggregate regardless of LUI: Sfor, Cacao and Yfor versus Chr and Crop (Figure 8).

Discussion

Overall species richness

The number of species recorded in this survey is approximately 68% higher than the 133 species so far identified across similar disturbance gradients in the humid forest zone of West-Africa where our study was carried out (Eggleton et al., 2002); new species accounted for 43% which was close to 40% in the study by Eggleton et al. (2002). This striking species richness (evidenced by the lack of leveling in the species accumulation curves (Appendix 2)) might be explained by the relatively large number of villages (6) where the survey took place and it corroborates the hypothesis that the region is a hot spot of termite diversity (Eggleton et al., 1996). It may also be that the sampling period was ideal for maximum recovery of termites. Termites are active all year round but their activity is more obvious at higher temperature (Lavelle and Spain, 2001). Sampling took place in the short dry season when the soil had enough residual humidity and the average temperature of about 25-28oC and litter thickness were high due to through-fall caused by the previous rainy season, all conditions that favored termite activity (Lee, 1985; Wood, 1996; Lavelle and Spain, 2001). Dibog et al. (1998) found significant differences in termite diversity between sampling dates in the Mbalmayo Forest Reserve. However, the number of Apicotermitinae species was by far the largest, raising the question of possible over-splitting of species within this subfamily (Eggleton, personal comm.). Donovan et al. (2000) showed that morphological data alone are unlikely to fully resolve relationships between and within subfamilies.

Impacts of LUI and LUS on species richness, abundance and trophic groups

Overall termite species richness showed a strong negative correlation with LUS disturbance level, declining from Sfor to Crop (Table2 and Figure 2). Several previous studies across

similar gradients have revealed the same trend (Eggleton et al., 1995, 1996, 2002; Dibog, 1998; Dibog et al., 1998, 1999; Davies et al., 1999; Bignell et al., 2000; Zeidler et al., 2002). All 3 blocks had virtually the same species richness from low to high LUI indicating that at this scale of resolution, intensification had no direct effect on termite species richness. Species abundance and trophic group abundance were not affected either by LUI. Results on effects of LUI on diversity indices are similar to those on effects on species richness. This confirms the trend observed with data at LUS level for species richness (Figure 2). This result may suggest on the one hand that at the LUI level, there is no change in termite community structure due to agricultural intensity or that intensification as practiced in southern Cameroon had not reached a threshold that may cause losses of termite species and create imbalances in functional groups; on the other hand, it may well be that changes in termite community structure are masked due to the overall structural complexity of the entire southern Cameroon forest zone. This possibility stems from the specific significant differences found between LUI blocks for some LUSs (Figures 3 and 4 and Tables 4 and 5) suggesting the existence of some effect of intensity. Limited data on studies of intensification impacts on invertebrates at large scales allow only speculative conclusions. As shown in Lavelle and Spain (2001), termite communities comprise species of differing ecological strategies. Community structure is determined by factors operating at different spatial scales. The large-scale factors are those of biogeographic, climatic and vegetational variation, while topographic location and soil variability are influential at more local scales. At regional and local scale, the physical and other properties of certain soils may also limit termite colonization.

Significant effects of LUS on species richness, species abundance and trophic group abundance in our study are in conformity with those obtained in numerous previous studies carried out on similar gradients in West Africa (Eggleton et al., 1995, 1996, 2002; Dibog, 1998; Dibog et al., 1998, 1999), South East Asia (Davies et al., 1999; Bignell et al., 2000) and tropical Australia (Braithwaite et al., 988; King et al., 1998). In general, more undisturbed LUSs harbor more species in number and abundance than more disturbed ones. Difference in canopy cover, management history and physical factors were probably among the main driving forces underlying these differences. For termite richness specifically, differences found between LUSs within LUI blocks clearly indicate that LUSs with high canopy closure (Table 3) outnumbered those with low or open canopy, suggesting that high light and temperature in the latter may be the principal factors causing their low species number.

Longer fallow periods may also create better conditions for species conservation mainly with regard to physical perturbation of the soil.

The pattern of the differences in termite abundance due to disturbance was not as straight-forward as with species richness. The two extreme LUSs (Sfor and Crop) in the disturbance sequence are not affected by LUI (Figure 4); it may be that they have reached a high level of resilience for the resident termite species so that any disturbance would not bring in major changes on their abundance anymore. They may also become key entry points or pools for colonizing species due to their almost steady environments for long period of time.

The low species richness and abundance in Yfor in the medium LUI coupled with the lowest diversity indices is hard to interpret. As observed in the majority of previous studies, the regenerating LUSs often offer suitable conditions for food and shelter for higher termite abundance and diversity.

Significant differences due to disturbance levels between and across LUSs for trophic groups clearly show that soil feeders dominated numerically (Table 5), but wood feeders seemed more resilient to higher disturbance. The latter were exclusively more abundant in Crop in the high LUI (Figure 5). This may also be explained by the generally massive presence of larger buttresses and large tree logs left in the field for several years after clearing and burning forest for production purposes, thereby constituting shelter and food for wood feeding termites. This suggests that in Crop, decomposition of wood and litter, mediated by termites, will be enhanced while soil-mediated processes might be compromised. From the viewpoint of sustainability, this may have a negative effect on agricultural productivity, as there is accumulating evidence that soil-feeding termites are important for soil fertility (Dibog et al., 1999; Donovan et al., 2001). Furthermore, after depletion of woody material, a possible shift in feeding habits of certain species may increase the damage of termites to crops. Gilot et al. (1995) reported that in a five-year-old Hevea plantation in southern Côte d'Ivoire, termite communities comprised more than half of the total biomass of macroinvertebrate communities. This was due to the development of substantial populations of wood-feeding termites, which utilized the dead woody material remaining following forest clearance. Ten years later, this woody material had been exhausted and termite biomass fell to five times less than that of the original forest.

Diversity, evenness and similarity

The low diversity indices within blocks were predictable since they were calculated on the basis of abundance of species considered at monolith level. Clustering of LUSs can be interpreted in two ways (Figure 8): First, LUSs of similar disturbance are more close to each other (Table 3) and, secondly, LUSs of high to moderate canopy cover shared many species and those of the open canopy had some species in common. However, the high dissimilarities observed between species in the same LUS at different LUI suggest that termite assemblages of each land use may have derived from a different assemblage specific to the locality, or a selection process of species might have taken place due to the land use change. The distribution of vegetation is clearly important to community structure at a range of scales. At the broadest scale, the various biomes of the world offer different opportunities to the various ecological groupings and this also pertains to the vegetation types at a local scale (Lavelle and Spain, 2001).

Conclusion

Changes in termite community structure in the southern Cameroon forest zone are mainly due to the effect of LUS disturbance intensity. LUSs of similar disturbance level and canopy cover share a lot of species. However, the causes of high dissimilarity between species compositions in the same land use system at different land use intensities require further investigation.

Acknowledgement

Appendix 1. Compiled list of termite species sampled in the 6 villages surveyed from monolith and hand picking. Species with record equal to 0 in all 3 LUI sampling blocks were not sampled from monoliths. Underlind species are characteristic for low LUI. Species in bold are characteristic for medium LUI.

(sub)family	Species	Low LUI (Ng+Ak)	Medium LUI (Mb+Me)	High LUI (Nk+Mi)
Apicotermitinae	*Acholotermes chirotus* Sand, 1972	1	0	0
Apicotermitinae	*Acholotermes imbellis* Sand, 1972	2	2	1
Apicotermitinae	*Acholotermes* sp nov near *chirotus*	0	1	0
Apicotermitinae	*Acholotermes* sp nov near *epius*	0	0	0
Apicotermitinae	*Acholotermes* sp nov near *imbellis*	1	0	0
Apicotermitinae	*Acholotermes* sp nov near *tithasus*	1	0	0
Apicotermitinae	*Acholotermes tithasus* Sand, 1972	0	2	2
Apicotermitinae	*Adaiphrotermes* sp nov 1	2	3	0
Apicotermitinae	***Adaiphrotermes* sp nov 2**	**2**	**5**	**0**
Apicotermitinae	*Aderitotermes cavator* Sand, 1972	1	0	0
Apicotermitinae	*Aderitotermes fossor* Sand, 1972	1	1	0
Apicotermitinae	*Aderitotermes* sp nov near *fossor*	2	0	1
Apicotermitinae	*Aderitotermes* unnamed species	1	0	0
Apicotermitinae	*Adynatotermes* sp nov	0	0	0
Apicotermitinae	*Aganotermes oryctes* Sand, 1972	0	0	0
Apicotermitinae	*Aganotermes* sp nov 1	0	0	0
Apicotermitinae	*Aganotermes* sp nov near *oryctes*	0	0	0
Apicotermitinae	*Allognatotermes hypogeus* Silvestri	0	0	0
Apicotermitinae	*Alyscotermes kilimandjaricus* (Sjostedt), 1907	2	0	1
Apicotermitinae	*Alyscotermes* sp nov near *kilimandjaricus*	0	0	0
Apicotermitinae	*Amalotermes phaeocephalus* Sand, 1972	0	0	0
Apicotermitinae	*Amicotermes autothysius*	0	0	0
Apicotermitinae	*Amicotermes camerunensis*	0	0	0
Apicotermitinae	*Amicotermes dibogi*	1	0	0
Apicotermitinae	*Amicotermes gasteruptus*	0	0	0
Apicotermitinae	*Amicotermes mayombei*	0	0	0
Apicotermitinae	*Amicotermes mbalmayoensis*	0	0	0
Apicotermitinae	*Amicotermes multispinus*	0	0	0
Apicotermitinae	*Amicotermes* sp nov 1	1	0	1
Apicotermitinae	*Amicotermes* sp nov 13 near *congoensis*	0	0	0
Apicotermitinae	*Amicotermes* sp nov 2	0	0	1
Apicotermitinae	*Amicotermes* sp nov 8	0	0	1
Apicotermitinae	*Amicotermes* sp nov near *gasteruptus*	0	0	0
Apicotermitinae	*Anenteotermes amachetus* Sand, 1972	0	0	1
Apicotermitinae	*Anenteotermes ateuchestes* Sand, 1972	1	0	0
Apicotermitinae	*Anenteotermes cnaphorus* Sand, 1972	0	0	0
Apicotermitinae	*Anenteotermes disluctans* Sand, 1972	0	0	0
Apicotermitinae	*Anenteotermes hemerus* Sand, 1972	0	0	0
Apicotermitinae	*Anenteotermes nanus* (Sjostedt), 1911	0	0	0
Apicotermitinae	***Anenteotermes polyscolus* Sand, 1972**	**0**	**3**	**1**
Apicotermitinae	*Anenteotermes* sp nov 2	0	0	0
Apicotermitinae	*Anenteotermes* sp nov near *amachetus*	0	0	0
Apicotermitinae	*Anenteotermes* sp nov near *cnaphorus*	0	0	0
Apicotermitinae	*Anenteotermes* sp nov near *disluctans*	0	0	0
Apicotermitinae	*Anenteotermes* sp nov near *hemerus*	0	0	1
Apicotermitinae	*Anenteotermes* sp nov near *polyscolus*	0	1	0
Apicotermitinae	*Apagotermes* sp nov	0	0	0
Apicotermitinae	*Apagotermes stolidus* Sand, 1972	0	0	0

Apicotermitinae	*Astalotermes acholus* Sand, 1972	0	0	1
Apicotermitinae	*Astalotermes benignus* Sand, 1972	0	0	0
Apicotermitinae	*Astalotermes concilians* (Silvestri*), 1914	0	0	0
Apicotermitinae	*Astalotermes ignavus* Sand, 1972	0	0	1
Apicotermitinae	*Astalotermes incertator*	0	0	0
Apicotermitinae	*Astalotermes mitis* Sand, 1972	0	0	0
Apicotermitinae	*Astalotermes quietus* (Silvestri*), 1914	0	2	0
Apicotermitinae	*Astalotermes* sp nov 1	0	0	0
Apicotermitinae	*Astalotermes* sp nov 10	**2**	**0**	**0**
Apicotermitinae	*Astalotermes* sp nov 11	0	0	0
Apicotermitinae	*Astalotermes* sp nov 12	0	0	0
Apicotermitinae	*Astalotermes* sp nov 13	0	2	0
Apicotermitinae	*Astalotermes* sp nov 14	0	0	0
Apicotermitinae	*Astalotermes* sp nov 15	0	0	0
Apicotermitinae	*Astalotermes* sp nov 16	0	0	0
Apicotermitinae	*Astalotermes* sp nov 2	1	0	0
Apicotermitinae	*Astalotermes* sp nov 3	**3**	**0**	**0**
Apicotermitinae	*Astalotermes* sp nov 4	0	0	0
Apicotermitinae	*Astalotermes* sp nov 5	1	0	0
Apicotermitinae	*Astalotermes* sp nov 6	0	0	0
Apicotermitinae	*Astalotermes* sp nov 7	1	0	0
Apicotermitinae	*Astalotermes* sp nov 8	0	0	0
Apicotermitinae	*Astalotermes* sp nov 9	**0**	**0**	**2**
Apicotermitinae	*Astalotermes* sp nov near *acholus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *aganus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *amicus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *benignus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *brevior*	**0**	**0**	**2**
Apicotermitinae	*Astalotermes* sp nov near *empodius*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *eumenus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *ignavus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *irrixosus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *murcus*	0	0	0
Apicotermitinae	*Astalotermes* sp nov near *quietus*	0	0	0
Apicotermitinae	*Astalotermes*sp nov near *impedians*	0	0	0
Apicotermitinae	*Astratotermes hilarus* Sand, 1972	0	1	0
Apicotermitinae	*Astratotermes libanus*	0	0	0
Apicotermitinae	*Astratotermes prosenus* Sand, 1972	0	0	0
Apicotermitinae	*Astratotermes* sp nov 1	0	0	0
Apicotermitinae	*Astratotermes* sp nov 2	0	0	0
Apicotermitinae	*Astratotermes* sp nov near *aneristus*	0	0	0
Apicotermitinae	*Astratotermes* sp nov near *hilarus*	0	0	1
Apicotermitinae	*Astratotermes* sp nov *near mansuetus*	0	0	0
Apicotermitinae	*Astratotermes* sp nov near *pacatus*	0	0	0
Apicotermitinae	*Astratotermes* sp nov near *prosenus*	0	0	0
Apicotermitinae	*Ateuchotermes ctenopher* Sand, 1972	0	1	0
Apicotermitinae	*Ateuchotermes pectinatus* Sand, 1972	0	0	0
Apicotermitinae	*Ateuchotermes sentosus* Sand, 1972	1	0	1
Apicotermitinae	*Ateuchotermes* sp nov 1	1	0	1
Apicotermitinae	*Ateuchotermes* sp nov near *ctenopher*	0	1	0
Apicotermitinae	*Ateuchotermes* sp nov near *muricatus*	0	0	0
Apicotermitinae	*Ateuchotermes* sp nov near *pectinatus*	0	0	0
Apicotermitinae	*Ateuchotermes* sp nov near *sentosus*	0	0	0
Apicotermitinae	*Ateuchotermes* sp nov near *spinulatus*	0	0	0
Apicotermitinae	*Ateuchotermes* sp nov near *tranquillus*	0	0	0
Apicotermitinae	*Ateuchotermes spinulatus* Sand, 1972	0	0	0
Apicotermitinae	*Coxotermes boukokoensis*	0	0	0
Apicotermitinae	*Duplidentitermes furcatidens* (Sjostedt),	0	2	1

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	1924			
Apicotermitinae	*Eburnitermes* sp nov 1	0	1	1
Apicotermitinae	*Eburnitermes* sp nov 2	0	0	1
Apicotermitinae	*Jugositermes tuberculatus* Emerson	0	0	0
Apicotermitinae	*Labidotermes* sp nov 1	1	0	0
Apicotermitinae	*Labidotermes* sp nov 2	0	1	0
Apicotermitinae	*Machadotermes rigidus* Collins, 1977zr	0	0	1
Apicotermitinae	New genus 1 sp 1	2	1	3
Apicotermitinae	New genus 1 sp 2	0	0	0
Apicotermitinae	New genus 11	0	0	0
Apicotermitinae	New genus 4	1	0	0
Apicotermitinae	New genus 5 *Eburnitermes* like	0	0	0
Apicotermitinae	New genus 7 sp 1	0	0	2
Apicotermitinae	New genus 7 sp 2	0	0	1
Apicotermitinae	New genus 8	0	0	0
Apicotermitinae	New genus 9 *Labidotermes* like	0	0	1
Apicotermitinae	New genus *Aderitotermes* like	0	0	0
Apicotermitinae	New genus *Astalotermes* like	0	0	0
Apicotermitinae	New genus *Astratotermes* like	0	0	0
Apicotermitinae	New genus *Ateuchotermes* like	0	0	0
Apicotermitinae	New genus *Capritermes* like	0	0	0
Apicotermitinae	New genus near *Amicotermes*	0	0	0
Apicotermitinae	New genus near *Labidotermes*	0	0	1
Apicotermitinae	*Phoxotermes cerberus* Collins, 1977zr	0	0	0
Apicotermitinae	*Trichotermes* sp	1	0	0
Macrotermitinae	*Acanthotermes acanthothorax* (Sjostedt)	0	1	0
Macrotermitinae	*Ancistrotermes crucifer* (Sjostedt)	0	0	1
Macrotermitinae	*Ancistrotermes guineensis* (Silvestri)	0	0	0
Macrotermitinae	*Ancistrotermes* sp	0	0	1
Macrotermitinae	*Macrotermes bellicosus* (Smeathman)	0	0	0
Macrotermitinae	*Microtermes* sp	9	8	7
Macrotermitinae	*Odontotermes* sp 1	4	5	5
Macrotermitinae	*Odontotermes* sp 2	3	0	1
Macrotermitinae	*Odontotermes* sp 3	0	0	0
Macrotermitinae	*Odontotermes* sp 4	0	0	0
Macrotermitinae	*Protermes prorepens* (Sjostedt)	1	0	0
Macrotermitinae	*Pseudacanthotermes grandiceps* (Sjostedt)	0	0	0
Macrotermitinae	*Pseudacanthotermes harrisensis* Weidner, 1962zr	0	0	0
Macrotermitinae	*Pseudacanthotermes militaris* (Hagen)	4	5	5
Macrotermitinae	***Pseudacanthotermes spiniger* (Sjostedt)**	0	3	0
Macrotermitinae	*Sphaerotermes sphaerothorax* (Sjostedt)	1	2	3
Macrotermitinae	*Synacanthotermes heterodon* (Sjostedt)	2	3	1
Macrotermitinae	*Synacanthotermes* sp nov	0	0	0
Nasutitermitinae	*Eutermellus convergens* Silvestri	0	0	0
Nasutitermitinae	*Leptomyxotermes doriae* (Silvestri)	0	0	0
Nasutitermitinae	*Nasutitermes arborumSmeathman* (Sands, 1965zr)	1	0	1
Nasutitermitinae	*Nasutitermes diabolus* (Sjostedt)	1	0	0
Nasutitermitinae	*Nasutitermes ferranti* (Wasmann*)*	0	0	0
Nasutitermitinae	*Nasutitermes fulleri* Emerson	0	1	0
Nasutitermitinae	*Nasutitermes latifrons* (Sjostedt)	0	0	1
Nasutitermitinae	*Nasutitermes lujae* Wasmann (resurrected by Sands, 1965zr)	0	0	0
Nasutitermitinae	*Nasutitermes schoutedeni* (Sjostedt)	0	0	1
Nasutitermitinae	*Postsubulitermes parviconstrictus* Emerson, 1960	0	0	0

Nasutitermitinae	*Trinervitermes bettonianus* (Sjostedt)	0	0	0
Nasutitermitinae	*Verrucocositermes tuberosus* Emerson, 1960	1	0	0
Nasutitermitinae	*Verrucositermes tuberculatus*	0	0	0
Rhinotermitidae	*Coptotermes sjostedti* Holmgren	1	0	0
Rhinotermitidae	*Schedorhinotermes putorius* (Sjostedt)	1	1	0
Termitinae	*Apilitermes longiceps* (Sjostedt, 1899)	3	0	0
Termitinae	*Basidentitermes aurivillii* (Sjostedt)	0	2	2
Termitinae	*Basidentitermes demoulini* Harris, 1963zr	1	1	0
Termitinae	*Basidentitermes diversifrons* Silvestri	2	1	1
Termitinae	*Basidentitermes mactus* (Sjostedt)	1	0	1
Termitinae	*Basidentitermes* sp nov 1	1	0	0
Termitinae	*Basidentitermes* sp nov 2	1	0	0
Termitinae	*Basidentitermes* sp nov 3	0	1	0
Termitinae	*Cephalotermes rectangularis* (Sjostedt)	0	1	0
Termitinae	*Crenetermes albotarsalis (Sjostedt)*	0	0	0
Termitinae	*Cubitermes antennalis*	0	0	1
Termitinae	*Cubitermes banksi* (Emerson*)*	0	1	0
Termitinae	*Cubitermes comstocki* (Emerson)	0	0	0
Termitinae	*Cubitermes fungifaber* (Sjostedt)	**0**	**0**	**2**
Termitinae	*Cubitermes gaigei* (Emerson)	0	0	0
Termitinae	*Cubitermes heghi* Sjostedt, 1924	0	0	0
Termitinae	*Cubitermes severus* Silvestri	0	0	0
Termitinae	*Cubitermes* sp near *antennalis*	1	0	0
Termitinae	*Cubitermes* sp near *comstocki*	0	0	0
Termitinae	*Cubitermes* sp near *congoensis*	0	0	0
Termitinae	*Cubitermes* sp near *fungifaber*	0	0	0
Termitinae	*Cubitermes* sp near *gaigei*	0	0	0
Termitinae	*Cubitermes* sp near *heghi*	0	1	0
Termitinae	*Cubitermes* sp near *loubetsiensis*	0	0	0
Termitinae	*Cubitermes* sp near *sankurensis*	0	0	0
Termitinae	*Cubitermes* sp near *severus*	0	0	0
Termitinae	*Cubitermes* sp near *subarquatus*	0	0	0
Termitinae	*Cubitermes* sp nov near *ugandensis*	0	0	0
Termitinae	*Cubitermes subarquartus* Sjostedt	0	0	0
Termitinae	*Cubitermes sulcifrons* Wasmann	0	0	0
Termitinae	*Fastigitermes jucundus* (Sjostedt)	2	3	1
Termitinae	*Foraminitermes tubifrons* Holmgren	0	0	0
Termitinae	*Foraminitermes valens* (Silvestri)	1	0	1
Termitinae	*Furculitermes winifredae* Emerson, 1960	1	2	2
Termitinae	*Microcerotermes edentatus* Wasmann	0	0	0
Termitinae	*Microcerotermes fuscotibialis* (Sjostedt)	0	1	0
Termitinae	*Microcerotermes parvus* (Haviland)	1	1	1
Termitinae	*Mirocerotermes* sp nov 1	0	0	0
Termitinae	*Mirocerotermes* sp nov 2	0	0	0
Termitinae	*Mucrotermes* sp nov 1	1	0	2
Termitinae	*Mucrotermes* sp nov 2	0	0	1
Termitinae	*Nitiditermes* sp	0	0	0
Termitinae	*Noditermes indoensis* Sjostedt	0	0	0
Termitinae	*Ophiotermes grandilabius* (Emerson)	0	0	0
Termitinae	*Orthotermes depressifrons* Silvestri	1	2	2
Termitinae	*Pericapritermes chiasognathus* (Sjostedt)	3	1	1
Termitinae	*Pericapritermes minimus* Weidner, 1956	0	0	0
Termitinae	*Pericapritermes nigeriana* Silvestri, 1914 (stat. n., Sand, 1972)	0	0	0
Termitinae	*Pericapritermes* sp nov 1	4	1	5
Termitinae	*Pericapritermes* sp nov 3	0	0	0
Termitinae	*Proboscitermes* sp nov 1	1	1	1

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Termitinae	*Procubitermes arboricola* (Sjostedt)	0	0	0
Termitinae	*Profastigitermes putnami* Emerson, 1960	2	7	3
Termitinae	*Promirotermes redundans* Silvestri	0	0	0
Termitinae	*Termes hospes* (Sjostedt)	0	0	0
Termitinae	*Thoracotermes macrothorax* (Sjostedt)	0	0	0
Termitinae	*Unguitermes acutifrons* (Silvestri)	0	0	1
Termitinae	*Unguitermes* sp nov 2	0	0	1
Termitinae	*Unguitermes* sp nov 3	0	0	0
Termitinae	*Unguitermes* sp nov near *trispinosus*	0	0	1
Termitinae	*Unguitermes trispinosus* Ruelle, 1973zr	0	1	2

Appendix 2. Species accumulation curves for the 5 LUSs in the 6 villages surveyed.

Akok

Ngoungoumou
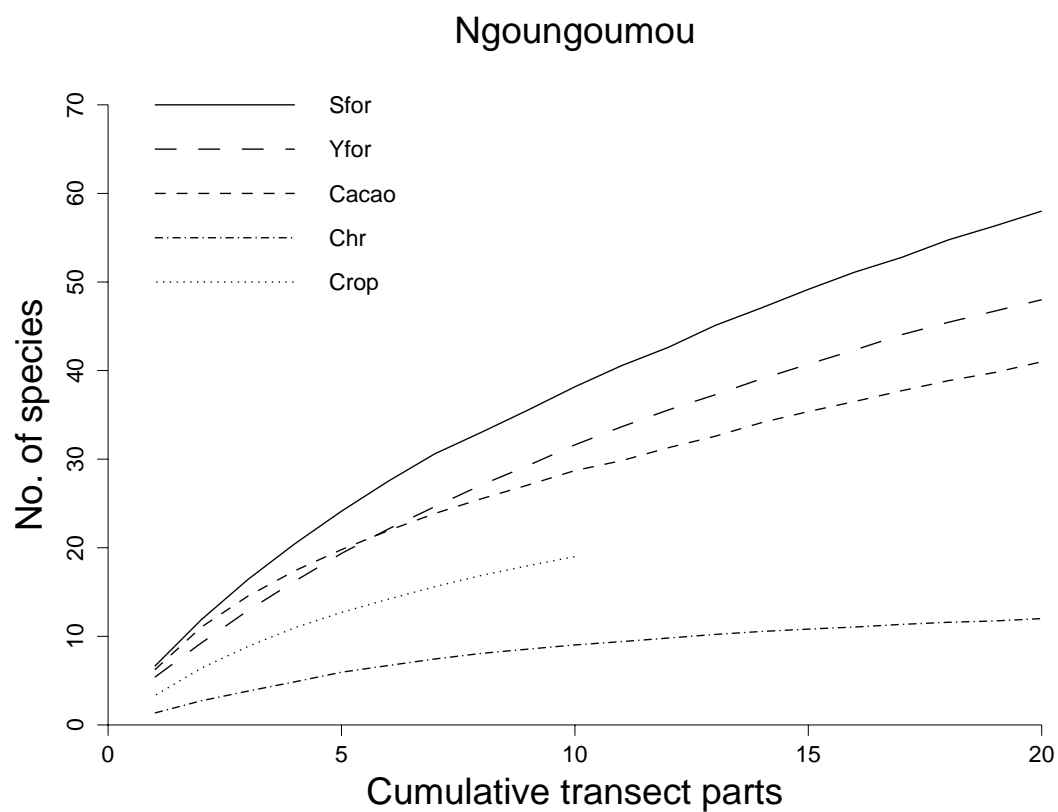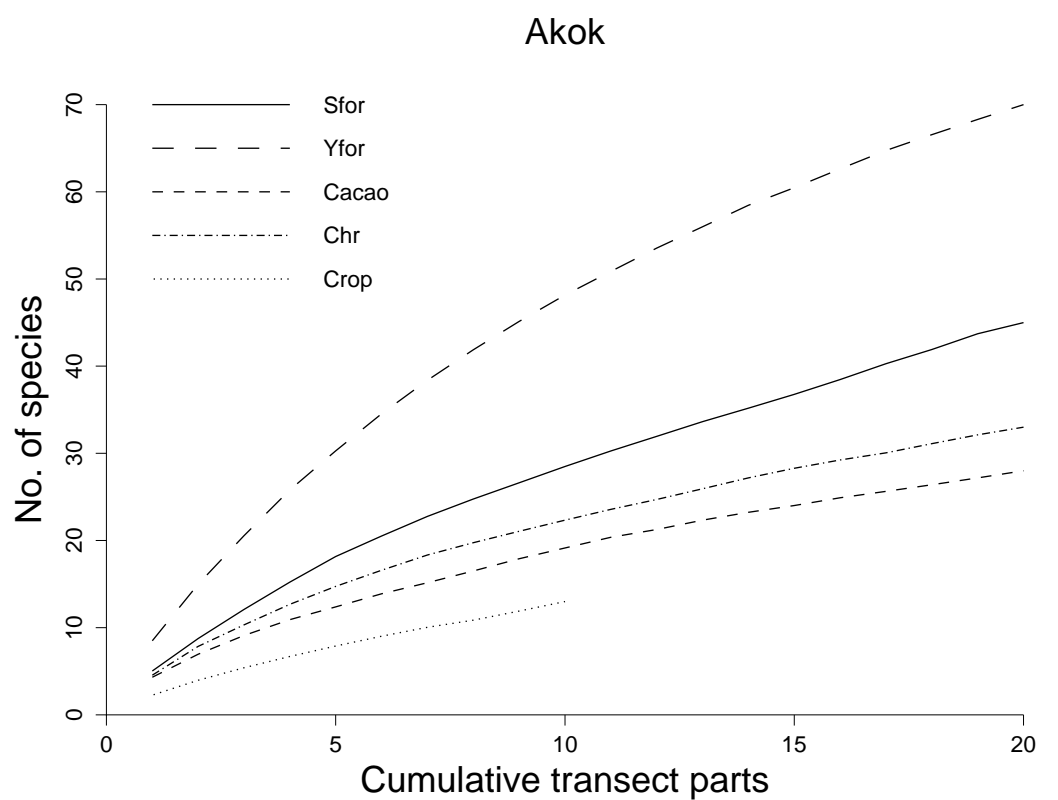
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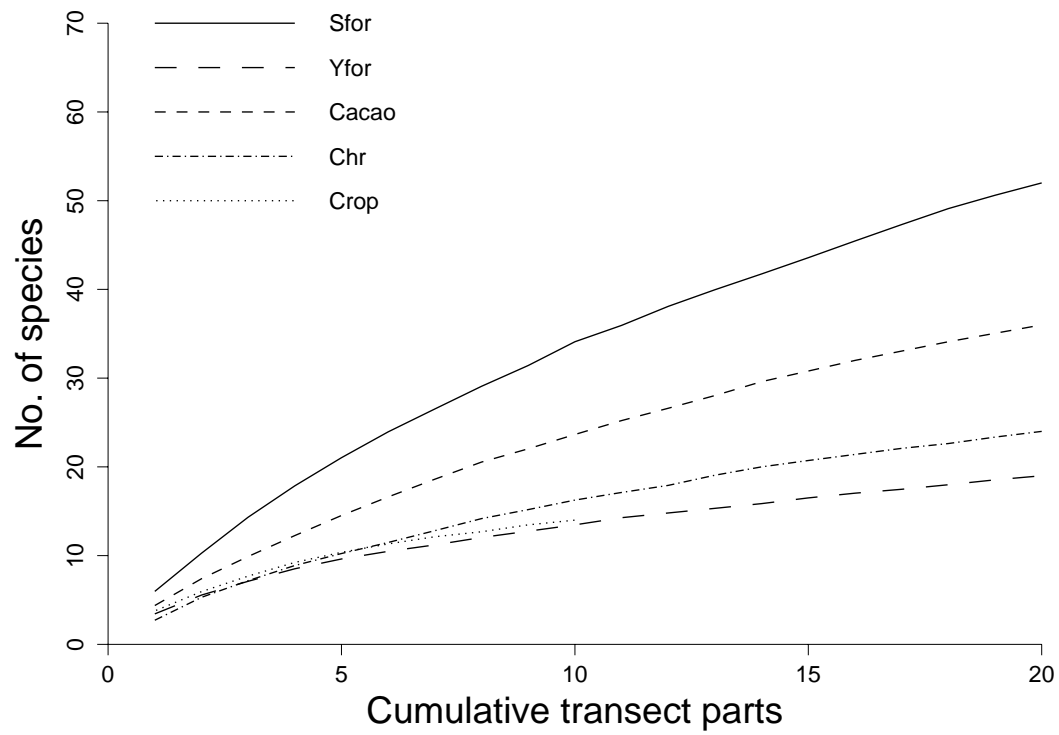
Mbalmayo
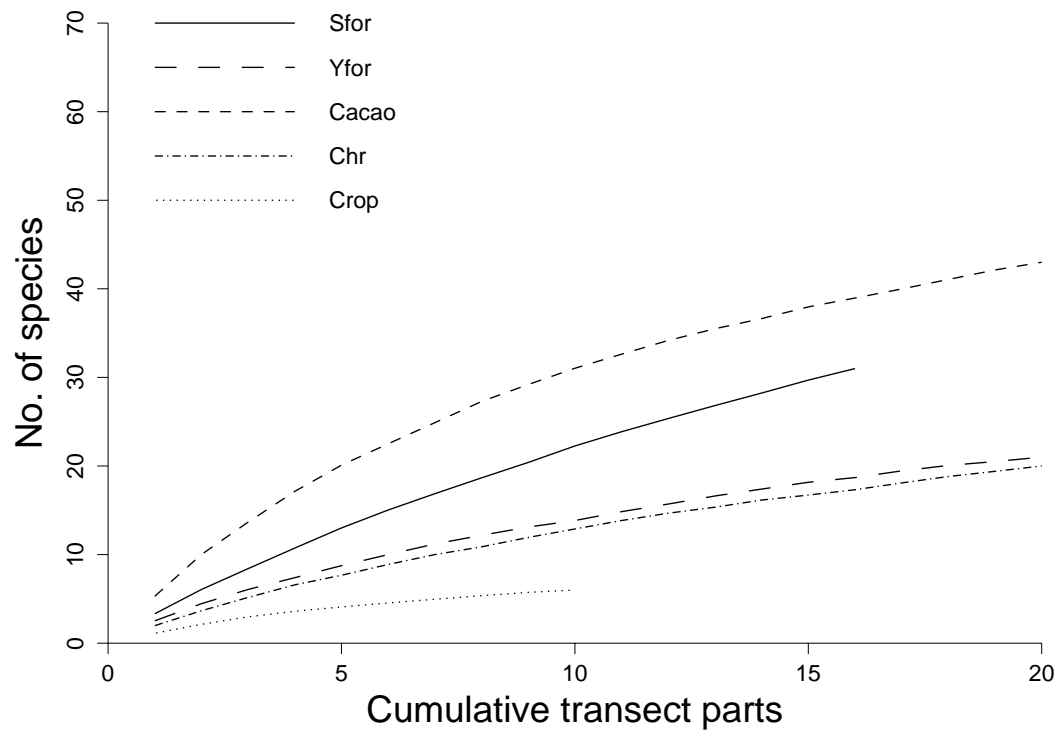
Nkometou
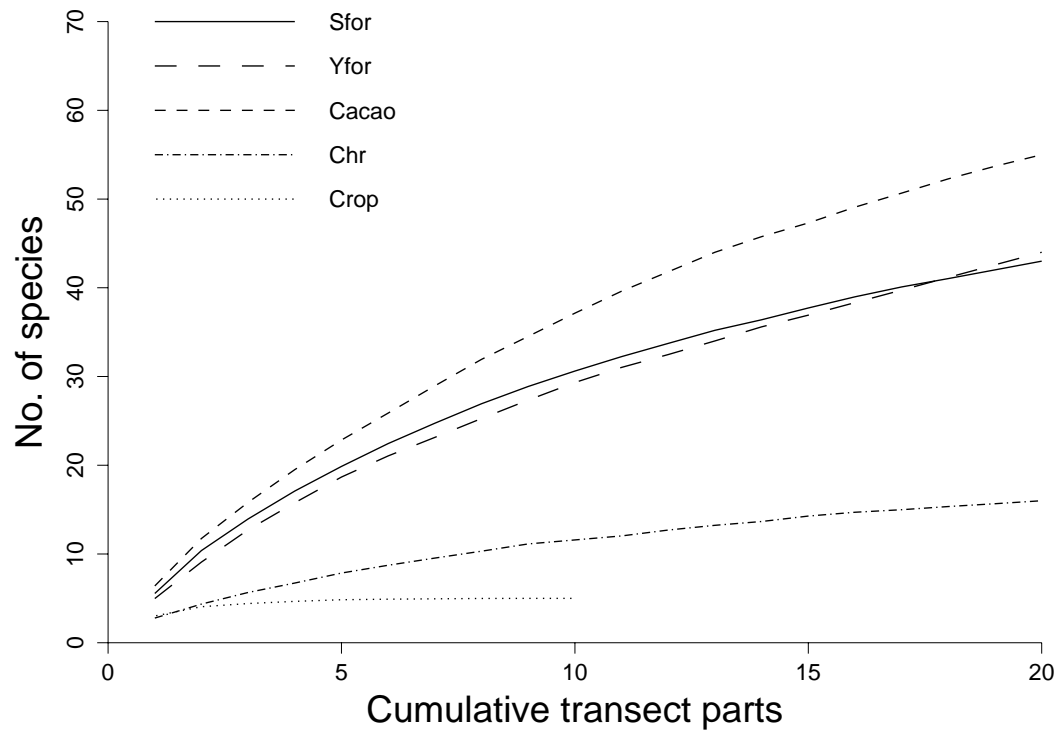
Minkoameyos
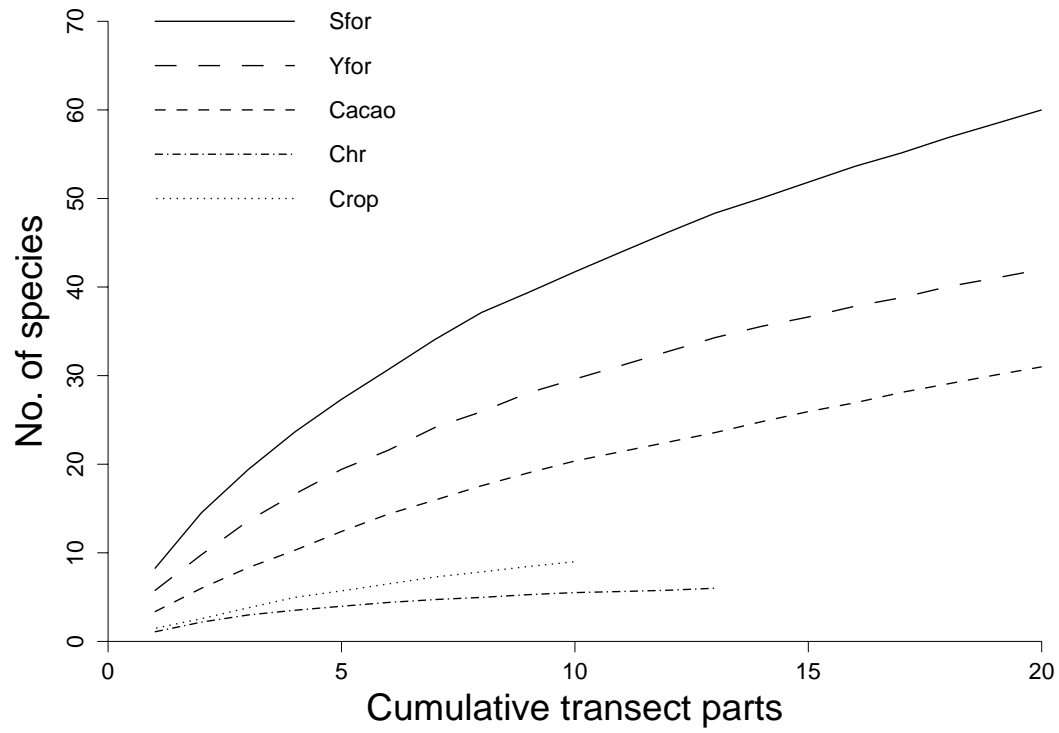
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Ant community structure along a gradient of land use intensification in the humid forest zone of southern Cameroon

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Summary

Ground-dwelling ant communities in most of the common land use systems edging the Congo Basin rainforest are poorly known as are the impacts of human activities.This study was carried out in order to describe the community structure of ants along a gradient of land use intensity (LUI) in the forest margin zone of southern Cameroon. High LUI (Nkometou and Minkoameyos villages), medium LUI (Mbalmayo and Metet villages) and low LUI (Akok and Ngoungoumou) are associated with the following degrees of deforestation: high (25% of forest cover left), medium (40%) and low (57% left). In each village, ants were collected during the short dry season in 5 land use systems (LUSs) of different levels of disturbance by hand-sorting 5 monoliths (50 x 50 x 30 cm). The sampled LUSs were: secondary forest >30 year old (Sfor), shaded cocoa plantation (Cacao), young forest of 12-15 years (Yfor), 4-5 year old *Chromolaena odorata* (Chr) and a groundnut/maize/cassava intercrop (Crop).

A total of 80 ant species were found belonging to 7 subfamilies. LUI and LUS had striking effects on ant communities with highest richness and abundance in the low LUI block, followed by medium and high LUI blocks respectively. Diversity indices (Shannon and Simpson's) significantly decreased along this LUI gradient. However, species were evenly distributed within and across LUSs and LUI blocks. Cacao plantation exhibited the highest diversity on average and harbored the highest number of saprovorous ant species. Crop showed the lowest diversity and abundance. Predator species dominated in all the LUSs. Ant communities of each LUI block were characterized by at least 3 dominant ant colonies. The low LUI block had the highest number of characteristic species (8) while the high LUI block had 3 such species and medium LUI block 5. A multivariate analysis (CA) on species incidence did not reveal a clear pattern of species association per LUI as suggested by the existence of characteristic species, but indicated that ant species assemblages in the forest zone of southern Cameroon were rather confined heterogeneously in the specific villages.

Key words: Community structure, land use intensity, land use system, Congo basin disturbance, south Cameroon.

Introduction

The importance of macrofauna to the promotion of tropical soil fertility has been stressed in a number of recent reviews (Lobry de Bruyn and Conacher, 1990; Brussaard and Juma, 1996, Lavelle et al., 1997). Soil ants and other macrofauna represent predators, herbivores (granivores) and bioturbators, bringing about important changes in the physical and chemical properties of soils, as well as dispersing plant propagules. Networks of galleries and chambers increase the porosity of the soil, increasing the drainage and aeration (Mando et al., 1997). Ants are among the most ubiquitous insects on the planet. They occur in all biomes except for the extreme polar regions. In biomes where ants are abundant, they affect many soil processes that contribute to the creation of patchy mosaics that characterize the soils and vegetation of many landscapes. The abundance and diversity of soil-nesting ants varies from as high as 7,000 colonies per hectare in tropical savanna to as few as 3–4 colonies per hectare on some periodically flooded, fine-textured soil, desert landscape units. Soil-nesting ants affect critical ecosystem processes such as nutrient cycling and water redistribution (Whitford, 2002).

Ground-dwelling ants are easily sampled and observed, are abundant and diverse, are sensitive to both small-scale and large-scale environmental variations, are characterized by strong behavioral and competitive interactions and may play a major role in the movement of materials in arid and semi-arid ecosystems (Morton et al., 1988). Ant communities are much more species-rich in the tropics than elsewhere, a pattern associated with habitat heterogeneity (Folgarait, 1996; Davidson and McKey, 1993). Ants represent up to 65% of the total number of faunal specimens in biomass collecting. With up to 150 species per hectare (>350 species including all ants), the leaf-litter ant fauna is diverse enough for the calculation of standard biodiversity measures. The taxonomy of ants is fairly well known by invertebrate standards. Because of their ecological importance, ants have the potential to deliver more reliable biodiversity data than often used indicator taxa such as plants, mammals, birds or even butterflies.

Deforestation and increased land use intensity are likely to change species composition in all groups of soil fauna including ants. In addition, the rate of intensification of agriculture in the tropics is greater than in other regions of the world, so that tropical ecosystems are under particular threat of major changes or loss (Izac et al., 1996). Therefore, there is a need to directly measure the impact of deforestation and forest disturbance on ant diversity. In the Congo Basin, information on ground-dwelling ants is limited. Most surveys

and collections of ants in West-Africa have focused on the description of ant's community structure or mosaics of either the canopy in forests and tree plantations or of specific ant habitats such as termitaries (Dejean and Cordoba, 2002; Kenne and Dejean, 1999;Watt et al., 2002; Dejean et al., 2000). Although some studies were devoted to the impact of forest conversion on ants communities (Watt et al., 2002), no reference was found on the effect of land use intensification. In recent years, socio-economic factors (including changing world price for cocoa, oil-palm, rubber latex and other cash crops), population growth, the restriction of urban employment opportunities and legal uncertainties over title to timber revenues, have led to an increase in clearance of forest for food or cash crop production and, concomitantly, an accelerated decline in the fertility of soil under cultivation as fallow periods have shortened (Woomer and Swift, 1994). All these factors have led to gradual agricultural intensification in an effort to assure reasonable land productivity. Intensification is a combination of a number of factors such as (1) the fraction of time land is used for crop production, (2) the fraction of total biomass harvested (3) the amounts of fertilizer, irrigation and pesticides used, as well as (4) the amount of (fossil) energy used in soil tillage and mechanized farm operations (Giller et al., 1997). This study was aimed at assessing the impact of land use intensity on soil-dwelling ant community structure in the forest margins of southern Cameroon. For this purpose, we made between-land use intensity (LUI) comparisons, and within LUI blocks, comparisons between land use systems (LUSs) to document how species and communities of ground-dwelling ants respond to local and regional gradients of disturbance, and to establish a baseline for understanding the long-term dynamics of these critical and sensitive components of the humid forest.

Materials and methods

Study area and treatments

The study was conducted in six villages in southern Cameroon classified into three blocks representing increasing levels of deforestation and land use intensity (LUI) within the benchmark established by ASB, IRAD and IITA (Thenkabail, 1999) known as: (1) Yaoundé block (high LUI), (2) Mbalmayo block (medium LUI) and (3) Ebolowa block (low LUI) (Figure 1 and Table 1). Annual rainfall in southern Cameroon is bimodal. Rains start in mid-March and end in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November. In 1999, annual rainfall was 1500 mm.

Table 1. Physical characterization of the 6 villages under study in southern Cameroon.

Block	Level of deforestation and LUI*	Village	Distance from Yaounde	Geo-references	Soil class	land under forest cover (%)	land under fallow (%)	land under crop (%)
Yaoundé	High	Nkometou (Nk)	40 km North	11°35'E, 4°05'N	Rhodic Kandiudult			
		Minkoameyos (Mi)	15 km West	11°27'E, 3°51'N		25	29	27
Mbalmayo	Medium	Mbalmayo (Mb)	50 km South	11°28'E, 3°27'N	Typic Kandiudult			
		Metet (Me)	90 km South	11°45'E, 3°25'N		40	16	19
Ebolowa	Low	Akok (Ak)	150 km South	11°14'E, 2°44'N	Typic Kandiudox	57	10	13
		Ngoungoumou (Ng)	130 South	12°01'E, 3°18'N				

*Land Use Intensity

Figure 1. Map of southern Cameroon and the three land use intensification blocks within the forest margins benchmark

The commonest 5 land use systems (LUS) of the region, representing a gradient of disturbance from low to high were selected such that the ages and plot histories of the LUSs of the same type in the different villages were approximately the same: a secondary forest (>30 years, Sfor), a shaded cacao plantation (Cacao), young forest fallow (12-15 years, Yfor), 4-5 year old *Chromolaena odorata* fallow (Chr), and a groundnut / maize / cassava intercrop field (Crop). For details, see Zapfack et al. (2002), who characterized the vegetation in several villages of these three blocks.

Sampling methods

<u>For qualitative assessment</u>

The sampling methods followed closely those of Anderson and Ingram (1993) and Bignell et al. (2000).

Transect sampling was used for a rapid biodiversity assessment from July to August 1999 during the short dry season. The transects were laid out to run through visually homogeneous surroundings, avoiding features that were not suitable for leaf litter ants and below-ground fauna, such as large streams, cliff edges or trails. We also avoided other

natural discontinuities such as hill slopes, streams or canopy gaps. The sampling was performed along a 100 m belt transect of two meter width, divided into 20 sections of five meter long each, numbered sequentially. Each section was sampled (hand-picking) by two trained persons for 30 minutes amounting to a total sampling time of one hour per section. The investigated microhabitats per section were as follows:

- ground surface and topsoil of at least five centimeters depth

- litter and humus on soil surface, at the base of trees, and between buttress roots if any

- soil within and beneath rotten logs

- epigeal termite mounds on ground surface and at the base of trees

- the inside of dead wood and logs, tree stumps, branches and twigs, damp and dead trees.

In addition 10 pitfalls traps were installed for day and night catches at 10 m intervals on a line situated 2 meters parallel to the transect. For pitfall traps, we used 50 cc glass jars of 10 cm opening diameter, half filled with a solution of water and drops of liquid detergent. The trap was checked after 24 hours and the collected ants preserved in a 70% ethyl alcohol solution.

For quantitative assessment

In each LUS five soil monoliths of 50 x 50 x 30 cm (L x W x D) were excavated along the 100 m transect at 20-m intervals and ants were hand-picked and specimens preserved in glass tubes containing 70% ethyl alcohol.

Identification

Taxonomy

Only soldiers and workers and, if possible, alates were identified, as immature forms (larvae and nymphs) are not identifiable. Their morphological characteristics alone were clear enough to identify genus and species. For the identification at the genus level, we used the dichotomous keys of Hölldobler and Wilson (1990) and Bolton (1994). For nomenclature we used the checklist of Bolton (1995). Some species could not be identified with certainty due to the generally poor species-level taxonomy of Cameroonian ants. Voucher specimens are kept at the Laboratory of Zoology of the Faculty of Sciences of the University of Yaoundé I, Cameroon.

Biological characterization of the ant fauna

The ant species were classified based on their nesting and feeding habits. We classified the

ant species into putative trophic groups: predators (P), nectarivores (N), saprovores (S) and omnivores (O) with additional categories for species that exhibited more than one feeding habit. Species with very restricted feeding habits were categorized as specialists, the others as generalists. In terms of nesting habits, tropical ants usually shelter in three microhabitats: (1) in below-ground nests (G), (2) in leaf litter and humus (L) (including epigeic termite mounds and inside dead wood and logs or trees) and (3) in arboreal nests (A). In cases where the species may nest in more than one stratum, we created a category which represented both strata.

Characteristic species

Species were counted per monolith and further pooled per LUS and LUI. Species recorded in only one LUI with more than one occurrence were considered characteristic of that LUI. Otherwise, the species should occur more than 5 times in a single LUI and less than 3 times in the others to be designated a characteristic species.

Diversity

Shannon diversity index (H') and evenness (E) were calculated based on species abundance in monoliths. Simpson's index of diversity (D) was used on the same data to reduce the bias that may rise from the interpretation of a single diversity index (Magurran, 1988). Steinhaus' coefficient (Legendre and Legendre, 1983) was used to determine the similarity of pairs of land use systems within each village and LUI on the basis of abundance: $S_A = 2W/ (A+B)$ where W=sum of the lower of the two abundances of each species and A and B are the sum of abundances of each community respectively. These data are presented at LUS level but were analyzed at monolith level.

Statistical analyses

For analyses of variance (ANOVA), the data were treated as a nested experimental design where land-use systems were nested within intensification levels using PROC GLM of SAS version 8 (1999). Where necessary for variance homogeneity, data were subjected to log transformation before analysis.Pair-wise comparison of least square means of selected treatments was performed using the Pdiff option. Correspondenceanalysis (CA) based on species presence/absence data was performed using CANOCO for Windows 4.5 (ter Braak and Smilauer, 2002) in order to assess affinities among species and among land use systems.

Reults

Species occurrence and composition

A total of 80 ant species belonging to 7 subfamilies were recorded in this study (Appendix 1). Of the 80 species, 14 were found in all three LUI blocks, 23 were only recorded from the low LUI block, 11 from the medium LUI block and 10 only from high the LUI block (Figure 2). Based on their occurrence, some species appeared to be characteristic of specific LUI blocks: 8 of such in the low LUI block, 5 in the medium LUI block and 3 in the high LUI block. Across LUI blocks, 11 species were recorded from all 5 LUSs under study, 9 species from 4, 10 from 3, 17 from 2 and 33 from 1. Of the 33 species found in only one LUS, only 1 morphospecies (*Myr005*) was recorded from Crop (Appendix 1).

Figure 2. Venn diagrams showing distribution of species among LUI
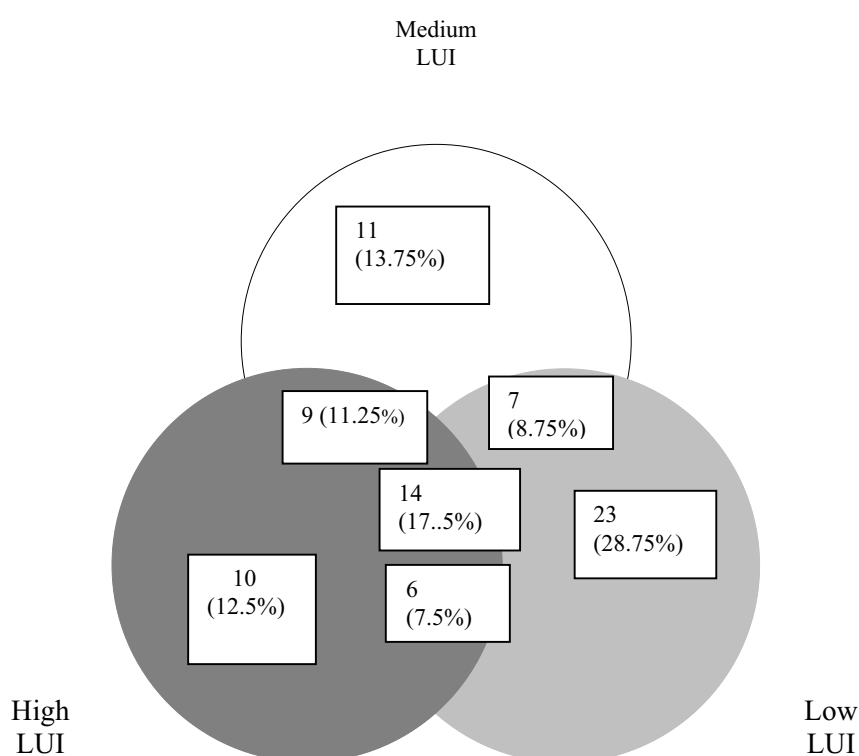
Table 2a. Characteristics of the ant community in the low LUI block[@]

Parameters	Sfor	Cacao	Yfor	Chr	Crop
Species number	11.5^{ab}	17^a	12.5^{ab}	12^{ab}	8.5^b
Abundance	32	43	30	41	30
Shannon (H')	2.03^b	2.59^a	2.17^{ab}	2.13^{ab}	1.78^b
Evenness (E)	0.83	0.92	0.86	0.87	0.84
Simpson (D)	0.84	0.93	0.87	0.86	0.81

Table 2b. Characteristics of the ant community in the medium LUI block

Parameters	Sfor	Cacao	Yfor	Chr	Crop
Species number	11.5^a	11^a	10^{ab}	7^{ab}	4.5^b
Abundance	40^a	34^a	24^a	25^a	16^b
Shannon (H')	2.11^a	2.16^a	2.08^a	1.76^{ab}	1.37^b
Evenness (E)	0.86	0.90	0.90	0.91	0.92
Simpson (D)	0.86	0.88	0.87	0.84	0.81

Table 2c. Characteristics of the ant community in the high LUI block

Parameters	Sfor	Cacao	Yfor	Chr	Crop
Species number	7.5	10.5	11.5	8.5	9.5
Abundance (ind m^{-2})	19^b	39^a	23^{ab}	15^b	22^b
Shannon (H')	1.69	2.19	2.12	1.97	2.01
Evenness (E)	0.84	0.94	0.91	0.92	0.91
Simpson (D)	0.79	0.89	0.90	0.89	0.88

[@] In a row, means followed by the same superscript are not significantly different at P<0.05

Species number and abundance (individuals m^{-2})

Species number

Species number ranged from 4.5 in the Crop in the medium LUI to 17 in the Cacao in the low LUI (Tables 2a and 2b). There were significant effects of LUI and LUS on species number (Tables 3 and 4). On average across LUSs, the low and medium LUI blocks harbored significantly more ant species than the high LUI block. Significant differences were found between the low and high LUI blocks for Cacao (P=0.045), for Chr between the low LUI and both the high (P=0.001) and medium LUIs (P=0.039) and both the low and medium LUI blocks were significantly higher than the low LUI block for Sfor (Figure 3). Within the low LUI block in table 2a, the only significant difference was between Cacao (17) and Crop (8.5) (P=0.012). In the medium LUI block, Cacao (11) and Sfor (11.5) harbored significantly more ants species than Crop (5) with P=0.015 and 0.0019, respectively. Within the high LUI block, no significant difference was found at the land use system scale (Table 2c).
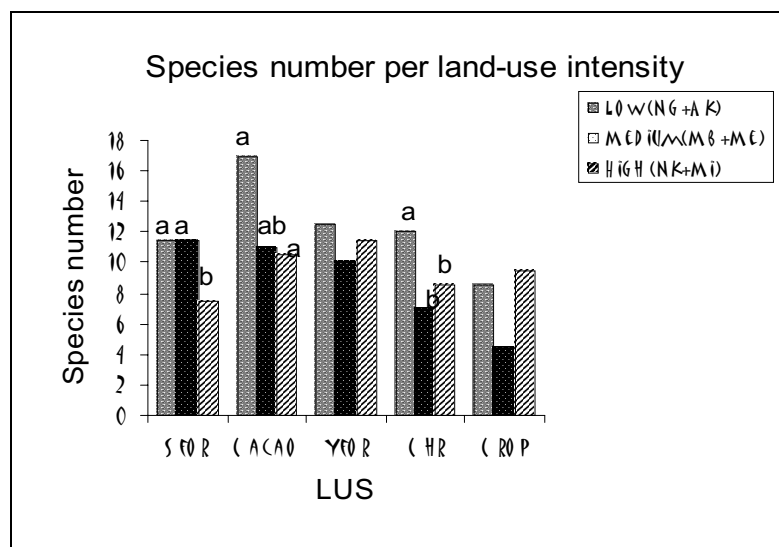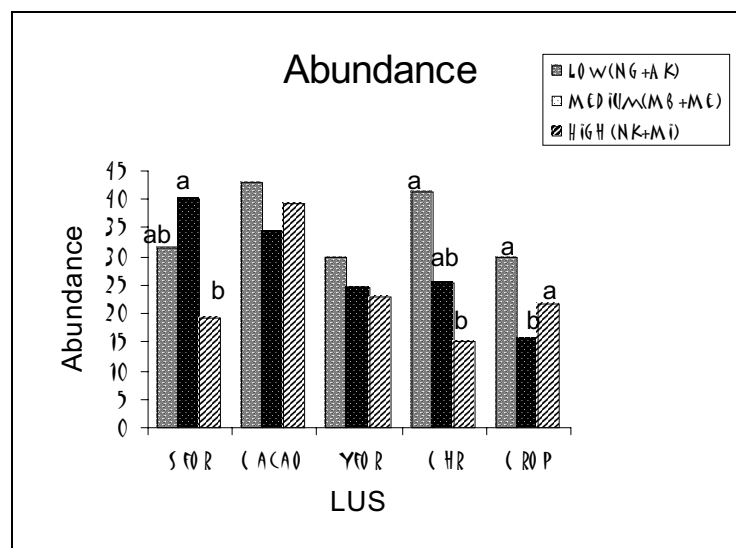
Figure 3. Ant species number per LUI block
In a LUS bars with the same letter (when present) are not significantly different at P=0.05

Abundance

Ant abundance ranged between 43 in Cacao in the low LUI block to 15 per square meter in Chr in the high LUI block (Table 2). There were significant effects of LUI and LUS on ant abundance (Tables 3 and 4). On absolute average across LUSs, the low and medium LUI blocks harbored more ants than the high LUI block; differences were significant between high and low, low and medium and not between medium and high LUI blocks (Table 4).

Table 3. ANOVA results of the effect of LUI and LUS within LUI on ant community characteristics in southern Cameroon.

Parameter	LUI		LUS within LUI	
	F (df=2)	P	F (df=12)	P
Species number	5.72	0.0041	2.41	0.0073
Abundance (ind m^{-2})	5.86	0.0036	3.59	0.0001
Predators	5.75	0.0040	2.89	0.0014
Nectarivores	1.89	0.155	1.26	0.24
Omnivores	9.44	0.0001	0.52	0.895
Saprovores	0.04	0.96	1.54	0.117
Shannon (H')	11.21	<0.0001	4.05	<0.0001
Evenness (E)	0.66	0.54	0.74	0.71
Simpson (D)	8.57	0.0003	4.14	<0.0001

Table 4. Significance of difference P-values in pair-wise comparison of LUI means (across LUSs)

Parameter	At the monolith level		
	High vs. Low	High vs. Medium	Low vs. Medium
Species number	0.001	0.2117	0.0384
Abundance (ind m^{-2})	0.0011	0.3409	0.0192
Predators	0.0013	0.0209	0.2861
Nectarivores	0.0405	0.3036	0.3023
Omnivores	0.5930	0.0013	0.0002
Saprovores	0.9337	0.9565	0.9771
Shannon (H')	<0.0001	0.9403	<0.0001
Evenness (E)	0.50	0.66	0.27
Simpson (D)	0.0192	0.0815	<0.0001

Significant differences in abundance were found between the high and low LUI block for Chr (P=0.0017), between the medium and both high (P=0.008) and low (P=0.0003) LUI blocks, respectively for Crop, and for Sfor between the high and medium LUI blocks (P=0.011) (Figure 4). Within the high LUI block (Table 2c), Cacao had significantly more ants than the other LUSs except Yfor. In the medium LUI block (Table 2b), Crop harbored significantly fewer ants than all the other LUSs. No difference was found between LUSs in the low LUI block (Table 2c).

Figure 4. Ant species average abundance per LUI block
In a LUS bars with the same letter (when present) are not significantly different at P=0.05

<u>Trophic groups abundance and distribution per LUI</u>

Differences in trophic group abundance are shown in Figure 5. In all 3 LUI blocks, predators and nectarivores make up the bulk of ant species. On average, predators have the highest proportions of ants in all blocks and LUSs except for Crop in the high LUI block, where nectarivores share the highest proportion. The other groups were in the decreasing order of ants proportion: nectarivores>omnivores>saprovores. The low LUI block contained all 4 trophic groups with saprovores exhibiting a very low proportion of ants. Saprovores were not recorded in Chr and Crop in the medium LUI block while omnivores were quasi absent in Sfor, Cacao and Crop. In the high LUI block, saprovores were not recovered in Yfor and Crop.

Differences due to LUI were significant only for predators and omnivores and LUS had a significant effect only on predators on an absolute number basis (Table 4). The low (52%) and medium LUI (59%) blocks had proportionally more predators than high LUI block (49%). Although LUI did not significantly affect nectarivorous ants, there were a significantly higher number of nectarivorous ants in the low LUI than in the high LUI block. There were no significant effects of LUS on saprovores and omnivores despite their absence in some LUSs.

Species diversity indices and evenness per LUI

<u>Diversity</u>

The Shannon diversity index ranged from 1.37 in Crop in the medium LUI block to 2.59 in Cacao in the low LUI block. Simpson's diversity index ranged from 0.93 again in Cacao in the low LUI block to 0.79 in Sfor in the high LUI block (Table 2). There were strongly significant effects of LUI and LUS on Shannon or on Simpson's diversity indices in the same direction. The low LUI block had significantly higher diversity indices than both the medium and high LUI blocks (Tables 3 and 4). The low LUI had a significantly higher H' for all the LUSs than the high LUI except Crop (Figure 6a). Within the low LUI block (Table 2a), Cacao has a higher H' than Crop (P=0.0073) and Sfor (P=0.048). Within the medium LUI block, Crop had a significantly lower H' than all the other LUSs except Chr (Table 2b). Within the high LUI block, Cacao had a higher H' than Sfor. For Simpson's index, the same trend was observed for Sfor and Cacao but in absolute values the high LUI had higher D indices than the medium and low LUI for Yfor,Chr and Crop (Figure 6b).
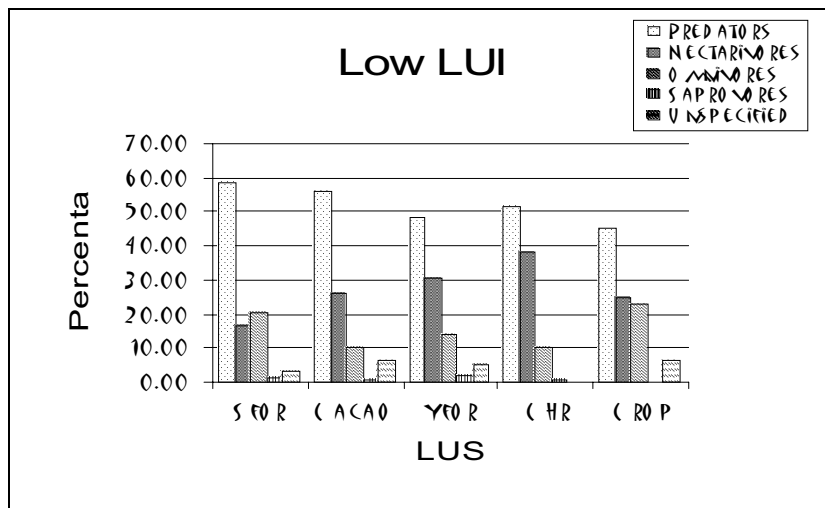
114

Figure 5a. Proportion of ant trophic groups in low LUI block
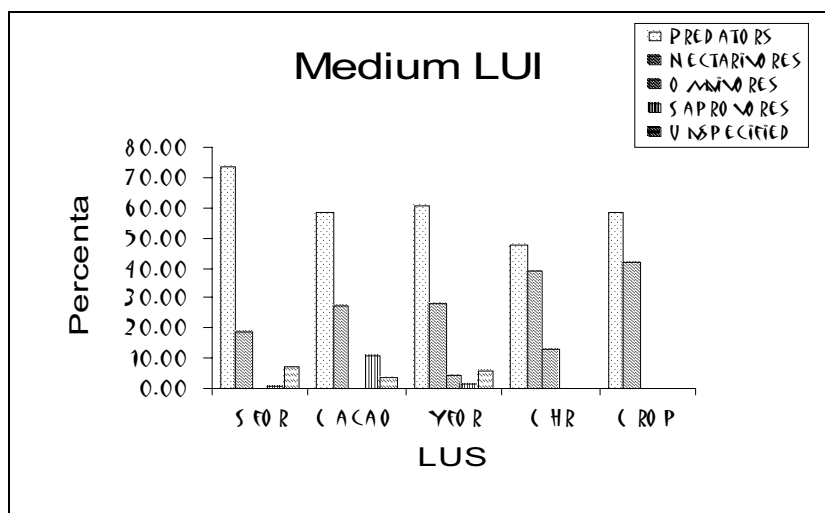

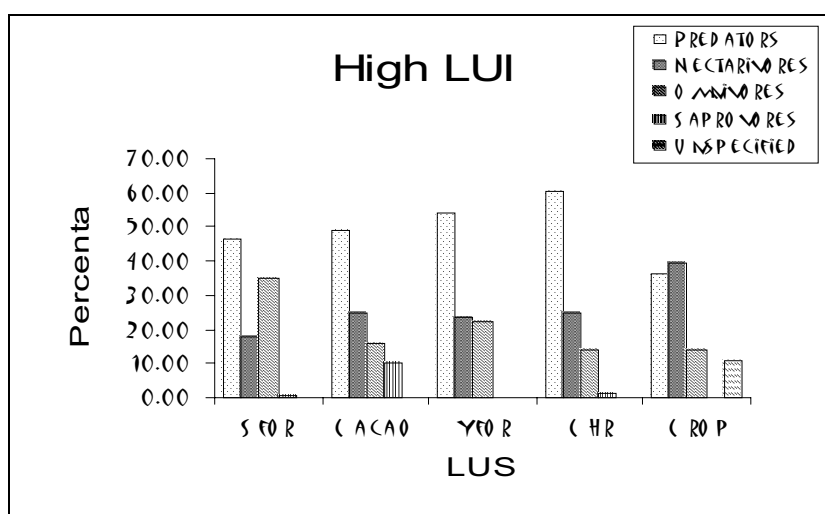**Figure 5b**. Proportion of ant trophic groups in medium LUI block

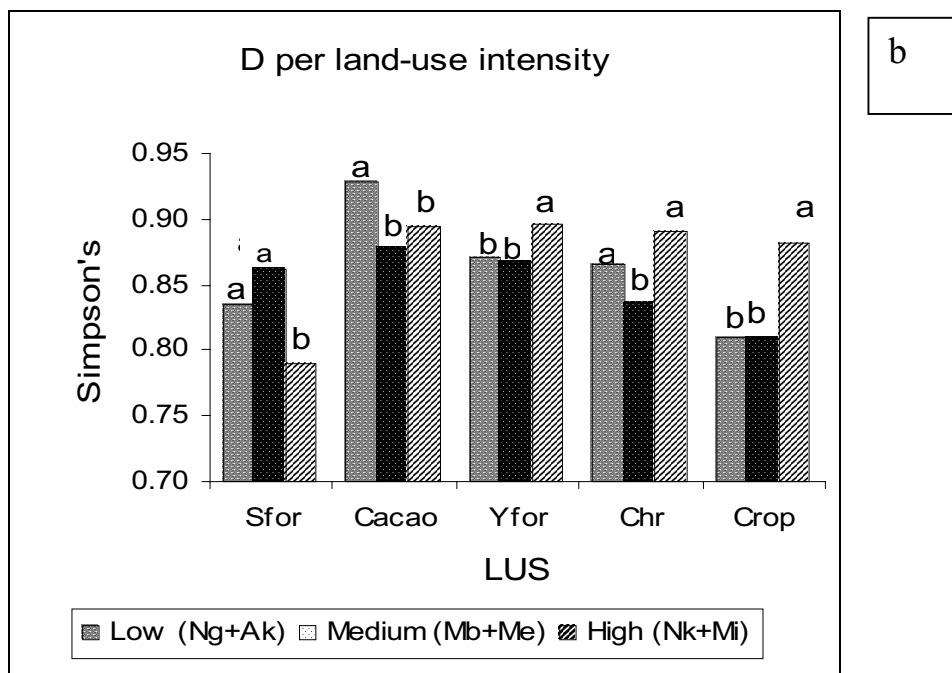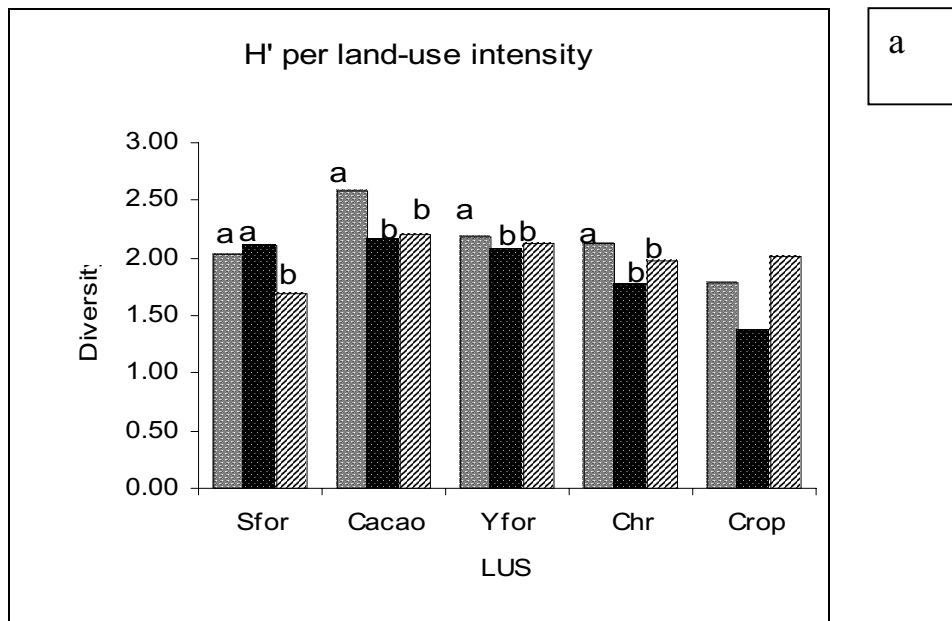**Figure 5c.** Proportion of ant trophic groups in medium LUI block

Figure 6. Ant species diversity indices
a= Shannon diversity index b=Simpson's diversity index
In a LUS bars with the same letter (when present) are not significantly different at P=0.05

Evenness

With a range of 0.83 in Sfor in the low LUI block to 0.93 in Cacao in the high LUI, evenness measures were very high in all LUSs. Ranges within blocks were very narrow (0.09 for the low and high LUI blocks and 0.05 for the medium LUI block), which suggests that ant species were evenly distributed within and across LUSs and LUI blocks. There was in fact no effect of LUI or LUS on evenness (Tables 2 and 3 and Figure 7).

Similarity

Steinhaus similarities (S_A) based on ant species abundance ranged from 0.09 (Sfor-Chr) in the medium LUI block to 0.59 (Cacao-Chr). The medium LUI block exhibited the lowest similarity indices between LUSs. On average, mean similarities between LUSs were higher in the low LUI (0.42) than in the high LUI (0.34) and the medium LUI (0.20) (Table 5).

Multivariate analysis

CA was based on species data (presence/absence) combining village and LUS. The first two factors explained 17.7 % of the total variance with respective eigenvalues of 0.599, 0.453. No clear distribution pattern of species could be derived from these analyses. However, land use systems tend to be grouped per village suggesting that ant species are largely confined to specific villages (Figure 8).
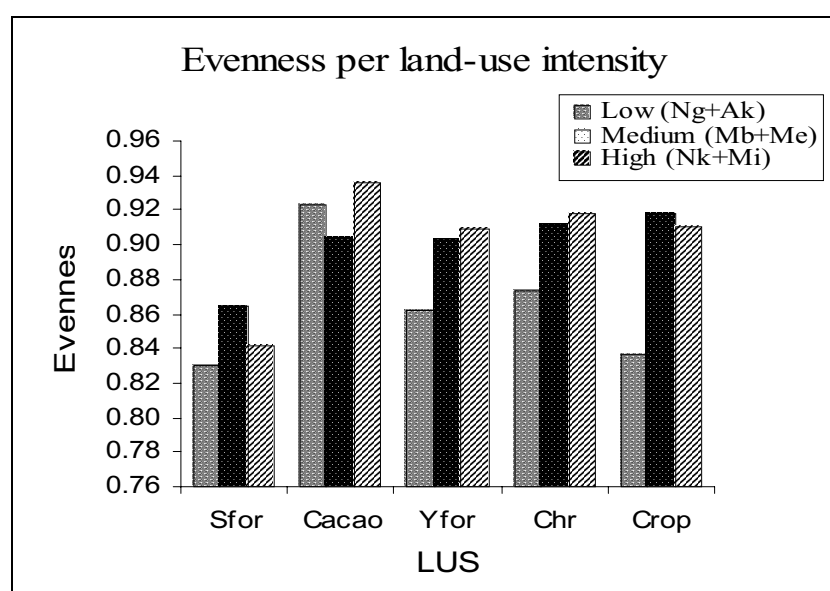

Figure 7. Ant species evenness per LUI block

Table 5. Matrix of similarity indices between pairs of LUSs per LUI

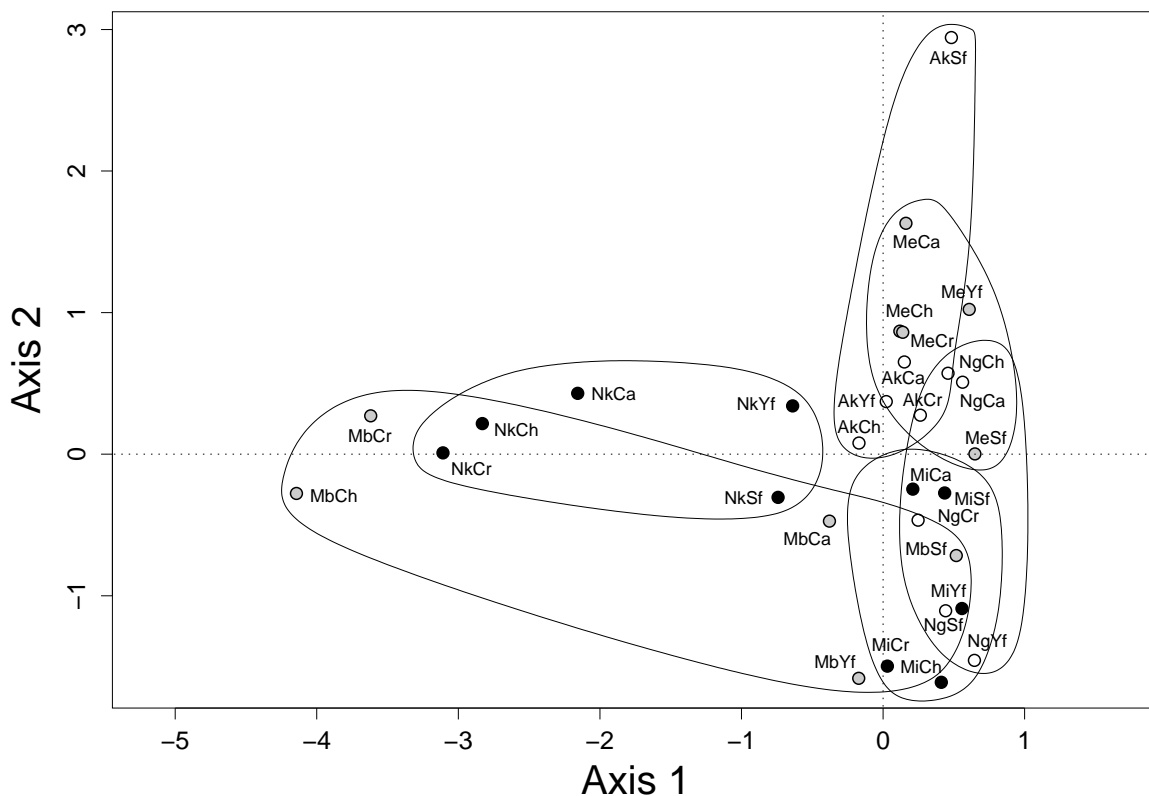| Low land-use intensity		Cacao	Yfor	Chr	Crop
	Sfor	0.31	0.38	0.30	0.49
	Cacao		0.37	0.59	0.43
	Yfor			0.36	0.51
	Chr				0.47
Medium land-use intensity		Cacao	Yfor	Chr	Crop
	Sfor	0.11	0.34	0.09	0.17
	Cacao		0.19	0.23	0.19
	Yfor			0.11	0.18
	Chr				0.43
High land-use intensity		Cacao	Yfor	Chr	Crop
	Sfor	0.48	0.42	0.37	0.13
	Cacao		0.28	0.29	0.29
	Yfor			0.36	0.36
	Chr				0.46

Figure 8. Ordination plot of samples (axes 1 and 2) based on correspondence analysis of the ant species composition data recorded from 5 LUSs in 6 villages in southern Cameroon. Data per village encircled; open symbols: low LUI; shaded symbols: medium LUI; black symbols: high LUI. The eigenvalues of the first four axes are 0.599, 0.453, 0.431 and 0.372, respectively. Total inertia is 5.965.

Discussion

Species richness, composition and abundance

The ant diversity recorded in this survey (80 species in 7 subfamilies) fits the literature on species number and types generally found across biogeographically similar regions. Majer et al. (1997) recorded 97 species of ants when comparing the ant litter fauna of forest, forest edges and adjacent grassland in the rainforest of Bahia in Brazil. Hamish (2002) found a total of 87 ant species and Bignell et al. (2000) found 57 species from 8 subfamilies using pitfall traps, dissected monoliths and transects when assessing ant species richness of a range of forest and forest-derived sites in The Pasir Mayang Forest Reserve in Sumatra (Indonesia). Watt et al. (2002) found a total of 111 leaf litter ant species in November 1993 in Mbalmayo Forest Reserve (Cameroon) when they sampled 3 uncleared forest plots and the corresponding partially and completely cleared plots. Ant abundance reported by Dejean et al. (1986) ranged from 166 individuals m^{-2} in Bamboo-grove to 5745 individuals m^{-2} in a wooded savannah in Congo. Contrary to our expectations, in our study the range was from 15 to 43 individuals m^{-2} only (Figure 4). Our figures are based on species recorded by hand-sorting monolith soil during one sampling expedition only. Dejean et al.(1986) did 6 to 9 evaluations of their sites. This suggests that a higher sampling intensity would have yielded higher ant numbers.

Ant colonies differ widely in their abundances depending on the subfamilies they belong to, colony ontogeny and their environment. The major driving force in ant communities is competition for resources, both between and within species. This competition is severe and unrelenting and results in continuing changes to the composition and community structure of ant populations and to their spatial disposition (Lavelle and Spain, 2001; Begon et al., 1996).

In our study, species richness and abundance were affected by LUI and LUS. From the low LUI to the high LUI block species number and abundance become lower and species composition changes with omnivores and saprovores missing in some LUSs in the high and mdedium LUI blocks (Figure 2 and Table 2). The same trend was also observed among LUSs within LUI blocks where in general richness and abundance were higher in less disturbed LUSs (Sfor, Cacao and Yfor) than in more disturbed ones (Chr, Crop). These results agree with previous studies which have also found species richness and densities to be highest in the

systems that conserved most of the characteristics of the original system from which they are derived (Lubertazzi and Tschinkel, 2003; Fisher, 1997; Majer et al., 1997; Majer and Delabie, 1999; Dejean et al., 1986). They correlated ant community structure changes to vegetation types and habitat destruction (intensification) which affect the resource abundance and quality. Holldöbler and Wilson's (1990) dominance impoverishment rule, which states that low-diversity ant communities are often numerically and behaviorally dominated by a single species does not conform with our study, evidenced by the presence of at least 3 dominant species in the least diverse communities (high LUI block) suggesting that, as a whole, the entire southern Cameroon forest zone still can maintain enough heterogeneity in habitats to support a diverse community. Furthermore, we assumed that the 'ecotone' or 'intermediate disturbance hypothesis' (which states that disturbances, intermediate in both magnitude and frequency, allow more species to exist in the same area), could apply in our study in the medium LUI block. This was not the case since the low LUI block kept more species diversity and abundance (Figure 2).

Diversity, evenness and similarity

Land use intensity effects on ant species richness and abundance along the LUI gradient are reflected in the diversity indices. Low LUI exhibited the highest diversity indices on average. Ants forming the assemblages of the 3 LUI blocks are distinctive communities overlapping only slightly with each other (Figure 2). LUSs clearly showed structural heterogeneity within each LUI block, evidenced by a low similarity (S_A) found between pairs of LUSs (Table 5). In line with these results, the CA of ant species presence/absence data showed a trend towards confinement of species to a village (Figure 8). Evenness was equal among LUI blocks (Table 4). These results can be explained by the competitive and behavioral characteristics of ants, which tend to have highly spatially heterogeneous distributions on a local scale, because their activities are centred around nest sites and because of competitive interactions between species (Majer, 1993; Floren and Linsenmair, 2000; Floren and Linsenmair, 2001).

Conclusions

Species richness and abundance of ants declined with increasing LUI and was generally lower in relatively disturbed LUSs. The ant community composition was highly location-specific.

Acknowledgements

Appendix 1. List of species recorded from the LUI blocks#

Subfamily	Species	Low (Ng+Ak)	Medium (Mb+Me)	High (Nk+Mi)
Cerapachyinae	*Cerapachys sp.1*	1	1	2
Dolichoderinae	*Tapinoma sp.1*	4	2	3
	Tapinoma sp.3	2	3	1
	Tapinoma sp.5	1	0	0
	*Technomyrmex sp.1**	2	0	0
Dorylinae	*Anomma nigricans*	0	1	1
	Dorylus sp.1	4	2	2
	Dorylus sp.2	2	3	0
Formicinae	*Anoplolepis tenella*	9	5	5
	*Camponotus acvapimensis***	<u>0</u>	<u>0</u>	<u>2</u>
	*Camponotus brutus**	4	1	0
	Camponotus flavomarginatus	0	2	3
	Camponotus melanocnemis	0	2	3
	Camponotus sp.1	3	0	2
	Camponotus sp.2	0	0	1
	Oecophylla longinoda	1	0	1
	Plagiolepis sp.	1	0	0
	Polyrhachis decemdentata	0	0	1
	Polyrhachis militaris	0	1	0
	*Polyrhachis sp.1***	<u>0</u>	<u>2</u>	<u>0</u>
	Polyrhachis weissi	1	0	0
Myrmicinae	*Atopomyrmex mocquerysi*	1	0	0
	*Cataulacus sp.1**	4	0	0
	Cataulacus sp.2	1	0	0
	*Cladarogenys sp.1***	<u>0</u>	<u>2</u>	<u>0</u>
	Crematogaster sp.1	7	5	4
	*Crematogaster sp.2****	<u>0</u>	<u>0</u>	<u>3</u>
	Crematogaster sp.3	1	0	0
	*Decamorium sp.1****	<u>0</u>	<u>0</u>	<u>6</u>
	Decamorium sp.2	0	0	1
	Meranoplus sp.1	1	1	0
	Monomorium (?) bicolor	0	2	2
	Myr001	2	1	0
	Myr002	0	1	0
	Myr003	2	1	0
	Myr004	1	0	0
	Myr005	0	0	1
	Myr006	1	0	0
	Myrmicaria opaciventris	6	6	5
	Pheidole megacephala	8	0	10
	Pheidole sp.1	2	1	0
	Pheidole sp.2	3	0	1

	Pheidole sp.3**	2	0	0
	Pheidole sp.4	0	2	4
	Tetramorium aculeatum	1	0	0
	Tetramorium coloreum	0	1	0
	Tetramorium sp.1	1	0	0
	Tetramorium sp.2**	<u>0</u>	<u>2</u>	<u>0</u>
Ponerinae	*Anochetus sp.1**	2	0	0
	Anochetus sp.2	0	1	1
	Centromyrmex bequaerti**	<u>2</u>	<u>6</u>	<u>2</u>
	Centromyrmex sp.2*	2	0	0
	Cryptopone sp.1	2	2	0
	Cryptopone sp.2	0	1	1
	Hypoponera sp.1	1	4	5
	Hypoponera sp.3	1	0	0
	Hypoponera sp.4	1	0	0
	Hypoponera sp.6	0	0	1
	Leptogenys sp.1	2	1	0
	Leptogenys sp.2	1	0	0
	Odontomachus assiniensis	5	4	1
	Odontomachus troglodytes	0	1	0
	Pachycondyla analis*	2	0	0
	Pachycondyla sennaarensis	0	2	3
	Pachycondyla sp.1	5	6	4
	Pachycondyla sp.2	1	0	0
	Pachycondyla sp.3	1	0	0
	Pachycondyla sp.4	1	0	3
	Pachycondyla sp.5	3	0	1
	Pachycondyla sp.6	3	1	3
	Pachycondyla sp.8	0	1	0
	Pachycondyla tarsata*	7	2	3
	Phrynoponera sp.1	1	0	0
	Phrynoponera sp.2	1	0	0
	Plectroctena minor	0	1	0
	Plectroctena sp.1*	<u>0</u>	<u>2</u>	<u>0</u>
	Probolomyrmex sp.1	0	0	1
	Proceratium sp.1	0	0	1
	Psalidomyrmex sp.1	0	1	0
Pseudomyrmecinae	*Tetraponera anthracina*	0	2	1

#Figures represent the number of LUSs out of 10 in which the species was recorded.
Species followed by *, ** and *** are characteristics species for low, medium and high
LUI blocks respectively.

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Belowground/aboveground biodiversity relationships in the humid forest zone of southern Cameroon

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Abstract

A survey was undertaken from July to November 1999 in five land-use systems differing in disturbance levels in six villages along a land-use intensification gradient in the benchmark of the forest margins zone of southern Cameroon. Simultaneous samplings for earthworms, termites and ants were done in the same sites using transect samplings and hand-sorting of monoliths; soil sampling and vegetation structure and description were also performed in the same site in order to establish the relationships between the invertebrates and the environmental variables as well as the impact of land management on the distribution of these animals. Direct ordination (RDA) of the samples with the whole species structural variables and environmental variables yielded significant eigenvalues of 0.303 for the first axis and 0.191 for the second axis. We found low correlations between the parameters of the different groups of fauna. Species richness and diversity of the three groups of soil fauna were clearly separated. Soil macrofaunal species richness and diversity were more responsive to soil and vegetation parameters than macrofaunal abundances. These results suggest that there is a positive relation between the structure and production of the vegetation and the structure of the faunal community in terms of species richness and diversity.

Key words. Land-use intensification, land management, vegetation structure, soil invertebrates, community structure, soil characteristics

Introduction

Soils differ greatly in composition, particle size, structure, depth and compaction, and whether they are under trees, grassland or cultivation. The role played by soil-dwelling macro-invertebrates (earthworms, termites, ants) in soil processes has been widely recognized and these organisms have been defined as 'ecosystem engineers' (Lavelle et al., 1997; Lawton et al., 1998; Jones et al., 1994). Soil ecosystem engineers are able to alter soil structure and other physical properties of their environment. It is known that at least at a local scale, soil ecosystems are among the most species-rich environments in the world. Many of the soil biota significantly modify the rate of key global biological, geological and chemical processes and provide critical links between terrestrial, aquatic and atmospheric realms. Therefore, losses in belowground taxonomic diversity may bring about changes in aboveground diversity as well as reductions in ecosystem functioning that are likely to result in changes in various other environments (Hooper et al., 2000; Decaens et al., 1999; Edwards, 1999). Functional groups of soil organisms are sensitive to ecosystem disturbance. Generally large-sized fauna such as earthworms, ants and termites disappear first. Although climate does have a direct effect on soil biota, soil biota are more strongly directly affected by vegetation changes than they are by atmospheric condition. This is for two reasons: (1) The structural characteristics of vegetative cover determine the degree to which particular vegetation modifies the thermal and hydric characteristics of the soil that affect the soil biota (Whitford, 1992), and (2) the vegetation provides a vast amount of organic matter (i.e. energy supply) and nutrients which may affect the species composition and structure of soil communities (Shakir and Dindal, 1997).

The relationships between earthworms, termites and ants and the factors and components of their respective habitats have been the topics of many investigations. Also responses of plants to climate change, such as loss of plant cover, changes in plant species diversity, density, or biomass, will regulate to some degree the belowground environment. Moreover, human activity in forest land-use will greatly influence changes in vegetation composition (Armbruster et al., 2000).

Understanding factors influencing the diversity and structure of natural communities is a fundamental goal of ecological studies. However, often studies of ecological processes at the community level are faced with particularly challenging problems (Lawton, 1999). For example although the definition of communities as species assemblages, which co-occur in space and time, is intuitively appealing (Begon et al., 1996) the logical difficulties of working

with communities defined in this way can be overwhelming. Consequently, the vast majority of studies in community ecology focus on a single taxonomic group. Understanding the extent to which these taxonomically restricted studies accurately describe patterns and processes in complete ecological communities represents an important challenge for community ecologists (Hooper et al., 2000).

In southern Cameroon, we surveyed six villages and a total of 30 sites classified in 5 land-use systems in order to characterize vegetation and soil ecosystem engineers, and explored relationships that could exist between these two groups and the soil that supports them. In preceding studies, we have characterized the species diversity, abundance and distribution of earthworms (Birang et al., subm. a), termites (Birang et al., subm. b) and ants (Birang et al., subm. c) that were concomitantly sampled along a gradient of land use intensification in the forest zone of southern Cameroon. In the present study, this complete dataset has been analyzed in combination with vegetation parameters and soil physical/chemical characteristics, in order to:

1) Provide baseline insight in the relationships between environmental parameters (vegetation cover, plant species richness and plant functional type diversity and soil characteristics as well as human land management) and soil ecosystem engineer communities and to describe the factors that co-occur in the main land use systems of southern Cameroon.

2) Shed light on the ecological processes connecting vegetation and soil biological diversity in the forest zone of southern Cameroon.

Materials and Methods

Study area and treatments

The study was conducted in six villages in southern Cameroon classified into three blocks representing increasing levels of deforestation and land use intensity (LUI) within the benchmark established by ASB, IRAD and IITA (Thenkabail, 1999) known as: (1) Yaoundé block (high LUI), (2) Mbalmayo block (medium LUI) and (3) Ebolowa block (low LUI) (Figure 1 and Table 1). Annual rainfall in southern Cameroon is bimodal. Rains start in mid-March and end in mid-July, followed by a short dry season of 6 to 8 weeks, then recommence in September and stop at the end of November. In 1999, average annual rainfall was 1500 mm. For the analysis in the study, the three blocks of the benchmark are ordinally ranked (high to low) with respect to intensity of land use (LUI). The Yaoundé block, at the northern

extreme, has few original forests remaining. With an average population density of around 80 persons km^{-2} and most of the land in some phase of an agricultural cycle, it exhibits land constraints at the household level resulting in shorter fallow periods. Road infrastructure and market access are well developed leading to a process of agricultural intensification. In contrast, the Ebolowa block at the southern end of the benchmark has a low population density of around 5 persons km^{-2} and large tracts of intact primary forest. There is still reliance on natural resource-based activities. Local agricultural markets are comparatively small, agricultural input markets are underdeveloped and road infrastructure is poor and not maintained. Between these two extreme conditions lies the Mbalmayo block where market access is fair (ASB, 2000).

The commonest 5 land use systems (LUS) of the region, representing a gradient of disturbance from low to high were selected such that the ages and plot histories of the LUSs of the same type in the different villages were approximately the same: a secondary forest (>30 years, Sfor), a shaded cacao plantation (Cacao), young forest fallow (12-15 years, Yfor), 4-5 year old *Chromolaena odorata* dominated fallow (Chr), and a groundnut / maize / cassava annual intercrop field (Crop). For details on vegetation, see Zapfack et al. (2002), who characterized the vegetation in several villages of these three blocks.
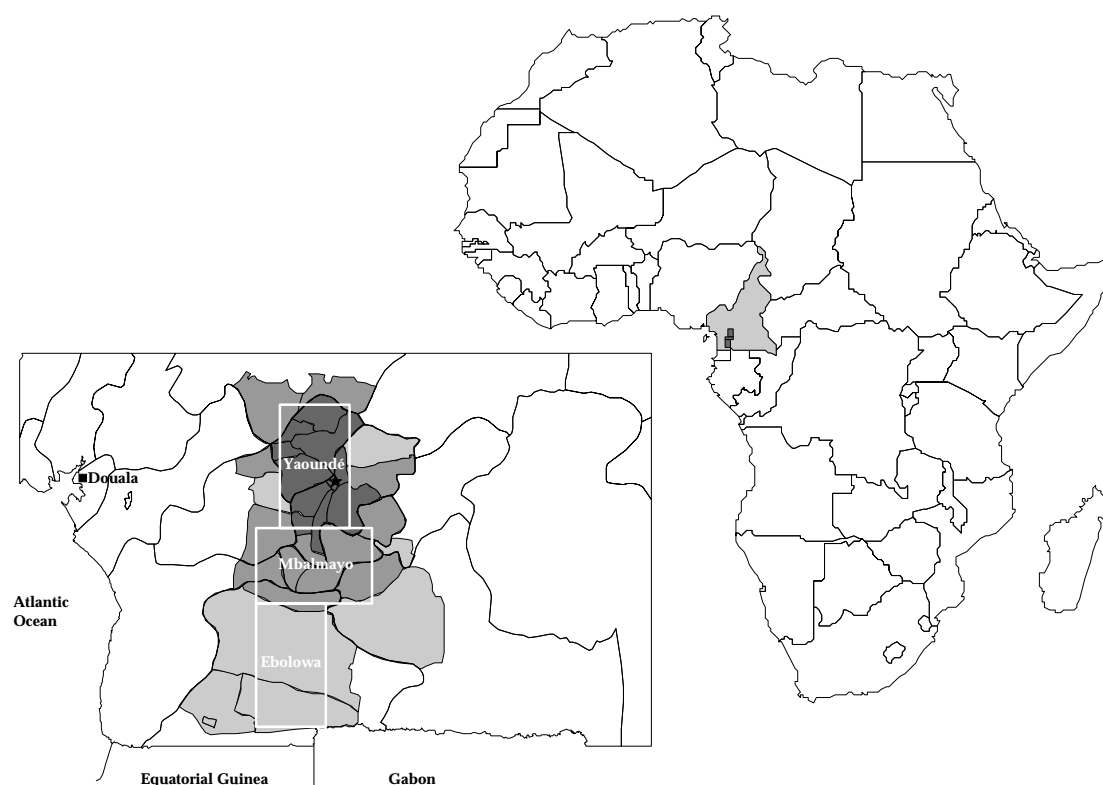

Figure 1. Map of southern Cameroon and the three land use intensification blocks within the forest margins benchmark

Table 1. Characterization of the 6 villages under study in southern Cameroon.

Block	Level of deforestation and LUI[*]	Village	Distance from Yaoundé	Geo-references	Soil type	Land under forest cover (%)	Land under fallow (%)	Land under crop (%)
Yaoundé	High	Nkometou (Nk)	40 km North	11°35'E, 4°05'N	Rhodic Kandiudult			
		Minkoameyos (Mi)	15 km West	11°27'E, 3°51'N		25	29	27
Mbalmayo	Medium	Mbalmayo (Mb)	50 km South	11°28'E, 3°27'N	Typic Kandiudult			
		Metet (Me)	90 km South	11°45'E, 3°25'N		40	16	19
Ebolowa	Low	Akok (Ak)	150 km South	11°14'E, 2°44'N	Typic Kandiudox	57	10	13
		Ngoungoumou (Ng)	130 South	12°01'E, 3°18'N				

*Land Use Intensity

Table 2. Earthworms, termites and ants characteristics (mean values of 6 replicates) of the five land-use systems (transects) surveyed at 0-10 cm depth

LUS	Sfor		Cacao		Yfor		Chr		Crop	
Variable	Mean	SEM*	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
ER	7.67	1.15	0.99	6.00	7.00	1.15	6.00	1.03	5.00	0.58
AE	134.67	24.04	33.59	140.00	86.67	16.42	140.00	58.86	114.00	19.59
HE	1.36	0.12	0.19	1.38	1.51	0.20	1.38	0.18	1.26	0.13
EB	1.36	0.18	1.95	4.94	1.12	0.14	4.94	2.04	2.65	0.53
Epa	7.17	0.83	5.66	5.50	4.00	1.24	5.50	1.57	5.00	1.98
Ena	26.00	5.05	6.20	29.17	16.83	4.32	29.17	13.68	23.50	5.05
TR	10.67	2.08	1.77	3.83	6.67	2.11	3.83	0.54	4.00	0.73
TA	268.53	66.23	35.71	228.80	355.47	180.16	228.80	119.66	71.07	16.83
TSf	201.89	61.36	34.93	96.67	275.57	145.67	96.67	34.94	34.48	14.11
TWf	44.82	24.49	14.90	27.87	86.46	60.53	27.87	14.10	47.13	26.74
HT	1.49	0.09	0.17	0.79	0.93	0.23	0.79	0.12	0.72	0.16
AR	10.17	0.95	1.74	9.17	11.33	1.26	9.17	1.42	7.50	1.18
AA	30.27	4.71	6.55	27.20	25.73	3.85	27.20	7.54	22.40	5.37
AP	23.21	4.62	5.26	18.13	17.25	2.56	18.13	5.65	12.75	3.55
AN	7.17	2.04	1.45	10.92	9.00	1.52	10.92	2.35	9.54	2.36
AO	5.33	2.12	2.31	4.83	4.50	1.52	4.83	2.44	3.83	1.47
AS	0.29	0.16	2.03	0.13	0.42	0.15	0.13	0.09	0.04	0.04
HA	1.94	0.11	0.12	1.95	2.12	0.08	1.95	0.14	1.72	0.13

*SEM=standard error of the mean. Abbreviations are defined in table 8.

Fauna sampling and identification

Sampling for fauna was performed from May to mid August 1999. Two different sampling methods were used for diversity and abundance assessment. The methods used were the standard 100 m transect hand sampling and monolith hand-sorting; they followed closely those described by Anderson and Ingram (1993), Eggleton et al. (1997) and Jones and Brendell (1998). For details see Birang et al. (subm. a, b, c). Average values of each community parameter are in Table 2.

Vegetation description, sampling and identification

Observations and sampling of the flora were made along the same transects with a larger width of 5 m subdivided in 20 quadrates of 5m x 5m following a modified method used by Gillison et al. (1997). The following observations on functional attributes were recorded on vascular plant species: biological type, type of leaves, and type of chlorophyll, shape and inclination of the leaves (Gillison et al., 1997; Gillison, 2000). From the combination of these characteristics were derived the number and types of the so-called modi that permit to assess and evaluate the level of degradation of the flora in the land use system. Basal area of all woody plants (m^2 ha^{-1}), diameter at breast height (dbh), average canopy height and average crown coverage were assessed and pooled per transect along with the number of species and

plant functional types. Geographic coordinates were recorded in each land use by a GPS. The samples collected were preserved in used journal papers imbibed with 70% ethyl alcohol and identified to species within known genus or family, enumerated by quadrate and then pooled by transect. Thereafter, they were classified into functional types following Gillison et al. (1997). All specimens were preserved in the laboratory at the Cameroon National Herbarium based at IRAD, Yaoundé. Mean values of characteristics of the vegetation used in the study are presented in Table 3.

Soil sampling and analyses

Soil physical properties

Samples were taken for the analysis of soil physical properties of every land use system from each of the five monoliths (50x50x30 cm (LxWxD)) where macrofaunal samplings took place along the 100 m transect. Three undisturbed soil cores (100 cm^3) were horizontally collected from the walls of each monolith at 10 cm intervals and used for determining soil bulk density and total porosity. Bulk soil samples were horizontally collected, air-dried, ground to pass a 2-mm mesh sieve and used for determining soil textural classes and chemical characteristics.

Soil Chemical properties

Soil was sampled from the same monoliths as above at 10 cm intervals in every land use system in the villages of study and used for determining routine soil properties such as pH (H_2O, 1:2.5), C, N, Ca, Mg, K, and exchangeable Al. Analyses were performed at the IITA chemistry laboratory as follows:

- Basic cations were extracted in a Mehlich-3 extractant 1:10 ratio and analysed using atomic absorption spectrophotometry, reported as cmol(+)/kg which is the same as meq/100g

- Organic carbon using Heanes improved chromic digestion and spectrophotometric procedure; reported as a percentage (org. C %)

- Total nitrogen (N) by acid digestion and using ammonia electrode analysis reported as a percentage (N %)

- Extractable aluminum acidity extracted in 1M KCl and analyzed colorimetrically by the pyrocathecol violet (PCV) method and reported as milliequivalent per 100g of soil or as cmol(+)/kg

- Available P extracted in Mehlich-3 extractant and analyzed colorimetrically using malachite green reagent and reported as parts per million (ppm P)

Mean values for soil properties per transect are given in Table 4.

Table 3. Vegetation characteristics (mean values of 6 replicates) of the five land-use systems (transects) surveyed

	Sfor		Cacao		Yfor		Chr		Crop	
Variable	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Pmod	64.17	3.16	57.50	3.89	60.00	4.40	47.83	3.39	33.75	2.63
Prich	122.33	7.54	105.00	10.34	105.00	9.40	74.67	5.49	46.50	5.81
pricmod	1.92	0.12	1.81	0.08	1.76	0.09	1.57	0.08	1.36	0.06
Caht	17.00	0.82	11.33	2.44	8.83	0.83	14.17	11.18	0.74	0.03
Crcov	69.50	13.87	44.17	10.36	61.33	11.02	55.00	17.84	0.00	0.00
Basare	13.58	3.89	13.33	0.80	8.06	1.32	3.83	0.65	0.00	0.00

Abbreviations are defined in table 8

Table 4. Soil characteristics (mean values of 6 replicates) of the five land-use systems (transects) surveyed at 0-10 cm depth

	Sfor		Cacao		Yfor		Chr		Crop	
Variables	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Bd	1.14	0.07	1.25	0.02	1.21	0.04	1.22	0.04	1.20	0.05
PH	4.63	0.17	4.78	0.16	4.80	0.16	4.98	0.13	4.94	0.16
Lutum/sand	1.38	0.17	1.22	0.19	1.12	0.10	1.36	0.21	1.35	0.16
C:N	13.13	0.30	13.04	0.46	13.46	0.40	13.11	0.49	13.27	0.36
Al	2.17	0.58	1.31	0.50	1.31	0.38	1.37	0.36	1.62	0.36
SB	1.31	0.30	1.58	0.31	1.98	0.43	1.92	0.48	2.13	0.64

Abbreviations are defined in table 8.

Table 5. RDA summary statistics with soil and vegetation as environmental variables. Biplot in Figure 2. Sum of all canonical eigenvalues 0.582

Axes	λ	Species-Environment correlation	Cumulative % variance of species data
Axis 1	0.303	0.74	30.3
Axis 2	0.191	0.80	49.5
	Correlations (r)		% Variation explained
Variables	Axis 1	Axis 2	
Pricmod	0.5915	0.3608	22.8
Prich	0.3514	0.5467	15.8
Pmod	0.080	0.560	0.098
Basare	0.3329	0.1654	8.2
Caht	0.3329	0.1654	7.2
Lutum	-0.2405	0.2085	6.7
pH	-0.142	0.0476	4.2
P	0.113	-0.118	1.7
Al	0.0405	0.3037	3.6
SB	-0.0239	-0.2002	1.8
C:N	-0.1426	-0.0032	1.7
Bd	-0.0082	0.0476	1.3

Statistical and numerical analysis

Analysis of variance (Proc GLM) was performed on each individual data set to examine the influence of LUI and LUS on the distribution of each faunal community structure variable as well as on the vegetation and soil physical/chemical parameters. The data collected were analyzed using a nested structure design with two factors: (1) level of intensification with 3 levels (low, medium and high) and (2) land use system nested within the level of intensification with 5 levels (Sfor, Cacao, Yfor, Chr and Crop). The 2 villages belonging to each intensification block were treated as replicates. For this study, we did some correlations and simple regression analysis to preliminary assess the degree of association between environmental variables and faunal data and to determine how much variation in fauna was explained by each environmental variable using Procedure Corr and Procedure Reg of SAS version 8 (SAS, 1999). These two procedures were used to identify the sets of variables to use in the ordination analysis in addition to those proposed in the literature. Redundancy analysis (RDA) was used to reveal the patterns in the relationships between the faunal community structural parameters and (1) the environment (vegetation structural variables and soil physical/chemical properties) (2) land-use (resource management) characteristics included as environmental variables. The data matrix had 150 sampling points (monoliths), which were pooled per land-use to form a dataset of 30 samples (sites) subjected to CANOCO for Windows 4.5 (Ter Braak and Smilauer, 2002).

Results

Correlation and redundancy analyses

For clarity of the ordination figure and because of a strong colinearity between some parameters, only a subset of them was actually introduced in the ordination. However, we added some variables suggested by the literature as having important influence on invertebrate communities although they did not show any significant correlation in the preliminary analysis.

The direct ordination (RDA) of the samples with species structural variables and environmental variables yielded eigenvalues of 0.303 for the first axis and 0.191 for the second axis (Monte Carlo permutation test for the first canonical axis F=7.38, P= 0.043, all canonical axes together F=2.069, P=0.02) (Table 5 and Figure 2). Vegetation (biotic)

variables together explained two third of the total variation, while abiotic variables explained one third (Table 5).
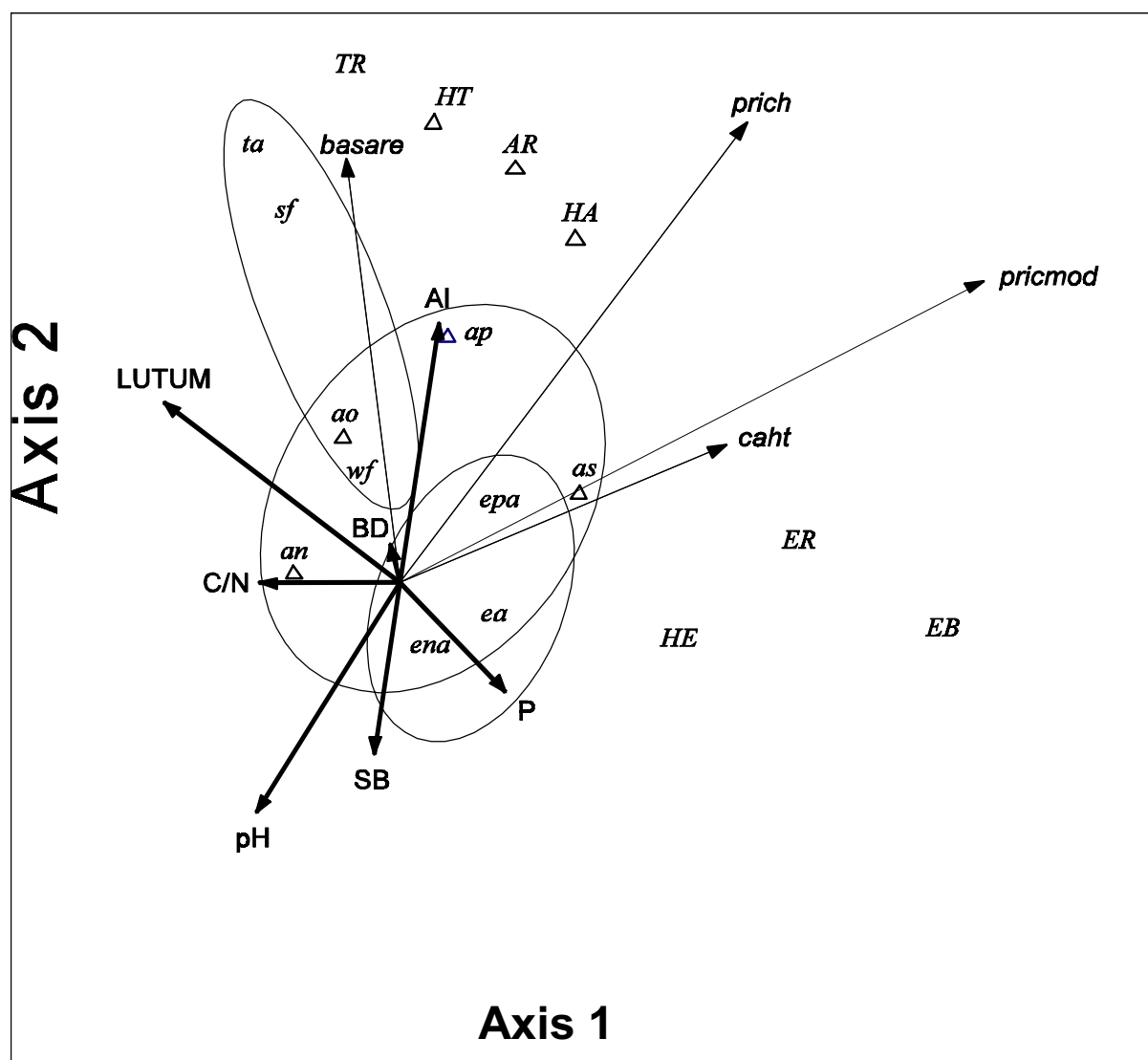

Figure 2. Biplot of RDA axis 1 and 2 showing the selected soil and vegetation variables and the positions of the faunal species parameters. The eigenvalues of the first two axes are 0.303, 0.191, respectively. The sum of all canonical eigenvalues is 0.58. Abbreviations are defined in table 8.

The first axis exhibited high positive correlations with Pricmod and Prich and negative correlations with pH and C:N ratio. The second axis was more determined by vegetation diversity with soil sum of bases negatively correlated.

Canonical analysis of the subset of faunal data and management data gave eigenvalues of 0.133 and 0.056 for the first two axes respectively. Correlation coefficients of the management variables indicated that the first axis represented the gradient of land-use systems disturbance, while the second axis mainly represented land use intensity (Table 6 and Figure 3). Sfor, Cacao and Yfor (negative scores) were opposed to Chr and Crop (positive

scores) on axis 1. The parameters of the three groups of fauna exhibited low correlation coefficients (Table 7) and few were significant.

Earthworm-termite-ant relationships with environment and management

Figure 2 shows a clear separation of species richness and diversity between the three groups of soil animals. Abundances of the three groups are also separated but less so than species richness and diversity. Soil and vegetation parameters are largely separated along the two axes.

Table 6. RDA summary statistics with LUS and LUI
as environmental variables. Biplot in Figure 3. Sum of all canonical eigenvalues 0.203

Axes	λ	Species-Environment correlation	Cumulative % variance of species data
Axis 1	0.133	0.64	13.3
Axis 2	0.056	0.73	18.9
	Correlations		Variation explained (%)
Variables	Axis 1	Axis 2	
LUI	0.023	0.497	2.7
Sfor	-0.447	0.383	8
Cacao	-0.121	-0.350	2.6
Yfor	-0.111	-0.14	0.9
Chr	0.329	-0.054	3.8
Crop	0.411	0.19	5.9

Table 7. Pearson correlation coefficient (r) between soil invertebrate community parameters across a land-use intensification gradient (N=30)

parameters	TR	ta	sf	wf	ER	ea	EB	epa	ena
TR					0.13	0.17	-0.16	0.20	0.15
Ta					-0.15	-0.07	-0.36*	-0.02	-0.04
Sf					0.01	-0.05	-021	-0.04	-0.02
Wf					0.07	-0.05	-0.10	-0.07	0.09
AR	0.37*	0.32	0.17	-0.00	0.12	0.01	0.03	0.12	-0.03
Aa	0.16	0.16	0.02	-0.002	0.19	0.27	0.11	0.20	0.21
Ap	0.28	0.17	0.11	-0.08	0.23	0.27	0.13	0.20	0.21
An	0.03	0.21	0.01	0.18	0.06	0.33	-0.03	0.14	0.24
Ao	-0.07	0.04	-0.12	-0.12	-0.32	-0.29	-0.03	-0.03	-0.23
As	-0.10	-0.26	-0.20	-0.07	0.22	0.17	0.36*	0.22	0.03

After Bonferroni correction *P≤0.05; **P≤0.01; ***P≤0.001 Abreviations are defined in Table 8.
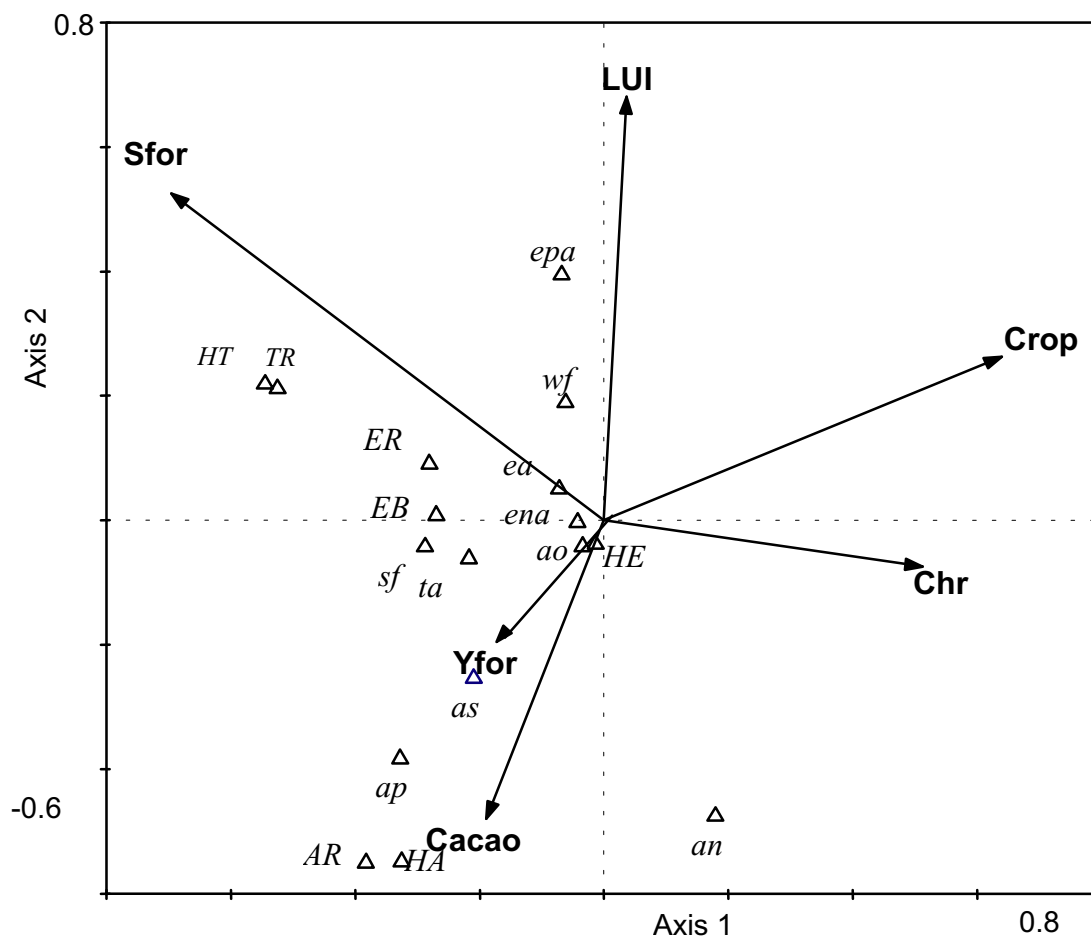
Figure 3. Biplot of RDA axis 1 and 2 showing land use (nominal variables) and LUI (scale variables) and the positions of faunal species parameters as linear combinations of these variables. The eigenvalues of the two axes are 0.133, 0.056 respectively. The sum of all canonical eigenvalues is 0.20. Abbreviations are defined in table 8.

Most of the faunal parameters are positively linked to vegetation variables. Taken singly, the strongest positive correlations are found between earthworm variables (ER, EB and HE) and Caht, Pricmod and Prich. Termite and ant diversities exhibit close relationships with plant basal area, Pmod and Prich and are negatively correlated to SB and pH. Earthworm biomass responds negatively to C:N ratio. In Figure 3, the influence of management was assessed using LUSs and LUI as proxies for soil and vegetation parameters. Axis 1 clearly separates the land use systems in open-canopy (Chr and Crop; most disturbed LUSs), half closed canopy (Yfor and Cacao; less disturbed) and closed-canopy (Sfor; least disturbed) LUSs. Axis 2 indicates that ants are negatively affected by LUI.

Discussion

In their review on belowground/aboveground biodiversity interactions, Hooper et al. (2001) suggested that the sizes of soil organisms and their spheres of influence vary over several orders of magnitude, temporally and spatially, and that, hence, the various processes that link aboveground and belowground biodiversity operate at different scales, influencing for example, species richness and composition and diversity of functional groups. It is therefore perhaps not surprising that in a biodiversity baseline study in a rain forest/land-use mosaic of southern Cameroon, Lawton et al. (1998) found little evidence to support the use of one taxon to predict the presence of another. Also in our study the structural characteristics of the three faunal groups showed low correlations at the scale of our analysis (Table 7). Lawton et al. (1998) did not use plant predictors and it was later suggested by Kotto-Same et al. (2000) that, because animals ultimately depend on plants and because the distribution of many taxa extends beyond the immediate bounds of closed forest, it is likely that the predictive performance of their study could have been considerably improved, had plants been included and had the samples been extended to a wider array of land use types. Indeed, in our study we found close relationships between plant species/functional type richness and diversity and soil faunal species richness and diversity (Figure 2 and Table 5). This is in accordance with the results of other studies that have shown positive relationships between herbivorous macroinvertebrate species richness and plant diversity (Gillison et al. 2003, Haddad et al. 2001, Jones et al. 2003). These results may imply that with an increasing number of plant functional types and plant species, the food resource from litter would be qualitatively and quantitatively diverse enough to fulfill the feeding requirements of an increasingly larger number of animal species at any time. Variation in resource availability over time is of considerable importance since interactions between consumers sharing the same resource will depend on both the timing of its availability and the capacities of consumers to respond to it by dispersal and/or increasing their populations (Lavelle and Spain, 2001). Symstad et al. (2000) tested the hypothesis that the functional group composition and diversity of a plant community may affect the composition and diversity of the herbivore community and higher trophic levels associated with that community. They found that two parameters explained most of the effects of plant functional group diversity on arthropod species richness: plant nutritional quality and plant taxonomic diversity. Siemann et al. (1998) experimentally tested the effects of plant productivity and diversity on aboveground grassland arthropods. He found that a history of high fertilization of the site and lowering plant species richness did

significantly decrease herbivore species richness; however, historical fertilization also significantly increased herbivore species richness indirectly by significantly increasing parasite and predator species richness. He concluded that the species composition or diversity of plants and the productivity of plants all influence the diversity of higher trophic levels. It can be assumed that when the food resource shrank, guilds with higher locomotory ability and behaviour would outnumber those of lesser mobility; the latter would not be able to scavenge over long distances to reach patches of higher food availability. Under such conditions, ants with their high mobility would be favoured, whereas termites, whose activities concentrate around their nests, might be more negatively affected. Epigeic earthworms would seem to have even lower survival ability, whereas endogeic eearthworms, depending on the older decomposed organic matter could remain relatively unaffected.

Soil characteristics are also known to be determinants of macro-invertebrates (Lee, 1985; Lavelle and Spain, 2001). In our study, they explained one third of the total variation in the faunal data. Earthworms were inversely related to soil C:N ratio, while all faunal groups were inversely related to pH and sum of bases which may be regarded as a proxy of soil fertility status. The latter indicates that the fauna in our study area is well adapted to acid and nutrient-poor conditions. Likewise, Lavelle and Spain (2001) reported that pH determines the dominance of litter-feeding (epigeic and anecic) earthworms in nutrient poor and/or acid soils and, in general, tropical earthworms appear to be more acid-tolerant than those in temperate climates.

An inverse relationship between termite species richness and soil nutrient status has also been shown across 30 tropical Australian sites representing five habitat types (Braithwaite, 1988). In Malaysian rainforests, however, termite species richness, functional group richness and population densities were all positively correlated with a soil productivity index, based on soil nutrients (Salick and Tho, 1984). This may be due to the fundamental difference in species composition between the two tropical biomes with soil feeding termites being less predominat in Malaysia (Jones et al (2003). Eggleton at al. (1995) also found strong positive correlations between termite abundance and the concentration of available soil N in a disturbance series of plots in a rainforest environment in Cameroon. In contrast to our study which encompassed a 500 km gradient across three blocks of increasing LUI, Eggleton's results were obtained in one forest-margin area (Mbalmayo Forest Reserve) in one village with all plots derived from the same.

Although it is quite common to derive soil faunal species richness and diversity from that of plants, as we have done above, Lavelle et al. (1997) argue that the diversity of soil

ecosystem engineers tracks that of the living plant community. Most likely, there are feedbacks between soil faunal and plant species richness and diversity, which have developed over evolutionary time and cannot be meaningfully disentangled in terms of cause and effect. It would therefore seem obvious that drastic reduction of plant species richness and diversity, e.g., due to land use (intensity) change, will lead to negative effects on soil faunal species richness and diversity with positive feedbacks (in a technical sense, not in a normative sense) on plant species richness and diversity. Evidence for this inference comes from our study, with more detailed information given by Birang et al. (subm. a, b and c). In Figure 3 LUSs and LUI are used as proxies for vegetation and soil parameters. All fauna parameters are positively associated with land use systems characterized by less anthropogenic disturbance (Sfor, Cacao and Yfor) as opposed to more disturbed ones (Chr and Crop). Crop and Chr are positively associated with soil parameters (SB, pH and C:N ratio), and negatively with vegetation parameters, in contrast with the (almost) closed-canopy LUSs (compare Figures 2 and 3 and see decreasing values for Pmod, Prich and Pricmod in Table 3 and increasing values for pH and SB in Table 4 with decreasing canopy closure).

Eggleton et al. (1996) also reported markedly reduced termite species richness (and biomass and abundance) in a Cameroon rainforest in plots recently cleared and either replanted with young trees or left as a weedy fallow, in comparison to nearby primary forest and older woody sites. In a study of termite diversity across an anthropogenic disturbance gradient in the humid forest zone of West-Africa, Eggleton et al. (2002) found that termite species composition was also strongly correlated with disturbance level. Watt et al. (1997, 2002) examined a range of forest sites in Cameroon representing a disturbance gradient and found that litter-ant abundance was severely reduced in the heavily disturbed sites while sites of intermediate to low disturbance yielded the larger abundances respectively.

Barros et al. (2002) also monitored the effects of land-use system on the soil macrofauna in Western Brazilian Amazonia and they found a significant impact of land-use practices on soil macrofauna. Their results showed that Shannon diversity values decreased gradually with increasing intensification of land use system Thus, diversity of macroinvertebrates was higher in forest than in the other systems in the following decreasing order: fallow, agroforestry, pasture and annual crop system.

Conclusions

It has been suggested before that the structures of soil ecosystem engineer communities are influenced by plant community parameters, which may themselves be determined by the pattern of agricultural practices and by soil nutrient status (e.g., Fragoso and Lavelle, 1992; Wardle and Lavelle, 1997). In the present study we give, for the first time, comprehensive evidence for this statement and for feedbacks among plant and animal groups from species richness and diversity data on the four main groups of ecosystem engineers (plants, earthworms, termites and ants), collected concomitantly in the same area. This constitutes the main scientific result from the present study.

Although the percentage of variation explained by Figure 3 (20.3%) is much less than that of Figure 2 (58.2%), comparison of the two figures nicely shows that LUSs and LUI scaled variables can be used as proxies for vegetation and soil nominal variables. Figure 2 also shows that soil macrofaunal species richness and diversity are more responsive to soil and vegetation parameters than are soil macrofaunal abundances. We therefore suggest that the impact of forest disturbance on soil macrofaunal communities can be assessed for land use evaluation purposes without the need of collecting detailed quantitative soil and vegetation data and soil macrofaunal abundance. This constitutes the main practical result from the present study.

Acknowledgement

Table 8. List of variables and abbreviations (codes) used in the RDA matrix and in correlations table

Faunal community parameters			
Code	Definition	Code	Definition
ER	earthworm species richness (number of species)	*wf*	log termite wood feeder abundance
AE	Earthworm abundance (individuals/m^2)	*HT*	Shannon termite diversity
ea	Log earthworm abundance	*AR*	ant species richness
HE	Shannon earthworm diversity	*AA*	ant species abundance
EB	earthworm biomass (g m^{-2})	*aa*	log ant abundance
Epa	epigeic earthworm abundance	*AP*	ant predator abundance
Ena	endogeic earthworm abundance	*ap*	log ant predator abundance
epa	Log epigeic abundance	*AN*	ant nectarivore abundance
ena	Log endogeic abundance	*an*	log ant nectarivore abundance
TR	termite species richness	*AO*	ant omnivore abundance
AT	termite species abundance	*ao*	log ant omnivore abundance
ta	Log termite abundance	*AS*	ant saprovore abundance
TSf	termite soil feeder abundance	*as*	log ant saprovore abundance
sf	Log termite soil feeder abundance	*HA*	Shannon ant diversity
TWf	termite wood feeders abundance		
Soil parameters		Vegetation parameters	
Bd	bulk density	*pmod*	Plant unique modus (plant functional type richness)
pH	Soil acidity (pH-H$_2$O)	*prich*	Plant species richness
lutum	%clay + %silt	*pricmod*	Plant richness-unique modus ratio
CN	C:N ratio	*caht*	canopy height (m)
P	available P (Mehlich-3)	*crcov*	crown cover (%)
Al	exchangeable Al	*basare*	basal area (m^2/ha)
SB	sum of bases		
Management variables			
LUI	Land use intensity	*Yfor*	Young secondary forest
Sfor	Secondary forest	*Chr*	*C. odorata* dominated fallow
Cacao	Cacao plantation	*Crop*	Annual (inter) crop

8

General discussion

General discussion

In this thesis we investigated the structure of soil macrofauna communities in six villages in southern Cameroon, classified into three blocks representing increasing levels of deforestation and land use intensity (LUI) within the benchmark characterized by ASB, IRAD and IITA. In each village the study focused on the five most common land use systems (LUSs) of the region, presenting a gradient of disturbance from low to high: a secondary forest (Sfor), a shaded cacao plantation (Cacao), a young forest fallow (Yfor), a *Chromolaena odorata* fallow (Chr) and a groundnut/maize/cassava intercrop field (Crop).

The major findings of the study were:
1. Farmers appreciated that earthworms can serve as indicators of soil fertility;
2. They predominantly believed that earthworms have positive effects on crop yield;
3. Slash-and-burn agriculture had negative effects on earthworm surface casting activity and thus on nutrient cycling;
4. This effect was dependent on fallow type before slashing and burning and recovery started immediately after crop establishment;
5. Undescribed earthworm species occured in all the LUI blocks and LUSs under study;
6. Earthworm species richness did not drastically change along the LUI gradient and each LUI harbor characteristic species;
7. The high LUI block has a completely different earthworm community structure; whereas there was no clear delineation between earthworm community structures under low LUI and medium LUI;
8. Within LUI blocks, highly disturbed LUSs had less earthworm abundance and biomass than less disturbed ones;
9. Termite species composition appeared to be primarily related to LUS;
10. LUI and LUS had no major effects on termite species richness and abundance;
11. LUS had some effect on termite functional groups; wood feeders dominated in Crop regardless of LUI;
12. Ant communities were largely location-specific, which constitutes a strong case for preservation;
13. Soil ecosystem engineer community structure was strongly linked to vegetation community structure;

Henceforth we will discuss these findings in the framework of major topics of scientific and societal concern.

Community structure of soil macrofaunal engineers in the humid forest zone of southern Cameroon

Much of the debate on natural resource management in the humid tropics revolves around forests, deforestation or forest conversion, the consequences it has and the way the process of change can be managed. Land use for agricultural purposes is agreed to be the strongest catalyst for changes in biodiversity. The humid tropics are an area where biodiversity levels are extremely high but also where forest conversion is increasing in response to rapidly increasing population levels (van Noordwijk et al., 2002). In Cameroon, 85% of the deforestation is caused by smallholder agriculture (Kotto-Same et al., 2000).

We took a close look at the practice of slash-and-burn in three blocks with different land intensities and the impact on three soil macrofauna guilds: earthworms, termites and ants.

We found in chapter 3 that, in general, earthworm species richness did not differ significantly throughout the land use intensity blocks. This may suggest that the entire pool of earthworm fauna of the southern Cameroon may still be present. However, in an absolute sense, the data show a trend for species loss since the high level of intensification block harbored a lower species number (18) than the medium (21) and low (24) LUI blocks, and, furthermore, less disturbed land use systems in the gradient harbored more species than the most disturbed ones. In terms of abundance and biomass, LUI affected earthworm communities in different ways. The medium LUI exhibited the highest range in values, the high LUI the lowest and the low LUI block was between the two extremes suggesting that in the medium LUI block, there is more differentiation between LUSs. Long-term deforestation and high pressure put on land due to an increasing human population and subsequent shortened fallow phases (80 inhabitants km^{-2} on average, highest frequency of fallow/cropped cycles) may have created conditions leading to the elimination of original species and favoring the migration of new species well adapted to the high LUI, thereby leading to the build-up of a completely different earthworm community in the high LUI block. It may also be that this block has already reached a low resilience as far as earthworms are concerned because of the lack of significant differences in the gradient of LUS disturbance and the high similarity indices found between LUSs. The intermediate disturbance hypothesis (which states that disturbances, intermediate in both magnitude and frequency, allow more species to

exist in the same area), could apply in our study to the medium LUI block for earthworms in southern Cameroon.

Concerning termites (chapter 4), all 3 blocks had virtually the same species richness from low to high LUI indicating that at this scale of resolution, intensification had no direct effect on termite species richness. As opposed to earthworms, species richness of termite showed a strong negative correlation with LUS disturbance level, declining from Sfor to Crop. Species abundance and trophic group abundance were not affected either by LUI. Our results on termites may suggest on the one hand that, at the LUI level, there is no change in termite community structure due to agricultural intensity or that intensification as practiced in southern Cameroon had not reached a threshold that may cause losses of termite species and create imbalances in functional groups; on the other hand, it may well be that changes in termite community structure are masked due to the overall structural complexity of the entire southern Cameroon forest zone. This part of the tropical rainforest has known the highest termite diversity (Eggleton et al., 1995, 1996).

Species richness and abundance of ants were affected by LUI and LUS. From the low LUI to the high LUI block species richness and abundance became lower and in addition we noticed a change in species composition. The same trend was also observed among LUSs within LUI blocks, where in general richness and abundance were higher in less disturbed LUSs (Sfor, Cacao and Yfor) than in more disturbed ones (Chr, Crop). There seems to be a correlation between ant community structure and vegetation complexity which in turn is related to habitat transformation. The presence of at least 3 dominant species in the least diverse communities (high LUI block) may suggest that, as a whole, the entire southern Cameroon forest zone still can maintain enough heterogeneity in habitats to support a diverse ant community.

It appears that LUI had a an effect on earthworms. For termites this was not demonstrable in terms of species richness, abundance and diversity, but there is an effect if species composition is taken into account. Conversion of natural forest to different land use systems more clearly induce differences in species richness and abundance in all three groups with termites being more susceptible. It is therefore imperative to propose alternative management systems to slash-and-burn agriculture that will maintain or restore their habitats. The high number of undescribed species calls for a great effort in taxonomic work as well as an intensive collection program considering the importance potential of the region in terms of biodiversity.

Impact of land use systems on earthworm surface casting activity

The status of soil fauna in undisturbed and converted natural systems can be monitored by their activity. Earthworms produce casts characterized by their higher C and nutrient contents compared to the adjacent soil from which they are derived. We clearly demonstrated that where surface casting is moderate to high such as in Ngoungoumou (low LUI) and Metet (medium LUI), slash-and-burn agriculture has a negative effect on earthworm surface casting and thus nutrient cycling. However, as this effect was dependent on the fallow type and as recovery started immediately after cropping, long-term effects could not be assessed. Hence, further research on individual factors affecting surface casting and its recovery during fallow phases is required. Among those factors are the edaphic conditions in the land use, the resilience of the species assemblages of the systems and the time required to reach full recovery of casting.

Relationships between above and below-ground biodiversity

It has been suggested before that the structures of soil ecosystem engineer communities are influenced by plant community parameters, which may themselves be determined by the pattern of agricultural practices and by soil nutrient status (e.g., Fragoso and Lavelle, 1992; Wardle and Lavelle, 1997). There were positive responses of species richness of all the faunal groups to plant species richness and to the ratio of plant species richness to plant functional type richness and woody vegetation basal area. Soil properties (pH, sum of bases, C:N ratio and lutum) explained only one third of the variation in fauna parameters. Soil macrofaunal diversity parameters were positively associated with less disturbed land-use systems characterized by high canopy cover. The present study (chapter 7) gives, for the first time, comprehensive evidence for this. This constitutes the main scientific result from the present study. In chapter 5 we also showed that a simple scaling of LUSs in terms of disturbance results in a relationship with macrofaunal community characteristics that is similar to such a relationship based on detailed vegetation and soil analyses. Hence we suggest that the impact of forest disturbance on soil macrofaunal communities can be assessed for land use evaluation purposes without the need of collecting detailed quantitative soil and vegetation data. This constitutes the main practical result from the present study.

Farmers' perception of biodiversity in the humid forest

Successful approaches to sustainable forest management are bound to full involvement and cooperation of all stakeholders, which includes the traditional rights of local populations

(Onguene, 2000). This was in our minds in deciding to ask farmers what they knew on soil fauna and whether they are open to technologies that would enhance soil macrofauna. We found that farmers appreciated earthworms as soil fertility indicators and they predominantly believed in their positive effects on crop yields. This constitutes a good basis for the introduction of alternative technologies, such as slash and mulch and green manure cover crop systems without prior burning, which may maintain diverse earthworm communities. The conservation of the (largely undescribed) earthworm fauna of southern Cameroon has to target agricultural productivity in already deforested land to reduce further clearing of forest. However, some farmers consider earthworms as pests probably because many causal agents of crop damage are not visible (nematodes, fungi, bacteria, viruses). Some also believe that earthworms feed on damaged plant tissue. This misconception needs to be addressed through awareness and training on the virtues of earthworms and of soil macrofauna as a whole prior to introducing the best-bet alternative technologies to slash-and-burn agriculture.

The knowledge gathered on the present state of earthworm, termite and ant communities and the effects of land use change on these macrofauna in southern Cameroon constitutes the baseline information necessary for the design and /or implementation of measures of conservation in which farmers should play a pivotal role.

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Summary

Summary

Earthworms, termites and ants are important components of the soil ecosystem. Based on their size, they are part of the soil macrofauna and are recognized as principal 'ecosystem engineers'. Ecosystem engineers are known to have sufficient numerical and biomass densities to exert a predominant influence in the formation and maintenance of the soil structure and to regulate soil processes to an extent that overrides organisms in other functional categories. In this thesis, the community structure of these engineers is described along a gradient of land use intensification in the humid forest zone of southern Cameroon. The general objective of this thesis is to provide baseline information on the soil macrofauna distribution and the impact of land use change on their diversity. Insight into their relationships with the environment in which they live is also explored.

Slash-and-burn agriculture is the main agricultural practice in southern Cameroon and contributes to 85% of deforestation and subsequent direct and indirect impacts on the belowground biodiversity. Because farmers in this region rely mostly on the biological fertility of their soil, it is important to determine the level of diversity of ecosystem engineers under which the integrity of the system is maintained. This knowledge will provide options to introduce soil management techniques to farmers , which reduce negative impacts of land use and land use changes on these species and the processes they fulfill, thereby reducing the pressure on the remaining forest.

This study was carried out in three land use intensification blocks (LUI): high LUI (Nkometou and Minkoameyos villages), medium LUI (Mbalmayo and Metet villages) and low LUI (Akok and Ngoungoumou). In each village, 5 land use systems (LUS) of different level of disturbance were sampled. The sampled LUS were: secondary forest>30 year old (Sfor), shaded cocoa plantation (Cacao), young forest of 12-15 years old (Yfor), 4-5 year old *Chromolaena odorata* (Chr) and a groundnut/maize/cassava intercrop (Crop).

The methodological approach used in this study involved several steps:

1. Assessment of the perception and appreciation by land users of soil faunal diversity and their effect on soil fertility and crop performance.
2. Evaluation of the effect of land use management on the activity of soil ecosystem engineers, in particular the earthworm surface casting activity on slash-and- burn cropped land and in *Chromolaena odorata* and young forest fallow.

3. Inventory and characterization of soil macrofauna diversity and density in 5 land use systems of different disturbance regimes along a gradient of land use intensification using a spatial gradient of land use intensification as a substitute for long term changes in macrofaunal diversity and composition that would be seen in a chronosequence of land degradation

4. Exploration of the relationships between vegetation cover, soil ecosystem engineers and the condition of the soil across the main land use systems used in southern Cameroon (are below and above ground biodiversity interdependent?)

In chapter 2, the knowledge and perception of earthworm effects on soil fertility and crop performance is reported. To assess if the fallow phase has attained sufficiently high levels of fertility, soil macrofauna was used by 42% of the farmers as an indicator. The presence of earthworm casts was used by 35% of the farmers to determine if the land was ready for cropping. Earthworms were not believed to have an effect on soil fertility by more than 98 % of the farmers. Less than 1% of the farmers believed that earthworms either increased or decreased soil fertility. Farmers made no distinction between different crops or fallows. Across all crops, 72% of the farmers reported that earthworms have no effect on crop yields. Positive effects were regarded as crop-specific: 30% of farmers believed that groundnut (*Arachis hypogaea*) and cassava (*Manihot esculentus*) yields increased if earthworms were present. For maize (*Zea mays*), plantain (*Musa* spp.), cocoyam (*Xanthosoma sagittifolium*) and cacao (*Theobroma cacao*), between 19 and 27% of the farmers believed in yield increases. Few respondents (mean across crops less than 2%) believed that earthworms reduced crop yields, with the highest proportion in plantain (almost 4%). Farmers' perception of earthworm effects on cassava and groundnut yields was highly dependent on location and related to the levels of surface casting

In chapter 3, the effect of slash-and-burn agriculture on earthworm surface cast deposition was assessed in 4-5 year old *Chromolaena odorata* (Chr) and young forest (Yfor) fallow (12-15 years old) in Ngoungoumou (low land use intensity (LUI)) , Metet (medium LUI), and Nkometou (high LUI) in 2000 and 2001. In 2000, surface cast deposition was different between villages, in both fallow types and cropped land. At Nkometou casting was lowest and no effects of fallow type or land use were found. At Metet and Ngoungoumou, more casts were deposited in fallow than in the cropped treatment. Cropping reduced cast deposition in both fallow types, yet more so in Chr than in Yfor. In 2001, as in 2000, no differences were found at Nkometou. At Metet and Ngoungoumou, more casts were deposited

in undisturbed controls than in the other treatments. Cast deposition was higher in plots in the first year of fallow after cropping than in double-cropped plots, indicating an immediate recovery after cropping. Cast production was not correlated with soil chemical properties across villages. Earthworm species assemblages were different between villages, with large-bodied, endogeic and anecic species most abundant at Metet. The more severe reductions in casting in cropped Chr than in Yfor indicated that either edaphic conditions in Yfor are maintained more favorably for earthworm survival and continued activity, or that the Yfor assemblages are more resilient. It is concluded that earthworm species assemblage is probably the main factor determining surface cast deposition and thus differences between villages.

Chapter 4 describes the community structure of earthworms. A total of 36 earthworm species were found, of which 1 new genus and 17 undescribed species, belonging to 3 families: Acanthodrilidae, Eudrilidae and Ocnerodrilidae. Abundance ranged from 64 to 236 individuals m^{-2}. Biomass ranged from 2 to 16 g m^{-2}. Low LUI harbored more species (24) than medium (21) and high (18) LUI but these differences were not significant. The only anecic species (*Rosadrilus camerunensis*) was collected in high canopy land use systems. Epigeic earthworms in Yfor in the medium LUI were 3 times more abundant than endogeic earthworms and this LUS significantly outnumbered all the other LUS in earthworm abundance and biomass. Diversity was low but evenness high in all 3 LUI. LUI had a significant effect on the diversity indices of all the LUS based on species data. There was a significant effect of LUI and a highly significant effect of LUS on Simpson's diversity index on a biomass basis. A completely different and specific earthworm assemblage composed mainly of small endogeic and exotic earthworms was found at the high LUI, while low and medium LUI had a lot of species in common in the various functional groups. It is concluded that land use intensification probably determined the differences in community structures.

Chapter 5 presents the community structure of termites. A total of 223 species were recorded of which 43% (91) were undescribed and 6% (14) were new genera; 80% were soil-inhabiting species and 13% were potential pests to agricultural crops. The number of species found was 68% higher than the previous figure from the region. There was no significant effect of LUI but, in contrast, a strong effect of LUS on termite species richness and abundance. Overall termite richness declined with increasing intensity of disturbance from Sfor to Crop. Soil-feeding species numerically dominated except in Crop in the high LUI. Regardless of the LUI blocks, LUS of similar disturbance level and canopy cover shared a lot of species. It is concluded that termite assemblages of each LUS are derived from different assemblages or very local assemblages may determine the community in a LUS.

Ground-dwelling ant communities are described in chapter 6. A total of 80 ant species were found belonging to 7 subfamilies. LUI and LUS had striking effects on ant communities with highest richness and abundance in the low LUI block, followed by medium and high LUI blocks, respectively. The diversity significantly decreased along this LUI gradient. Species were evenly distributed within and across LUS and LUI blocks. Cacao plantation exhibited the highest diversity on average and harbored the highest number of saprovorous ant species. Crop in the most disturbed LUS showed the lowest diversity and abundance. Predator species dominated in all the LUS. Ant communities of each LUI block were characterized by at least 3 dominant ant colonies. The low LUI block retained the highest number of characteristic species (8) while the high LUI block had 3 such species and the medium LUI block 5. There was no clear pattern of changes in ant species assemblages within LUI, but the species assemblages were rather specific to each village.

In short, earthworms, termites and ants reacted quite differently on LUI and LUS:

- Land use intensification appeared to shape the community structure of earthworms, for example evidenced by the invasion of exotic species in the high LUI. At the same time the medium block appeared to offer the best conditions for earthworm development.

- Land use systems (disturbance) were the driving force for termite community structure.

- Ant community structure was more local and species assemblages were influenced by the combination of land use intensity and land management.

In chapter 7, relationships between the soil macrofauna and the environmental variables as well as the impact of land management on the distribution of these animals are investigated. There were significant correlations between the parameters of the environment and those of the fauna. Biotic (vegetation) variables together explained two third of the total variation in faunal parameters, while abiotic (soil) variables explained one third. Earthworms, termites and ants did not correlate among themselves. Species richness and diversity were clearly separated by faunal group. Taken singly, the strongest positive correlations were found between earthworm variables (richness, biomass and Shannon diversity) and canopy height, the ratio species richness : number of functional groups and the species richness of plants. Termite and ant diversities exhibited close relationships with plant basal area, the number of plant functional groups and the species richness of plants and were negatively correlated to base saturation and pH. Earthworm biomass responded negatively to C:N ratio. Soil macrofaunal species richness and diversity were more responsive to soil and vegetation

parameters than macrofaunal abundances. It is concluded that a positive relation between the complexity and production of the vegetation and the complexity of the faunal community in terms of species richness and diversity exists.

The major findings of the study are twofold:

1. There is comprehensive evidence that the structures of soil ecosystem engineer communities are influenced by plant community parameters, which are themselves determined by the pattern of agricultural practices and by soil nutrient status;

2. The impact of forest disturbance on soil macrofaunal communities can be assessed for land use evaluation purposes without the need of collecting detailed quantitative soil and vegetation data.

The knowledge gathered on the present state of earthworm, termite and ant communities and the effects of land use change on these macrofaunal groups in southern Cameroon constitutes the baseline information necessary for the design and /or implementation of measures of conservation in which farmers should play a pivotal role.

Samenvatting

Regenwormen, termieten en mieren zijn belangrijke componenten van het bodemecosysteem. Zij maken deel uit van de bodemmacrofauna en worden beschouwd als belangrijke 'ecosystem engineers'. 'Ecosystem engineers' zijn door hun aantal en biomassa van overheersende invloed op de vorming en instandhouding van de bodemstructuur. Hierdoor zijn ze van groter belang voor het reguleren van bodemprocessen dan bodemorganismen in andere functionele categorieën. In dit proefschrift wordt de gemeenschapstructuur van deze 'ecosystem engineers' beschreven langs een gradiënt van intensivering van het landgebruik in de humide boszone van Zuid-Kameroen. Het doel van het proefschrift is om basisinformatie te verstrekken over de verspreiding van de macrofauna en de invloed die landgebruikverandering heeft op de diversiteit van deze macrofauna. Ook de relatie met het leefmilieu is onderzocht.

Zwerflandbouw is het belangrijkste landbouwsysteem in Zuid-Kameroen. Het draagt voor 85% bij aan de ontbossing, en als gevolg hiervan heeft het directe en indirecte invloed op de ondergrondse biodiversiteit. Aangezien boeren in de regio afhankelijk zijn van de biologische vruchtbaarheid van hun bodems, is het van belang om te bepalen in hoeverre de diversiteit van de 'ecosystem engineers' wordt behouden. Met behulp van deze kennis kunnen de boeren opties aangereikt krijgen om bodemmanagement-technieken te introduceren, waarmee negatieve gevolgen van landgebruik en landgebruikverandering op de macrofaunasoorten en de bodemprocessen waaraan zij bijdragen, kunnen worden verminderd. Hierdoor wordt de druk op het resterende bos verlicht.

Het hier beschreven onderzoek is uitgevoerd op drie niveaus van landgebruikintensivering (LUI): hoge LUI (de dorpen Nkometou en Minkoameyos), matige LUI (de dorpen Mbalmayo en Metet) en lage LUI (de dorpen Akok en Ngoungoumou). In elk dorp zijn vijf landgebruiksystemen (LUS) van verschillend niveau van verstoring bemonsterd. De bemonsterde LUS zijn: secundair bos > 30 jaar oud (Sfor), beschaduwde cacao aanplant (Cacao), jong bos van 12-15 jaar oud (Yfor), 4-5 jaar oude *Chromolaena odorata* (Chr) en een aanplant van aardnoten/maïs en cassave (Crop).

De methodologische aanpak van het onderzoek bestond uit verschillende stappen:

1. Beoordeling van de perceptie en waardering door landgebruikers van de bodemfauna-diversiteit en het effect van deze diversiteit op de bodemvruchtbaarheid en het gewas.
2. Evaluatie van het effect van landgebruikmanagement op de activiteit van de bodem-'ecosystem engineers', in het bijzonder de afzetting van regenwormexcrementen aan

de oppervlakte op bouwland waar de zwerflandbouwtechniek wordt toegepast, op *Chromolaena odorata* en op jonge bosbraak.

3. Inventarisatie en karakterisering van de bodemmacrofauna-diversiteit en -dichtheid in vijf landgebruiksystemen van verschillend verstoringniveau langs een gradiënt van intensivering van het landgebruik. Hierbij werd een ruimtelijke gradiënt van landgebruikintensivering beschouwd als substituut voor veranderingen in de diversiteit en samenstelling van de macrofauna welke gezien zou worden in een chronosequentie van landdegradatie.

4. Onderzoek naar de relatie tussen vegetatiebedekking, bodem-'ecosystem engineers'en de bodemtoestand in de belangrijkste landgebruiksystemen in Zuid-Kameroen (zijn boven- en ondergrondse biodiversiteit afhankelijk van elkaar?)

In hoofdstuk 2 wordt de kennis en perceptie van de effecten van regenwormen op de bodemvruchtbaarheid en het gewas in de humide boszone van Zuid-Kameroen besproken. Van de boeren gebruikte 42% de bodemfauna als indicator om te beoordelen of de braakfase voldoende was om de gewenste vruchtbaarheidniveaus te behalen. De aanwezigheid van regenwormexcrementen werd door 35% van de boeren gebruikt om te bepalen of het land gebruiksklaar was. Regenwormen werden niet verondersteld een effect te hebben op de bodemvruchtbaarheid bij 98% van de boeren. Minder dan 1% van de boeren geloofde dat regenwormen de bodemvruchtbaarheid verlagen of verhogen. Boeren maakten geen onderscheid tussen verschillende gewassen of braak. Van de boeren rapporteerde 72% dat bij geen van de gewassen de wormen een effect op de oogst hebben. Positieve effecten werden als gewasspecifiek gezien: 30% van de boeren geloofde dat de oogst van aardnoten (*Arachis hypogaea*) en cassave (*Manihot esculentus*) verbeterde wanneer regenwormen aanwezig waren. Bij maïs (*Zea mays*), bakbanaan (*Musa* spp.), cocoyam (*Xanthosoma sagittifolium*) en cacao (*Theobroma cacao*) geloofde tussen de 19 en 28% van de boeren in oogsttoename. Slechts weinig respondenten (gemiddeld minder dan 2% over de verschillende gewassen, met een maximum van 4% bij bakbanaan) geloofden dat wormen de gewasopbrengst verminderden. De perceptie bij boeren van het effect van wormen op de oogst van cassave en aardnoten was afhankelijk van de locatie en gerelateerd aan de hoeveelheid regenworm-excrementen aan de oppervlakte.

In hoofdstuk 3 wordt het effect van zwerflandbouw op de afzetting van regenworm-excrementen aan de oppervlakte besproken. Dit effect is bestudeerd in 2000 en 2001 in 4-5 jaar oude braak van *Chromolaena odorata* (Chr) en jong bos (Yfor; 12-15 jaar oud) in

Ngoungoumou (lage landgebruikintensiteit (LUI)), Metet (matige LUI) an Nkometou (hoge LUI). In 2000 was er een verschil in afzetting van regenworm-excrementen tussen de dorpen, in beide braaktypen en in bouwland. De afzetting van excrementen was het laagst in Nkometou, waar geen effect van braaktype en landgebruik werd waargenomen. In Metet en Ngoungoumou werd meer afzetting gevonden in de braakvelden dan in de behandeling met gewas. Gewas reduceerde de afzetting in beide typen braak, echter meer in Chr dan in Yfor. Noch in 2000, noch in 2001 werden er verschillen gevonden in Nkometou. In Metet en Ngoungoumou werden meer excrementen afgezet in de ongestoorde controle dan in de andere behandelingen. De afzetting van excrementen was hoger in de velden tijdens het eerste braakjaar na verbouw van een gewas dan in de velden waar voor een tweede maal een gewas geproduceerd werd. Dit duidt op een onmiddellijk herstel na een gewasjaar. De productie van excrementen was niet gecorreleerd met verschil in bodemchemische eigenschappen tussen de verschillende dorpen. Tussen de dorpen werd een verschil geconstateerd in de soortensamenstelling van regenwormen, waarbij grote, in de bodem levende en naar de oppervlakte pendelende soorten het meest voorkwamen in Metet. In Chr werd een belangrijkere reductie van excrementen geconstateerd dan in Yfor, wat erop duidt dat ofwel de bodemcondities van Yfor gunstiger waren voor wormen en hun activiteit, ofwel dat de soortengroep in Yfor veerkrachtiger was. De conclusie is gerechtvaardigd dat de soortensamenstelling van de wormen de belangrijkste factor is die de mate van afzetting van regenwormexcrementen aan de oppervlakte bepaalt.

Hoofdstuk 4 beschrijft de structuur van de regenwormgemeenschappen. Er werden 36 wormensoorten gevonden (waaronder 1 nieuw genus en 17 onbeschreven soorten, behorend tot 3 families: Acanthodrilidae, Eudrilidae en Ocnerodrilidae). De abundantie varieerde van 64 tot 236 individuen m^{-2}. De biomassa varieerde van 2 tot 16 g m^{-2}. Lage LUI huisvestte meer soorten (24) dan matige (21) en hoge LUI (18), maar deze verschillen waren niet significant. De enige pendelende soort (*Rosadrilus camerunensis*) werd gevonden in landgebruiksystemen met hoog kroondak. Oppervlakkig levende soorten in Yfor in matige LUI waren 3 keer zo talrijk als in de bodem levende soorten. Bij deze LUI waren significant meer wormen (in aantal en biomassa) aanwezig dan in alle andere LUS. De diversiteit was laag in alle 3 LUI, maar de 'evenness' was hoog. LUI had een significant effect op de diversiteitindices van alle LUS op basis van de soorten. Er was een significant effect van LUI en een zeer significant effect van LUS op Simpson's diversiteitindex, op basis van de biomassa. Een geheel afwijkende en specifieke groep regenwormen, voornamelijk bestaande uit in de bodem levende en exotische wormen werd gevonden in de hoge LUI, terwijl in de

lage en matige LUI overeenkomst bestond in de soortensamenstelling van de verschillende functionele groepen. De conclusie is gerechtvaardigd dat intensivering van het landgebruik waarschijnlijk het verschil in de structuur van de wormengemeenschap bepaalt.

Hoofdstuk 5 beschrijft de structuur van de termietengemeenschap. Er werden 223 soorten gevonden waarvan 43% (91) onbeschreven en 6% (14) nieuwe genera waren; 80% waren bodemsoorten en 13% waren een potentiële plaag voor landbouwgewassen. Het gevonden aantal soorten was 68% hoger dan de soortenrijkdom die in voorgaand onderzoek in de regio was geconstateerd. Er was geen significant effect van LUI, maar daarentegen een sterk effect van LUS op de soortenrijkdom en abundantie van de termieten. De soortenrijkdom van termieten nam af met een toename van intensiteit van verstoring van Sfor naar Crop. Bodemetende soorten waren numeriek dominant behalve in Crop en hoge LUI. Er was een grote overeenkomst in soorten tussen LUS van gelijk niveau van verstoring en kroonbedekking, onafhankelijk van de LUI- blokken. De conclusie is gerechtvaardigd dat de termieten in elke LUS afkomstig zijn van verschillende groepen of dat zeer lokale groepen bepalend zijn voor de gemeenschap in een LUS.

Hoofdstuk 6 beschrijft de bodembewonende mierengemeenschappen. Er werden 80 mierensoorten gevonden die tot 7 subfamilies behoren. LUI en LUS hadden een enorm effect op de mierengemeenschappen. De grootste soortenrijkdom en abundantie werden gevonden in de lage LUI, gevolgd door de matige en hoge LUI-blokken. De diversiteit nam langs deze LUI-gradiënt significant af. De 'evenness' van de soorten was hoog binnen en tussen de LUS en de LUI. Cacao-aanplant toonde gemiddeld de hoogste diversiteit en huisvestte het hoogste aantal saprovore mierensoorten. Crop in het meest verstoorde LUS vertoonde de laagste diversiteit en abundantie. Predatore soorten domineerden in alle LUS. In elk LUI-blok werd de mierengemeenschap gekarakteriseerd door ten minste 3 dominante mierenkolonies. Het lage LUI-blok had het hoogste aantal karakteristieke soorten (8), terwijl de matige LUI er 5 en de hoge LUI er 3 hadden. Er was geen duidelijk patroon van verandering in groepen mierensoorten binnen een LUI, maar de soortengroepen waren wel specifiek voor elk dorp.

Kortom, regenwormen, termieten en mieren reageerden verschillend op landgebruikintensiteit en landgebruiksysteem:

- Landgebruikintensivering bleek de structuur van wormengemeenschappen te bepalen, zoals bijvoorbeeld blijkt uit de invasie van exotische soorten in de hoge LUI. Tegelijkertijd bleek matige LUI de beste condities voor regenwormen te bieden.
- (Verstoringen van) landgebruiksystemen waren de drijvende factor voor de structuur van de termietengemeenschap.

- De gemeenschapstructuur van mieren was meer lokaal van aard en de soortengroepen werden beïnvloed door de combinatie van landgebruikintensiteit en -management.

In hoofdstuk 7 wordt gezocht naar de relaties tussen de bodemmacrofauna en omgevingsvariabelen en naar de invloed van management van het land op de verstoring van deze dieren. Er waren significante correlaties tussen omgevingsparameters en faunaparameters. Biotische (vegetatie-) variabelen verklaarden tezamen tweederde van de totale variatie van de faunaparameters, terwijl abiotische (bodem-) variabelen een derde verklaarden. Regenwormen, termieten en mieren correleerden niet met elkaar. Soortenrijkdom en diversiteit waren duidelijk gescheiden per diergroep. Per diergroep bezien werd de sterkste positieve correlatie gevonden tussen de soortenrijkdom, biomassa en diversiteit van regenwormen enerzijds en anderzijds kroonhoogte, de verhouding soortenrijkdom : rijkdom aan functionele groepen van planten en de soortenrijkdom van planten. De diversiteit van termieten- en mierensoorten vertoonde sterke relaties met de oppervlakte van de plantbasis, de rijkdom aan functionele groepen planten en de soortenrijkdom van planten en deze waren negatief gecorreleerd met de basenverzadiging en de pH. De biomassa van regenwormen reageerde negatief op de C:N ratio. De soortenrijkdom en diversiteit van de bodemmacrofauna reageerden meer op bodem en vegetatie dan de abundantie. De conclusie is gerechtvaardigd dat er, wat betreft soortenrijkdom en diversiteit, een positieve relatie bestaat tussen de complexiteit en productie van de vegetatie en de complexiteit van de faunagemeenschap.

De belangrijkste conclusies van dit proefschrift zijn:

1. de structuur van de gemeenschappen van bodem-'ecosystem engineers' wordt beïnvloed door parameters van de plantengemeenschap, die zelf worden bepaald door het landgebruik en de nutriëntentoestand van de bodem;

2. de invloed van bosverstoring op de bodemmacrofauna-gemeenschappen kan worden vastgesteld voor beoordeling van het landgebruik zonder dat het nodig is om gedetailleerde kwantitatieve bodem– en vegetatiegegevens te verzamelen.

De kennis die bijeengebracht is over de huidige staat van regenwormen-, termieten- en mierengemeenschappen en de effecten van veranderingen in het landgebruik op deze macrofauna in Zuid-Kameroen vormt de basisinformatie die nodig is voor het ontwerp en de uitvoering van maatregelen voor behoud van natuurlijke hulpbronnen, waarbij boeren een centrale rol zouden moeten spelen.

Résumé

Les vers de terre, les termites et les fourmis ne sont pas que les habitants du sol, ils font partie intégrante de l'écosystème. Sur la base de la taille, ils sont classés dans le groupe de la macrofaune du sol et sont appelés organismes ingénieurs du sol. Les organismes ingénieurs du sol sont généralement abondants et de biomasse élevée au point d'exercer une grande influence dans la formation et la conservation de la structure du sol et de réguler les activités des organismes appartenant à d'autres groupes fonctionnels (Lavelle et. al, 1997). Cette thèse décrit la structure des peuplements de ces ingénieurs à travers un gradient d'intensification de l'utilisation du sol dans la zone forestière humide du Sud Cameroun dans le but de procurer des informations de base sur leur distribution et l'impact qu'imposent les changements de type d'utilisation du sol sur leur diversité qui du reste, est un facteur crucial dans la performance des processus pour lesquels ils sont importants. Les relations avec les facteurs de l'environnement dans lequel ils vivent sont aussi explorées.

La pratique agricole la plus répandu dans le sud du Cameroun reste l'agriculture itinérante sur brûlis qui contribue à hauteur de 85% dans le phénomène de déforestation et les effets subséquents sur la biodiversité du sol. Considérant l'intérêt de la fertilité biologique chez les agriculteurs qui utilisent peu ou pas d'intrants, il s'avère important de déterminer les seuils de diversité des ingénieurs du sol qui permettent de maintenir l'intégrité fonctionnelle du système. Cette connaissance permettra l'introduction de techniques alternatives de gestion des terres aux agriculteurs afin de limiter les effets néfastes causés par l'intensification de l'utilisation des sols et les changements de type d'utilisation du sol sur ces espèces et les foncions qu'elles remplissent, et par conséquent réduire la pression potentielle sur le reste de la forêt.

L'approche méthodologique utilisée pour cette étude comporte plusieurs étapes:
1. L'évaluation de la perception et de l'appréciation par les agriculteurs de la diversité de macroinvertébrés du sol et de leur effet sur la fertilité du sol et la performance des cultures
2. L'évaluation de l'impact de la gestion des sols sur les activités des organismes ingénieurs du sol: le cas d'étude comparée de la production des terricoles des vers de terre dans une jachère à *Chromolaena odorata* et dans une jeune jachère forestière et dans des champ cultivés dérivés

3. L'inventaire et la caractérisation de la diversité et de la densité de la macrofaune du sol dans 5 types d'utilisation du sol présentant de niveaux de perturbation différents à travers un gradient d'intensification de l'utilisation du sol en considérant le gradient d'intensification dans l'espace comme substitut pour des changements à long terme de la diversité et de la composition de la macrofaune qui serait interprétés comme une chrono séquence de la dégradation du sol.

4. L'exploration des relations qui existent entre le couvert végétal, les ingénieurs du sol et les propriétés du sol qui les héberge à travers les principaux types d'utilisation du sol du Sud Cameroun (Y a t'il une interdépendance entre la biodiversité superficielle et la biodiversité souterraine?)

Le chapitre 2 reporte sur la connaissance et la perception par les agriculteurs des effets des vers de terre sur la fertilité du sol et la performance des cultures dans la zone de forêt humide du Sud Cameroun. Pour évaluer si le niveau de fertilité de la jachère est suffisant pour la mise en culture, 42% d'agriculteurs utilisent la macrofaune du sol comme indicateur de fertilité. La présence des terricoles de vers de terres est utilisée par 35% d'agriculteurs pour déterminer le niveau de fertilité du sol. Pus de 98% d'agriculteurs ne croient pas que les vers de terre ont un effet sur la fertlité des sols. 0.7% d'agriculteurs seulement croient que les vers de terre diminuent ou augmentent la fertilité des sols. Les agriculteurs ne font pas de distinction entre les champs cultivés et les champs de jachères.

En combinant les résultats obtenus de tous les champs, 71.6% d'agriculteurs ont reporté que les vers de terres n'ont aucun effet sur le rendement des cultures. Ils considèrent que les effets positifs observés sont spécifiques aux cultures: 30.1% d' agriculteurs pensent que les rendements de l'arachide (*Arachis hypogaea*) et du manioc (*Manihot esculenta*) augmentent en présence des vers de terre. Entre 19.2 et 27.7% d'agriculteurs croient que les rendements du maïs (*Zea mays*), du bananier-plantain (*Musa spp)*, du macabo (*Xanthosoma sagittifolium*) et du cacao (*Theobroma cacao*) augmentent. Peu de répondants (moyenne combinée de toutes les spéculations égale à 1.8%) pensent que les vers de terre diminuent les rendement des cultures, la banane-plantain étant la plus susceptible (3.8%). La perception que les vers de terre ont un effet sur les rendements de l'arachide et du maïs a été fortement dépendante de la localité et liée à la production des terricoles.

Dans le chapitre 3, les effets de l'agriculture sur brûlis ont été évalués en 2000 et 2001 dans un champ de jachère à *Chromolaena odorata* de 4-5 ans (Chr) et dans une jeune jachère forestière de 12-15 ans (Yfor) à Ngoungoumou (bloc à faible intensification), Metet (bloc à

intensification intermédiaire) et à Nkometou (bloc à forte intensification). En 2000, la production des terricoles a été différente entre les villages, dans les deux types de jachère et les champs cultivés dérivés. A Nkometou, la production des terricoles a été la plus faible et aucun effet de type de jachère ni de type d'utilisation du sol n'a été observé. A Metet et Ngoungoumou, plus de terricoles ont été déposés dans les parcelles (controls) non perturbés que dans les champs cultivés dérivés. La mise en culture réduit la production des terricoles dans les deux types de jachère, cependant cette réduction est beaucoup plus prononcée dans Chr que dans Yfor. En 2001, il n'y a pas eu de différence de production à Nkometou comme en 2000. A Metet et à Ngoungoumou, par contre, il y a eu plus de terricoles déposés dans les controls non perturbés que dans les autres traitements. Il y a eu plus de terricoles dans les parcelles en première année de jachère après la culture que dans celles en culture continue, ce qui indique une reprise immédiate de production de terricoles après la mise en culture. La production des terricoles n'est pas corrélée aux propriétés chimiques du sol à travers les villages. Les peuplements de vers de terre sont différents entre les villages, Metet abritant beaucoup de grands vers de terre endogés et anéciques. Les réductions de production des terricoles ont été plus sévères dans les champs cultivés dérivés de Chr que de Yfor; ce qui indique que soit les conditions édaphiques dans Yfor sont conservées plus favorablement pour la survie des vers de terre et la poursuite de leurs activités ou que les espèces dans Yfor sont plus résiliants. En conclusion, la composition spécifique des peuplements de vers de terre est responsable de la production des terricoles et partant de la différence de production entre les villages.

La structure de la communauté des vers de terres est décrite au chapitre 4. Au total, 36 espèce de vers de terre ont été récoltées dont un genre nouveau et 17 espèces non-encore décrites. Elles appartiennent à 3 familles: Acanthodrilidae, Ocnerodrilidae et Eudrilidae. La densité numérique varie de 64 à 236 individus m^{-2}. La biomasse varie de 2 à 16 g m^{-2}. Le bloc de faible intensité abrite plus d'espèces (24) que le bloc d'intensité intermédiaire (21) et le bloc de forte intensité (18); cependant ces différences ne sont pas significatives. L'unique espèce de vers de terre anécique (*Rosadrilus camerunensis*) a été récoltée dans les types d'utilisation du sol caractérisé par une canapé haute. Les vers épigés dans Yfor dans le bloc á intensité intermédiaire étaient 3 fois plus abondants que les vers endogés et ce type d'utilisation du sol contenait plus d'espèces de vers que tous les autres types en densité numérique et en biomasse. L'indice de diversité spécifique était bas mais l'équitabilité était élevée dans les 3 blocs. L'intensification avait un effet significatif sur les indices de diversité de tous les types d'utilisation sur la base de données sur les espèces. Il y avait un effet

significatif de l'intensification et un effet très significatif du type d'utilisation sur l'indice de diversité de Simpson calculée sur la base de la masse. Une faune de vers de terre complètement différente, principalement composée de petits vers endogés et de vers exotiques est formée dans le bloc à forte intensité. En même temps, les blocs á intensité faible et intermédiaire comportaient beaucoup d'espèces de vers en commun. Nous concluons que l'intensification de l'utilisation du sol serait à l'origine de la différence dans la structure des 3 peuplements.

Au chapitre 5 les peuplements des termites sont décrits. Un total de 223 espèces de termites ont été récoltées parmi lesquelles 43% (91) ne sont pas encore décrites et 6.25% sont nouvelles à la science; 80% d'espèces trouvées habitent le sol et 13% sont de ennemis potentiels de cultures. Il y a eu une augmentation de 68% par rapport au nombre d'espèces précédemment collectées dans la région. On a pas trouvé de différence significative due à l'effet de l'intensification mais au contraire le type d'utilisation du sol semble avoir un effet très élevé sur la richesse spécifique et l'abondance numérique des vers de terre. La richesse spécifique des termites diminue avec l'augmentation de la perturbation du milieu dans le gradient partant de la forêt au champ cultivé dans le bloc à forte intensification. Le termites humivores sont numériquement dominants. Indépendamment du bloc, les types d'utilisation du sol (types de perturbation et de canopée similaires)gèrent les mêmes espèces de termites. Nous concluons que les communautés de termites de chaque type d'utilisation du sol proviennent de peuplements différents ou alors que des peuplements très localisés déterminent la communauté de termites dans le type d'utilisation du sol.

La structure des peuplements des fourmis est présentée dans le chapitre 6. Un total, 80 espèces de fourmis ont été récoltées; elles appartiennent à 7 sous-familles. Le type d'utilisation du sol et le degré d'intensification ont des effets très significatifs sur la communauté des fourmis; le bloc à faible intensification présente la plus grande richesse spécifique et la plus grande abondance des populations de fourmis, suivi par celui à intensification intermédiaire (modérée). Par conséquent, la diversité spécifique diminue aussi dans le sens de ce gradient d'intensification. Les espèces sont uniformément distribuées à travers et à l'intérieur des types d'utilisation du sol et des blocs d'intensification. En moyenne, la cacaoyère présente la plus grande diversité spécifique et abrite le plus grand nombre de saprovores. Le champ cultivé, le type d'utilisation du sol le plus perturbé, présente la pus petite diversité spécifique et contient le plus petit nombre de fourmis. Les espèces de fourmis prédateurs dominent dans tous les types d'utilisation du sol. Dans chaque bloc d'intensification, les peuplements de fourmis sont caractérisées par au moins 3 colonies

dominantes. Le bloc à faible intensification abrite le plus grand nombre d'espèces caractéristiques (8) alors que celui de forte intensification n'en compte que 3 et le bloc d'intensification modérée 5. Nous n'avons pas trouvé un modèle particulier de changement d'espèces dans le peuplement des fourmis à l'intérieur de chaque bloc d'intensification; mais les peuplements apparaissent plutôt spécifiques à chaque village.

L'intensification de l'utilisation des sols semble être le facteur déterminant la structure des peuplements des vers de terre, ceci est attesté par l'invasion des espèces exotiques dans le bloc à forte intensification; en même temps, le bloc à intensification modérée semble offrir les meilleures conditions pour le développement des vers de terre. Le type d'utilisation du sol apparaît comme responsable de la structure de peuplements de termites alors que les peuplements des fourmis semble être plus locaux et sont influencés par la conjugaison des effets du d'utilisation du sol et l'intensification de son utilisation.

Le chapitre 7 présente les relations entre les macroinvertébrés du sol et les paramètres de l'environnement ainsi que l'impact de la gestion des sols sur la distribution de cette faune. Les résultats obtenus montrent des corrélations significatives entre les paramètres de l'environnement et ceux de la faune. Les variables de la végétation expliquent les deux tiers de la variation des paramètres de la faune alors que celles du sol en expliquent seulement le tiers. Des corrélations significatives n'ont pas été trouvées entre les vers de terre, les termites et les fourmis. La richesse et la diversité spécifiques sont associées par groupe d'invertébrés. Les plus fortes corrélations ont été obtenues entre les paramètres des vers de terre (richesse spécifique (ER), biomasse (EB) et indice de diversité de shannon (EH)) et le canapé de la végétation (cath), sa richesse spécifique (prich) et le ratio richesse spécifique/richesse fonctionnelle (pricmod). La diversité spécifique des termites et des fourmis sont liées positivement au diamètre de base des arbres, à la richesse spécifique, et à la richesse fonctionnelle (pmod) ; mais sont négativement corrélées à la somme de cations et au pH. La biomasse des vers de terre répond négativement au pH du sol. Nos résultats démontrent que la richesse et la diversité spécifiques de la macrofaune répondent mieux aux paramètres du sol et de la végétation que leur abondance. Nous en avons conclu qu'une relation positive existent entre la complexité et la production de la végétation et la complexité des peuplement des invertébrés en termes de richesse et diversité spécifiques.

Les résultats les plus originaux de l'étude présentée dans cette thèse portent sur 2 aspects (i) sur une base scientifique, nous présentons de façon compréhensible l'évidence que la structure des peuplements des ingénieurs du sol est influencée par les paramètres de la communauté des végétaux, qui seraient eux-mêmes déterminés par les systèmes de pratiques

agricoles et le niveau de fertilité du sol; (ii) sur une base pratique, nous suggérons que dans le cadre de l'évaluation de l'utilisation du sol, l'impact de la perturbation de la forêt sur les peuplements de la macrofaune du sol peut être déterminé sans qu'on ait à faire des prélèvements détaillés des données du sol et de la végétation.

Nous concluons que les connaissances acquises sur le statut actuel des peuplements de vers de terre, de termites et de fourmis et les effets qu'induisent sur eux les changements de type d'utilisation du sol dans la zone forestière du Sud Cameroun constituent une base d'informations nécessaires pour la conception et la mise en œuvre de mesures de leur conservation, processus dans lequel le paysan devrait jouer un rôle capital.

Curriculum Vitae

Birang à Madong was born on 23 January 1959 in Bafia, Cameroon. After 7 years of primary school respectively at 'Ecole Presbyterienne' de Djoungolo and 'Ecole Catholique' de Nkol-Eton in Yaoundé, he went to College François-Xavier Vogt in Yaoundé and Lycée de Mbalmayo for high school. He obtained the high school diploma BAC-C in Mathematics and Physics in 1979. The same year, he passed the competitive examination to enter the Institute of Agricultural Technology of the then University Centre of Dschang (University of Dschang) and obtained a bachelor in agriculture (Agricultural Techniques Engineer degree) in July 1982. The same year, he was hired by the Ministry of Agriculture and served as chief sub-divisional agricultural extension officer in Yoko until August 1983, then was appointed as chief divisional agricultural section officer for the Nyong-et-So'o at Mbalmayo. He then was transferred to the Institute of Agricultural Research (IRA) on his demand in September 1984 and joined the Station IRA of Dschang where he served in the Crop protection research section as research assistant from January 1985 to January1989. Upon return from a 8-months long specialization training course in Cereal Production at IFOA, Reggio-Emilia, in Italy in September 1989, he joined the National Cereal Research and Extension Project funded by USAID as Rice Agronomist. He served in this capacity until December 1991. In January 1992, he was admitted to the Graduate School of the University of Arkansas at Fayetteville (USA) under a USAID fellowship to pursue a Master of Science degree programme and was hired as a research assistant at the Soil Fertility Laboratory in the Agronomy Department. He earned his Master of Science in Soil fertility and Plant nutrition in May 1994 and returned to Cameroon. He was posted at IRA Nkolbisson in Yaoundé to do research on legume agronomy and in addition he was a member of the multi-disciplinary research team of the World Bank-funded National Agricultural and Extension Programme to serve as liaison unit between research and extension until August1998 when he was admitted to the PhD Sandwich Fellowship of Wageningen University within the department of Soil Quality. Mr. Birang also holds a Certificate on Legume Research and Production from IITA-Cotonou, Benin, obtained in 1986, a Certificate on Integrated Pest Management (IPM) from IRRI, Los-Banõs, The Philippines, obtained in 1987 and a Certificate on Plant Genetic Resource Utilization and Conservation from IPGRI, Cotonou, Benin, obtained in 1997. He is married to Marie-Louise Meyengue and has 6 children. He can be reached at: mbirang@cgiar.org or Birangmadong@hotmail.com