The impact of forest management on saproxylic beetles and other arthropods in a semi-deciduous forest in Southern Benin

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Biodiversity threats in tropical forests

At the World Summit on Sustainable Development held in Johannesburg in 2002, the international community committed itself to protect and restore the integrity of our planet's ecological systems. Reaffirming the goals and objectives already laid down in the Rio Declaration on Environment and Development and the Agenda 21, including the Convention on Biological Diversity, the community considered measures to reduce the rate of biodiversity loss at national and global levels as a high priority. However, despite the actions foreseen in the Rio Declaration in 1992 and reaffirmed in the Johannesburg Declaration, poverty kept deepening and environmental degradation worsening over the last decade. Human populations in tropical countries are growing at a rate of 2–3% annually. Hence, the pressure on tropical forests due to an increasing demand for cropland, timber, fuelwood and other forest resources is unbroken (Ravindranath and Hall 1996). Furthermore, weak government institutions and poor policies, increasing trade liberalization, and industrial logging are considered as key drivers of forest destruction in many tropical countries (Laurance 1999).

The destruction, fragmentation and degradation of forests are major threats to the protection of biodiversity in tropical regions (Myers 1984). Tropical forests are the most ancient, diverse and ecologically complex terrestrial ecosystems (Myers 1984). While occupying only 7% of the land surface, they probably sustain over half of the planet's life forms (Wilson 1988). Thus, the loss of biodiversity resulting from tropical forest destruction signifies an ecological crisis of global importance (Wilson 1988).

To counter these adverse consequences, it is necessary to develop new strategies for the sustainable management and use of tropical forests, which in turn requires the strengthening of research into functional and structural characteristics of tropical biodiversity.

State of African forests

With ≈ 650 million ha of forest (21.8% of the land area), Africa accounts for one sixth of the global forest cover (FAO 2003a). The Congo basin is home to the second largest contiguous block of tropical rain forest in the world (FAO 2003b). Unfortunately, these forests disappear at alarming rates. Between 1990 to 2000, the annual net change in forest cover was -0.8%. This rate is based on losses or gains in the cover of both natural and plantation forests. At the continental level, the rate is the highest in the world, and about twice as high as the second highest rate in South America (-0.4%).

Considering forest plantations, Africa accounts for only 4.4% of the global area. For every hectare reforested, the area deforested reaches 41 hectares. In view of this, there is growing consensus about the need to reduce deforestation, to use forests sustainably, and to establish forest plantations in order to meet the increasing demand for woody biomass (Ravindranath and Hall 1996). Commercial plantation forests are designed to produce maximum yields of timber or fuelwood. This seems to preclude any environmental benefit in terms of biodiversity conservation. However, recent analyses have shown that forest plantations can be managed to harbour an important proportion of the former biodiversity without compromising economic benefits (Lamb 1998). Different measures have been proposed to this end, including the creation of plantation species mosaics, embedding monocultures in a matrix of intact or restored vegetation, using indigenous species rather than exotic species, or preserving micro-habitats such as dead wood that are known to be particularly species-rich.

Forest (FAO 2001)

Land with a canopy cover (or equivalent stocking level) of more than 10 percent and an area of more than 0.5 hectares. The trees should be able to reach a minimum height of 5 meters at maturity *in situ.*

Forest plantations (FAO 2001)

Forest stands established by planting or/and seeding in the process of afforestation or reforestation. They are composed of introduced species (planted stands), or intensively managed stands of indigenous species, meeting all of the following criteria: one or two species at planting, even age class, regular spacing.

Afforestation is defined as the establishment of forest on land that was not forested within living memory or the past 10 years, and reforestation as the establishment of forest on land that had been forested in the recent past.

Despite the potential of tropical forest plantations for biodiversity conservation, only few studies have been completed to date (e.g., Davis et al. 2001; Lawton et al. 1998; Watt et al. 1997). These studies have shown that plantations are not necessarily biodiversity deserts (Speight and Wylie 2001) but that they can support a rich and varied fauna. The importance of tropical forest plantations for the conservation of wildlife and as nuclei for natural forest regeneration has been demonstrated in

Madagascar (Goodman et al. 1996), Sri Lanka (Ashton et al. 1993), Thailand (Elliott et al. 1998) and Australia (Tucker and Murphy 1997).

Nevertheless, assuming that the current scenario persists, the predictions for the next two decades are very pessimistic (FAO 2003 b). The scenario assumes that deforestation will continue more or less at current rates, forest plantations expand only in few countries, and that fuelwood remains the main source of energy. As a consequence, the loss of biodiversity is expected to continue. With only 10% of the original forest remaining and at an annual decline in forest cover of -1.26%, west African forests are particularly vulnerable to human disturbance. In view of this and considering the exceptional concentration of endemic species, West African forests have been designated as biodiversity hotspots (Myers et al. 2000).

The Lama forest reserve in Southern Benin — one of the last remnants of natural forest in the Dahomey Gap (Sinsin et al. 2003) — appears to be an exception to the regional deforestation trend and might serve as a model for future conservation programs. Since 1988, a central part (*Noyau central*) covering 4,800 ha lies under strict protection, and the population living therein has been resettled. The forest is composed of a small-scale mosaic of remnants of natural or degraded semi-deciduous forest of variable size and successional stage (Specht 2002). It is surrounded by teak (*Tectona grandis*) and fuelwood (mainly *Senna siamea* and *Acacia auriculiformis*) plantations, covering 7,000 ha and 2,400 ha, respectively. These plantations provide timber and fuelwood for the local, national as well as international market.

Arthropods in biodiversity studies

Forget about pandas, elephants and tigers. If we want to understand how to sustain biodiversity, then we should be concerned about arthropods. Whether measured by species, individuals or biomass, arthropods dominate terrestrial ecosystems (Kremen et al. 1993). They have been referred to as the little things that run the world (Wilson 1988) because they occupy the widest possible diversity of ecosystems and microhabitats, and because they play many key ecological roles (Collins and Thomas 1991). Studies on the impact of forest disturbance on arthropods, particularly on tropical insects, have increased substantially over the last decades (e.g. Eggleton et al. 2002; Grove 2000, 2001, 2002; Holloway et al. 1992; Nummelin and Hanski 1989; Vasconcelos et al. 2000). These studies have been inspired by concerns about the rapid modifications of tropical habitats and by findings that invertebrates are highly sensitive to such modifications (Basset 1998). This vulnerability makes them potential early warning indicators of environmental change (Kremen et al. 1993). Furthermore, they are often more representative of overall biodiversity than plant and vertebrate surveys (Oliver et al. 1998). Finally, they are often more amenable to statistical analyses than vertebrates (Basset 1998).

Even though, African forest arthropods have been very little studied, and studies of arthropods associated with dead wood (saproxylics) are basically absent. In Lama forest, with the exception of preliminary insect inventories (Boppré 1994; Emrich et al. 1999; Fermon et al. 2001; Tchibozo 1995), arthropod assemblages were not studied at all, let alone their distribution in different types and successional stages of forest in the reserve.

Dead wood and saproxylic invertebrates

Over the last decades, dead wood has become an important research focus in the Northern hemisphere. Dead wood provides habitat for a sizable proportion ─ perhaps the majority ─ of forest organisms, from fungi through invertebrates to vertebrates (Elton 1966; Speight 1989; Grove 2001). Furthermore, it is a main store of nutrients. These are gradually released through decomposition, thereby improving soil fertility (Laiho and Prescott 1999). While dead wood has been recognised as an ecologically important component of temperate and boreal forests, there has been little consideration of its role in tropical forests, nor of the effects that management might have on it (Harmon 2002). In African developing countries, where 91% of the wood is used as fuelwood (FAO 2003b), dead wood is not a waste. Rather, it is systematically collected as fuelwood. Consequently, where firewood is scarce, the amount of dead wood in natural forests or plantations is low, especially the amount of pieces of larger size or advanced stage of decay.

Saproxylic invertebrates (Speight 1989)

Species that are dependent, during some part of their life-cycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics.

Saproxylic invertebrates, in particular saproxylic beetles ─ one in five species known on Earth is a beetle ─ contribute greatly to biodiversity. Moreover, they play an important role in wood decomposition, influencing the nutrient supply of plants and thus primary production (Didham et al. 1996). By boring and tunnelling the wood, they create important infection courts for wood-rotting fungi and provide access into the wood to other wood-boring and -dwelling insects which in turn induce and accelerate the decomposition process (McIntosh et al. 2001). They can be regarded as ecosystem engineers, i.e., organisms that cause physical changes in their environment and modulate the availability of resources to other species (Jones et al. 1997). The diversity of saproxylic fauna depends on the availability and diversity of dead wood habitats (Grove 2002), which in turn are governed mainly by forest management. At a time when more and more forests are logged and cleared worldwide, studies of dead wood and the associated fauna can reveal a great deal about the ecological impact of forest destruction and degradation, and provide baseline data for dead wood management, the so-called morticulture (Harmon 2002).

Objectives

The overall goal of this thesis is to enhance the scientific understanding of the Lama forest arthropod fauna, with particular emphasis on saproxylic beetles, as a basis for an improved, conservation-oriented forest management. Specifically, we aim (i) to elucidate the role of different forest habitats (natural, degraded and plantation forests) for biodiversity conservation and (ii) to recommend management measures for the conservation of arthropod diversity.

In Chapter I, we focus on arthropods that are involved in the decomposition of litter and dead wood, comparing the diversity and composition of arthropod assemblages in nine different forest types, including natural, degraded and plantation forest as well as forest patches outside of the reserve. Based on arthropod data and measured habitat attributes, we evaluate the value of forest plantations for biodiversity conservation, and identify indicator taxa for specific forest habitats.

Chapter II reports on a study of dead wood colonizer beetles. We investigated, in two baiting experiments in the field, the primary attraction of native and exotic, freshly cut wood to these beetles. For these experiments, we used a newly designed dead wood bait trap, the so-called twin-Malaise trap. Apart from providing evidence of primary attraction and host tree selection of West African colonizer beetles, we also give an account of ecological traits of one potential pest species of logs.

Chapter III summarises results from a dead wood inventory and a saproxylic beetle diversity assessment. This is the first study of the relationship between dead wood and saproxylic beetle assemblages in a tropical African forest. The influence of forest management on dead wood quantity and quality, and on saproxylic beetle species richness, was assessed in natural as well as plantation forests. The study examines dead wood habitat attributes such as the type (tree species) or stage of decay of dead wood that determine the diversity and composition of saproxylic beetle assemblages.

In Chapter IV, we followed up on our previous findings and evaluate the importance of standing dead trees (snags) for the conservation of saproxylic beetle assemblages. We compare assemblages from native snag tree species in remnants of natural forest and in degraded forest with those from exotic snag tree species in monospecific plantations.

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CHAPTER 1 – ARTHROPOD DIVERSITY

Arthropod diversity in Lama forest reserve (South Benin), a mosaic of natural, degraded and plantation forests

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Brice Sinsin and Ralf Peveling

Biodiversity and Conservation, in press

Arthropod assemblages were examined in Lama forest reserve, a protected area situated in the Dahomey gap, southern Benin, composed of plantations, degraded forest and remnants of natural forest. The objectives were to compare assemblages in relation to forest type and use, to elucidate the value of forest plantations for biodiversity conservation and to identify indicator species for specific forest habitats. Arthropods were collected over an 11-month period, using standardized sets of traps (pitfall, emergence, Malaise and flight intercept traps). Nine different habitats were studied, including natural and degraded forest, forest plantations (*Tectona grandis* and *Senna siamea*) of different age, and isolated forest fragments. Our analysis focused on detritivorous and xylophagous arthropods but also included ground beetles and heteropterans, totalling 393 species. We found no differences in species richness among natural and degraded forest habitats in the centre of the reserve (*Noyau central*). Outside of the *Noyau central*, species richness was highest in old teak plantations and isolated forest fragments and lowest in young teak and fuelwood plantations. Detrended correspondence analysis (DCA) separated three main groups: (1) natural forest, (2) degraded forest and young plantations, and (3) old plantations and isolated forest fragments. Multiple regression of DCA scores of the first two axes on environmental variables identified one natural and three disturbance-related predictors of arthropod assemblages in Lama forest: soil type (texture), canopy height, naturalness (proportion of Guineo-Congolian plant species) and understorey vegetation cover. We identified 15 indicator species for six different forest habitats. The highest numbers were found in abandoned settlements and old teak plantations. Beta-diversity was similar among the three DCA ordination groups (degraded forest excluded). Values for β-diversity were relatively high, suggesting that all major forest habitats contribute significantly to regional species pools und should therefore be protected. To enhance arthropod diversity, we propose that management practices in Lama forest should aim to encourage the development of species-rich understorey vegetation of the Guineo-Congolian phytogeographical region.

Key words: Arthropod assemblages, Biodiversity conservation, Dahomey gap, Degraded forest, Forest plantations, Indicator species, Natural forest

Introduction

West African forests are listed among the 25 hotspots considered as priority areas for biodiversity conservation (Myers et al. 2000). At the same time, there is consensus that secondary forests are becoming increasingly important for biodiversity conservation (Gemerden et al. 2003; Zapfack et al. 2002), and that the contribution of forest plantations to the conservation of tropical forests must be evaluated.

Forest plantations are extending world-wide. Since 1990, the area planted has quadrupled. In Africa, plantations account for only 1.2% of the total forest cover (FAO 2000), but the proportion in Benin is relatively high (4.2%). Forest plantations provide a range of forest products on a relatively limited land surface, and can therefore contribute to reducing deforestation and degradation of natural forests (FAO 2001). Being a man-made type of forest, plantations are considered to support low biodiversity and hence be of little interest for biodiversity research and conservation. Thus, only few studies on the biodiversity in tropical forest plantations have been completed to date (e.g. Watt et al. 1997; Lawton et al. 1998; Davis et al. 2001). These studies showed that forest plantations are not necessarily “biodiversity deserts” (Speight and Wylie 2001) but that they can support a rich and varied fauna. The importance of tropical forest plantations for the conservation of wildlife and as nuclei for natural forest regeneration has been demonstrated in Madagascar (Goodman et al. 1996), Sri Lanka (Ashton et al. 1993), Thailand (Elliott et al. 1998) and Australia (Tucker and Murphy 1997).

Several authors studied the response of insects (ants, termites, moths, dung and carrion beetles) to the degradation of tropical forests (e.g. Nummelin and Hanski 1989; Holloway et al. 1992; Vasconcelos et al. 2000; Eggleton et al. 2002). These studies showed that the composition and species richness of arthropod assemblages vary depending on disturbance levels, regional species pools and the spatial and temporal scale of the study. However, little information is available on the effects of different forest management regimes on the composition of arthropod assemblages in West Africa.

As one of the last remnants of natural forest within the Dahomey gap (Ballouche et al. 2000), and an important refuge for several endangered plants and animals, Lama forest reserve is of key concern for biodiversity conservation in Benin. Only few studies have been conducted so far, the majority focusing on natural forest. Despite their larger size, degraded forests and forest plantations have received little attention. With the exception of litter-dwelling arthropods (Attignon et al. 2004) and butterflies (Fermon et al. 2001), arthropod assemblages have not been well studied, let alone surveyed in different habitat types and successional stages of forest in the reserve.

The goal of the present study was to enhance the scientific understanding of the Lama forest arthropod fauna as a basis for improved, conservation-oriented forest management. The specific objectives were (1) to compare arthropod diversity and assemblages in the principal forest types of Lama forest, (2) to assess the value of forest plantations for biodiversity conservation and (3) to identify indicator taxa for specific forest habitats.

Materials and Methods

Study site

The Lama forest reserve is situated about 80 km north of Cotonou (6°55.8' to 6°58.8' N and 2°4.2' to 2°10.8' E), covering an area of 16,250 ha in a shallow depression between the Allada and Abomey plateaus. The forest is located in the Dahomey gap, a low rainfall zone separating the western and eastern part of the humid Guineo-Congolian evergreen and semi-evergreen forests of West and West-central Africa (White 1983). The climate is relatively dry (ca. 1200 mm rainfall), with a pronounced dry season from November to March (Sayer et al. 1992). The prevailing soils are hydromorphic vertisols rich in nutrients and clay, as well as sandy ferralsols. The natural vegetation is a semi-deciduous forest, belonging to the drier peripheral semi-evergreen Guineo-Congolian rain forest system (White 1983).

Despite having been legally protected since 1946, deforestation for agriculture in Lama forest continued until 1988, leading to the reduction of natural forest cover from 11000 ha to 1900 ha. Since then, a central part covering 4800 ha, the so-called *Noyau central*, lies under strict protection. Peasants living in the *Noyau central* were resettled in nearby agroforestry schemes. Reflecting the traditional farming system, the *Noyau central* is composed of a small-scale mosaic of natural and degraded forest patches of variable size and successional stages (Specht 2002). The *Noyau central* is surrounded by young and old teak plantations (7000 ha, *Tectona grandis*) and fuelwood plantations (2400 ha, mainly *Senna siamea*, interspersed with *T. grandis*, and a few stands of *Acacia auriculiformis*) (Figure 1). The present study focused on nine different forest types representing all major habitats within the reserve boundaries plus a few forest remnants outside of the reserve. Five forest types were situated within the *Noyau central* and four outside:

1. Semi-deciduous forest (1937 ha) is dominated by tree species such as *Afzelia africana*, *Ceiba pentandra*, *Dialium guineense*, *Diospyros mespiliformis*, *Drypetes floribunda*, *Celtis brownii*, *Mimusops andongensis*. The understorey vegetation can be dense and canopy height reaches 16 to 21 meters (Table 1).

2. *Cynometra megalophylla* lowland forest (< 100 ha) grows in seasonally flooded areas. This forest is characterized by *C. megalophylla* and other plants adapted to

seasonal flooding. The understorey vegetation is usually less dense than in semi-deciduous forest.

3. *Anogeissus leiocarpa* dry forest (1222 ha) is a secondary forest developing on former slash-and-burn patches. *A. leiocarpus* can reach 20 m in height and promotes the establishment of shade-tolerant plants.

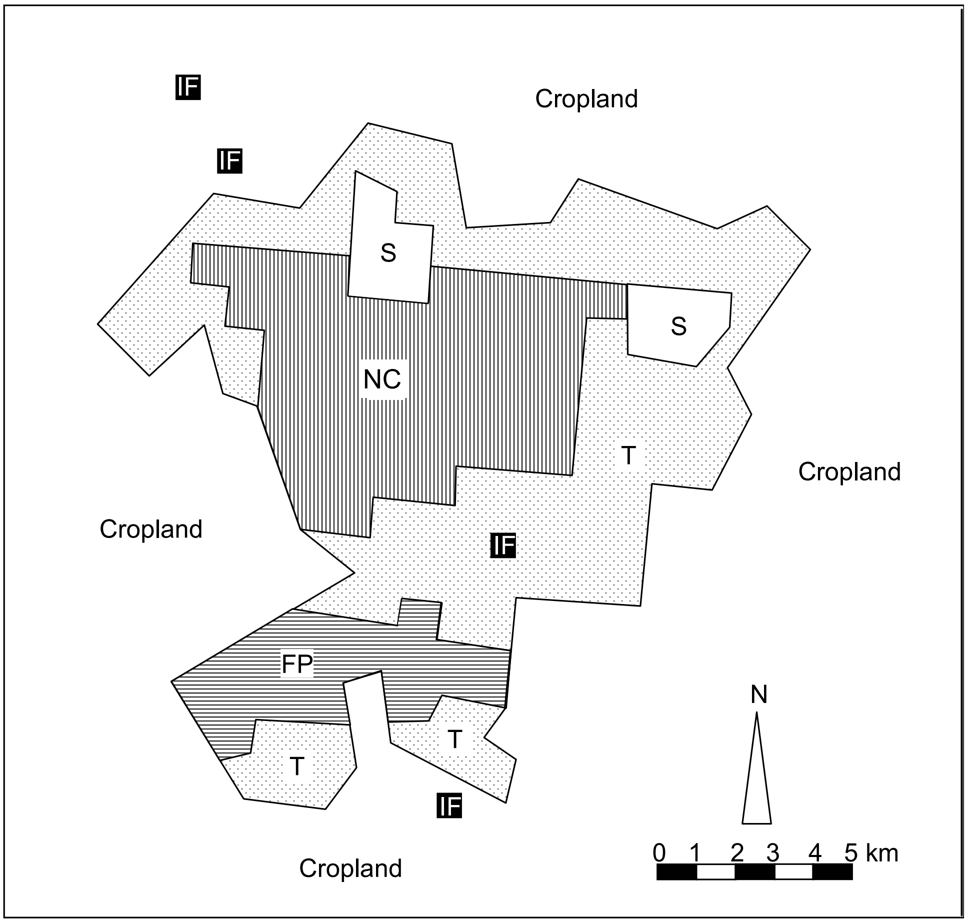

Figure 1. Schematic view of Lama forest reserve. NC, Noyau central; T, Teak plantations; FP, Fuelwood plantations; S, Settlements; IF, Isolated forest fragments (the latter not to scale).

4. Abandoned settlements (166 ha) of the resettled population present a characteristic vegetation type composed of cultivated trees such as oil palm (*Elaeis guineensis*) and guava (*Psidium guajava*), and secondary regrowth.

5. Perennial *Chromolaena odorata* thicket (1452 ha) grows on former farmland. *C. odorata* is an alien, invasive species of neotropical origin encroaching open-canopy forest patches, clearings, as well as fallow land. It is rapidly shaded out if the forest canopy cover exceeds about 40%.

6. Young teak plantations (7200 ha) were planted between 1985 and 1995 on vertisol around the *Noyau central*.

7. Old teak plantations (2200 ha) were planted between 1955 and 1965 on sandy ferralsol (transition between vertisols in the valley and ferralitic soils on the surrounding plateaus).

8. Fuelwood plantations (2400 ha) were planted between 1988 and 1996. They are composed of *S. siamea*, *T. grandis* and *A. auriculiformis*.

9. Most isolated forest fragments are located outside of the reserve. These widely scattered sacred groves are embedded in a matrix of farmland and degraded savannah. They are used as ceremonial places and remain in a relatively natural state. The remnants are usually very small (1–2 ha).

Sampling sites were selected according to three criteria: (1) spatial representativeness, (2) patch size and (3) accessibility. Each forest type was represented by four replicates. Thus, the total number of sites was 36 (Table 1). Distances between sites of the same forest type ranged from 0.3 km to 19.0 km. A minimum distance of 20 m (small patches) or 50 m (large patches) was maintained between sampling sites and patch borders.

A botanical survey was also conducted within the scope of our study, using the Braun-Blanquet system. Two hundred ninety plant species in 77 families were sampled (unpublished data).

Sampling methods

On each site, we installed an equal number of sampling devices, comprising (1) three funnel pitfall traps, each consisting of a collecting jar inside a plastic sleeve, an 11 cm diameter funnel and a transparent plastic roof 20 cm in diameter (Southwood 1978), (2) one Malaise trap (after Townes 1972) with a 1.5 m^2 black vertical mesh panel, (3) one flight intercept trap intercepting insects flying between 1.0 and 1.5 m above the ground, consisting of two crossed black vertical mesh panels, each measuring 0.25 m^2 (0.5×0.5 m), and top and bottom funnels 50 cm in diameter (Wilkening et al. 1981), and (4) one pyramid-shaped emergence trap (ground photo-eclector) covering an area of 0.75 m^2 ($\approx 0.86 \times 0.86$ m), equipped with a collecting jar on the top and one pitfall trap (Mühlenberg 1993). The traps were spaced out along 30 m north-south transects. The placement design was similar at all sites. We used formalin (0.5%) as a preservative, adding some detergent to lower the surface tension. A preliminary two-week sampling was conducted in May 2001 to establish the methodology. The sampling period for the present study was one week per month from June 2001 to April 2002. Specimens were sorted, counted, labelled and stored in alcohol (75%) for later identification.

Table 1. Site characteristics of the forest types studied in Lama forest.

	Classified forest								Sacred grove
	Inside of the *Noyau central*					Outside of the *Noyau Central*			
Forest type:	Semi-deciduous forest	Lowland forest	*A. leiocarpa* dry forest	Abandoned settlements	*C. odorata* thicket	Young teak plantations	Old teak plantations	Fuelwood plantations	Isolated forest fragments
Forest code:	SF1–4	LF1–4	DF1–4	AS1–4	CT1–4	YT1–4	OT1–4	FP1–4	IF1–4
Soil type % clay[m]	Vertisol 75 (45–75)	Vertisol 75	Vertisol 75	Vertisol 75	Vertisol 75	Vertisol 60 (45–75)	S. ferralsol 11 (8–15)	Vertisol[b] 35 (8–75)	S. ferralsol[c] 25 (15–45)
Naturalness (%)[a]	67	67	23	23	23	13	36	20	48
Nearest distance to natural forest (km)[m]	0.0	0.0	0.75 (0.05–0.10)	0.10 (0.05–0.20)	0.08 (0.05–0.20)	0.98 (0.20–2.20)	3.80 (2.50–6.40)	4.90 (4.30–5.70)	3.28 (1.90–7.00)
Temperature (°C)[d] Min–Max	25.9 24.1–28.9	25.0[d] 24.0–26.5	26.9 24.5–30.4	27.0[e] 25.2–29.3	26.5 24.7–29.3	26.8 24.8–30.3	27.4 25.4–30.6	27.2 25.2–28.6	26.6 24.5–29.7
Relative humidity (%)[d] Min–Max	92.2 81.0–99.0	94.3[e] 90.3–98.1	85.2 72.9–94.1	86.2[f] 78.6–95.4	86.2 76.1–93.4	86.8 73.8–95.3	84.5 73.6–91.9	83.5 75.6–91.5	85.6 75.2–93.4
Tree cover (%)[m]	55 (50–67)	69 (65–80)	60 (48–65)	55 (55–77)	12 (3–45)	78 (65–85)	67 (47–72)	63 (55–65)	55 (40–72)
Canopy height (m)[m]	17.5 (16–21)	21.0 (21–23)	17.5 (16–20)	17.0 (15–19)	20.0 (8–25)	18.5 (13–21)	24.0 (22–26)	14.0 (12–20)	24.5 (18–28)
Tree species richness[m]	7 (6–8)	6 (4–11)	7 (6–10)	7 (6–10)	8 (5–14)	2 (2–3)	1 (1–2)	2 (2–5)	9 (8–11)
UV cover (%)[m]	83 (37–92)	68 (55–75)	75 (29–90)	72 (45–80)	81 (17–97)	20 (8–30)	35 (27–75)	66 (45–70)	85 (65–97)
UV height (m)[m]	1.3 (1.0–1.5)	1.5 (1.4–1.5)	1.1 (1.0–1.3)	1.0 (0.9–1.4)	1.2 (0.7–1.3)	1.0 (0.5–1.3)	1.4 (1.3–1.4)	1.3 (1.2–1.4)	1.5 (1.2–1.5)
UV species richness[m]	35 (28–52)	45 (30–47)	42 (29–52)	38 (28–43)	23 (14–40)	42 (21–45)	35 (34–37)	36 (17–40)	49 (41–63)

[a] Dominance of plant species of the Guineo-Congolian phytogeographic type; [b] except FP4 (sandy vertisol); [c] except IF4 (vertisol); [d] measured on only one site per forest type (monthly average); [e] November–March not available; [f] August–November not available; [m] median (range); S. ferralsol = Sandy ferralsol; UV = Understorey vegetation

Sorting scope and identification

Among the wide range of invertebrates sampled, we focused on detritivorous and xylophagous arthropods because of their important role in nutrient cycling in forest ecosystems (Didham et al. 1996). These taxa comprised fourteen coleopteran families, as well as representatives of Isoptera, Diplopoda and Isopoda. We also included epigeal predators (Carabidae and Chilopoda), omnivorous beetles (Tenebrionidae) and both herbivorous and predatory bugs (Heteroptera). These additional taxa were retained for a more comprehensive characterization of arthropod assemblages and because some have been used as representative indicators in previous biodiversity assessments (Duelli and Obrist 1998; Giulio et al. 2001; Rainio and Niemelä 2003).

All arthropods were first sorted to morphospecies (*sensu* New 1998) and then taxonomically identified at the International Institute of Tropical Agriculture (IITA) in Benin. Voucher specimens were deposited at the IITA Biodiversity Center and partly at the Museum of Natural History, Basel, Switzerland. The analysis was done at the morphospecies level for taxa with difficult taxonomy (e.g. most Diplopoda).

Environmental variables

Soils were classified according to the FAO system (FAO-UNESCO 1974), and the percentage of clay (soil texture) was estimated by touch. Temperature (°C) and relative humidity (RH) were recorded every hour from April 2002 to March 2003, using one data logger (Hobo Pro RH/Temp) per forest type. Loggers were attached to tree trunks about one meter above ground level. The naturalness (*sensu* Angermeier 1999) of the different forest types was calculated based on the proportion of plant species belonging to the Guineo-Congolian phytogeographical region. We also determined cover, height and species richness of the main vegetation strata (Table 1). The nearest distance between sampling sites and natural forest patches was measured with a geographic information system (ArcView 3.1), using the vegetation map of Specht (2002) (Table 1).

Measures of diversity

We used species richness as a measure of α-diversity (the number of species within a habitat). Beta-diversity (the degree of change in species composition between habitats) was evaluated for selected groups of forest habitats according to Whittaker's formula $\beta_w = \gamma / \bar{\alpha}$, where γ is the species pool within a group of habitats (γ-diversity) and $\bar{\alpha}$ is the average number of species per site (Whittaker 1960).

Data analysis

We used the total catch per taxon and per sampling site for statistical analyses. This was done by pooling specimens from all sampling periods and traps within sampling sites.

One-way analysis of variance (ANOVA) was conducted to test differences in arthropod assemblages among forest types (Zar 1999), followed by Bonferroni multiple comparison of means. In view of an unfavourable ratio between factor levels ($n = 9$) and replicates ($n = 4$), we also performed a *post hoc* power analysis (SPSS 12.0).

To determine the similarity of forest types based on their arthropod assemblages, we performed detrended correspondence analysis (DCA) (Hill and Gauch 1980), using PC-ORD 4.27 (McCune and Mefford 1999). Abundances of species rarer than $F_{max}/5$ (where F_{max} is the frequency of the most common species) were down-weighted in proportion to their frequency. Axes were rescaled with a threshold of zero, and the number of segments was set to 26 (default). Reciprocal averaging (RA), also known as correspondence analysis, revealed the same grouping, but DCA was preferred because it squashed the arch effect associated with RA and corrected the compression of the axis ends. The proportion of variance represented by the ordination axes was calculated according to an after-the-fact method, using the relative Euclidean distance (McCune and Mefford 1999). Stepwise multiple regression with forward selection (SPSS 12.0) was conducted to relate DCA ordination scores of the first two axes to the environmental variables listed in Table 1.

A hierarchical cluster analysis based on presence/absence data was employed to distinguish groups of sites in the DCA ordination plot (SPSS, 12.0, settings: Ward's method, squared Euclidean distance). Clusters were grouped in probability ellipses whose axes are proportional in length to a specified percentage of the x and y coordinates (Jennrich and Turner 1969). The inclusion probability was set to $P = 0.90$. Computation of the ellipses was done with ArcView 3.1.

We used Mantel tests to evaluate the relationship between arthropod assemblages and the distance to the nearest natural forest patch (Mantel 1967). These tests were performed with PC-ORD 4.27 (McCune and Mefford 1999), using binary data (Sørensen distance) and Monte Carlo randomisation (1000 runs).

Indicator species

Indicator species for the different forest types were determined according to Dufrêne and Legendre (1997). The method combines data on the frequency of occurrence (faithfulness) and relative abundance (concentration) of species in a particular habitat. The significance of indicator values was tested using Monte Carlo randomisation (1000 runs). The threshold level for the indicator value was 25%. This implies that the frequency of occurrence of a species indicative of a particular habitat must be $\geq 50\%$, and its relative abundance therein $\geq 50\%$ of its total abundance at all sites (Dufrêne and Legendre 1997). The significance level was $p \leq 0.01$, as proposed by the authors. The analysis was performed with PC-ORD 4.27 (McCune and Mefford 1999). Note that indicator organisms may include both species restricted to a certain habitat and those more widely distributed yet especially abundant in a particular type of forest.

Estimation of true species richness

True species richness was estimated by computing the abundance-based coverage estimator (ACE) and the incidence-based coverage estimator ICE (1000 runs) for the eleven collecting periods, using EstimateS 6.0 (Colwell 1997). The ACE is based on species with ≤ 10 individuals in the sample (Chao et al. 1993). The corresponding ICE, likewise, is based on species found in ≤ 10 sampling sites (Lee and Chao 1994). These estimations were the most appropriate for our data set which was characterized by a large number of singletons (species occurring with one individual only) and uniques (species occurring in one sample only).

Results

A total of 9431 specimens belonged to the taxonomic groups examined in the present study, representing 393 species (Appendix 1). More than one third of all species were singletons, and only fourteen were collected in all forest types. Seventy one percent (ACE) and 66% (ICE) of the estimated true species number were sampled.

Coleoptera

We collected 264 species in 16 families of Coleoptera, representing 67% of the total number of species and 58% (5499 specimens) of the total number of arthropods included in the analysis. Except for carabids, the high number of specimens was due to a few very abundant species. Of 37 scarabaeid species, six represented over 63% of all specimens. One of 17 species of Elateridae represented 97% of the total catch in this family, and one of 12 species of Scolytidae 58% of the total catch. All but one scarabaeid species of the dominant taxa were found in all forest types. Thirty eight percent of all coleopteran species were singletons. Most coleopterans were collected in isolated forest fragments (111 species, 42% of all coleopterans) and old teak plantations (94 species, 36%), and the smallest number in young teak plantations (64 species, 24%) and fuelwood plantations (59 species, 22%). Forest types within the *Noyau central* had about the same number of coleopteran species, with an average of 81 ± 1 species (mean ± SE).

Heteroptera

Within 15 families of Heteroptera, we found 75 species (19% of the total number of arthropod species analysed) and 558 specimens (6% of the total catch analysed). Forty-one percent of the Reduviidae (22 species) and 54% of the Lygaeidae (17 species) were represented by three species only. One of five species of Alydidae made up 95% of the total catch for this family. More than 41% of all heteropterans were singletons. Species numbers were highest in isolated forest fragments (32 species) and lowest in semi-deciduous forest (13 species). The other forest types within the *Noyau central* presented an average species number of 23 ± 1 (mean ± SE).

Chilopoda, Isopoda, Diplopoda and Isoptera

For the classes Isopoda, Diplopoda and Chilopoda and for the order Isoptera, the analysis was performed at the morphospecies level. Forty eight percent of all Diplopoda (27 species) were represented by only one species occurring in all forest types. Two of 14 species of Isopoda made up 52% of the total catch of this taxon. Only six species of Isoptera were sampled, with one species representing 96% of all specimens.

Arthropod diversity

Despite the unfavourable ratio between factor levels and replicates, the statistical power of the analyses of variance was satisfactory (0.996). Differences in species richness among forest types were significant at $p < 0.001$ ($F_{8,27} = 5.76$). Isolated forest fragments and old teak plantations showed the highest number of species (Figure 2), with an average of 71 ± 5 and 67 ± 2 species, respectively (mean ± SE). Species richness was lowest in young teak (40 ± 6) and fuelwood plantations (43 ± 6). Natural and degraded forest in the *Noyau central* had intermediate levels of species richness, ranging from 50 ± 2 in *C. megalophylla* lowland forest to 57 ± 2 in abandoned settlements. Statistically significant differences were found between young plantations (teak and fuelwood) and old teak plantations or isolated forest fragments (Figure 2).

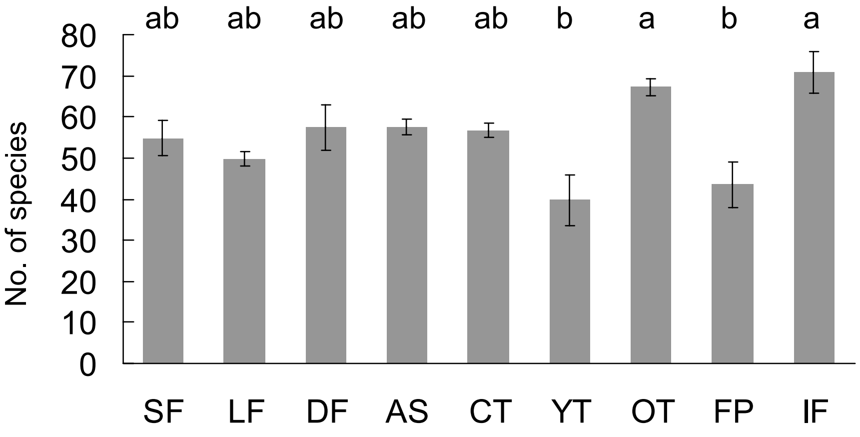

Figure 2. Species richness in nine different forest habitats in Lama forest. Bars show means ± standard error (n = 4). SF, Semi-deciduous forest; LF, C. megalophylla lowland forest; DF, A. leiocarpa dry forest; AS, Abandoned settlements; CT, C. odorata thicket; YT, Young teak plantations; OT, Old teak plantations; FP, Fuelwood plantations; IF, Isolated forest fragments. Means marked with different letters are significantly different at $p < 0.05$.

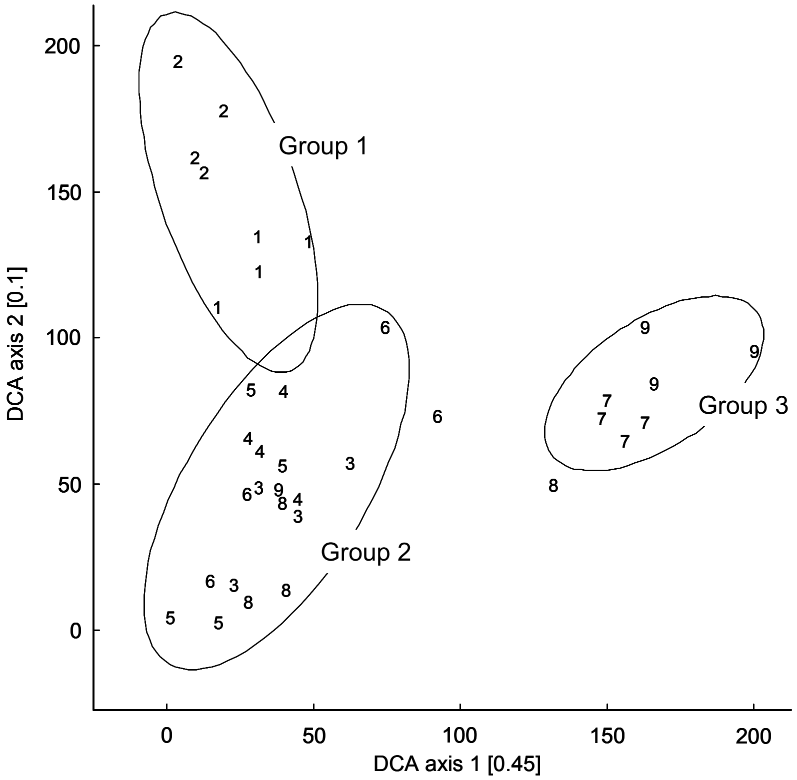

Figure 3. Detrended correspondence analysis (DCA) of sampling sites in species space [proportion of variance]. Groups 1, 2 and 3 are defined by probability ellipses (p = 90%). 1, Semi-deciduous forest; 2, C. megalophylla lowland forest; 3, A. leiocarpa dry forest; 4, Abandoned settlements; 5, C. odorata thicket; 6, Young teak plantations; 7, Old teak plantations; 8, Fuelwood plantations; 9, Isolated forest fragments.

Beta-diversity of arthropod assemblages was computed for the three habitat (site) groups obtained by the DCA ordination (see below). Two of these groups (group one and three, Figure 3) contained two forest types each, including all old-growth forests, and one group (group two) the remaining forest types. Of these, we selected young teak and fuelwood plantations as representatives of young-growth forest. Because some groups comprised only three of the four replicate sites per forest type, we randomly excluded one replicate site of each complete sample to achieve an equal number of sites per group which is a prerequisite for comparing β_w-diversity. Thus, each group contained three replicate sites of two different forest types (n = 6). Beta-diversity was very similar among these three groups of forest habitats, ranging from $\beta_w = 2.8$ in group three (old teak plantations and isolated forest fragments) and $\beta_w = 3.1$ in group two (young teak and fuelwood plantations) to $\beta_w = 3.2$ in group one (semi-deciduous forest and *C. megalophylla* lowland forest).

Arthropod assemblages

DCA of sampling sites in species space revealed three distinct groups of forest habitats: (1) natural forest, comprising semi-deciduous forest and *C. megalophylla* lowland forest, (2) degraded forest and young plantations, including *A. leiocarpa* dry forest, abandoned settlements, *C. odorata* thicket, young teak plantations (all but one site) and fuelwood plantations (all but one site), and (3) old teak plantations and isolated forest fragments (all but one site) (Figure 3).

The proportion of variance represented by the first axis of the DCA ordination was 0.45. Multiple regression identified two significant predictors of DCA axis one scores, soil texture and canopy height ($F_{2,33} = 76.6$, $R^2 = 0.823$, $p < 0.001$). The regression equation is:

$$\text{Axis 1} = 78.3 - 1.6\,(\text{PC}) + 3.8\,(\text{CH}),$$

where PC = Percentage of clay and CH = Canopy height; *t*-values for the partial regression coefficients were –9.0 ($p < 0.001$) and 3.6 ($p = 0.001$), respectively, indicating that soil texture was the major explanatory variable in this model.

The proportion of variance represented by the second axis was 0.10. DCA axis two scores were also best predicted by two variables only, naturalness and understorey cover ($F_{2,33} = 49.7$, $R^2 = 0.751$, $p < 0.001$). For the second axis, the regression equation is:

$$\text{Axis 2} = 26.8 + 2.3\,(\text{PG}) - 0.6\,(\text{PU}),$$

where PG = Percentage of Guineo-Congolian plant species and PU = Percentage of understorey vegetation cover; *t*-values for the partial regression coefficients were 10.0 ($p < 0.001$) and –3.3 ($p = 0.002$), respectively. Thus, naturalness was the more important explanatory variable.

The remaining environmental variables listed in Table 1 had no significant effect on the ordination scores.

Mantel tests revealed that arthropod assemblages of replicate sites within young teak and fuelwood plantations were not correlated with the distance to the nearest natural forest patches ($r_s = 0.436$, $p = 0.260$ and $r_s = 0.533$, $p = 0.169$, respectively).

Indicator species

We identified 15 indicator species for six different forest habitats, ranging from one to five species per forest type (Table 2). No indicators were found for dry forest, *C. odorata* thicket and young teak plantations. The indicators included 11 species of Coleoptera, two species of Isopoda and one species each of Diplopoda and Heteroptera. Most indicator species were recorded for abandoned settlements ($n = 4$) and old teak plantations ($n = 5$).

Table 2. Indicator species sensu Dufrêne and Legendre (1997) for Lama forest.

	Indicator value (%)	*p*
Semi-deciduous forest		
Chlaenius (*Chlaenites* s.l.) sp. (Carabidae, Chlaeniinae)	80.0	0.001
Scolytidae sp. 9	58.7	0.001
C. megalophylla lowland forest		
Stenocoris southwoodi Ahmad, Alydidae	95.8	0.001
Abandoned settlement		
Onthophagus sp. 1, Scarabaeidae	66.7	0.001
Onthophagus sp. 3, Scarabaeidae	54.8	0.003
Sisyphus sp. 1, Scarabaeidae	66.7	0.004
Elateridae sp. 3	31.1	0.007
Old teak plantations		
Hoplolenus obesus (Murray, 1858) (Carabidae, Oodini)	72.2	0.001
Trochalus sp. 1, Scarabaeidae	75.0	0.008
Trochalus sp. 2, Scarabaeidae	72.1	0.002
Tenebrionidae sp. 24	60.9	0.007
Diplopoda sp. 1	31.3	0.002
Fuelwood plantations		
Isopoda, Eubelidae sp. 3	68.9	0.005
Isopoda, Eubelidae sp. 5	61.5	0.001
Isolated forest fragments		
Tetragonoderus (s.str.) *quadrimaculatus* Gory, 1833 (Carabidae, Cyclosomini)	87.5	0.001

No indicator species were found for *A. leiocarpa* dry forest, *C. odorata* thickets and young teak plantations.

Discussion

Arthropod diversity

Against our expectations, α-diversity was similar among the different forest types within the *Noyau central*. We would have expected lower species richness in disturbed habitats such as *C. odorata* thicket. However, not only was species richness similar, but the similarity in species composition was also high, ranging from 38% (*C. odorata* thicket vs. lowland forest) to 58% (*C. odorata* thicket vs. dry forest) species in common (Lachat, unpublished data). This suggests a high connectivity between natural, secondary and degraded parts of the *Noyau central* whose spatial structure is characterized by contiguous patches of variable size, sometimes covering less than one hectare (Specht 2002). Moreover, forest cover was relatively high (≤ 45%) even in degraded patches, which would be expected to facilitate movements between forest habitats. This is corroborated by observations in the Amazon which showed that secondary growth reduces the barrier effect of cleared forest for forest dung and carrion beetles (Klein 1989).

Our results confirm those of other studies that found no major difference in species richness of arthropod assemblages between primary forest and secondary and/or degraded (logged) forest (e.g. Nummelin and Hanski 1989; Holloway et al. 1992; Kalif et al. 2001).

Significant differences in species richness were found only among forest habitats outside of the *Noyau central* (Figure 2). Notably, species richness in old teak plantations was as high as in forest fragments and in the *Noyau central*, which demonstrates the importance of old teak for arthropod diversity conservation. The low species richness in young teak and fuelwood plantations came as no surprise. These forests are more exposed to silvicultural practices. Moreover, despite a fire exclusion strategy adopted by the forestry authorities, agricultural fires sometimes escape into young teak and fuelwood plantations.

Beta-diversity was similar between the three groups obtained by the DCA-ordination (natural forest, young plantations, old plantations and isolated forest fragments). Furthermore, β_w-values were relatively high (2.8–3.2), compared to a theoretical minimum of $\beta_w = 1$ (each species occurs on all sites) and a maximum of $\beta_w = 6$ (each species occurs on one site only) for $n = 6$ sites per group. Beta-diversity — hence species turnover — increases with increasing spatial heterogeneity, resource selectivity and the diversity of refugia available to rare species (Stanton 1979; Deshmukh 1986). From a conservation point of view, high β-diversity implies that the preservation of diversity is most effective if habitats are protected entirely.

The importance of plantations for biodiversity conservation

Several modifications to the design and management of tropical plantations have been proposed that may enhance regional biodiversity without compromising economic benefits (reviewed in Lamb 1998). Among the various approaches, two are pertinent to Lama forest: the establishment of plantations in the vicinity of natural forest — which may act as a reservoir and source of forest species — and the development of understorey vegetation. The second option is only feasible for long-rotation sawlogs such as teak. The growth of understorey vegetation and a concomitant increase in biodiversity is enhanced by the selective harvesting of logs which creates gaps for plant colonization. In Lama forest, this process seems to be supported by the fire exclusion practice. Contrary to timber plantations, understorey development is unlikely in short-rotation forests such as fuelwood plantations (Lamb 1998). Fuelwood in Lama forest is harvested at an age of 20 years or less. These plantations obviously contribute less to biodiversity conservation, as reflected by the low species richness found in our study. Even though, the production of fuelwood itself may reduce the pressure on natural forest resources.

The evidence provided in the present study shows that old teak plantations are important habitats for forest species. This is supported by the presence of typical forest specialists such as *Paussus excavatus*, *P. liber* and *P. bicornis* (Carabidae, Paussinae). Similar observations were made in mature plantations of endemic hardwood in Cameroon where butterfly assemblages were undistinguishable from those found in natural forest (Stork et al. 2003). An elevated arthropod diversity in old plantations may have consequences not only from a biodiversity conservation but also from a pest management perspective. A high degree of naturalness and/or close distance to natural forest may benefit natural enemies of forest pests, thereby reducing the risk of infestations of plantation forests (Speight and Wylie 2001).

The distance between natural forest and sampling sites in young teak plantations varied from 0.2 to 2.2 km, and the distance to sampling sites in fuelwood plantations from 4.3 to 5.7 km. Thus, one might hypothesise that assemblages within plantations differ depending on their distance to the nearest natural forest patch. Yet, a border effect was dismissed on the basis of the Mantel tests performed, suggesting that plantations adjacent to the *Noyau central* may act as dispersal corridors. However, our study design was not conceived to monitor movement pathways between forest patches.

Influence of environmental variables on arthropod assemblages

Arthropod assemblages in the different forest types were most strongly related to soil type (DCA axis 1), a natural site character, and to naturalness of the vegetation (DCA axis 2), an indicator of disturbance. The other two statistically significant explanatory variables were canopy height (DCA axis 1) and understorey cover (DCA axis 2), representing disturbance indicators related to land use and management.

Soil may have influenced arthropod assemblages in two ways. First, the prevailing vertisols show distinct seasonal swelling-shrinking cycles. During the dry season, they harden and form deep cracks. In the rainy season, they are saturated with water, leading to flooding in depressions. This in turn might reduce the habitat available to epigeal species not tolerating temporary flooding, forcing them to retreat to mounds of the so-called gilgai micro relief (irregular land surface with alternating mounds and depressions in areas with vertisol). To the contrary, physical properties of the sandy ferralsols in old teak plantations and isolated forest fragments do not change dramatically between seasons, and the soil may offer suitable habitats throughout the year. Second, soil influences arthropods indirectly by affecting the vegetation. However, ordination of our vegetation data did not clearly segregate plant associations of forests stocking on vertisol and ferralsol (Djego, unpublished data), suggesting that soil type had a more pronounced influence on arthropod assemblages than on plant associations.

The importance of soil as a co-determinant of arthropod assemblages was also evidenced by the sites plotted outside of the corresponding probability ellipses in the

DCA ordination (Figure 3). For example, the soil of one of the fuelwood plantation sites (label 8) was a sandy vertisol. This site plotted next to group three which also comprised sites on ferralsol. Likewise, the only isolated forest fragment (label 9) located on vertisol — and being embedded in a matrix of young teak plantations — was plotted together with group two sites, all of which shared the same soil.

The remaining environmental predictors of arthropod assemblages in Lama forest (naturalness, canopy height, understorey vegetation cover) are related to land use and silvicultural practices. Naturalness is an indicator of human disturbance (clearing for agriculture, conversion to plantation forests and other land uses). Highly disturbed parts of Lama forest have a higher proportion of plant species with wide (sometimes pantropical) distribution, while Guineo-Congolian species dominate in less disturbed parts. Naturalness increases not only from degraded to natural forest, but also from young to old plantations. Unfortunately, little is known about the biogeography of the arthropod species sampled, which makes it difficult to define geographic types and to draw parallels with phytogeographic types.

Canopy height reflects a succession towards old-growth forest. The tallest canopy trees were found in old teak plantations and isolated forest fragments (c.f., Table 1). The similarity in vegetation structure may have contributed to the high similarity of arthropod assemblages among these forests.

The development of understorey vegetation is a characteristic of old-growth stands (Lamb 1998). However, understorey cover in Lama forest was highly variable within and among the different forest types (Table 1) and should therefore be interpreted with caution. For example, disturbed, open-canopy forests were often dominated by uniform *C. odorata* thicket, whereas a diversity of native, shade-tolerant plants prevailed in closed-canopy forests (Djego, unpublished data). Thus, understorey cover alone appears to be an insufficient predictor of arthropod assemblages, but together with naturalness it defines environmental conditions relevant to their composition.

Edge effects in old teak plantations and isolated forest fragments

In contrast to other studies (Didham et al. 1998; Barbosa and Marquet 2001), the highest species richness was encountered in isolated forest fragments and old teak. Moreover, the similarity of arthropod assemblages was high, despite long distances among replicate sites (16–19 km).

Another common trait of these forest types — apart from soil type and naturalness — is their adjacency to open country (degraded savannah and/or cropland). Forest edges are likely to attract arthropods from open landscape as well as forest, thereby increasing overall species richness (Laurance et al. 2002). Some forest species may even increase in abundance near edges, in particular those adapted to the microclimate prevailing in open forest or treefall gaps (Kapos 1989; Laurance et al.

2002). Such edge effects ─ along with the combined effect of the four environmental explanatory variables ─ may explain the high diversity and distinctiveness of arthropod assemblages in old teak plantations and isolated forest fragments.

Indicator species

Indicator species have been defined as taxa that "mirror changes in a wider array of groups as a consequence of environmental change" or that "reflect overall diversity and complexity of an assemblage" (New 1998). The idea to focus on indicator species is also owed to limitations in processing and identifying the huge numbers of samples typically collected during invertebrate surveys. The four most important criteria for choosing invertebrate indicators are that they have a well known taxonomy and ecology, are accessible to sampling and respond to environmental changes (New 1998). Strictly speaking, none of the species identified in the present study fulfils all of these criteria. At this initial stage of research, they are therefore simply considered as species characteristic of certain forest habitats. Their role as indicators of successional changes requires validation in future monitoring programmes.

Notably, the highest numbers of indicators were found in abandoned settlements and old teak plantations. This can be interpreted as an indication of the importance of these two forest types to regional biodiversity.

Taxonomically, most species belong to the family Scarabaeidae (chafers, Melolonthinae, and dung beetles, Scarabaeinae). Dung beetles have often been used as indicators because of their reliance on vertebrate dung or carrion and their sensitivity to habitat disturbance (Klein 1989; Nummelin and Hanski 1989; Hill 1995). Carabidae are also well represented. While being common indicators in temperate ecosystems, their suitability for tropical forests is as yet not well established (Rainio and Niemelä 2003).

Conclusions

This study provides a first overview of the arthropod diversity in Lama forest reserve, one of the last and largest vestiges of natural forest in southern Benin, and highlights its importance for biodiversity conservation. No differences in arthropod species richness were found among habitats within the *Noyau central*, a small-scale mosaic of natural and degraded forest. However, great differences were observed among forest plantations separating the *Noyau central* from the matrix of agricultural land. We identified four environmental variables as significant predictors of arthropod assemblages. Of these, soil type is a natural factor promoting high species richness in old plantations and isolated forest fragments. The remaining variables naturalness, understorey cover and canopy height are related to silvicultural practices and are therefore amenable to an improved, conservation-oriented forest management. To enhance arthropod diversity in Lama forest, we propose that management practices should aim to encourage the development of species-rich understorey vegetation of the Guineo-Congolian phytogeographical region. Animals higher up the food chain, in particular insectivorous reptiles, birds and mammals, may also benefit from increased arthropod diversity. In this respect, arthropod conservation is not an end in itself but a contribution to overall biodiversity conservation.

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Primary attraction of beetles to native and exotic tree species in natural and plantation forests in Lama forest reserve, Benin

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Manuscript

Wood-associated beetles have evolved specialised foraging techniques to rapidly locate and colonize suitable host substrate. Many species rely on olfactory stimuli such as volatiles released by dead or injured wood. We studied the primary attraction of beetles to freshly cut wood in natural forest and teak plantations of the Lama forest reserve in Benin, West Africa, using a newly designed bait trap (twin-Malaise trap). Traps were baited for four weeks with the native tree species *Dialium guineense* or *Antiaris africana* and with the exotic plantation species *Tectona grandis*, or they were left unbaited. We found six beetle species showing primary attraction (species whose relative abundance was higher in baited than in unbaited traps), and two species showing primary repulsion (species whose relative abundance was higher in unbaited than in baited traps). Three species preferred native wood over teak, but none teak over native wood. Different beetles showed different temporal patterns in relative abundance, reflecting different sensitivities to injured or recently dead wood volatiles. Moreover, primary attraction differed depending on whether the bait wood was offered in natural forest or teak plantations, indicating an effect of forest type on colonisation patterns. Among the beetles attracted to teak logs, we found no pest species of economic importance.

Key words: Saproxylic beetles, Native and exotic trees, Natural forest, Plantations, Primary attraction, Twin-Malaise trap, Wood decomposition

Introduction

The decomposition of dead wood is a slow process, starting immediately after a tree or part of it has died. The causes for the death of trees are manifold, including natural mortality and natural or anthropogenic disturbances such as windstorm, fire, diseases, or logging and forest clearing activities. Wood-boring beetles are pioneers of wood decay. By boring and tunnelling the wood, they create important infection courts for wood-rotting fungi and provide access into the wood to other wood-boring and -dwelling insects (McIntosh et al. 2001). In a companion study conducted in the Lama forest reserve in Benin, we found an extraordinary diversity of dead wood-associated (saproxylic) beetle assemblages on dead wood of all decay stages (Chapter 3). However, little is known about the first colonizers of dead wood in Lama forest or in other tropical forests. Understanding processes and biological clues governing the colonisation of dead wood by beetles is not only of scientific interest but also of importance in tropical forestry.

Recently dead or severely stressed trees release higher amounts of volatile chemicals than live and healthy ones, and these volatiles may act as kairomones attracting wood-boring beetles (Byers 1996). Unless responding to pheromones emitted by conspecifics that have already colonized a dead wood resource, beetles follow two different strategies to find and select their substrate, primary attraction or random attack. Species following the primary attraction strategy select dead wood *prior* to landing. This selection behaviour is initiated by olfactory and visual stimuli (Byers 1996) and requires the ability to detect suitable dead wood in flight (Tunset et al. 1993). For species following the random attack strategy, dead wood encounters are by chance, and only after landing – and possibly feeding – the resource is accepted or rejected as a host substrate (Brattli et al. 1998; Tunset et al. 1993).

De Groot and Nott (2001) suggested that many saproxylic beetles rely mainly on visual cues such as dark silhouettes for host finding. In contrast, Barata and Araújo (2001) found that cerambycid beetles do not respond to visual stimuli unless associated with olfactory stimuli (dead wood volatiles).

In the present study, we investigated the attraction of native and exotic, freshly cut wood for colonizer beetles (pioneers). Our aims were to test primary attraction and host tree selection of beetles in two different forest types (natural and plantation forests) within the Lama forest reserve, and to determine ecological traits of potential pest species.

Material and methods

Study site

The study was conducted about 80 km north of Cotonou in the Lama forest reserve (6°55.8’ to 6°58.8’ N and 2°4.2’ to 2°10.8’ E), an area covering 16,250 ha in a large, shallow depression between the plateaus of Allada and Abomey. The natural vegetation is a semi-deciduous Guineo-Congolian forest (White 1983). The mean annual rainfall is about 1,200 mm. The dominant soil types are hydromorphic vertisols in the centre and sandy ferralsols towards the plateaus.

The fully protected core of the reserve, the so-called *Noyau central* (4777 ha), is composed of a small-scale mosaic of natural and degraded forest (Specht 2002). It is surrounded by teak (*Tectona grandis*) plantations (9000 ha). Plantations bordering on the *Noyau central* have been planted between 1985 and 1995 and those located at the periphery of the reserve between 1955 and 1965.

Sampling

We designed a new type of Malaise bait trap (twin-Malaise trap) to collect beetles attracted to freshly cut wood (Figure 1). The trap consisted of two Malaise traps (after Townes 1972) – hence the term twin-Malaise trap. The two traps were put up alongside each other and stitched together along the bordering edges of the front, back and roof mesh panels. The left half of the one trap and the right half of the other enclosed a compartment (about 1.0 m^3) that was stocked with about 0.2 m^3 of bait wood. The lower edges of the mesh panels were covered with soil. Thus, the compartment was inaccessible to beetles or other insects entering the trap via the open flanks. Insects

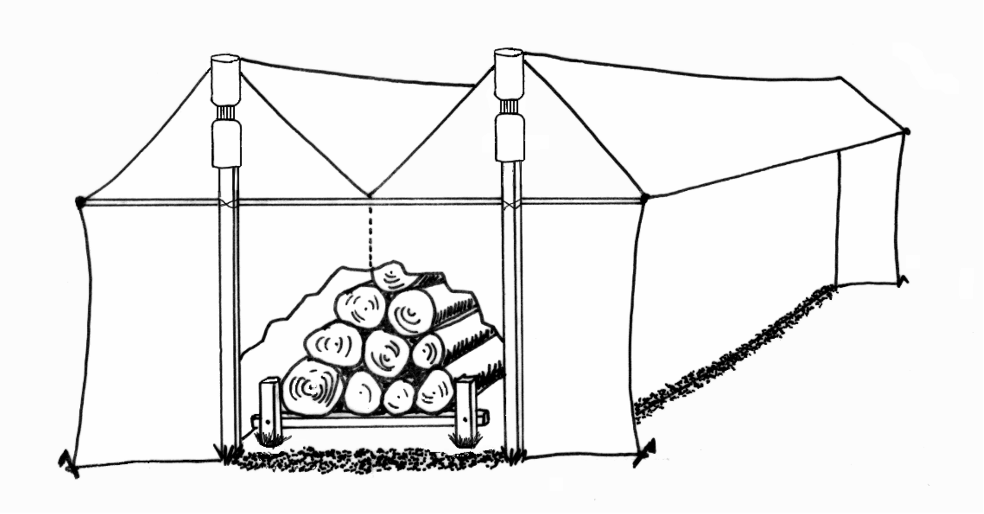

Figure 1. Twin-Malaise trap and bait wood.

were collected in two 0.25 L vials at the top of each of the two front gables, using a 0.5% formaldehyde preservative with a few drops of liquid detergent to lower the surface tension. During the experiments, the vials were emptied weekly.

Bait wood

The bait wood was cut from healthy trees outside of Lama forest reserve a few hours before installing the traps. The logs were one meter long and had a diameter between 5 cm and 25 cm. The logs were piled up on a support rack (10 cm above the ground) in the bait wood compartment of the twin-Malaise trap. We used bait wood from one plantation (exotic) and two native tree species. The exotic species was *Tectona grandis* (Verbenaceae), a species introduced from tropical Asia and widely cultivated in West Africa. In Lama forest, it is the dominant plantation tree. The indigenous species included *Dialium guineense* (Caesalpiniaceae) and *Antiaris africana* (Moraceae). *D. guineense* is the most common and widespread tree in West-African semi-deciduous forest. The tree is to 20 m high, but may also grow as a shrub (Keay 1989). Densities in Lama forest have been estimated at 205 stems ha^{-1} (≥ 10 cm diameter at breast height) (Emrich et al. 1999). *Antiaris africana* (Moraceae) is a tree of lowland rainforest and outlier forest in the savannah regions to 40 m high. In Lama forest, it is a common yet widely scattered tree. Along with *Afzelia africana* and kapok (*Ceiba pentandra*), *Antiaris africana* is one of the tallest trees in the reserve (Paradis and Houngnon 1977).

Experimental design

We selected four sites each in tracts of natural forest in the *Noyau central* and in old-growth teak plantations. At each site, two baited traps and one unbaited control trap were installed in random order along an axis oriented North-South. A minimum distance of 10 m between traps was maintained to reduce neighbour effects. Two independent four-week experiments were conducted, hereafter referred to as experiment I and II, respectively.

Experiment I

Experiment I was carried out from 9 April to 7 May 2003. At each site, one trap was baited with freshly cut logs from *T. grandis*, a second one with logs from *D. guineense*, and a third one was left unbaited.

Experiment II

The same sites and traps were used in the second experiment which lasted from 14 May to 11 June 2003. The traps were re-baited in a similar fashion as in the first experiment, using logs from *T. grandis* and *A. africana*. Treatments were allocated to traps at random.

Observations on xylophagous beetles

For xylophagous beetles showing primary attraction and being considered as potential pests of logs (species with wood-boring larvae), individuals were sexed by examining the genitalia. We also counted the presence of developed eggs in order to assess sexual maturity. Body size and antennal length were measured with a micrometer.

Data analysis

The two experiments were analysed separately. Only those beetles were included whose relative abundance over the entire four-week sampling period was ≥ 10 specimens (all weeks pooled). Catch data were first $\log_{10}(x+1)$-transformed and then subjected to one-way analysis of variance (ANOVA, SPSS 12.0), using species as dependent variable and bait wood (*T. grandis* and *D. guineense* or *A. africana*) and forest type (natural *versus* plantations forests) as fixed factors. Sampling sites were considered as random factor nested in forest type. We used Bonferroni multi comparison of means as *post hoc* test, using an experimentwise error rate of $P \leq 0.05$.

To analyse the change in relative abundance over time, we compared the number of beetles showing host wood attraction during the first (first two weeks pooled) and the second (last two weeks pooled) half of the experiments, using Wilcoxon signed rank test (SPSS 12.0).

Morphological measurements (body size and antennal length) of potential pest species were compared with an independent sample *t*-test.

Results

In the first experiment, we sampled 3354 beetle specimens in 185 species. Corresponding values in the second experiment were 1819 specimens in 147 species. Table 1 summarises species richness and relative abundance of families with ≥ 5 species per family.

Experiment I

Thirty-one beetle species had ≥ 10 specimens and were included in the analyses. Of these, only two species showed significant preferences for particular types of bait wood and forest. Curculionidae sp. 1 was more abundant in teak plantations than in natural forest, and preferred teak logs over unbaited controls (Table 2). Moreover, there was a significant interaction between bait wood and forest type. Conversely, Dermestidae sp. was more abundant in natural forest and preferred *D. guineense* logs over both controls and teak logs. We found non interaction between the main factors. Surprisingly, one species (Mordellidae sp.) was found to be significantly more abundant in control traps than in traps baited with teak, indicating a repellent effect of teak logs. *D. guineense* baits were also avoided, but this effect was not significant. Mordellidae sp. showed no forest preference.

Table 1. Beetles collected in the twin-Malaise traps (experiment I and II).

	Experiment I		Experiment II	
	Individuals	Species number	Individuals	Species number
Anthribidae	20	17	16	11
Buprestidae	13	5	15	6
Carabidae	18	8	7	6
Cerambycidae	48	18	102	17
Chrysomelidae	329	25	562	18
Curculionidae	90	23	45	14
Elateridae	541	18	199	9
Erotylidae	1015	15	112	12
Mordellidae	326	13	169	10
Scaphidiidae	15	6	49	6
Scarabaeidae	693	18	399	19
others families	246	19	144	19
Total	3354	185	1819	147

Experiment II

Thirty-five beetle species (≥ 10 specimens) were included in the analyses. Four species showed a significant preference for one type of bait wood, and one species was more abundant in the unbaited control (Table 2). Cerambycidae sp., Curculionidae sp. 2 and Scaphidiidae sp. preferred logs of *A. africana* over teak logs and unbaited controls. Similar to the first experiment, only a curculionid was more abundant in teak plantations than in natural forest, and only for this species was a significant interaction between bait wood and forest type found. All remaining species were either more abundant in natural forest or equally abundant in both forest types. One species, Erotylidae sp., was more abundant in control than in both baited traps, but differences were only significant among control and *A. africana*. Finally, Lycidae sp., while being more abundant in natural than in plantation forest, preferred teak logs over *A. africana* logs and unbaited controls, but only the latter effect was significant.

Table 2. Attracted beetle species to freshly cut wood in Lama forest (experiment I and II).

	Attraction (F-value, df = 2)	Bait wood selection Percent of individuals by tree species			Forest type (F-value, df = 1)	Forest preference	Bait wood*forest type (F-Value, df = 2)
Experiment I		***T. grandis***	***D. guineense***	**Control**			
Curculionidae sp. 1 (29 ind.)	7.8**	72 a	28 ab	0 b	7.9*	Teak plantations	5.0*
Dermestidae sp. (10 ind.)	7.8**	10 b	80 a	10 b	11.3*	Natural forest	3.2
Mordellidae sp. (35 ind.)	5.0*	4 b	27 ab	69 a	1.0	None	0.8
Experiment II		***T. grandis***	***A. africana***	**Control**			
Cerambycidae sp. (62 ind.)	21.6**	2 b	98 a	0 b	0.6	None	0.3
Curculionidae sp. 2 (11 ind.)	4.4*	20 ab	80 a	0 b	6.7*	Teak plantation	4.4*
Erotylidae sp. (18 ind.)	5.6*	17 ab	22 b	61 a	1.9	None	0.4
Lycidae sp. (46 ind.)	5.2*	67 a	30 ab	3 b	15.0**	Natural forest	2.9
Scaphidiidae sp. (25 ind.)	5.3*	8 b	84 a	8 b	9.8*	Natural forest	1.7

*significant at $P = 0.05$, **significant at $P = 0.01$. Percent with different letters are significantly different at $P < 0.05$.

Temporal patterns

Beetles with significant preferences for particular types of bait wood and/or forest showed different temporal patterns in relative abundance (Figure 2). Curculionidae sp. 1 attracted to teak were caught mainly during the first sampling week. In contrast, species such as Dermestidae sp. (*D. guineense*) and Curculionidae sp. 2 (*A. africana*) showed no distinct temporal patterns. The relative abundance of Cerambycidae sp. was highest in traps baited with *A. africana* during the entire experiment, but there was a gradual decrease over time. Species such as Lycidae sp. (teak and *A. africana*) and Scaphidiidae sp. (*A. africana*) showed the opposite pattern, their abundance gradually increasing towards the end of the experiments. However, differences in the relative abundance of Lycidae sp. attracted to teak among the first and the second sampling period were not significant (see Figure 2).

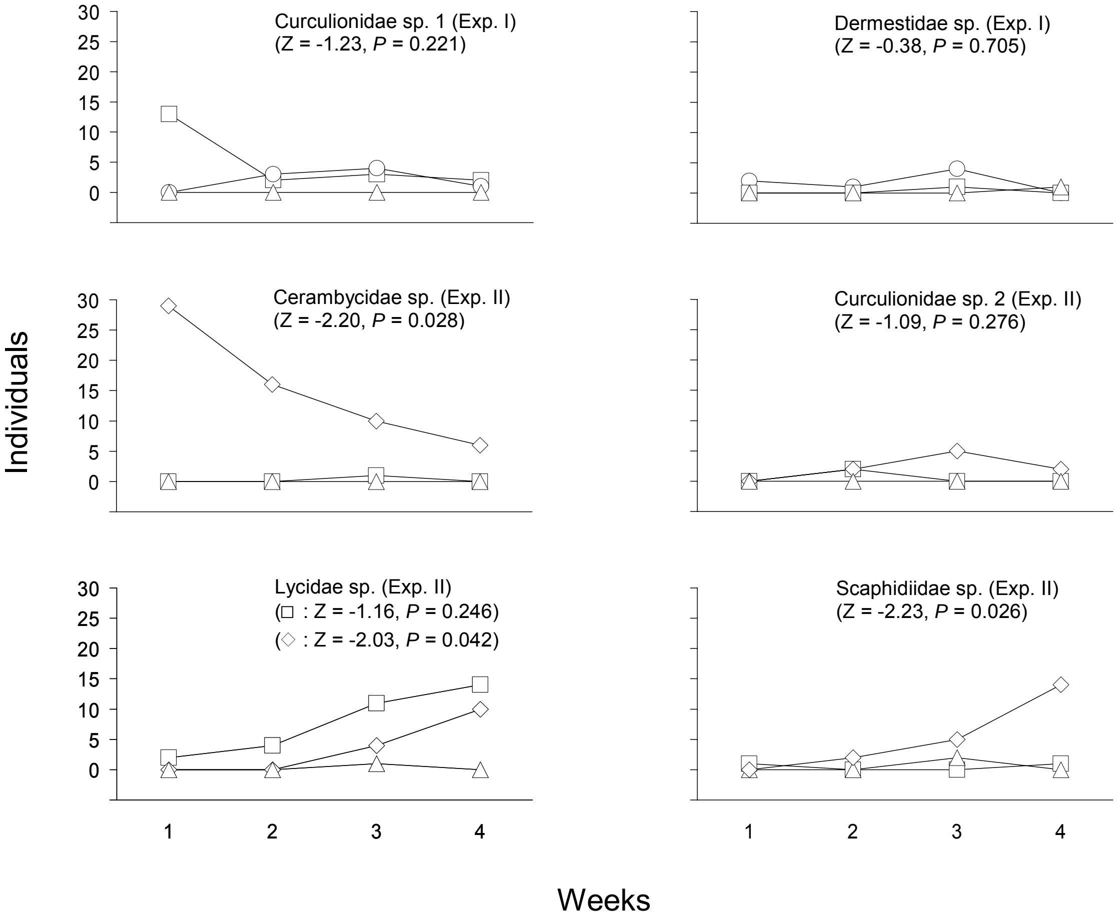

Figure 2. Total catch over time of beetles showing primary attraction in experiment I (Exp. I) and II (Exp. II) (forest types pooled); square = *T. grandis*; circle = *D. guineense*; diamond = *A. africana*; triangle = unbaited control.

Graciella pulchella

The most abundant species collected was *Graciella pulchella pulchella* Klug (Cerambycidae, Lamiinae, see annex 1 for other determinations). Ninety eight percent of all individuals (n = 62) of *G. pulchella* were found in traps baited with *A. africana*. The sex-ratio was 1.16 (male/female). Body length and antennal length were not significantly different between sexes (Table 3). Nevertheless, females seemed to be larger than males because most (93%) carried well developed eggs.

Table 3. *G. pulchella*: body size and antennae length (mm) of males and females.

	Male	Female	T-value (df = 20)	*P*-value
Body size (mm)*	7.0 ± 0.17	6.9 ± 0.10	0.53	0.601
Antennae length (mm)*	16.1 ± 3.60	16.0 ± 2.74	0.23	0.819

*Mean ± Standard Error

Discussion

Primary attraction

The random attack hypothesis does not apply for species showing primary attraction and host wood selection (Brattli et al. 1998 and Table 2). In our study, six of eight species were significantly more abundant in traps baited with freshly cut wood than in unbaited traps. Furthermore, three of them discriminated significantly between different types of bait wood (Dermestidae sp., *G. pulchella* and Scaphidiidae sp.). All of these species preferred logs of native trees over teak logs and can be considered as native wood specialists. Moreover, two species were more abundant in traps baited with teak than in traps baited with native logs, but these differences were not significant. Thus, neither species can be considered as teak specialist. Nevertheless, both preferred baited over unbaited traps – as indicated by the absence (Curculionidae sp. 1) or very low number (Lycidae sp.) of specimens in control traps, providing clear evidence of primary attraction to freshly cut wood.

Two species were significantly more abundant in unbaited than in baited traps (Mordellidae sp. and Erotylidae sp.), indicating a repellent effect of dead wood odours. This negative attraction or *primary repulsion* (beetles avoiding a wood resource prior to landing) is difficult to interpret. Both families are associated with decaying wood or fruiting bodies of dead wood-decomposing fungi (Scholtz and Holm 1996). Therefore, these species are more likely to colonize dead wood at a more advanced stage of decay. However, the ecological benefit of avoiding logs is a matter of speculation. Predator avoidance or reducing competition with other saproxylic insects might explain this behaviour, but we have no data to test this assumption.

Temporal abundance patterns

Species attracted to bait wood showed different temporal patterns in relative abundance, reflecting variable attractiveness of dead wood over time. The cerambycid *G. pulchella* was most abundant at the beginning. This species was obviously attracted by primary volatiles immediately released from freshly cut wood (i.e., components of the sap). Fast reacting, early colonizer such as *G. pulchella* may have an advantage over slower ones, especially if they rely on subcortical tissues of stressed or dying trees, an ephemeral, limited and unpredictable resource heavily competed for by intra- and interspecific competitors (Allison et al. 2001; Hanks 1999).

Species whose relative abundance increased towards the end of the four-week experiments (Lycidae sp. and Scaphidiidae sp.) may have responded to secondary volatiles such as ethanol which are formed during the decay. Ethanol is an important attractant for a wide range of wood-associated beetles. Release rates are low in live trees but high in stressed plants and decaying woody tissue (Brattli et al. 1998). Thus, the release of ethanol from recently dead wood increases as the decay progresses, thereby also increasing the attraction of colonizer beetles sensitive to this agent (Joseph et al. 2001; Jonsell et al. 2003). During wet periods, the vascular tissue of dead wood fills with water, impeding the gas exchange and leading to an accumulation of ethanol in the tissue (Kelsey and Joseph 1999). These ethanol stores are released in pulses when the wood dries up, attracting beetles and other wood-associated insects.

Very little is known about the biology of Lycidae, especially those from tropical forests. There is some evidence that lycid larvae consume sap from freshly cut surfaces (Bocak, personal communication) or from decomposing wood (Pototskaya 1981).

Imagoes of Scaphidiidae feed on fungal spores and hyphae (Scholtz and Holm 1996). Even though no fruiting bodies were visible at the end of the four-week experiments, cryptic mycelia may have developed already and attracted scaphidiids. On dead or injured wood, fungi can develop very fast. For example, in a study of fungal communities of beech, superficial brown mottling of wood cuts was already visible after three weeks (Coates and Rayner 1985). However, in the present study we could not distinguish fungal mottling and wood oxidation.

The duration of our experiments was only four weeks. Morewood et al. (2002) warned that firm conclusions about primary attraction cannot be drawn if the experiments are conducted only during part of the wood beetle flying season. Furthermore, responses to olfactory stimuli varies greatly even within species, depending on the physiological state at different times of the year. To detect such seasonal fluctuations, it would therefore be necessary to conduct experiments lasting for one year.

Habitat preference and host-finding

The composition and relative abundance of arthropod assemblages in Lama forest reserve differs greatly among natural forest and teak plantations (Lachat et al., in press, see Chapter 1). In view of these differences, we also expected different habitat preferences of species showing primary attraction to recently dead wood, and hence different host-finding ability. On the other hand, it is known that some wood-associated beetles are able to disperse over very long distances (Nilssen 1984), suggesting that locating and colonizing the dead wood resource may be more important than living in a particular forest habitat.

The beetles examined in the present study can be loosely divided into three groups, reflecting different habitat preferences and host-finding abilities.

1. The first group is represented only by *G. pulchella*. This species showed no forest preference but a strong preference for *A. africana* wood, irrespective of whether the logs were located in natural forest or in teak plantations. Foraging techniques that combine high host-finding ability with strong flight capacity are typical for species specialised on resources that are sparsely distributed (Jonsell and Nordlander 1995).

2. The second group comprises species preferring wood characteristic of their preferred habitat. Dermestidae sp. and Scaphidiidae sp. were more abundant in natural forest dominated by *D. guineense* than in teak plantations, and consequently preferred *D. guineense* logs. These beetle species seem to have poor dispersal capacities because they were unable to locate and colonize suitable wood outside of their preferred habitat.

3. The third group (Curculionidae sp. 2 and Lycidae sp.) includes species preferring wood that was untypical of their preferred habitat (teak in natural forest and native wood in plantations). This shows that the attractiveness of certain dead wood varies depending on the habitat. This in turn may be related to differences in the resource base (dead wood quantity and quality) and in the dead wood fauna, leading to different colonisation patterns and competition regimes.

For the two Curculionidae species (spp.1 and 2) we found an interaction between dead wood and forest type, indicating dissimilar preferences for dead wood across forest types. However, it is difficult to interpret this observation in an ecologically meaningful way.

Catchability of twin-Malaise traps

We used a newly designed bait trap to capture wood-associated beetles. These new traps have several advantages. First, large volumes (≈ 0.2 m^3) of bait wood can be used. Higher volumes release higher amounts of volatiles and may attract colonizer beetles over larger distances. Second, insects lured into the trap by olfactory cues have no direct contact with the bait, reducing a confounding effect of secondary attraction (Tunset et al. 1993). Third, once installed, twin-Malaise traps require very little maintenance. Fourth, ordinary Malaise traps are common and widely used devices and can be easily transformed into twin-Malaise traps.

However, no trap collects the whole species spectrum (New 1998), and this is also true for twin-Malaise traps. For example, very few Scolytidae and Platypodidae were sampled, even though these families are known to be colonizers of freshly cut wood (Beaver and Löyttyniemi 1991; Byers 1996). They may have been excluded for different reasons. First, Malaise and related traps sample only insects moving upwards. Species with different escape behaviour do not reach the collecting vial at the top. Other traps are more efficient to catch these taxa (see Flechtmann and Gaspareto 1997; Tunset et al. 1988). Second, according to Wood (1982) and Brattli et al. (1998), host wood selection by many Scolytidae requires probing of the outer bark into the phloem tissue or reception of host volatiles at close range. In the twin-Malaise traps, the distance between bait wood and mesh may have been too long (> 10 cm). Other authors suggest that host tree volatiles are not important at all in the host finding and selection of many bark beetles (Byers 1996).

Ecological traits of Graciella pulchella

G. pulchella was attracted nearly exclusively to *A. africana* (61 of 62 individuals). Of all the species showing primary attraction in our study, *G. pulchella* was certainly the most selective. In the following we provide an overview of the ecology and behaviour of this interesting species, based on our observations and existing literature.

This longhorn beetle bores into the phloem and oviposits on bark (Wagner et al. 1991). It is considered a typical stressed host species (Hanks 1999). A common trait of stressed host species is that they oviposit mainly on freshly fallen trees or cut logs. A single generation of stressed host species develops in the host wood which gradually becomes infested with other species preferring dead wood in a more advanced stage of decay.

In contrast to ambrosia and bark beetles, most cerambycids respond to contact or short-range pheromones to mate (Ginzel et al. 2003; Ginzel and Hanks 2003; Reagel et al. 2002). Thus, beetles are first attracted by dead wood volatiles. Once landed on the wood, short-range pheromones govern short distance mate-finding. This may explain the balanced sex ratio between males and females collected in our study. Most species copulate immediately after the first antennal contact and mate recognition. The presence of eggs in 93% of the females can be explained in two ways. First, most members of the Lamiinae subfamily emerge with their eggs fully developed (Hanks, personal communication). Alternatively, mating may already have taken place before arriving at the trap. Depending on stressed hosts, *G. pulchella* mates and oviposits in a short period. However, a long time may lay between adult emergence and oviposition because this requires locating rare and widely dispersed stressed hosts.

From an economic point of view, damages caused by stressed host cerambycids are negligible, because larvae feed exclusively within the subcortical tissue and enter the sapwood only to pupate (Hanks 1999). More observations are certainly needed to draw a more complete picture of the larval development of cerambycid beetles.

Conclusions

The present study found different beetle species showing primary attraction (six species) or repulsion (two species). Three of them were native wood specialists, but none were teak specialists. Among the beetles showing primary attraction, we found no economically important pest species.

The twin-Malaise trap proved to be a suitable device to examine the primary attraction of beetles, even though the entire spectrum of wood-associated beetles was not sampled. Baiting experiments conducted over longer periods of time would be useful to validate and follow up on our findings, and to monitor potential pests on logs.

Because plantation systems plays an increasing role in tropical forestry (Speight and Wylie 2001), the mechanism of primary attraction and host tree selection in natural and plantation forest ecosystems should receive more attention. Direct observations of ecological traits as well as chemical analyses of plant odours may improve our understanding of both host stimuli and beetle responsiveness. This knowledge is of great interest for both the conservation and management of tropical forest resources (Brattli et al. 1998).

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Annex

Annex 1. Identification of beetle species showing primary attraction and repulsion in Lama forest.

Experiment	Identification
Experiment I	
Curculionidae sp. 1	Camptorhinus sp. (Cryptorhynchinae, Cryptorhynchini, Tylodina)
Dermestidae sp.	*Orphinus* sp. or *Thaumaglossa* sp. (♀!) (Megatominae, Megatomini)
Mordellidae sp.	?
Experiment II	
Cerambycidae sp.	*Graciella pulchella pulchella* Klug (Lamiinae, Tragocephalini).
Curculionidae sp. 2	Entiminae, Trachyphloeini
Erotylidae sp.	?
Lycidae sp.	*Xylobanus* sp. (Lycinae, Metriorrhynchyni)
Scaphidiidae sp.	*Antongilium* sp. (Scaphidiinae, Scaphisomatini, Baeoceridiina)

CHAPTER 3 – DEAD WOOD AND SAPROXYLIC BEETLES

Dead wood and saproxylic beetle assemblages in a semi-deciduous forest in Southern Benin

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Saproxylic (dead wood associated) beetles play an important role in all forest ecosystems and are known to be highly susceptible to forest management and fragmentation. Contrary to temperate forests, there has been very little research on saproxylic beetle assemblages in tropical forests. In Africa, large tracts of natural forest have been converted to tree plantations and cropland, and these land use changes are expected to have a dramatic effect on saproxylic beetle assemblages. In the Lama forest reserve in Southern Benin, we conducted an inventory of dead wood and the associated saproxylic beetle fauna, focusing on three different forest types, natural semi-deciduous forest, teak plantations and fuelwood plantations. The dead wood recorded included all coarse woody debris, standing dead trees (snags) and dead branches or stems on live trees (limbs). Saproxylic beetles were reared from dead wood of different decay stages and tree species, using emergence traps. Both the quantity and quality of dead wood resources differed greatly among natural forest and plantations. Average volumes were about thirty, four and one cubic meter per hectare in natural forest, teak and fuelwood plantations, respectively. Dead wood of advanced decay was basically absent in plantations, due to wood collecting activities of the local population. The overall species richness of saproxylic beetles was higher in natural forest, and detrended correspondence analysis clearly segregated dead wood beetle assemblages from natural forest and plantations. Multiple regression found four significant predictors of the first two ordination axes, the volume of (a) recently dead wood, (b) large pieces of dead wood and (c) coarse woody debris (axis one), or to the volume of (a) recently dead wood and (b) snags (axis two). Despite the overall paucity of dead wood, in particular the lack of strongly decayed wood, saproxylic beetle diversity in teak and fuelwood plantations was surprisingly high, providing evidence of the importance of dead wood for biodiversity conservation. Different management measures are proposed to increase the amount of dead wood in plantations so as to protect and enhance the diversity of the saproxylic fauna.

Key words: Dead wood, Emergence traps, Forest management, Plantations, Saproxylic beetles, Tropical forest

Introduction

Saproxylic insects comprise “species that are dependant, during some part of their life cycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics” (Speight, 1989). Over the last decades, saproxylic insects have been subject of intensive research in Europe and Australia. Results emerging from these studies show that dead wood insect assemblages are exceptionally rich in species diversity. For example, an estimated 21% of all beetles living in the canopy of subtropical rainforests in Australia are xylophagous (Hammond et al., 1996). In Central Europe, 56% of all forest beetles were found to be associated with dead wood (Köhler, 2000). However, the fraction of species living on dead or decaying wood seems to be larger in temperate and boreal forests than in tropical and temperate forests (Hanski and Hammond, 1995).

The diversity of saproxylic fauna depends on the availability and diversity of dead wood habitats, which in turn are governed mainly by the physicochemical quality and stage of decomposition of dead wood (Grove, 2002a). Moreover, dead wood is an important medium-term store of carbon (Mackensen et al., 2003), and as it decays nutrients are gradually returned to the soil, thereby restoring soil fertility (Laiho and Prescott, 1999). Thus, dead wood represents a valuable resource in all forest ecosystems, and its removal may lead to a depletion of soil nutrients and an impoverishment in biodiversity.

Saproxylic invertebrate assemblages are highly susceptible to forest management and fragmentation, over time scales ranging from decades to millennia (Kaila et al., 1997; Martikainen et al., 2000; Grove, 2000, 2001, 2002b). In the tropics, dead wood habitats are threatened mainly by the conversion of forests to cropland or intensively managed tree plantations, and by the fragmentation of pristine forests. Even selective logging may endanger the fauna associated with overmature trees and the dead wood they generate because mature trees are felled before they die naturally. In view of the manifold risks to saproxylic fauna and the ecological functions they mediate, it is important to study their diversity and ecology, and to devise dead wood management measures for their protection (Okland et al., 1996).

Despite the important role of saproxylic fauna in all forest ecosystems (Elton, 1966), only few studies have been conducted in tropical forests, most of them in Australia (Grove, 2000, 2001, 2002a, 2002b, 2002c). To our knowledge, the research reported here is the first to examine the diversity of saproxylic insects and their interaction with dead wood in African tropical forests. The objectives of our study were (i) to quantify and qualify dead wood habitats in different forest types of the Lama forest reserve in Benin, West Africa, (ii) to compare saproxylic beetle assemblages in relation to different forest management regimes (natural and plantation forests), (iii) to identify dead wood habitat attributes determining the diversity and composition of beetle assemblages and (iv) to evaluate preferences of saproxylic beetles for particular species or decay stages of dead wood.

Material and Methods

Study area

The Lama forest reserve is situated in southern Benin in a shallow depression between the Allada and Abomey plateaus (6°55.8’ to 6°58.8’ N and 2°4.2’ to 2°10.8’ E). The reserve covers an area of 16,250 ha and comprises remnants of semi-deciduous forest as well as timber and fuelwood plantations. The mean annual rainfall is about 1,200 mm. The dominant soil types are hydromorphic vertisols in the centre and sandy ferralsols towards the plateaus.

Despite having been protected since 1946, human encroachment and deforestation in the reserve continued until 1988 when only 1,900 ha of natural forest were left. Since then, a central part (*Noyau central*) covering 4,800 ha lies under strict protection, and the population living therein has been resettled. The *Noyau central* is composed of a small-scale mosaic of natural and degraded forest patches of variable size and successional stage (Specht, 2002). It is surrounded by teak (*Tectona grandis*) and fuelwood (predominantly *Senna siamea*) plantations, covering 7,000 ha and 2,400 ha, respectively.

Three different forest types were studied, each covering about 2,000 ha and representing different management systems:

1. Semi-deciduous natural forest is composed of trees such as *Afzelia africana*, *Ceiba pentandra*, *Dialium guineense*, *Diospyros mespiliformis*, *Drypetes floribunda*, *Celtis brownii* and *Mimusops andongensis*. The understorey vegetation can be very dense throughout all seasons, and canopy height is about 20 m, with some emergent trees reaching 30 meters. The average basal area on the study plots was 28.2 m^2 ha^{-1}, and the stand density of stems with ≥ 5 cm diameter at breast height (DBH) 904 stems ha^{-1} (Fig. 1a). The remnants of natural forest within the *Noyau central* are unmanaged. However, various management measures are being practiced on adjacent patches of degraded forest to assist the restoration of natural forest, including enrichment plantings with native trees and annual weeding.

2. Old-growth teak plantations were planted between 1955 and 1965. Canopy height is about 25 meters. The understorey vegetation cover may reach 75% during the rainy season. The average basal area on the study plots was 20.8 m^2 ha^{-1}, and the stand density 203 stems ha^{-1} (≥ 5 cm DBH) (Fig. 1b). Mature teak plantations are selectively logged for the local production of floor tiles.

3. Fuelwood plantations were planted between 1988 and 1996. These forests are up to 20 m high and have an understorey vegetation cover of up to 70% during the rainy season. The average basal area on the study plots was 11.8 m^2 ha^{-1}, and the stand density 304 stems ha^{-1} (≥ 5 cm DBH) (Fig. 1c). The rotation period of fuelwood plantations is about 20 years. Contrary to natural forest and teak plantations, these forests are sometimes affected by anthropogenic fires.

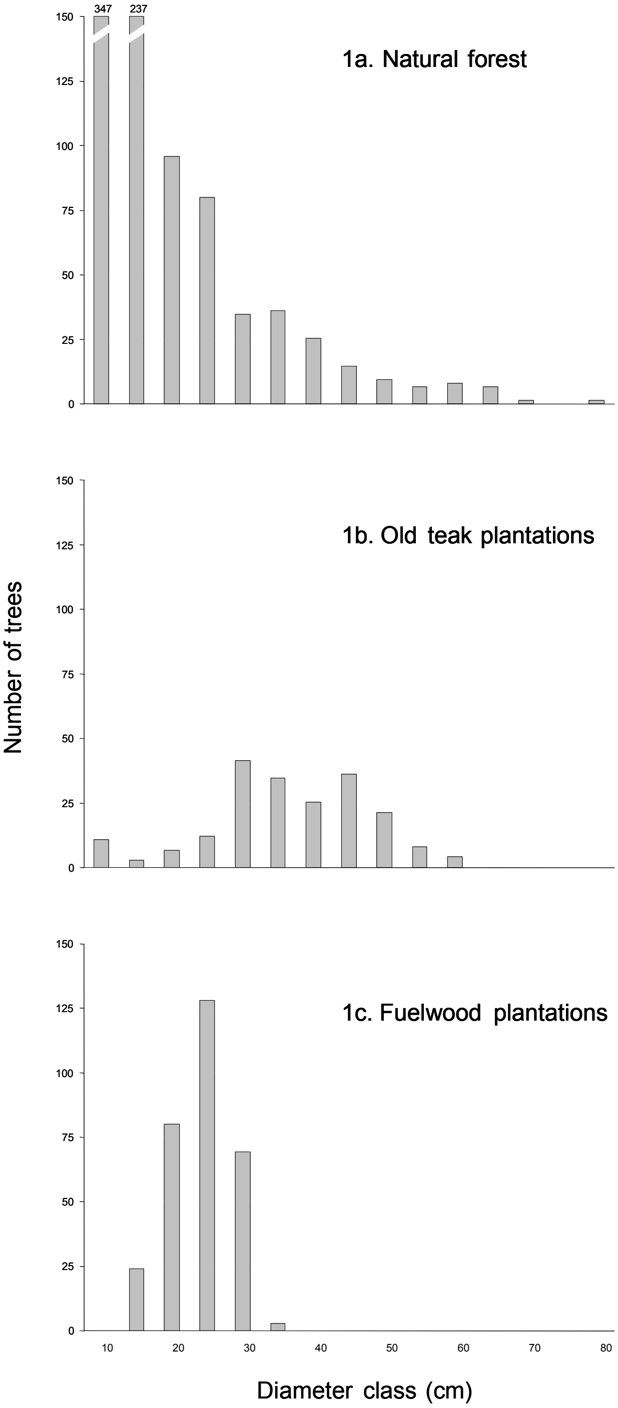

Fig. 1. Distribution of stem diameter classes in natural forest (1a), teak (1b) and fuelwood plantations (1c). Values are means of three replicate plots.

Assessment of dead wood

The amount of dead wood was assessed on three replicate 1 ha plots in natural forest and on three replicate 0.25 ha plots in the more uniform teak and fuelwood plantations. All plots were divided into grids of 16 (natural forest) or four (plantations) contiguous cells (subplots) measuring 625 m^2 (25 m × 25 m). These subplots were systematically searched for dead wood. The assessment was conducted before collecting dead wood for the rearing of saproxylic insects (see below).

Within each subplot, we recorded the size of all coarse woody debris (CWD) on the ground, snags (standing dead trees) as well as dead branches or stems (limbs) on live trees. Length and circumference (at both ends and the middle) of items down to a minimum circumference of 15 cm were measured with a tape. Of the pieces lying partially outside a grid cell, we included only the portion lying within the respective cell. Length and circumference of inaccessible items or parts of dead wood (e.g. snags and limbs) were visually estimated. Each item was classified according to its stage of decay, using a four-scale classification key (Table 1). We further distinguished small (stem diameter < 30 cm) and large (stem diameter ≥ 30 cm) items of dead wood.

Table 1. The classification adopted for determining decay stage of dead wood in the Lama forest reserve (after Bretz-Guby and Dobbertin, 1996; Irmler et al. 1996)

Stage	Characters
I	Wood recently dead, bark and all wood sound, current year twigs still attached, no insect holes
II	Wood still sound, bark loose from sapwood or absent, insect holes, twigs absent
III	Wood soft, not sound, numerous insect holes
IV	Wood soft and rotten, partly integrated to the forest soil (humus)

Volume calculation

Homologising the shape of dead wood items with truncated cones, we used Newton’s formula to calculate individual volumes of each dead wood item:

$$V = L \times (A_b + 4 \times A_m + A_t) / 6$$

where V = Volume, L = length, and A_b, A_m, A_t = area at the base, middle and top, respectively (Harmon and Sexton, 1996). Individual volumes of all dead wood items were summed for each plot, yielding the total dead wood volume. In natural forest, this value corresponded to the total volume per hectare (V ha^{-1}). Volumes for plantation plots were multiplied by four to yield the same unit.

Emergence traps

Samples of dead wood were transferred into sealed emergence traps fabricated from solid black tissue. Sealing the entire trap was important to assure that only saproxylic insects reared from dead wood were collected. The traps were equipped with translucent collecting vials. These provided the sole source of light in order to attract newly emerged, positively phototactic insects. Assuming that traps were inaccessible to other insects, all specimens collected were considered as saproxylic (New, 1998). This assumption was necessary because many species were only identifiable on the morphospecies level, and because the ecology of most species was basically unknown. However, full exclusion of non-saproxylic species throughout the 15-month rearing period could not be achieved. This was evident from sporadic occurrences of clearly non-saproxylic taxa such as Chrysomelidae. These specimens were therefore discounted. Collecting vials were filled with formaldehyde solution (5%). They were emptied every three weeks from the 25 December 2002 to 31 March 2004 (22 sampling dates). Within the scope of this study, we used two kinds of emergence traps:

Pyramidal emergence traps

Pyramidal emergence traps (PETs) had a space volume of about 0.2 m^3 (86 × 86 cm wide, 70 cm high) and were stocked with 0.08 m^3 of dead wood on the average. The lateral faces were covered with fine black mesh reinforced with black cotton tissue on the outside. Dead wood pieces were first cut into pieces up to 70 cm long and then heaped up on fine plastic mesh (ground mesh) to exclude epigeal and hypogeal arthropods. Subsequently, the pyramids were placed over the dead wood heaps. Their base covered the ground mesh and was buried in the soil to a depth of about 5 cm to seal the interior space. The top was equipped with a translucent collecting vial (Mühlenberg, 1993).

Cylindrical emergence traps

Cylindrical emergence traps (CETs) were based on the same principle as PETs but were easier to fabricate and to install. They consisted of fine black mesh bags (150 cm circumference, 120 cm long) with a space volume of about 0.18 m^3 when closed. One end was connected to a translucent collecting vial attached to a pole about 60 cm above the ground. At the opposite end, the bag was tightly closed with a cord after having been stocked with dead wood (average dead wood volume: 0.04 m^3). The whole trap (except the collecting vial) was covered with black cotton tissue.

Rearing experiments

Representative samples of dead wood items (> 5 cm diameter) were collected from the three study plots (and their surroundings, as appropriate) used for the dead wood assessment, plus one additional plot per forest type. Thus, the total number of replicate samples of dead wood was four in all rearing experiments. In natural forest, emergence traps were installed on the sites from where the dead wood had been collected. However, for logistical reasons, and to avoid the damage of traps through vandalism ─ a problem sometimes encountered in plantations ─ all rearing experiments with dead wood collected from plantation forests were conducted at a single protected site in the teak plantations. Within this site, traps were distributed in random order. A shade roof of palm leaves (2 m high) was constructed to protect the emergence traps from direct sun exposure during the dry season.

PETs were used to rear saproxylic beetles from dead wood of different decay stages. In natural forest, all decay stages were found. Thus, one representative sample of each stage was collected on each replicate plot (4 decay stages × 4 replicates). In teak and fuelwood plantations, decay stages 3 and 4 were not encountered in sufficient quantities. Therefore, only stages 1 and 2 were sampled (2 decay stages × 4 replicates × 2 plantation types). The total number of PETs employed was 32 (16 in natural forest and 8 in teak plantations and 8 in fuelwood plantations).

CETs were used to rear saproxylic beetles from dead wood of certain tree species. Only dead wood of decay stage 2 was used for these rearing experiments. In natural forest, we selected dead wood of the seven most abundant species: *A. africana* (Caesalpiniaceae), *Anogeissus leiocarpus* (Combretaceae), *C. pentandra* (Bombacaceae), *D. guineense* (Caesalpiniaceae), *D. mespiliformis* (Ebenaceae), *M. andongensis* (Sapotaceae) and *Zanthoxylum zanthoxyloides* (Rutaceae). In plantation forests, we only sampled dead wood of cultivated trees, i.e., *T. grandis* (Verbenaceae) and *S. siamea* (Caesalpiniaceae) in teak and fuelwood plantations, respectively. The total number of CETs employed was 36 (9 tree species × 4 replicates).

Note that the overall sampling effort in terms of the total number of emergence traps employed (PETs plus CETs) was dissimilar among natural forest (11 traps per plot, all decay stages and dead wood species pooled) and forest plantations (3 traps per plot).

Species identification

All specimens were sorted to morphospecies and determined to the family level. Voucher specimens were deposited at the IITA-Benin in Cotonou, and partially at the Natural History Museum in Basel.

Statistical analyses

Differences in dead wood volumes and attributes among forest types were compared by one-way analysis of variance (ANOVA), followed by Bonferroni multiple comparison of means (SPSS 12.0). All data were $\log_{10}(n+1)$-transformed prior to the analyses to achieve homogeneity of variances.

Similar analyses were conducted to examine the effect of forest type on *measured* species richness (= species richness per trap, as opposed to *estimated* species richness, see below), relative abundance and evenness of saproxylic beetle assemblages. Abundance and species richness data were also $\log_{10}(n+1)$-transformed.

In order to standardise species richness estimates by sampling effort, we combined species accumulation and rarefaction, two closely related analytical techniques (Magurran, 2003). The former was employed for plantation plots because the number of sampling units (traps) therein was insufficient for rarefaction ($n = 3$). The latter was used for natural forest plots ($n = 11$). Computations were done with the programme EstimateS 6.0b1 (Colwell, 1997). Smoothed accumulation curves were obtained after 50 randomisations. Rarefaction curves were calculated according to Colman's random placement method (Coleman, 1981). Species richness was estimated for the highest possible equivalent sampling effort (= three traps per plot) among the more and the less intensively sampled forest types (Gotelli and Colwell, 2001). Hence species richness estimates for natural forest plots represent rarefied values, and those for plantation plots cumulated ones (Magurran, 2003).

All *P*-values reported are for individual analyses. Where appropriate, we also give significance levels after sequential Bonferroni adjustments for multiple testing.

Saproxylic beetle assemblages from individual traps were further analysed with detrended correspondence analysis (DCA), using PC-Ord 28.0 (McCune and Mefford, 1999) (default parameters). Prior to the analysis, abundance data were $\log_{10}(n+1)$-transformed. We only interpreted the ordination space determined by the first two axes.

We used linear multiple regression with forward selection to analyse the relationship between dead wood variables (characters) and measures of saproxylic beetle assemblages (species richness, abundance, evenness and DCA ordination scores). Cut-off values for the F-statistics determining inclusion or exclusion of explanatory variables in the regression models were set to $P = 0.1$ and $P = 0.4$, respectively (Okland et al., 1996; Grove, 2002c).

We adopted a method for the determination of indicator species (Dufrêne and Legendre, 1997) to assess preferences of certain beetle species and families for certain dead wood species or decay stages. The threshold level for the indicator value was 25%, and the significance level $P \leq 0.01$. Species abundance data were stored in a main matrix and grouping variables for the computation of indicator species in a second matrix. All indicator species were identified using the same main matrix by changing the grouping variables in the second matrix. This method is available in the programme PC-Ord 28.0 (McCune and Mefford, 1999).

Results

Dead wood

Altogether, we recorded 1,847 pieces of dead wood, corresponding to a mean volume across all sites of 12.0 m^3 ha^{-1}. The highest total volume of dead wood was found in natural forest and amounted to 30.2 ± 5.8 m^3 ha^{-1} (mean ± SE). This volume was seven and 25-fold higher, respectively, than the dead wood volume in teak (4.3 ± 1.5 m^3 ha^{-1}) and fuelwood plantations (1.2 ± 0.3 m^3 ha^{-1}). All dead wood attributes except the volume of limbs were significantly different among forest types (Table 2). All nominally significant effects were also significant at $P < 0.05$ after sequential Bonferroni adjustment.

Table 2. Mean (± SE) volumes (m^3 ha^{-1}) of different categories of dead wood in natural and plantation forests in the Lama forest reserve. *P*-values for individual ANOVAs are given.

Dead wood category	Natural forest	Teak plantation	Fuelwood plantation	$F_{2,6}$	*P*	Pairwise compar.
Decay stage I	3.4 ± 0.9	1.0 ± 0.5	0.6 ± 0.1	8.4	0.018	NF > FP
Decay stage II	8.2 ± 2.0	3.1 ± 1.5	0.6 ± 0.2	11.7	0.008	NF > FP
Decay stage III	10.3 ± 3.5	0.1 ± 0	0	64.4	<0.001	NF > TP NF > FP
Decay stage IV	8.4 ± 2.7	0	0	64.1	<0.001	NF > TP NF > FP
Coarse woody debris	21.2 ± 3.8	3.3 ± 1.71	0.5 ± 0.3	29.8	0.001	NF > TP NF > FP
Dead limb	1.7 ± 0.4	0.7 ± 0.2	0.6 ± 0.3	3.9	n.s.	
Snag	7.4 ± 2.2	0.4 ± 0.2	0	40.5	<0.001	NF > TP NF > FP
Snag (> 30 cm)	4.7 ± 2.3	0	0	16.2	0.004	NF >TP NF > FP
Dead wood (total)	30.2 ± 5.8	4.3 ± 1.5	1.2 ± 0.3	44.7	<0.001	NF > TP NF > FP
Dead wood (> 30 cm)	10.1 ± 4.8	0.4 ± 0.1	0	23.1	0.002	NF > TP NF > FP

n.s. = not significant; NF = natural forest; TP = teak plantation; FP = fuelwood plantation

The amount of dead wood of decay classes I and II was significantly higher in natural forest than in fuelwood plantations, but was not different from the one in teak plantations. For all other dead wood variables, values were significantly higher in natural forest than in both types of plantation (Table 2).

In natural forest, the highest proportion of dead wood belonged to the advanced decay stages III and IV, representing 34% and 28%, respectively, of the total amount of dead wood (Fig. 2). In contrast, about 95% of the total amount of dead wood in teak and fuelwood plantations belonged to decay stages I and II.

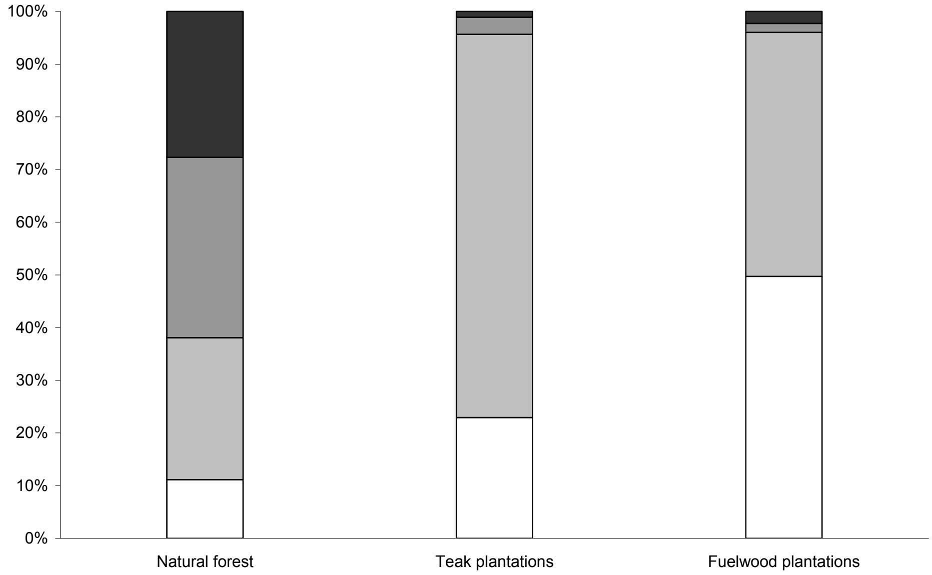

Fig. 2. Proportion of dead wood of different decay stages in natural forest, teak and fuelwood plantations. Progressive shading of columns indicates successive decay stages, ranging from stage I (white) to IV (black).

Dialium guineense was the dominant dead wood tree species in natural forest, representing at least 50% of the total amount of dead wood on all sampling sites, followed by *A. africana* and *M. andongensis* (about 10% each). In plantation forests, *T. grandis* (teak plantations) and *S. siamea* (fuelwood plantations) represented > 95% of the total amount of dead wood.

Saproxylic beetle assemblages

The total volume of dead wood used in the rearing experiments was 4.1 m^3 (all 68 traps pooled). During the 15-month rearing period, we collected 7,474 specimens in 469 species and 33 identified families of saproxylic beetles (Table 3).

Twenty-nine percent of all species were singletons, and 26% occurred with > 10 individuals. We reared 4,168 individuals from dead wood of decay stages I to IV in pyramid-shaped emergence traps, representing 349 species. Corresponding values for beetles reared from specific dead wood in cylinder-shaped emergence traps were 3,306 individuals and 319 species. One hundred ninety-nine species were reared in both types of trap.

Even though the dead wood volume contained in PETs was significantly higher than the one in CETs (0.08 *versus* 0.04 m^3 per trap; Mann-Whitney test, U = 53.0,

$P < 0.001$), neither species richness nor the total number reared were different among traps (paired samples *t*-tests, $P > 0.05$). Therefore, the different traps were considered as replicates in subsequent statistical analyses.

Table 3. Saproxylic beetles reared from dead wood in the Lama forest reserve

Family	Species richness	Relative abundance	Family	Species richness	Relative abundance
Cerambycidae	55	887	Nitidulidae	8	45
Staphylinidae	49	691	Pselaphidae	9	36
Tenebrionidae	38	402	Scolytidae	8	926
Anthribidae	34	256	Brentidae	7	78
Carabidae	34	200	Bostrichidae	6	77
Curculionidae	24	555	Endomychidae	6	54
Elateridae	21	149	Erotylidae	6	45
Mordellidae	17	161	Trogossitidae	6	22
Scarabaeidae	13	86	Histeridae	6	10
Cleridae	12	22	Lagriidae	5	15
Lycidae	11	132	Anobiidae	4	80
Buprestidae	11	114	Lucanidae	4	14
Colydiidae	10	565	Platypodidae	2	449
Anthicidae	10	530	Lampyridae	2	110
Cucujidae	10	205	Drilidae	2	2
Scaphidiidae	9	162	Ceratocanthidae	1	17
Eucnemidae	9	158	Undetermined	20	219

Species richness

The measured species richness of beetle assemblages (in terms of mean number of beetles reared per trap) was significantly higher for dead wood collected in natural forest than for dead wood collected in teak plantations (Table 4). However, we found no significant differences between natural forest and fuelwood plantations. Multiple regression of dead wood variables on species richness retained limb volume as the sole explanatory variable, resulting in the following regression model:

$$\text{Species richness} = 22.9 + 4.8 \times \text{Limb vol.}$$

However, the model obtained was only marginally significant ($R^2 = 0.318$, $P = 0.056$).

Comparing species richness estimates standardised by sampling effort ($n = 3$ sampling units, see methods) and derived from individual accumulation or rarefaction curves (Fig. 3) revealed highly significant differences among forest types. Pairwise comparisons showed higher species richness in natural forest than in old teak and fuelwood plantations. Multiple regression retained two explanatory variables for estimated species richness, the volume of snags and the volume of limbs. The linear regression model was:

Species richness = 52.9 + 2. 6 × Snag vol. + 12.8 × Limb vol.

Contrary to the model for measured species richness presented above, this model was highly significant ($R^2 = 0.799$, $P = 0.001$).

Table 4. Mean (± SE) species richness, relative abundance and evenness of saproxylic beetle assemblages in the Lama forest reserve. For species richness, analyses were performed for *measured* and for *estimated* data derived from individual species accumulation or rarefaction curves. Sequential Bonferroni adjustment for multiple testing retains all significant effects except for evenness whose critical level drops to $P = 0.052$.

Variable	Natural forest	Teak plantation	Fuelwood plantation	$F_{2,9}$	P	Pairwise compar.
Species richness (measured)[1]	31.3 ± 1.5	22.3 ± 2.3	29.4 ± 1.2	7.0	0.014	NF > TP
Species richness (estimated)[2]	94.6 ± 2.4	54.0 ± 2.9	68.3 ± 5.1	31.4	< 0.001	NF > TP NF > FP
Relative abundance	114.8 ± 9.5	71.9 ± 12.3	312.3 ± 132.5	4.0	0.058	
Evenness	0.85 ± 0.02	0.88 ± 0.02	0.79 ± 0.02	5.7	0.026	TP > FP

NF = natural forest; TP = teak plantation; FP = fuelwood plantation; [1] mean per trap; [2] mean per plot, standardised for sampling effort

Relative abundance

Relative abundance was highest in fuelwood plantations (due to the superabundance of one species in a single trap) and lowest in teak plantations. However, differences among forest types were only marginally significant (Table 4). We found no relationship between dead wood attributes and relative abundance.

Evenness

Evenness was significantly different among forest habitats (Table 4). A significantly lower value was encountered in firewood than in teak plantations. However, we found no significant regression model for evenness.

Species richness and dead wood decay

Seventy-two saproxylic beetle species were found only in dead wood of advanced decay stages (26 species in decay stage III, 25 species in decay stage IV and 21 species in both these stages). Individual species accumulation curves for different forest types and decay stages are plotted in Fig. 4. The highest levels were observed for decay stages III and IV (natural forest), and the lowest levels for decay stages I and II (teak plantations).

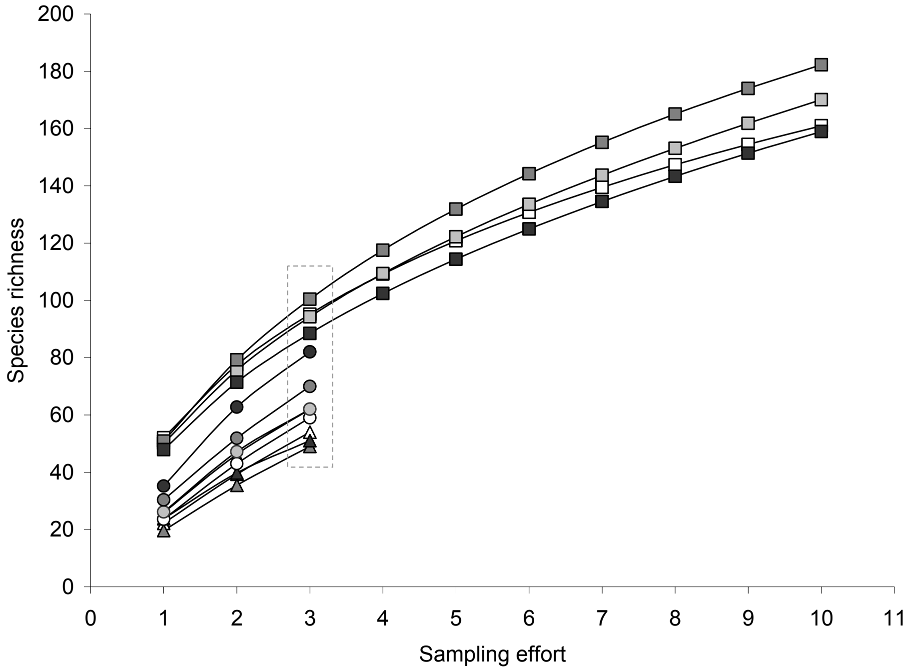

Fig 3. Rarefaction curves for natural forest (square) and accumulation curves for fuelwood (circle) and teak (triangle) plantations. Computation was done using all traps per site. Progressive shading of markers indicates replicate sites one (white) to site four (black).

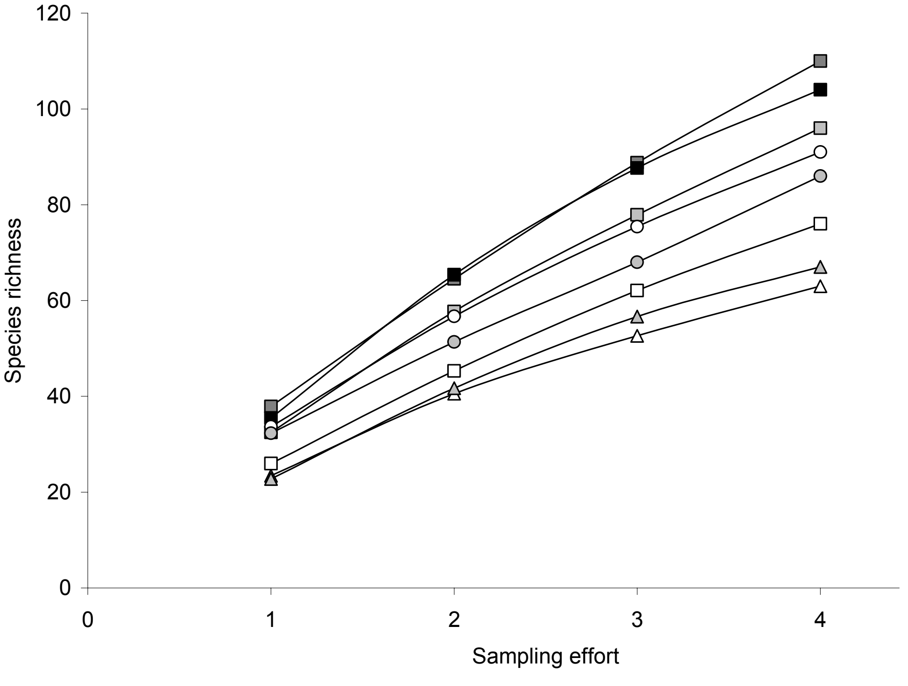

Fig. 4. Accumulation curves for different decay stages and forest types. Progressive shading of markers for natural forest (square) indicates four successive decay stages, ranging from early decay stage I (white) to advanced decay stage IV (black). Markers for fuelwood (circle) and teak plantations (triangle) indicate decay stages I (white) and II (grey).

Preferences for specific tree species

Sixteen beetles were identified as indicator species and can be considered as specialists for specific dead wood tree species. Eight indicators were cerambycids. The other ones were species of Tenebrionidae, Curculionidae, Eucnemidae and Carabidae. Half of the dead wood specialists were reared from *D. guineense*. A separate indicator analysis for all leguminous trees (*D. guineense*, *A. africana* and *S. siamea*) found no specialist beetles for this plant family as a whole.

Preferences for specific decay stages

The analysis of specialists for particular decay stages found two species for decay stage I (Cerambycidae and Curculionidae) and one species for decay stage III (Tenebrionidae). However, when pooling early (I and II) and advanced (III and IV) decay stages, the analysis was more discriminative and revealed seven species in the early decay stages (species of Cerambycidae, Curculionidae, Cucujidae, Bostrichidae) and six in the advanced decay stages (species of Cerambycidae, Mordellidae and Scarabaeidae).

Saproxylic beetle assemblages

The DCA ordination of dead wood (all emergence traps included) clearly segregated dead wood assemblages from natural forest (left) and those from plantations (right) (Fig. 5). No other ecological grouping of traps was evident from the ordination.

The proportion of variance represented by the first axis of the DCA was 0.378. Multiple regression identified three significant predictors of axis one scores, the volumes of coarse woody debris (CWD), dead wood of decay stage I (DW-I) and large dead wood items (DW-30) ($R^2 = 0.786$, $F_{3,64} = 76.6$, $P < 0.001$). The regression equation is:

$$\text{Axis 1} = 283.0 - 8.9 \times \text{CWD vol.} - 19.5 \times \text{DW-I vol.} + 4.9 \times \text{DW-30 vol.}$$

The proportion of variance represented by the second axis was 0.055. Axis two scores were best predicted by two variables, the volume of snags and the one of dead wood of decay class I (DW-I) ($R^2 = 0.165$, $F_{2,65} = 6.4$, $P = 0.003$). The corresponding regression equation is:

$$\text{Axis 2} = 112.6 - 5.7 \times \text{Snag vol.} + 12.0 \times \text{DW-I vol.}$$

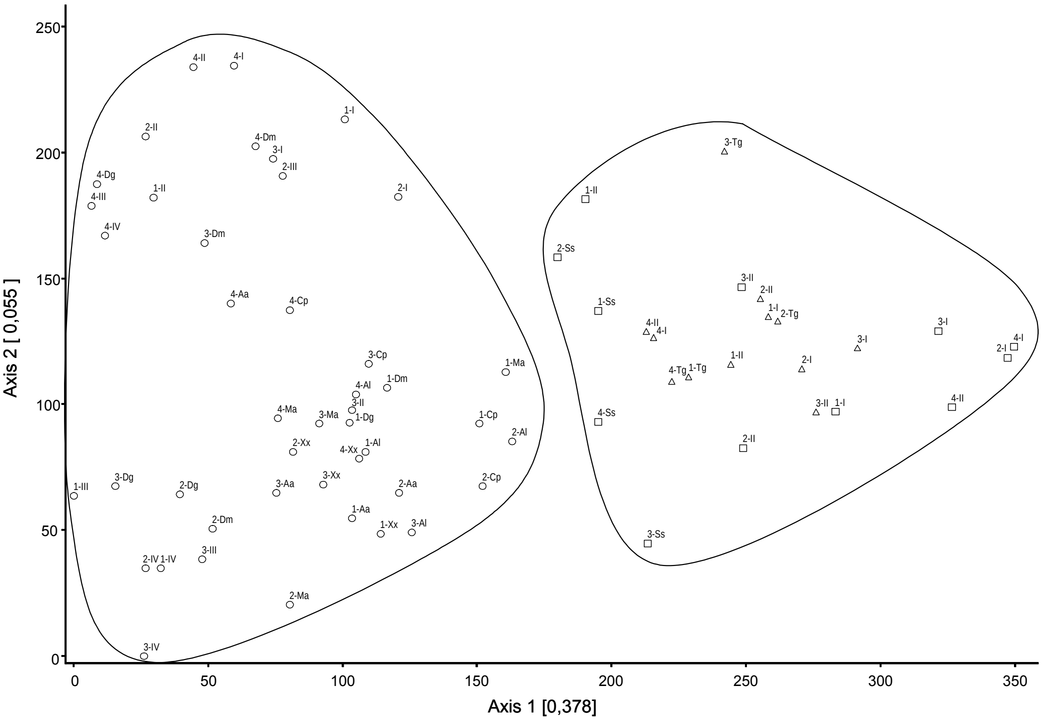

Fig. 5. Detrended correspondence analysis of sampling units (traps) in species space. Circle = natural forest, square = fuelwood plantations, triangle = teak plantations; replicate sites are marked with numerals 1 to 4 and decay stages with I (early decay stage) to IV (advanced decay stage); Aa = *Afzelia africana,* Al = *Anogeissus leiocarpus*, Cp = *Ceiba pentandra*, Dg = *Dialium guineense*, Dm = *Diospyros mespiliformis*, Mm = *Mimusops andongensis*, Zz = *Zanthoxylum zanthoxyloides*, Tg = *Tectona grandis* and Ss = *Senna siamea*.

Discussion

Dead wood

The amount of dead wood of all different types, decay stages and size classes was generally higher in natural forest than in plantations, reflecting the importance and diversity of dead wood habitats in natural forest remnants of the *Noyau central.* The overall paucity of dead wood items in teak and fuelwood plantations, in particular the lack of strongly decayed wood, results from various human activities. First, plantation trees cannot reach overmature stages that would generate dead wood since the intention is to harvest trees before they die naturally (Nicholson et al., 1983). This holds particularly for fuelwood plantations which are harvested at a maximum age of 20 years. Second, after the felling of trees, logging residues are systematically collected by the local population, either for their own use or as a commodity. The cumulative effect of these practices is the near absence of strongly decayed and a deficit in newly generated dead wood. In particular, dead wood originating from large trees is essentially absent from plantations. It is this type of dead wood which is known to provide the most diverse and favourable habitats for a variety of rare and highly specialized saproxylic species (Jonsell et al., 1998). Hence, these species can hardly survive in plantations.

In natural forest, advanced decay stages dominated. Since the eviction of residents from the *Noyau central* in 1988, anthropogenic removal of dead wood has been negligible. Thus, dead wood is decomposed mainly *in situ*. The residence time of moderately decayed dead wood may be relatively short, leading to the dominance of dead wood of advanced decay stages. In boreal forests of central Europe, dead wood volumes can reach as much as 300 m^3 ha^{-1} (Korpel, 1995). In Lama forest, the maximum volume found was 41.8 m^3 ha^{-1}. This confirms results from studies in other tropical forests which found volumes between 33 and 126 m^3 ha^{-1} (Harmon et al., 1995). The lower amount in tropical forests compared to most temperate and boreal forests appears to be due mainly to higher decay rates (Grove, 2001). For example, the mean residence time of coarse litter in central Amazonia was only 5.9 years (Chamber et al., 2000). A study in Lama forest showed that leaf litter decay in natural forest was faster than in most other tropical forests (Attignon et al., in press). We would therefore also expect a rapid wood decay.

Besides, the low amount of dead wood may also be related to the peculiar structure and physiognomy of natural forest patches in the *Noyau central*. Most study sites were characterised by a high frequency of stems in small diameter classes (Fig. 1a), indicating a relatively young age structure which in turn may be due to earlier anthropogenic disturbances incurred before the resettlement of forest settlers in 1988. Young forests generate only a low amount of dead wood. Oldeman (1983) found that dead wood generation in tropical forest reaches a peak in late successional stages. This is supported by our observation that the highest volume of dead wood (41.8 m^3 ha^{-1}) in Lama forest was recorded on a site showing the lowest basal area (19.7 m^2 ha^{-1}), suggesting that this site may have reached a senescent stage.

In the present study, no snags were found on the study sites located in forest plantations. Subsequent surveys, however, revealed that snags occur at very low densities in both teak and fuelwood plantations. Saproxylic beetle assemblages of snags will be the subject of Chapter 4.

Species richness of saproxylic beetles

Both *measured* and *estimated* species richness of saproxylic beetle assemblages were significantly higher in natural forest than in plantations. However, the latter was clearly the more discriminative variable because it integrated species richness data from various types of dead wood, including all decay stages and different tree species. This was achieved by first determining total species richness in natural forest (species from all traps pooled) and then rarefying species richness to the point where the sampling effort was equivalent to the one for plantation forests, i.e., at three sampling units. Such a high diversity of dead wood was not available in plantations, which explains why we reduced the sampling effort. Putting equal effort into the rearing of saproxylic beetles from dead wood collected in plantations – with only one tree species and two decay stages each – would not only have produced redundant data but would also have surpassed our sampling capacity. To conclude, a higher sampling effort in natural forest was necessary because of the high diversity of dead wood therein. Rarefaction was an *a posteriori* means of standardisation by sampling effort so as to compare species richness of saproxylic beetles from natural and plantation forests.

Quality and quantity of dead wood and hence saproxylic species richness in the plantations of Lama forest are greatly affected by the anthropogenic removal of dead wood. These activities result in a scarcity of large and/or strongly decayed dead wood items. Even though, the number of species reared from dead wood collected in plantations was not as low as expected. To the contrary, species richness was high relative to the low amount and diversity of dead wood habitats. This may explain why only few of the many dead wood character variables showing significant differences among natural forest and plantations were significant explanatory variables in multiple regression analyses. In particular, factors such as the amount of large-sized and strongly decayed dead wood pieces which are known to enhance species richness (Kleinevoss et al., 1996; Kolström and Lumatjärvi, 2000) did not seem to be so important in our study. Nevertheless, rarefied (estimated) species richness was significantly related to two similar variables, the volume of limbs and the volume of snags, i.e., species diversity increased with increasing volumes of limbs and snags. These two types of dead wood share several ecological and management properties. (i) Not lying on the ground, they provide habitats for saproxylic species adapted to drier and warmer conditions (Jonsell and Weslien, 2003). (ii) They usually collapse before reaching an advanced degree of decay. (iii) Due to their size and architecture, they are not systematically removed by the local population.

Overall arthropod diversity

Our finding that the diversity of saproxylic beetles was higher in natural forest than in plantations – while being equal among teak and fuelwood plantations – contrasts with a previous study on arthropod diversity which showed that old teak plantations were among the most species-rich forest habitats and fuelwood plantations the poorest (Lachat et al., in press, see Chapter 1). Moreover, the same study found no difference in species richness among natural forest and plantations. This shows that overall diversity of invertebrates in tropical forests can hardly be predicted from single inventories of selected taxonomic or functional groups. A more comprehensive account requires repeated inventories of a wide spectrum of invertebrate assemblages.

Superabundance in fuelwood plantations

In fuelwood plantations, saproxylic beetle assemblages were dominated by several small-sized, superabundant species of the families Cucujidae, Colydiidae, Platypodidae and Scolytidae. The dominance was also reflected in a significantly lower evenness compared to teak plantations. The massive emergence of these species in fuelwood plantations may be due to the wood quality of *S. siamea.* This species is a fast growing, soft wood leguminous (not nitrogen fixing) plantation tree whose dead wood appears to be rapidly colonized by small saproxylic invertebrates with short life-cycles.

Singletons

The proportion of singletons (29%) in our study was lower than the one found in an Australian tropical forest (≈ 43%; Grove, 2001). However, the Australian study used window (flight intercept) traps which capture a different portion of the saproxylic fauna. Specifically, they are designed to intercept flying insects. Thus captures depend on the flight activity. In contrast, emergence traps measure the abundance of beetles reared from a definite quantity of dead wood. Because most saproxylic beetles lay more than one egg on the same piece of decaying wood, the probability to rear and capture several individuals of the same species is higher than with intercept traps.

Saproxylic beetle assemblages

The two main groups of saproxylic beetle assemblages obtained in the DCA reflect the gross division of Lama forest into two different forest types, natural forest and plantations. It underlines the importance of silvicultural and forest management practices for the composition of saproxylic beetle assemblages. Within these two main groups, it was not possible to clearly distinguish subgroups of sampling sites, decay class or tree species. An exception was the concentration of assemblages associated with teak wood in the centre of the main group “plantations”. Dead wood assemblages within the main group “natural forest” are more widely dispersed which may be due to the high heterogeneity of dead wood habitats (different tree species and decay stages).

Saproxylic beetle assemblages were related to the amount of (a) recently dead wood (decay stage I), (b) large pieces of dead wood and (c) coarse woody debris (axis one), or to the amount of (a) recently dead wood and (b) snags (axis two).

In both regression models, the regression coefficient was highest for the variable “decay stage I”, indicating that recently dead wood was crucial to the composition of beetle assemblages. In natural forest, recently dead wood passes through all decay stages, and the nutrients are recycled *in situ*. In plantations, wood items are usually collected before reaching advanced decay stages. The removal of dead wood leads to a depletion of soil nutrients and reduces the diversity of habitats for saproxylic beetles. Despite the short residence time of dead wood in plantations we found characteristic and species-rich saproxylic beetles assemblages. These appear to be well adapted to a dead wood decomposition regime in which habitats are available only for short periods of time (McPeek and Holt, 1992).

Larger pieces of dead wood are known to provide important habitats to saproxylic arthropods, including rare and threatened species. They are generated mainly in old-aged forests with a high proportion of trees of large diameters. A positive relationship between the diversity of saproxylic insects and the frequency of large diameters has been found in several studies (Kleinevoss et al., 1996; Jonsell et al., 1998; Martikainen et al., 2000; Grove, 2002c). The ecological value of larger-diameter material is due to several reasons. First, decomposition is slow. Thus, large dead wood pieces may harbour species with long life cycles. Second, as the decomposition proceeds, they develop a diversity of habitats (e.g., different decay stages) and resources (e.g., different fungal species). Thus, highly specialised saproxylics may colonize different micro-habitats within the same piece of wood at the same time (Kolström and Lumatjärvi, 2000).

The importance of the other predictors included in the models (CWD and/or snags) shows that dead wood architecture and exposure may also influence the composition of the saproxylic fauna. Abiotic (e.g., humidity, temperature) and biotic (e.g., fungal growth) features of decay depend on whether or not dead wood is in contact with the soil. To maintain a high diversity of saproxylic beetle assemblages, both of these types of dead wood must be present.

Dead wood preferences

The association of saproxylic beetles with specific types of dead wood depends on a range of factors, including tree species or family (hence wood quality), decay stage, size, exposure as well as the composition of wood-decomposing fungal communities. Preferences for specific host wood are rare at the species level but common at higher taxonomic levels (genus, family) (Basset et al., 1996, Tavakilian et al., 1997). Some saproxylic species show clear preferences for recently dead wood (Hamilton, 1978; see Chapter 2). A high degree of specificity in host wood selection might be advantageous in forests dominated by few abundant species (Beaver, 1979). In Lama forest, *D. guineense* is the most abundant tree, its dead wood representing more than 50% of the total amount of dead wood. It was therefore not surprising that half of the specialist beetles identified preferred this species.

Several beetles showed significant preferences for the exotic trees *T. grandis* (three species) or *S. siamea* (one species). Unfortunately, we have no information about their origin and biogeography that would allow us to decide whether they are introduced or indigenous species. The interpretation is further complicated by the lack of taxonomic and ecological data. Further studies are required to collect this information.

Caesalpiniaceae was the only family represented by several species for which we could test dead wood preferences at the family level. However, we found no significant preferences for caesalpiniaceous dead wood. While a preference for the family as a whole may indeed not exist, it is also possible that the distance between natural forest with *D. guineense* and *A. africana* on the one hand and *S. siamea* fuelwood plantations on the other hand was too long (> 4 km), or that the exotic tree species was not attractive to Caesalpiniaceae specialists.

As the diversity and biomass of dead wood-decomposing fungi increases, the range of saproxylic colonisers of decaying wood broadens. For many species, these saprophytic fungi are the essential factor in dead wood habitat or host selection (Jonsell et al., 1998). We found only three species with significant preferences for individual decay stages (I and III) but 13 species when distinguishing early (classes I and II pooled) and late (classes III and IV pooled) decay. This suggests that the different decay classes represent a spatio-temporal continuum of wood decomposition rather than distinct decay sequences, and that preferences for certain decay stages become apparent only towards the extremes (i.e., recently dead *versus* rotten wood).

To conclude, we found more preferences for individual tree species than for individual decay stages. Similar observations were made in a boreal forest in Scandinavia (Jonsell et al., in press). However, more tree species should be investigated to confirm host tree fidelity of specialists identified in this study.

Conclusions

To our knowledge, this is the first study of saproxylic beetle assemblages in tropical West Africa and their relationship with dead wood attributes. Our objective was to provide an overview of this important and largely neglected functional group in Lama forest, and to explore conditions for its conservation.

The overall amount and quality of dead wood in teak and fuelwood plantations was lower than in natural forest. Types of dead wood known to be particularly species-rich were either rare or absent (snags, large and/or strongly decomposed wood items). Due to the low dead wood habitat diversity in forest plantations, a full complement of saproxylic beetles was not retained. Consequently, species richness was lower than in natural forest, and species assemblages were found to be distinctly different from those in natural forest. Nevertheless, given the low amount and quality of dead wood, saproxylic beetle diversity in plantations was surprisingly high. Moreover, nearly 25% of all species were found only in plantations (Lachat, unpublished data). This demonstrates that even small quantities of dead wood, however dispersed, may enhance the diversity of saproxylic insect assemblages.

The plantations in Lama forest have been established mainly to provide the human population with alternative timber and fuelwood resources, thereby preserving the remaining tracts of natural forest. From a conservation standpoint, this is certainly the most important objective. However, single-objective forest management and protection approaches are considered to be increasingly unattractive (Lamb, 1998). Creating plantations to reduce the pressure on natural forest should not preclude measures enhancing the biodiversity in plantations. Moreover, plantations can be managed so as to enhance dead wood resources available to saproxylic insects without compromising economic benefits. At the landscape level, management measures should aim to promote and maintain ecological processes characteristic of natural forests by allowing some trees to live to ecological maturity and subsequent decay without intervention (Grove, 2002b). To create dead wood habitats in the short term, some logs or high stumps should be retained during logging or harvesting operations (Jonsell et al., in press). In the teak plantations in Lama forest, such measures are unlikely to cause economic losses, because the wood at buttress level is often of inferior quality (hollow trunks). In order to restore natural forest dynamics in the long term, restoration of natural forest patches should be promoted.

The provision of dead wood resources in plantations would not only benefit saproxylic insect assemblages, but also vertebrates feeding on them, e.g. woodpeckers, soricids and lizards.

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CHAPTER 4 – SAPROXYLIC BEETLES ON SNAGS

Saproxylic beetle assemblages on native and exotic snags in a West African tropical forest

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Manuscript

Abstract

Standing dead trees (snags) and their saproxylic (dependent on dead wood) beetle assemblages were studied in the Lama forest reserve in Benin, West Africa. The study comprised several snag species in different forest systems (native snag species in protected forest and exotic snag species in plantations) and types (natural semi-deciduous forest, degraded forest, teak plantations, fuelwood plantations). We compared native snag species in protected forest and exotic snag species in plantations. The snag beetle fauna was sampled for a total of 12 weeks during one year, using trunk window traps. To distinguish saproxylic and non-saproxylic beetles, we also sampled an equal number of live trees (controls). Species richness, relative abundance and the number of singletons (species sampled only once) of saproxylic beetle assemblages were similar among native and exotic snags. However, overall species richness and beta-diversity of snag beetle assemblages were higher for native than for exotic snags, reflecting a high heterogeneity in habitat quality among the snags in natural forest. Thus, snag beetle assemblages were influenced mainly by the forest system. From a dead wood management point of view, it is suggested that the retention or creation of snags in natural forest as well as in plantations can enhance and preserve the diversity of the saproxylic beetle fauna.

Key words: Dead wood, Natural forest, Plantations, Snag, Saproxylic beetle assemblages, Trunk window trap

Introduction

In view of high deforestation rates on the one hand and a high demand for wood and wood products on the other, there is a growing need for large-scale reforestation and afforestation programmes in the tropics. However, single-objective forest plantation management in terms of maximizing wood production is an increasingly unattractive option (Lamb 1998). In addition to producing timber or fuelwood, plantation forestry should also aim to maintain and enhance biodiversity (Kolström and Lumatjärvi 2000), and to contribute to the protection of natural forests.

In tropical forests, dead wood-associated (saproxylic) invertebrates make up a large part of the total invertebrate diversity (Hammond et al. 1996). Therefore, the management of dead wood is crucial to the conservation of invertebrate diversity in both natural and plantation forests. Saproxylic organisms include species that are dependent, during some part of their life-cycle, upon dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics (Speight 1989). Decaying wood is an extremely heterogeneous substrate with hundreds of different microhabitats hosting a great variety of species, especially beetles (Siitonen 2001). Moreover, saproxylic beetle assemblages differ greatly among different types of dead wood (Sverdrup- Palm 1959; Thygeson and Ims 2002). Dead wood lying on the ground is exposed to more humid conditions than standing dead wood (snags), which is exposed to drier conditions and to higher temperature and humidity fluctuations (Hunter 1990). To design and adopt effective and practicable conservation strategies for saproxylic beetles, it is therefore important to understand their respective specialization patterns (Kaila et al. 1994).

During the past 20 years, saproxylics were studied mainly in temperate forests of the northern hemisphere (e.g. Speight 1989; Siitonen 1994; Köhler 2000; Martikainen et al. 2000; Schiegg 2000; Jonsell et al. 2004; Martikainen and Kaila, in press). These studies revealed that saproxylic beetle assemblages are highly susceptible to forest management. In contrast, only few studies have been done in tropical forest ecosystems, most of them in tropical Australia (Grove 1999, 2000, 2001, 2002a, 2002b, 2002c). The results of these studies await validation from tropical forests of all other continents.

With more than 650 million ha, the African continent represents one sixth of the world forest area. The annual decline in forest cover (-0.8%) due to deforestation or conversion to cropland is the highest in the world (FAO 2003). These changes are expected to cause dramatic changes in the diversity and composition of saproxylic invertebrate assemblages. A study conducted in the Lama forest reserve in Benin, West Africa, showed great differences of the saproxylic fauna among natural and plantation forests (see Chapter 3). These were related to different forest management practices and use patterns, including the removal of dead wood for fuelwood by the local population. Notably, the study found that even small amounts of dead wood in plantation forests harbour a high diversity of saproxylic beetles, and that the volume of snags is an important factor determining saproxylic beetle assemblages.

The goal of the present study was to follow up these findings by evaluating the importance of snags for the conservation of saproxylic beetle assemblages in Lama forest. Our specific objective was to compare beetle assemblages from native snag tree species in remnants of natural forest (including degraded forest) in the central part of the reserve (*Noyau central*) with those from exotic snag tree species in monospecific plantations surrounding the *Noyau central*.

Materials and Methods

Study area

The Lama forest reserve is located about 80 km north of Cotonou (6°55.8' to 6°58.8' N and 2°4.2' to 2°10.8' E), covering an area of 16,250 ha in a shallow depression between the Allada and Abomey plateaus. The forest is situated in the Dahomey gap, a low rainfall zone separating the western and eastern part of the humid Guineo-Congolian evergreen and semi-evergreen forests of West and West-central Africa (White 1983). The annual rainfall is about 1,200 mm, with a pronounced dry season from November to March (Sayer et al. 1992). The prevailing soils are hydromorphic vertisols and sandy ferralsols. The natural vegetation is a semi-deciduous forest, belonging to the drier peripheral semi-evergreen Guineo-Congolian rain forest system (White 1983). Remnants of this forest type are nowadays confined to the *Noyau central* (4,800 ha) which has been strictly protected since 1988. The forests within the *Noyau central* are characterised by of a small-scale mosaic of natural forest and abandoned, gradually recovering slash-and-burn patches (Specht 2002). The *Noyau central* is surrounded by teak (*Tectona grandis*, 7,000 ha) and fuelwood plantations (mainly *Senna siamea* and *Acacia auriculiformis*, 2,400 ha).

Study sites

We studied snags in each of two different forest types within two main forest systems, *protected forest* (*Noyau central*) and *forest plantations*. The forest types comprised (1) natural and (2) degraded forest in the *Noyau central* (native tree species), and (3) teak and (4) fuelwood plantations in forest plantations (exotic tree species).

The vestiges of natural forest within the *Noyau central* are dominated by tree species such as *Afzelia africana*, *Ceiba pentandra*, *Dialium guineense*, *Diospyros mespiliformis*, *Drypetes floribunda*, *Celtis brownii* and *Mimusops andongensis*. The understorey vegetation is dense and canopy height reaches up to 25 meters.

Degraded forest in the *Noyau central* derives from abandoned cropland. The vegetation is characterised by the perennial weed *Chromolaena odorata*. Dominant trees are remnants of natural forest or post-fire pioneers such as *Anogeissus leiocarpus*. In some parts, forest regeneration has been assisted with enrichment plantings of native trees.

The old-growth teak plantations studied were planted between 1955 and 1965 on sandy ferralsol (transition between vertisols in the Lama valley and ferralitic soils on the surrounding plateaus). The understorey vegetation is well developed and species-rich, resembling the vegetation usually encountered in natural forest (Lachat et al. in press, see Chapter 1).

The fuelwood plantations were planted between 1990 and 1995 to satisfy the growing fuelwood demand. The understorey vegetation of these relatively open, short-rotation forests is often dominated by dense stands of *Chromolaena odorata*.

Sampling methods

Beetles were collected using trunk window traps (Kaila 1993). These consisted of 20 × 30 cm transparent plastic sheets attached radially to the trunk with two iron rods, about 30 cm long, driven into the wood. The longitudinal axes of the windows were oriented in vertical position. Plastic funnels (20 cm diameter, green colour) were suspended from the lower rod to collect intercepted insects. Funnel exits were connected to 0.25 litre sampling bottles containing the preservative solution (0.5% formalin plus some droplets of washing liquid to lower the surface tension). We installed two traps per tree, one at 70 cm and one at 200 cm above the ground (measured from the upper rod). The traps were generally east-west oriented.

Sampling design

The sampling effort was limited mainly by the availability of snags in plantations and degraded forest. Overall, we examined five snags in natural forest and four snags each in degraded forest, fuelwood and teak plantations. Snags were dead trees with a diameter at breast height (DBH) of ≥ 15 cm and a trunk height of at least 5 m. All snags had branches but no green leaves.

To distinguish the activity of saproxylic beetles from the one of non-saproxylic passengers, we also sampled one live control tree in the vicinity (20–50 m) of each snag, resulting in five (natural forest) and four (remaining forest types) snag-control pairs. Controls were young trees (5–20 cm DBH) with no signs of decay, hence unsuitable for saproxylic beetles (Kaila et al. 1994). In most cases, conspecific control trees were selected. Only in degraded forest we could not find live counterparts for all snag species. In these cases, different species with similar growth form were chosen (Table 1).

Table 1. Environmental factors measured on snags and control trees in Lama forest.

System	Forest type	Snag							Control tree		
		Tree species	Diameter[a]	Height[b]	Decay[c]	Polypore fungi	Bark[d]	Exposure[e]	Tree species	Diameter[a]	Height[b]
Noyau central	Natural forest	*D. guineense*	37	18	0	-	100	1	*D. guineense*	9	12
		D. guineense	38	8	1	-	100	1	*D. guineense*	10	16
		D. guineense	28	16	1	-	100	1	*D. guineense*	6	8
		D. mespiliformis	36	10	0	-	100	1	*D. mespiliformis*	15	12
		M. andogensis	38	10	1	-	40	2	*M. andongensis*	20	16
	Degraded forest	*A. africana*	90	22	1	Present	100	3	*A. floribunda*	11	6
		A. africana	80	20	0	-	100	3	*L. serriceus*	8	10
		A. leiocarpus	27	14	1	-	50	2	*A. leiocarpus*	13	8
Plantations	Old teak plantations	*T. grandis*	41	22	0	-	100	2	*T. grandis*	11	10
		T. grandis	30	18	0	-	100	2	*T. grandis*	8	8
		T. grandis	22	12	0	-	80	1	*T. grandis*	6	8
		T. grandis	39	14	1	-	0	2	*T. grandis*	14	12
	Fuelwood plantations	*S. siamea*	10	10	0	Present	100	2	*S. siamea*	10	12
		S. siamea	10	12	0	Present	100	2	*S. siamea*	10	10
		A. auriculiformis	11	12	0	-	85	3	*A. auriculiformis*	11	12
		A. auriculiformis	11	14	0	-	100	2	*A. auriculiformis*	11	12

[a] DBH in cm; [b] in m; [c] 0 = sound wood, 1 = soft wood, [d] percentage of remaining bark; [e] 1 = closed forest with low sun exposure, 2 = medium sun exposure, 3 = clearcuts with high sun exposure.

There is an elevated risk that snags collapse during studies extending over longer periods of time. Previous studies managed this problem by selecting nearby replacement snags similar in species, decay and size (Hammond 1997). In our study, two snags collapsed, one in degraded forest and one in fuelwood plantations. A suitable replacement snag was found in fuelwood plantations but not in degraded forest. The latter was therefore considered as missing.

Beetles were sampled from June 2002 to June 2003 for a total period of 12 weeks. Individual sampling periods lasted one or two weeks. During this time, the traps were emptied weekly.

Identification

Suspected saproxylic beetles were first identified and enumerated at the morphospecies level (Oliver and Beattie 1996). Beetles were regarded as saproxylic if so suggested by their habitat association found during this and other studies in the Lama forest reserve, or if their ecology could be inferred from the literature. Taxa whose saproxylic status was dubious or clearly wrong were discounted. Examples are the families Chrysomelidae, Curculionidae and Staphylinidae. To reduce sampling and computation bias due to passengers, the main analyses focused on the so-called true snag beetles (see analysis).

Environmental factors

A range of environmental variables were recorded, representing different scales and describing different (micro-) habitat attributes. These variables included tree species, trunk diameter (DBH), height, decay stage (sound and soft wood), sun exposure (closed forest with low or medium sun exposure, clear-cuts with high sun exposure; after Sverdrup-Thygeson and Ims 2002), the presence of polypore fungi growing in the wood and the percentage of bark remaining.

Data analysis

Beetle assemblages were examined using three summary variables, species richness, relative abundance and the number of singletons (species occurring with one individual only). All data of the summary variables were $\log_{10}(n+1)$-transformed prior to statistical analyses.

We first tested differences in beetle assemblages among traps positioned at 70 cm and 200 cm above the ground, using paired-sample *t*-tests (SPSS 12.0). Similar tests were employed to compare beetle assemblages on snags and paired control trees. In these and all remaining analyses, sequential Bonferroni adjustments were made to correct the error rate for multiple testing if significant effects were found (Manly 2001).

Beta-diversity (the degree of change in species composition between habitats) was calculated according to Whittaker's formula $\beta_w = \gamma / \bar{\alpha}$, where γ is the total species number recorded (γ-diversity or the local species pool) and $\bar{\alpha}$ is the average number of species per site (Whittaker 1960). β_w was then related to the maximum β_{w_max} to allow comparisons of samples with different size (Magurran 2003).

Trunk window traps intercept insects flying close to the trunk. This may reflect a specific relationship of these insects with the dead wood substrate (e.g., saproxylic beetles hatching from or attracted to snags). However, other insects intercepted may respond to clues that are not specific to dead wood, or travel in a quasi random fashion (Jonsell and Weslien 2003; Kaila et al.1994). These arbitrary passengers or transient visitors may introduce a bias in the analysis of dead wood beetle assemblages and reduce the variation among individual snags (Hammond 1997). To reduce this bias, we included only those species that were only found on snags, or – in case of common occurrence on snags and control – species whose relative abundance was at least four times higher on snags than on paired control trees. These beetles were considered as truly saproxylic (true snag beetles). Unless otherwise stated, all remaining analyses were done using this subset of data.

Differences in species richness, relative abundance and the number of singletons of true snag beetles among forest systems (*Noyau central versus* plantations) and forest types (natural *versus* degraded forest *versus* teak *versus* fuelwood plantations) were tested using factorial analysis of variance (ANOVA). Because the different tree species were not present in all forest types, and the latter not in all forest systems, we considered *tree species* as a factor nested in *forest type*, and the latter as a factor nested in *forest system*, with *tree species* being a random factor.

Differences in species richness, relative abundance and the number of singletons of beetle assemblages on snags with different environmental attributes were analysed with one-way ANOVA. For these analyses, quantitative variables were transformed into factor variables comprising four levels each (height: ≤ 10 m, > 10 to ≤ 15 m, > 15 to ≤ 20 m and >20 m; diameter: ≤ 20 cm, >20 to ≤ 30 cm, >30 to ≤ 40 cm and >40 cm; bark cover: 0%, >0% to ≤ 50%, >50% to < 100% and 100%).

True snag beetle species accumulation curves were generated for both forest systems (*Noyau central* and plantations) after 100 randomisations, using the programme EstimateS (Colwell 1997).

We performed detrended correspondence analysis (DCA; McCune and Grace 2002; Hill and Gauch 1980) to ordinate snags according to their saproxylic beetle composition and abundance. The analysis was run with the programme PC-Ord 4.28, using default parameter settings (McCune and Mefford 1999). Canonical correspondence analysis was conducted using the same programme to examine the relationship between selected environmental data and true snag beetle assemblages (CCA; Ter Braak 1986, 1994). For this analysis, categorical variables were transformed into binary dummy variables. Because inclusion of correlated groups of variables may yield unreliable results (Ter Braak 1986), variables were first tested for correlations using Pearson's correlation coefficient (SPSS 12.0). Four uncorrelated, biologically relevant variables were retained. Axis scores were standardised according to the method of Hill (1979) and scaled to optimise the representation of sampling units (snags). Snag scores were considered as linear combinations of environmental variables. The correlation between the species matrix and the environmental variables matrix was tested at 100 Monte Carlo randomisations. Following a recommendation of McCune (personal communication), we only report *P*-values for axis one because simple randomisation tests for subsequent axes may be constrained by the interdependence with previous axes.

To test the hypothesis of no difference between two or more groups of snags (e.g., exotic *versus* native trees), and to measure the average distance within groups (used as heterogeneity measure; Grove 2002a), we applied multi-response permutation procedures (MRPP, PC-Ord 4.28).

Beetle species showing preferences for particular tree species or forest systems were determined according to the indicator species method of Dufrêne and Legendre (1997), using PC-Ord 4.28. For this analysis, dead and live trees of the same species were considered as separate habitats, and the whole dataset was included.

Results

Overall, we collected 2,275 beetle specimens, representing 348 species in 38 families (Table 2). Singletons made up 41% of the total beetle catch. Sixty-seven and 163 species, respectively, were sampled only on control trees and snags, and 118 species on both live and dead trees.

We found no significant difference in species richness, relative abundance and the number of singletons between traps mounted at 70 cm and 200 cm above the ground (Table 3). Likewise, MRPP using rank-transformed Euclidean distance found no significant differences among traps ($P = 0.19$). For further analyses, catches of both traps were therefore pooled, yielding a single datum (total catch) per tree.

Table 2. Total species richness of beetle families sampled on both snags and control trees, and species richness of true snag beetles. Only families with at least four species are listed.

	Species richness	
Family	All beetles	True snag beetles
Tenebrionidae	48	24
Carabidae	42	25
Erotylidae	34	23
Cerambycidae	24	7
Elateridae	24	16
Scarabaeidae	21	9
Anthribidae	20	16
Histeridae	13	7
Mordellidae	13	5
Scolytidae	13	2
Colydiidae	10	8
Nitidulidae	10	1
Pselaphidae	9	4
Scaphidiidae	8	5
Buprestidae	5	3
Cucujidae	5	2
Endomychidae	5	5
Trogossitidae	5	5
Eucnemidae	4	1
Other families (18)	35	18
Total	348	186

Table 3. Mean (± SE) species richness, relative abundance and the number of singletons of beetles collected with trunk window traps at 70 cm and 200 cm above ground level (all traps included).

	Trap height (cm)		*t*-value	Significance
Summary variable	70	200	(df = 31)	(2-tailed)
Species richness	18.9 ± 1.4	18.6 ± 1.0	-0.256	0.800
Relative abundance	38.6 ± 6.1	32.4 ± 2.7	-1.437	0.161
Singletons	13.2 ± 1.0	12.6 ± 0.7	-0.646	0.523

In contrast, we found highly significant ($P < 0.001$) differences among snags and live control trees for all summary variables (Figure 1). Species richness ($t = -5.89$, df = 15), relative abundance ($t = -5.27$) and the number of singletons ($t = -4.73$) were always higher for snags than for control trees (species richness: 38.2 ± 1.7 *versus* 25.6 ± 1.7; relative abundance: 96.0 ± 15.5 *versus* 46.4 ± 5.2; number of singletons: 23.5 ± 1.2 *versus* 17.2 ± 0.8). All nominally significant effects were also significant at $P < 0.01$ after sequential Bonferroni adjustment.

Beta-diversity was similar among beetle assemblages collected on snags ($\beta_W = 7.3$) and control trees ($\beta_W = 7.2$), representing 46% and 45%, respectively, of the maximum value ($\beta_{W\_max} = 16$).

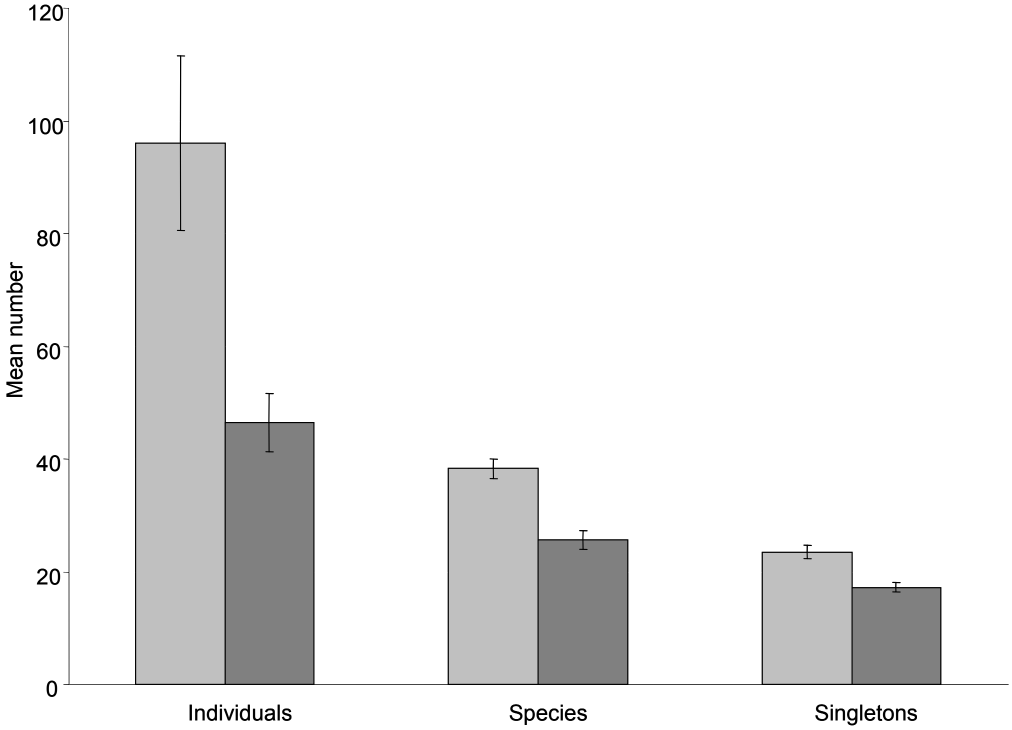

Figure 1. Mean (± standard error) species richness, relative abundance and number of singletons on snags (light grey) and live control trees (dark grey). All differences are significant at P < 0.01 after sequential Bonferroni adjustment.

One hundred eighty-six species (611 specimens) were found to be true snag beetles (Table 2). Fifty-two percent of these were singletons. Beta diversity of true snag beetle assemblages was 9.6, representing 60% of the maximum value ($\beta_{W\_max} = 16$). Beta-diversity was slightly higher in the *Noyau central* ($\beta_W = 5.85$) than in plantations ($\beta_w = 5.01$), representing 73.2% and 65.6%, respectively, of the maximum ($\beta_{W\_max} = 8$). Overall, more species were collected on native snags in the *Noyau central* than on exotic snags in plantations (Figure 2). Fifty-five and 104 species, respectively, were sampled only on exotic or on native snags, and 27 species on both exotic and native snags. Likewise, species richness, relative abundance and the number of singletons per snag were higher in the *Noyau central* than in plantations, however, these differences were not statistically significant (Table 4).

Table 4. Mean (± SE) species richness, relative abundance and the number of singletons of true snag beetles in the *Noyau central* and in plantations.

	Forest system			
Summary variable	Plantations	*Noyau central*	$F_{1,14}$	Significance
Species richness	16.4 ± 1.5	22.4 ± 2.6	3.211	0.095
Relative abundance	34.7 ± 8.1	41.6 ± 6.6	0.994	0.336
Singletons	11.0 ± 0.9	14.5 ± 1.6	3.006	0.105

We found no significant differences in species richness, relative abundance and the number of singletons among tree species (range of *P*-values: 0.110–0.186). Furthermore, most environmental factors had no significant effect on these summary variables after Bonferroni correction. An exception was the relative abundance of true snag beetles which was significantly higher on snags with fruiting bodies of polypore fungi than on snags without fruiting bodies ($F_{1,14} = 9.8$, $P = 0.007$).

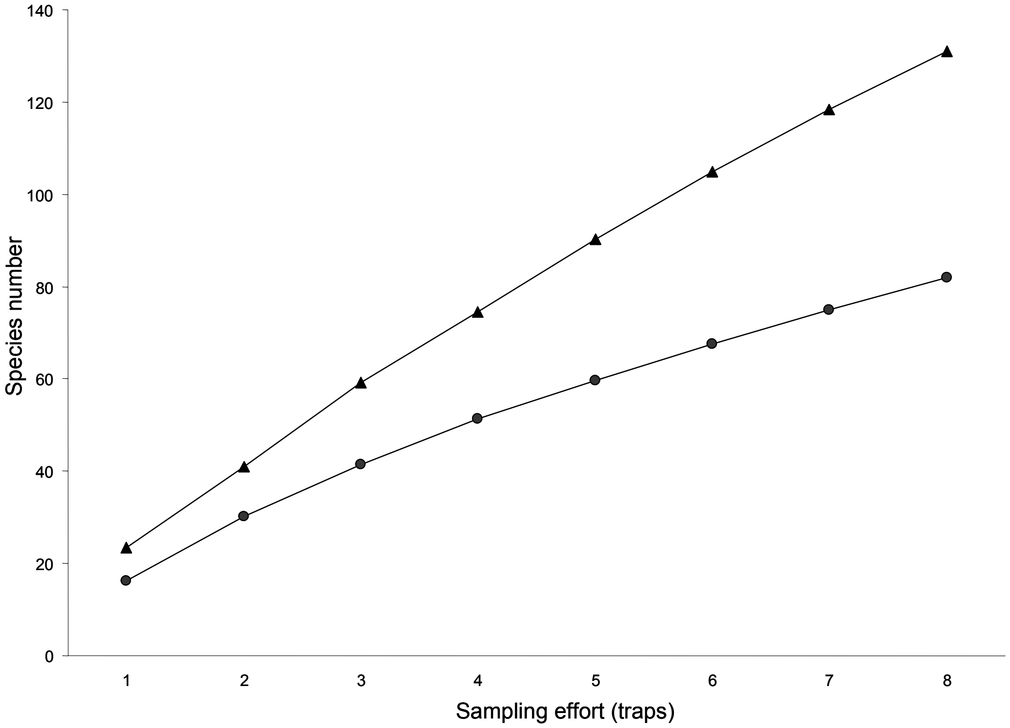

Figure 2. Species accumulation curves for true snag beetle assemblages in the *Noyau central* (triangles) and in plantations (circle).

Detrended correspondence analysis of true snag beetle assemblages differentiated exotic snags in plantations and native snags in the *Noyau central* (Figure 3). The grouping along axis one was more homogenous for exotic than for native snags which were more widely dispersed (average Euclidean distance: 0.365 *versus* 0.572). Furthermore, native snags from degraded forest of the *Noyau central* plotted close to exotic snags from plantations. Because DCA ordination axes are scaled according to the average standard deviation of species turnover, the first axis can be interpreted directly to assess the heterogeneity of snag assemblages (Bestelmeyer and Wiens 1996; McCune and Grace 2002). Standard deviations of one and four, respectively, correspond to approximately 50% and 100% species turnover. With an ordination length of six standard deviations, the species turnover observed in our study was one and a half times higher than the full turnover, indicating a very strong heterogeneity (high β-diversity) of snag beetle assemblages among snags.

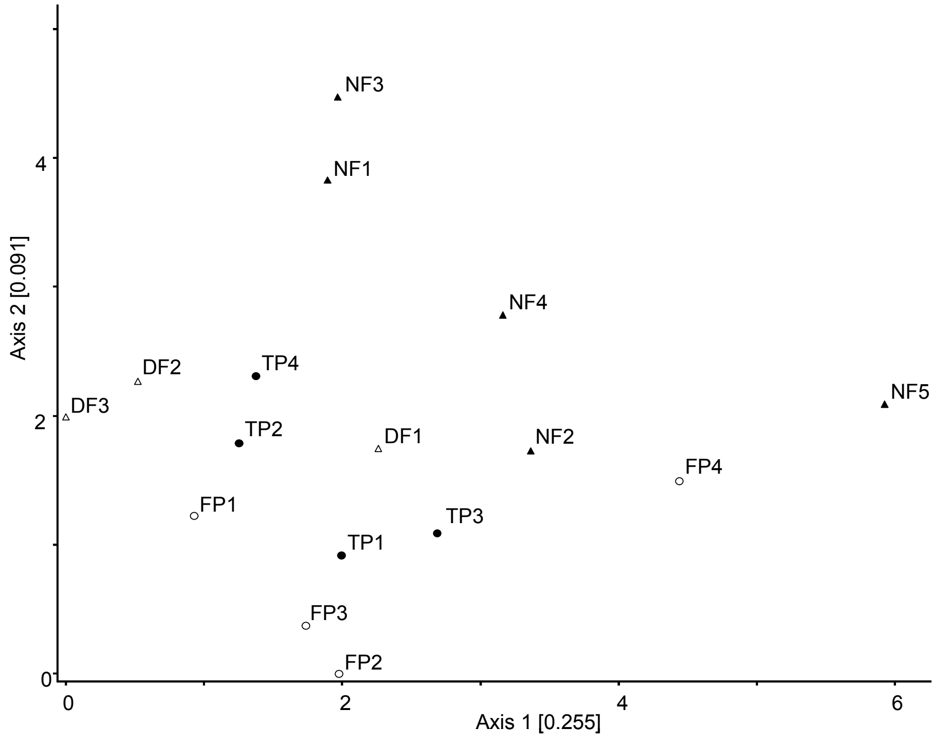

Figure 3. Detrended correspondence analysis of snag beetle assemblages in the *Noyau central* (triangle) and in plantations (circle). NF1–5 (filled triangle): natural forest; DF1–3 (open triangle): degraded forest; TP1–4 (filled circle): teak plantations; TP1–4 (open circle): fuelwood plantations.

The first three axes of the CCA-ordination explained only 23% of the total variance in the true snag beetle data (Table 5). Of the four environmental variables, forest system accounted for the highest percentage of the total variance explained. This value, even though relatively low, was significant at $P < 0.05$.

The number of beetle species with significant preferences for particular tree types or species differed. When comparing control trees and snags, we found only snag species specialists (two Scolytidae species, and one species each of Cerylonidae and Scydmaeidae). On the tree species level (based on an analysis of five species), we found seven snag specialists (one species in each of the families Anthribidae, Ceratocanthidae, Colydiidae, Scaphidiidae, Scarabaeidae, Scolytidae and Scydmaenidae) and one live tree specialist (Scarabaeidae).

Table 5. Summary statistics for the first three CCA axes. The analysis was performed using a primary matrix of snag beetle assemblages and a secondary matrix of four environment variables and their canonical coefficients.

Canonical axis	1*	2[a]	3[a]
Eigenvalue	0.718	0.641	0.535
Percentage of variance explained	8.7	7.8	6.5
Cumulative percentage of variance explained	8.7	16.5	23.0
Pearson correlation (species–environment variables)	0.993	0.983	0.967
Environmental variables (Canonical coefficients)			
Forest system	1.405	0.078	0.174
Sun exposure	-0.297	1.235	0.310
Percentage of bark remaining	-0.573	-0.191	1.029
Diameter	0.105	0.121	0.412

* significant at $P = 0.05$; [a] significance not computed (see explanations in data analysis)

Discussion

Abundant life in dead wood

The high diversity and abundance of saproxylic beetle assemblages on individual snags – irrespective of forest system – provides impressive evidence of the importance of this type of dead wood for invertebrate diversity in Lama forest.

Even though species richness, relative abundance and the number of singletons were slightly higher on snags from the *Noyau central* than on those from plantations (see Table 3), no significant differences were found. This surprising result shows that the widely scattered snags in plantation forests are a rare yet readily colonised resource for saproxylic beetles. This may be related to the greatly enhanced attractiveness of isolated, rare snags in forests that provide few alternative dead wood habitats (Schroeder et al. 1999). Nevertheless, as expected, overall species richness was much higher in the *Noyau central* than in plantation forests (see Figure 2), and about twice as many species were encountered exclusively there than in plantations, indicating a high species turnover among snags from natural and degraded forest.

Snags are not all the same

Window traps mounted on control trees were supposed to intercept insects flying in a random fashion, and those mounted on snags to intercept these random passengers plus insects that are specifically attracted to dead wood or fungi growing on dead wood. Therefore, we expected the snag fauna to be more homogenous. However, beta-diversity was similar among snags and control trees, indicating that snag beetle assemblages were as heterogeneous as passenger assemblages. This was also reflected in the large scale of DCA axis one which spanned six standard deviations, and in the low percentage of variance explained by the environmental variables. The heterogeneity of snag beetle assemblages mirrors a strong heterogeneity of dead wood habitats but may also be related to different spatio-temporal colonisation patterns. Kaila (1993) proposed that the colonisation of dead wood substrate strongly depends on the presence of similar substrates in the surroundings. In the plantations of Lama forest, the overall biomass of snags and other types of dead wood is low, and densities are less than one snag per hectare, compared to up to 15 snags in natural forest (see Chapter 3). This suggests that saproxylic beetle diversity might be greatly enhanced by management practices promoting snag and other dead wood resources.

Effects of environmental factors

Of the six snag habitat attributes (environmental factors) examined with ANOVA, only the presence of fruiting bodies of polypore fungi (sexual stage of the fungal life-cycle) had a significant effect, and this only with respect to the relative abundance of saproxylic beetles. Fruiting bodies of polypore fungi, in particular those that decay, are a substrate that hosts a very diverse beetle fauna (Kaila et al. 1994; Jonsell et al. 2003). In our study, fruiting bodies were found only on three snags, giving the impression that saproxylic beetles specialised on fungal substrate must be rare. However, many wood-decaying fungi are cryptic, and their actual density and diversity – hence the quantity and quality of fungal substrate available to saproxylic beetles – cannot be inferred from the abundance of fruiting bodies (Jonsell et al. 2003).

Fruiting bodies were not included as a factor in the CCA because their occurrence was significantly correlated with sun exposure. Of the four variables included in the CCA, forest system was the most important determinant of saproxylic beetle assemblages, followed by sun exposure and bark cover.

The dependence of the snag beetle fauna on the forest system is a straightforward result. Both natural and degraded forest of the *Noyau central* are composed of native tree species only and are no longer subjected to anthropogenic disturbances (Specht 2002). In contrast, plantations are composed mainly of exotic tree species and are exposed to high levels of disturbance such as thinning, logging, clearing and firewood collecting. However, our interpretation is strongly constrained by the nesting of snag species (representing dead wood quality) in forest system (representing an environmental matrix). As a consequence, differences in beetle assemblages may be related to only one or both of these factors. To distinguish these factors, it would be necessary to compare the fauna of exotic snags in natural forest and/or native snags in plantations. First evidence from translocation experiments with freshly cut wood showed that preferences of saproxylic beetles may differ depending on whether the resource is provided in natural forest or plantations (see Chapter 2). Further studies are clearly necessary to address this issue. An equally important aspect is the effect of snag and other dead wood biomass on snag beetle assemblages.

Sun exposure was the second most important habitat attribute affecting the snag beetle fauna in Lama forest. This confirms observations from boreal forests. These studies found that the species richness of dead wood specialists, including rare and threatened beetles, was correlated with sun exposure (Kaila et al. 1997; Sverdrup-Thygeson and Ims 2002). Even though no significant effect of sun exposure on species richness was found in our study, snags with the highest beetle species richness were situated in clearcuts, i.e. on sites with high sun exposure.

Snags in open areas are likely to be visited more frequently, because the flight activity of insects is greater in open sunshine than in shade (Jonsell et al. 2004). High flight activity in clearcuts, high attractivity of isolated snag and location in ecotone (between natural forest and plantations) may explain the ordination of snags of clearcuts around exotic snags of plantations.

The percentage of bark remaining also affected saproxylic beetle assemblages. Snags with a larger proportion of bark remaining provide a greater diversity and quality of microhabitats than nude snags. Moreover, bark substrate is rich in nutrients and protects dead wood-inhabiting invertebrates from predation and desiccation (Sverdrup-Thygeson and Ims 2002).

Snags support specialists

Despite an unfavourably high percentage of singletons, our indicator analysis identified several snag tree specialists. It has been suggested that the heterogeneity of dead wood habitats promotes a high degree of specialization among the saproxylic beetle fauna (Kaila et al. 1997), which in turn allows the co-occurrence of a diversity of species on a single dead tree. In the *Noyau central*, resource availability and diversity (tree species, stages of decay, exposure, etc.) may have been sufficiently high to reduce competitive exclusion. In contrast, the scarcity of dead wood resources in plantations makes competitive exclusion more likely, resulting in a more depauperate saproxylic beetle fauna (Hugueny and Cornell 2000; Grove 2002a).

Unfortunately, highly specialized species are particularly sensitive to environmental changes and disturbances, and may be threatened if their habitat is destroyed or highly fragmented (Lawton 1995).

Conclusions

The present study showed that dead native trees in natural and degraded forest and dead exotic trees in plantations harbour very different beetle assemblages. Thus, all snags, wherever they stand, contribute to the overall conservation of saproxylic beetles. Nevertheless, species richness and beta-diversity were clearly lower in plantation forests, which was probably related to the scarcity of dead wood substrate. This offers the opportunity to enhance the diversity of the saproxylic fauna in plantations by increasing the dead wood stock (Kirby et al. 1998). Different options are at hand, including the protection or creation of snags of plantation species. Moreover, when adopting a long-term strategies to integrate biodiversity conservation into tropical forestry, native trees could be planted or allowed to regrow spontaneously within plantation schemes so as to provide a stock of native trees that mature and die in plantations (Lamb 1998). The retention of snag is not the only measure that can be taken to protect saproxylic species. Limbs (dead branches on live trees), lying trunks and smaller dead wood items could also be retained or created to increase the diversity and quantity of dead wood substrate (Schiegg 1999; Ehnström 2001).

Further studies are required to elaborate specific dead wood management techniques for the protection of the saproxylic fauna in Lama forest.

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SUMMARY AND CONCLUSIONS

Tropical forest ecosystems worldwide are suffering from anthropogenic pressures leading to deforestation and forest degradation, and resulting in a loss of biodiversity. Because tropical forests sustain over half of the planet's life forms, their destruction might evoke an ecological crisis of global dimension. However, in spite of an increasing awareness of the general public and political authorities, tropical forests continue to deteriorate unabatedly, and numerous species are getting extinct every day. At the same time, large-scale reforestation and afforestation programmes in the tropics have been launched to produce timber and fuelwood. Moreover, it has been proposed that plantation forests have an important role to play in maintaining or enhancing regional biodiversity pools and in alleviating anthropogenic pressures on the natural forests remaining. Consequently, studies about the role of forest plantations for biodiversity conservation are emerging worldwide. However, there is a dearth of information from Africa, and basically none about the arthropod fauna in African forest plantations. The present study steps into this gap and aims to generate baseline data about the diversity of arthropods in natural and plantation forests in tropical West Africa. In doing so, it wishes to encourage and inspire the development and implementation of conservation-oriented forest management strategies.

We studied arthropod assemblages in the Lama forest reserve in Southern Benin, an area harbouring one of the last remnants of natural forest in the Dahomey gap. We compared arthropods from different types of forest, including natural, degraded and plantation forest. The fully protected core of the reserve, the so-called *Noyau central*, is composed of a small-scale mosaic of natural and degraded semi-deciduous Guineo-Congolian forest. It is surrounded by teak (*Tectona grandis*) and fuelwood (predominantly *Senna siamea*) plantations. The particular geographical configuration of the reserve provided an ideal set-up to study the impact of different forestry management systems on arthropod diversity and the role of plantations for biodiversity conservation.

In the first chapter, we give an **overview of arthropod diversity in the Lama forest reserve**, focusing on species related to biomass decomposition, and highlight its importance for biodiversity conservation. No differences in arthropod species richness were found among different forests types within the *Noyau central*. However, great differences were observed between forest plantations. Of the environmental variables influencing arthropod assemblages, soil type was the most important natural factor, and species richness was highest in soils with coarse texture (old plantations and isolated forest fragments). The remaining variables naturalness, understorey cover and canopy height are related to silvicultural practices and are therefore amenable to an improved, conservation-oriented forest management. High values for β-diversity suggest that all major forest habitats contribute significantly to regional species pools und should therefore be protected.

Chapters two to four deal with beetles dependent on dead wood (saproxylics). Saproxylic beetles are an exceptionally species-rich ecological group. Moreover, they are known to be highly sensitive to forest management and are therefore particularly endangered. Despite this, invertebrate diversity studies in Africa have largely ignored saproxylic beetles and their dead wood habitat.

In the second chapter, we investigate **the attraction of freshly cut wood for pioneer beetles, using a newly designed trap** (twin-Malaise trap) baited with native and exotic wood and exposed in both natural and plantation forests. Six species showed primary attraction and two repulsion. Three species were native wood specialists, but none were teak specialists. Among the beetles showing primary attraction, we found no economically important pest species. The twin-Malaise trap proved to be a suitable device to examine the primary attraction of beetles. However, our study also showed that the entire spectrum of wood-associated beetles cannot be sampled with this type of trap.

In the third chapter, the **diversity of saproxylic beetles and their interaction with dead wood** are examined for the first time in an African tropical forest. Both the quantity and quality of dead wood resources differed greatly among natural forest and plantations. Dead wood of advanced decay stage and larger size was basically absent in plantations. Despite this paucity of dead wood, saproxylic beetle diversity in teak and fuelwood plantations was surprisingly high. Nonetheless, overall species richness of saproxylic beetles was higher in natural forest, and wood beetle assemblages differed clearly between natural forest and plantations. The volumes of recently dead wood, large pieces of dead wood, coarse woody debris and standing dead trees were found to have the most significant influence on the composition of saproxylic beetle assemblages.

The last chapter focuses on **standing dead trees (snags)**. We found similar species richness of saproxylic beetle assemblages from native and exotic snags. However, overall species richness and β-diversity were higher for native snags, reflecting higher habitat heterogeneity in the protected forest. Species assemblage composition, influenced mainly by the forest system, revealed high heterogeneity, especially among snags of native tree species. Our results showed that retaining or even creating snags is crucial to the protection of saproxylic beetle assemblages.

The results presented here provide evidence that the cultivation of exotic trees in the vicinity of natural forest may be an important element in biodiversity conservation. The system practiced in Lama forest, which combines different management intensities from unmanaged natural forest to intensively managed, short-rotation fuelwood plantations, goes well beyond the single-objective forestry approaches practiced in other tropical areas. The functional and spatial diversity of Lama forest is reflected in a high diversity of saproxylic beetles and other arthropods. The forest ecosystem as a whole benefits from the diversity and abundance of these invertebrates and the ecological services they provide (decomposition, nutrient cycling). Last not least, the rich and varied invertebrate fauna promotes species higher up the food chain feeding on them.

Several conservation-oriented management measures can be proposed to foster the role of plantation forests as habitat surrogates for forest species. In the short term, the regeneration and development of species-rich understorey vegetation of the Guineo-Congolean phytogeographical region should be promoted in plantations. Moreover, different types of dead wood should be retained to improve the resource base for saproxylic beetles. When adopting long-term strategies that aim to integrate biodiversity conservation into tropical forestry, native trees should be planted or allowed to regrow spontaneously within plantation schemes so as to provide a stock of trees that mature and die in plantations.

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