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The diversity and abundance of ants in relation to forest disturbance and plantation establishment in southern Cameroon

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Summary

1. Tropical biodiversity is seriously threatened by deforestation but few studies have quantified its impact. We aimed to measure the impact of forest clearance and different methods of establishing *Terminalia ivorensis* (Combretaceae) forest plantations on the abundance, richness and composition of ants, the most abundant group of arthropods in tropical forest canopies, in the Mblamayo Forest Reserve in Cameroon. For canopy ants, we quantified the effects of different methods of plantation establishment by sampling two sets of plots subjected to complete clearance, partial mechanical clearance and partial manual clearance relative to uncleared forest reference plots. For leaf-litter ants, we quantified the impacts of different levels of forest disturbance along a gradient from near primary forest to complete forest clearance.

2. A total of 97 ant species was recorded from the canopy (from approximately 48 500 individuals), at an average of 213 (±45) ants m^{-2}. Jack-knife estimates of species richness showed that at one site, Bilik, 87% more species occurred in the partial manual clearance plot than the complete clearance plot, with the partial mechanical clearance plot intermediate. At the other site, Ebogo, ant richness did not vary between treatments. Ants were 20 times more abundant in the partial manual clearance plot in Ebogo than the partial manual clearance plot in Bilik, largely due to a numerous *Technomyrmex* species that might have reduced ant richness on this plot.

3. Cluster analysis of the similarities in ant species composition between plots, calculated by the Morisita index, showed that site and treatment affected species composition. Neither treatment nor site affected the relative number of species in different nesting categories.

4. A total of 111 ant species (from 3650 individuals) was recorded from the leaf litter, at an average of 52 (±4·6) ants m^{-2}. Species numbers were greatest in the two partial clearance plots in Ebogo (52–53 species), lowest in the two complete clearance plots (37), and intermediate and most variable in the three uncleared forest plots (40–52). Cluster analysis showed that species composition was not affected by treatment, while neither treatment nor site affected the relative number of ant species in different feeding categories.

5. Despite some local effects by dominant species, our results support the view that deforestation can reduce arthropod species richness. This study is unique in showing that reforestation methods (using a single tree species) can have a marked effect on arthropod species richness and composition. Specifically, it reveals that ant species richness can be greater in plantations established after partial manual clearance than complete clearance.

Key-words: deforestation, forest canopy, Formicidae, leaf litter, reforestation

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Introduction

It is generally considered that two groups of macro-arthropods, termites and ants, dominate tropical rain-forests in abundance, biomass and ecological roles. Termites are important as decomposers and by virtue of their numerical dominance of the below-ground arthropod community (Eggleton *et al.* 1995, 1996; Davies *et al.* 1999). In contrast, the arthropod community of tropical forests canopies is dominated numerically by ants (Erwin 1983; Adis, Lubin & Montgomery 1984; Floren & Linsenmaier 1997; Watt *et al.* 1997a,b). Ants also dominate the macro-arthropod ground fauna of tropical forests (Levings & Windsor 1985; Stork & Brendell 1990; Belshaw & Bolton 1993; Kaspari 1996a, b). This paper describes the impact of forest clearance and different methods of establishing forest plantations on the abundance, richness and composition of the ant fauna of the Mblamayo Forest Reserve in Cameroon. It is part of a series that details many aspects of the relationship between biodiversity, forest disturbance and reforestation at this same site (Eggleton *et al.* 1995, 1996; Watt *et al.* 1997a,b; Lawton *et al.* 1998).

Although not as speciose globally as the Coleoptera, Hymenoptera (Parasitica) and Diptera, ants can contribute significantly to local species richness. For example, Wilson (1987) recorded 43 species from a single tree in Peru; Harada & Adis (1997) recorded 82 species on a single tree in Brazil; Stork (1991) recorded 98 species from 10 trees in Borneo; and Floren & Linsenmaier (1997) recorded 192 species from 19 trees in Sabah, Malaysia. Ants are also relatively well known taxonomically, both in West and Central Africa, and for the world as a whole (Bolton 1994, 1995). Their biology has been recorded as well as almost any other invertebrate group (Hölldobler & Wilson 1990), and they are often used as indicators, for example of pollution and restoration success (Madden & Fox 1997; Rabitsch 1997; Majer & Nichols 1998). Ants perform several significant functional roles, particularly as predators of other arthropods and tenders of leaf-sucking insects (Hölldobler & Wilson 1990; Way & Khoo 1992; LaSalle & Gauld 1993, Itioka & Inoue 1996). Many species of tropical plants have a symbiotic relationship with ants because many ant species provide protection from other insects and perhaps from pathogens.

Tropical deforestation, estimated to be occurring at around 1% per annum overall and 2·2% in West Africa (Whitmore & Sayer 1992; World Conservation Monitoring Centre 1992), poses a major threat to the biodiversity of tropical rain forests. Although deforestation rates in Cameroon were lower during the 1980s than elsewhere in West Africa, at about 0·4–0·6% per annum, more recent data for tropical log production suggest an increasing rate of deforestation in Cameroon in particular (Johnson 1995). However, our understanding of the impact of deforestation on global species richness is extremely poor. Attempts have been made to quantify impacts on species extinction, resulting in estimates of global species extinction rates of 1–10% species per decade (Reid 1992; Mawdsley & Stork 1995). These estimates have all been obtained by extrapolating from known relationships between species richness and habitat area, global estimates of the species richness of arthropods and other organisms, and estimates of actual and projected deforestation.

However, the fate of many species of organisms following forest clearance is uncertain (Lugo 1988) and there is a need to measure directly the impact of deforestation and forest disturbance on insect diversity. There is also a need to quantify the impact on insect diversity of establishing forest plantations and other land uses after deforestation. We aimed, therefore, to quantify the impact on the richness and composition of the ant fauna in the Mblamayo Forest Reserve of (i) forest clearance and (ii) different methods of establishing plantations of the native tree *Terminalia ivorensis* A. Chev (Combretaceae). The values of contrasting methods of plantation establishment were studied, specifically the establishment of plantations after complete forest clearance and after different methods of partial forest clearance. Both canopy and leaf-litter ants were studied, in the former case to quantify the effects of different methods of plantation establishment, and in the latter to quantify the impacts of different levels of forest disturbance along a gradient from near primary forest to complete forest clearance.

Terminalia ivorensis is a rapidly growing tree that has been used in more than 100 plantations covering over 4000 ha of Côte d'Ivoire, Nigeria, Ghana and Cameroon, and it has also been planted in Trinidad, Fiji and Central Africa (Lawson *et al.* 1990; Lawson 1994). It is one of the most important timber trees in Africa, accounting for 2–5% of timber exported from Africa to Europe (Sayer, Harcourt & Collins 1992) and has been the subject of considerable research as a potential plantation tree (Lawson *et al.* 1990).

Materials and methods

FOREST MANAGEMENT AND REGENERATION PROJECT

The research described in this paper formed part of the Forest Management and Regeneration Project (FMRP; 1990–96), a bilateral project between the Government of Cameroon's Office National de Dévéloppement des Forêts and the UK Department for International Development. Details of this project are given by Lawson (1994), Lawson *et al.* (1990) and Watt *et al.* (1997b).

TREATMENT PLOTS

In 1987–88, two replicate sets of plots, 3 km apart, were established at Bilik and Ebogo within the Mbalmayo Forest Reserve, Cameroon (11°25′–11°31′E 3°23′–3°31′N), under the following treatments.

Complete clearance. All large trees were felled by chainsaw, then cleared along with the smaller trees and all remaining vegetation by bulldozer; the resulting effect was that all above-ground plant material was removed and there was considerable soil compaction due to the bulldozer.

Partial mechanical clearance. A bulldozer was used to remove most of the undergrowth and approximately 50% of the large trees, resulting in a reduction of about 50% in the canopy cover; the use of the bulldozer also resulted in some soil compaction.

Partial manual clearance. Ground vegetation and some small trees were removed by machete, and some other small trees were felled by chainsaw; this technique resulted in minimal soil compaction.

Uncleared forest reference. No trees were cut or removed, there was no ground disturbance by machinery, no trees were planted, and very little ground vegetation was cleared for narrow access lines.

In 1991, a more extensive series of plots was established in the Mbalmayo Forest Reserve. These plots, all near Eboufek village, included the following treatments (Lawson 1994).

Complete clearance. As in Bilik and Ebogo described above, except that felled trees were pushed into windrows (rows of cleared vegetation) every 40–50 m (i.e. two per 1-ha plot).

Uncleared forest reference. As for Bilik and Ebogo. All plantation plots sampled were planted with *T. ivorensis* (framiré) at spacings of 5 × 5 m. Although this species is found in Cameroon, it does not occur naturally in the wild in the Mbalmayo area. The related species *T. superba* occurs naturally within the Reserve and is the fifth most common tree species in Bilik and Ebogo (Lawson *et al*. 1990). Since 1972, several plantations of *T. ivorensis*, totalling about 1000 ha, have been established in the Mbalmayo area, although many have failed, principally through lack of management (Lawson *et al*. 1990). A total of three uncleared forest plots were sampled in the Mbalmayo Forest Reserve (at Bilik, Ebogo and Eboufek). While it is known that logging has taken place in the Reserve several times, there are no detailed accounts of where and when logging took place. However, the evidence, in particular the presence/absence of logging trails and the size of trees in each plot, strongly suggested that the Bilik plot had not experienced logging for some considerable time. This plot was, therefore, defined as 'near primary', and the Eboufek plot, which contained an old logging trail that was widened during the course of the study, as 'old secondary' (Eggleton *et al*. 1995). The Ebogo plot could also be classified as near primary.

CANOPY SAMPLING

Tree canopy sampling was carried out in the Bilik and Ebogo plots in the Reserve on three occasions between 1992 and 1993. On each occasion, approximately 15 *T. ivorensis* trees in each single hectare plantation plot were either fogged or sprayed with permethrin, an insecticide with a rapid knockdown effect on insects. On each occasion 10–40 (generally 25) collecting trays, each 1 m^2, were used. The use of species accumulation curves and jack-knife estimates allowed comparisons of the species richness in different plots despite small differences in the numbers of collecting trays used (Watt *et al*. 1997b).

LEAF-LITTER SAMPLING

A survey of leaf-litter dwelling ants was carried out in November 1993 in several plots within the Reserve (Table 1). Ten 1-m^2 samples of leaf litter and top soil were collected in an approximately 50-m transect across the centre of each of the plots and across the rows of planted trees, such that half the samples were from tree rows and half were from between-tree rows. The leaf litter and top few millimetres of soil were scraped up and placed in a bag. Each sample was sieved with a coarse 1-cm mesh sieve and the residue placed in mesh bags. These were suspended in 'Winkler bags' (Davies & Stork 1996) to allow the soil and leaf-litter residues to slowly dry out, causing the insects to drop down into a pot of alcohol at the bottom of the bag. Leaf-litter samples were dried in the Winkler bags for 2 days.

Table 1. Sampling programmes for ants in the Mbalmayo Forest Reserve, Cameroon (E, Ebogo; B, Bilik; K, Eboufek). Note that the complete clearance plot at Eboufek was cleared shortly before the insect sampling, whereas the other complete clearance plots were cleared (and replanted) several years before sampling

	Plantation and forest plots sampled			
	Plantation clearance treatment			
Insect group	Complete	Partial manual	Partial mechanical	Uncleared forest
Leaf-litter ants	K, E	E	E	K, E, B
Canopy ants	E, B	E, B	E, B	

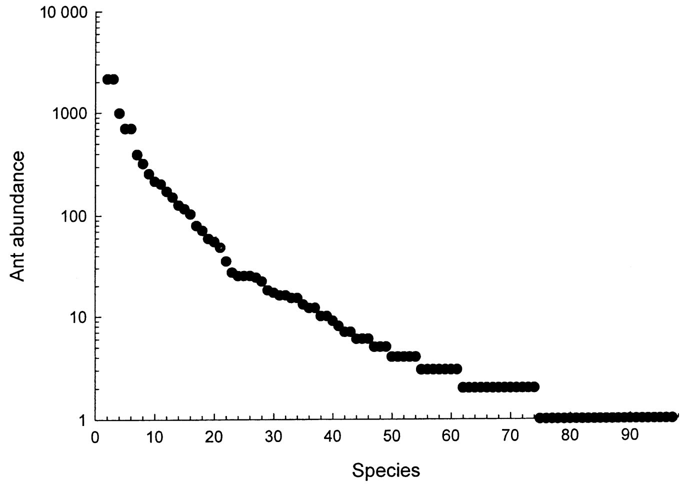

Fig. 1. Rank-abundance plot of canopy ants sampled in the Mbalmayo Forest Reserve 1992–93; abundance of each species shown on the vertical axis.

ANT IDENTIFICATION AND DATA ANALYSES

After ant identification in the Entomology Department of the Natural History Museum, London, UK, species richness was estimated by the jack-knife technique (Heltshe & Forrester 1983a,b; Krebs 1989; Colwell & Coddington 1994) using the program EstiMateS (R. K. Colwell, University of Connecticut, unpublished data). The species composition of different plots was compared with the Morisita similarity index (Krebs 1989) and cluster analysis (SAS 1990), techniques widely used to compare the species composition of plant and animal communities (Pinheiro & Ortiz 1992; Russell-Smith & Stork 1995). Canopy ant species were also classified according to their nesting strategy (B. Bolton, unpublished data): ground nesters, wood nesters, other arboreal nesters and unknown nesting habit. Litter ants were classified according to their feeding behaviour (B. Bolton, unpublished data): Collembola predators, generalists, feeding habits unknown and other categories combined (because of the small numbers recorded in some categories), i.e. termite predators, ant predators and small invertebrate predators.

Results

CANOPY ANTS

A total of 97 ant species (from approximately 48 500 individuals) was recorded from the canopy of *T. ivorensis* plantation plots in the Mbalmayo Forest Reserve in 1992 and 1993 (Appendix 1). Forty per cent of the ants were previously undescribed. The most common ant was a previously undescribed *Technomyrmex* species, which made up 80% of the total number of individual ants sampled. *Crematogaster stadelmanni*, *Crematogaster striatula* and *Crematogaster clariventris* (authorities for these and other species given in Appendix 1–2) were the next three most common species (11% of individuals) and eight other species of *Crematogaster* were among the 22 most common species overall (Appendix 1). The fifth most common ant species was *Oecophylla longinoda*, the African weaver ant. The 22 most common species together made up 99% of the total number of individuals sampled. The remaining 1% of the individuals sampled were from 75 species, 23 of which were represented by single individuals (Fig. 1).

Overall, an average of 213 (±45) ants m^{-2} was recorded, 180 (±46) m^{-2} of which were *Technomyrmex* species 2 (Appendix 1). The three most common *Crematogaster* species ranged in abundance from 3·5 to 7·5 (±1·9–1·2) m^{-2} and the average abundance of *O. longinoda* was 2·6 (±1·0) m^{-2}.

Different numbers of ant species were recorded in each of the six *T. ivorensis* plantation plots sampled (Table 2). However, the species accumulation curves showed that the numbers of species recorded was likely to be a considerable underestimate (Fig. 2a).

Jack-knife estimates of species richness showed differences in the number of species in each plot, particularly at Bilik (Table 2). At Bilik, the estimated number of ant species was greatest in the partial manual clearance plot (1993) and the partial mechanical clearance plot (1992), and lowest in the complete clearance plot (Table 2). When the data for the three sampling periods (i.e. November 1992, February 1993 and November 1993) were combined, they showed that there was an estimated 87% more ant species in the partial manual clearance plot than the complete clearance plot (with an intermediate number in the partial mechanical clearance plot) and this difference was statistically significant, as measured by 95% confidence limits (Fig. 3). No significant differences in the abundance of ants in different silvicultural treatment plots were found in Bilik (Watt *et al.* 1997b; Fig. 3).

At Ebogo, in contrast to Bilik, the estimated number of ant species was almost the same in the different plots in 1992, and was greater in the complete clearance plot than elsewhere in 1993 (although this difference was not statistically significant) (Table 2). When the data

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Table 2. The number of canopy ant species sampled and extrapolated (first-order jack-knife) in six plantation plots in the Mbalmayo Forest Reserve in November 1992 and February 1993; n = number of collecting trays ha^{-1}; CI, confidence interval

	Bilik			Ebogo		
Treatment	Complete	Mechanical	Manual	Complete	Mechanical	Manual
November 1992						
Species sampled	13	24	23	22	23	23
Jack-knife estimate	20·6	38·7	33·8	32·6	34·1	34·1
95% CI	8·9	7·4	6·6	7·1	8·7	8·7
n	15	15	15	15	14	15
February 1993						
Species sampled	22	25	32	27	17	16
Jack-knife estimate	26·7	32·7	42·3	31·0	23·7	23·5
95% CI	5·5	6·8	6·6	4·4	6·0	6·0
n	25	24	23	35	21	23

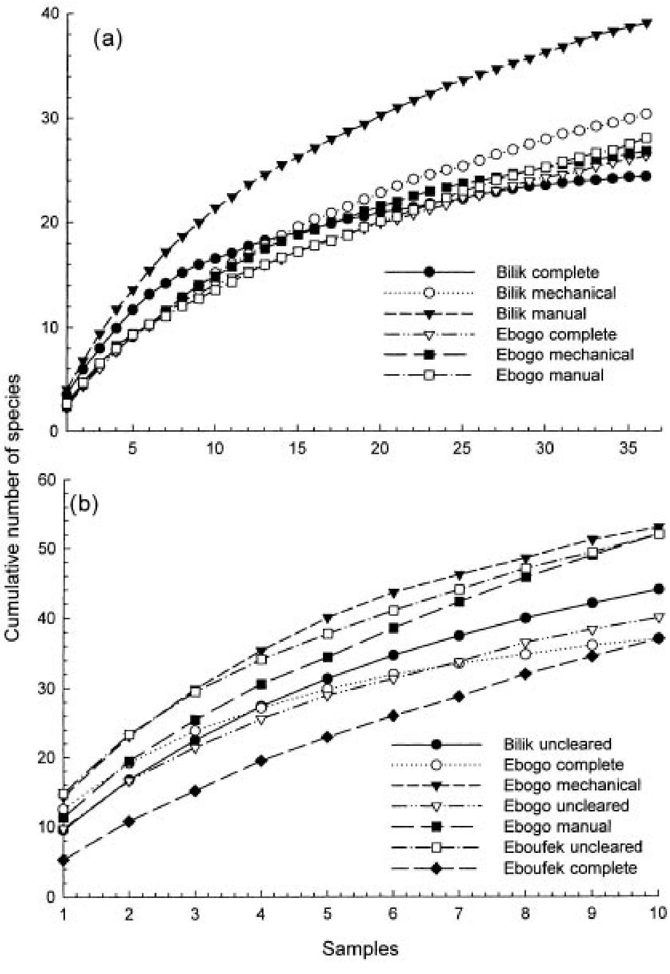

Fig. 2. Species accumulation curves for (a) canopy ants sampled in the Mbalmayo Forest Reserve 1992–93 and (b) leaf-litter ants sampled in the Mbalmayo Forest Reserve 1993.

for the three sampling periods were combined they showed that the estimated number of species was greatest in the partial manual clearance plot and least in the partial mechanical clearance plot (with an intermediate number in the complete clearance plot). However, these differences were not statistically significant (Fig. 3). In contrast to Bilik, the number of ants recorded in Ebogo was considerably higher in the partial manual clearance plots than the other plots (Watt *et al.* 1997b; Fig. 3).Thus, plantation establishment after partial manual forest clearance resulted in a greater number of ant species than establishment after complete forest clearance in both sites within the Mbalmayo Forest Reserve, but significantly at only one of the two sites.

Cluster analysis based on the Morisita index suggested that both treatment and site had an influence on

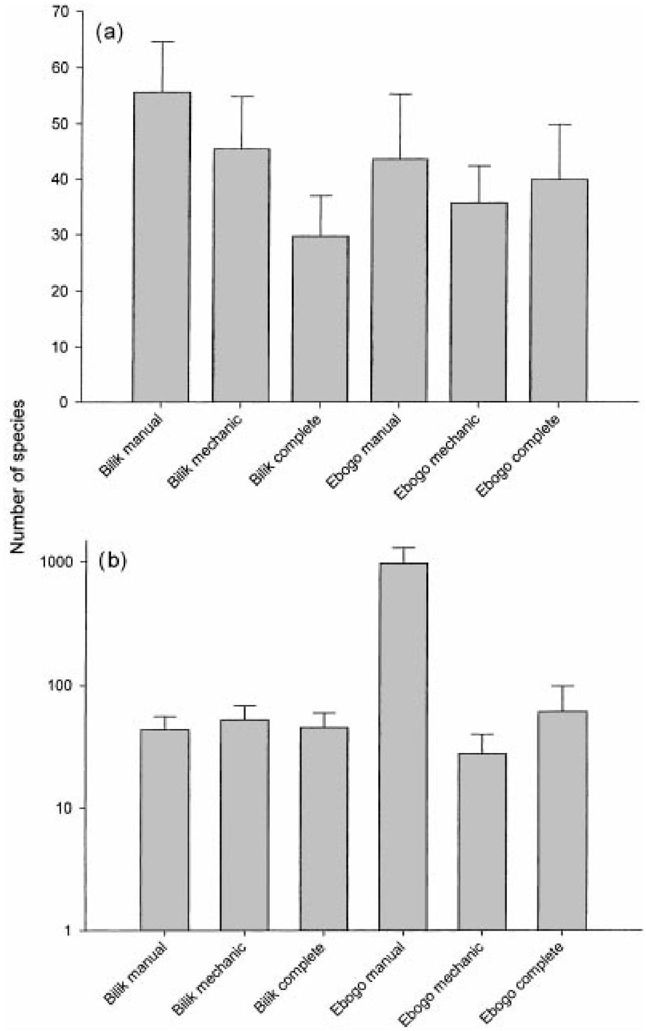

Fig. 3. Jack-knife estimates of species richness (a) and abundance (ants m^{-2}) (b) of canopy ants sampled in the Mbalmayo Forest Reserve 1992–93, sampling dates combined; standard errors given in each case.

Table 3. Similarities between the canopy ant species composition of different plots in the Mbalmayo Forest Reserve as measured by the Morisita index

Treatments	Ebogo complete	Ebogo mechanical	Ebogo manual	Bilik complete	Bilik mechanical
Ebogo mechanical	0·9803				
Ebogo manual	0·9674	0·9293			
Bilik complete	0·0552	0·0537	0·0072		
Bilik mechanical	0·0473	0·0590	0·0046	0·3916	
Bilik manual	0·0149	0·0289	0·0131	0·0736	0·4650

species composition (Table 3 and Fig. 4a). The two complete clearance plots formed one cluster and the partial clearance plots were grouped according to site.

Forty-six per cent of the ant species recorded from *T. ivorensis* canopies were arboreal nesting, 23% were ground nesting, 17% were wood nesting and 14% were of unknown nesting habit. Neither treatment nor site had an effect on the relative number of species in different nesting categories (Fig. 5).

LEAF-LITTER ANTS

A total of 111 ant species [from 3650 individuals, an average of 52 (±4·6) ants m^{-2}] was recorded from the leaf-litter samples in the Mbalmayo Forest Reserve in November 1993 (Appendix 2). The number of leaf-litter ant species recorded in different plots in the Mbalmayo Forest Reserve varied from 37 in both of the complete clearance plots to 52–53 in the (two) Ebogo partial clearance plots and the Eboufek uncleared forest plot (Fig. 2b). When the plots sampled were considered as three groups, separated according to type of management, the greatest numbers of species were in the two partial clearance plots in Ebogo (52–53), the lowest numbers of species were in the two complete clearance plots (37) and intermediate, and most variable,

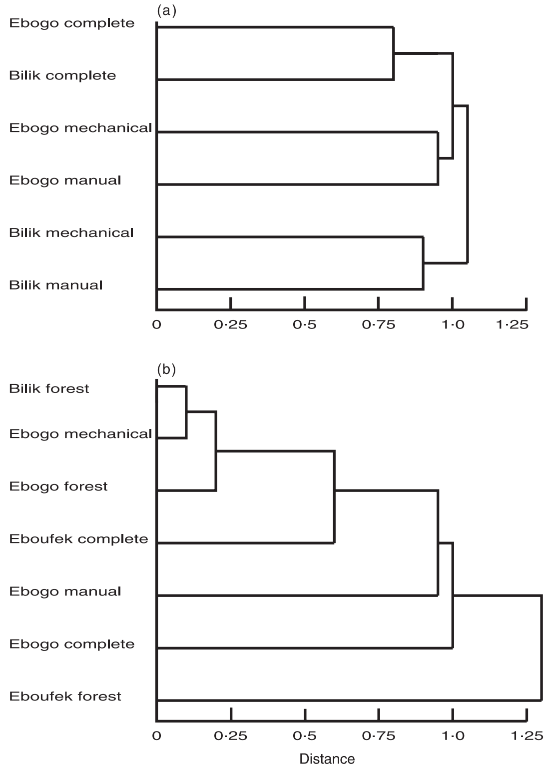

Fig. 4. (a) Plantation treatment plots grouped according to similarity of canopy ant species composition (using the Morisita index and average linkage cluster analysis). (b) Uncleared forest and plantation treatment plots grouped according to similarity of leaf-litter ant species composition (using the Morisita index and average linkage cluster analysis).

Table 4. Similarities between the litter ant species composition of different plots in the Mbalmayo Forest Reserve as measured by the Morisita index

Treatments	Bilik forest	Ebogo forest	Eboufek forest	Ebogo manual	Ebogo mechanical	Ebogo complete
Ebogo forest	0·9040					
Eboufek forest	0·7560	0·1738				
Ebogo manual	0·8669	0·5168	0·5510			
Ebogo mechanical	0·9493	0·9524	0·7168	0·8924		
Ebogo complete	0·6570	0·7327	0·5106	0·5441	0·7033	
Eboufek complete	0·7732	0·7553	0·6504	0·5404	0·8034	0·5577

numbers of species occurred in the three uncleared forest plots (40–52). The estimated species richness in each plot varied in a similar manner: an average of 76 species in the partial clearance plots, 52 in the complete clearance plots and 64 in the uncleared forest plots (Fig. 6). The confidence limits around these mean values showed that the numbers of ant species in the three treatments were not statistically different, but that the estimated ant species richness of the partial clearance plantation plots, together with two of the three uncleared forest plots, was significantly greater than those in the complete clearance and uncleared forest plots in Ebogo (Fig. 6).

These data were similar to the canopy ant data in that the plantation plots established after partial forest clearance tended to have a greater number of ant species than the plantation plots established after complete forest clearance. The data also provided some evidence to suggest that plantation establishment after partial forest clearance results in an increase in species richness in comparison to uncleared forest.

The cluster analysis for leaf-litter ants showed that species composition was not affected by treatment: there was no evidence of separate clusters for ants in the uncleared forest, partial clearance and complete clearance plots (Table 4 and Fig. 4b). Nor did the data show any effect of site (as the canopy ant data did), but it should be noted that plots used for the leaf-litter ant sampling did not provide replication of the partial clearance treatments at different sites and, therefore, the opportunity to detect site difference.

Thirty-three per cent of the litter ants had unknown feeding habits, 27% were generalists, 16% were Collembola predators, and the remainder were either arboreal species, termite predators or ant predators. Neither treatment nor site had an effect on the relative number of species of litter-dwelling ants in different feeding categories (Fig. 5).

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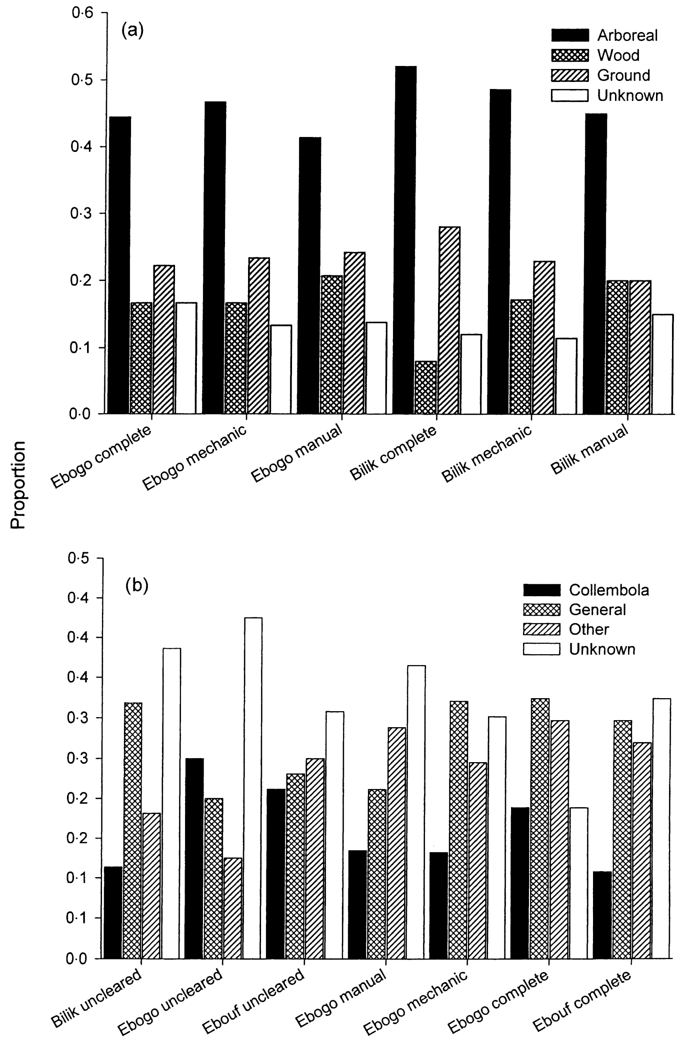

Fig. 5. Proportions of (a) canopy ants in different nesting categories [arboreal (except wood-nesting), wood, ground and nesting habits not known] and (b) leaf-litter ants in different feeding categories [Collembola-feeding, generalists, other categories (i.e. termite predators, ant predators and small invertebrate predators) combined and feeding habits not known].

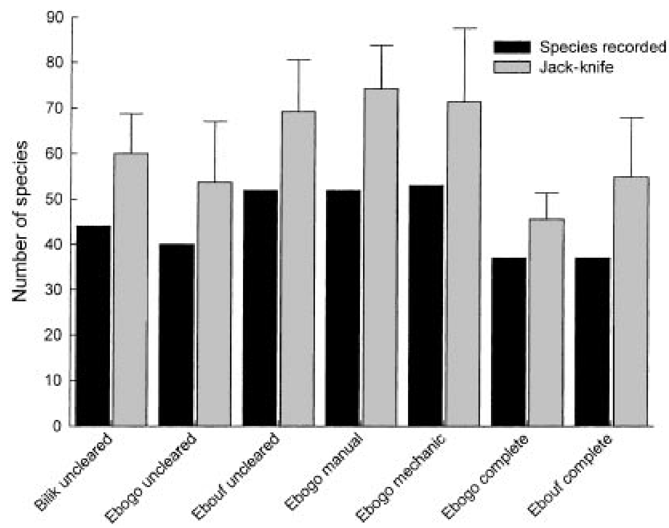

Fig. 6. Actual and jack-knife estimates of species richness of leaf-litter ants sampled in the Mbalmayo Forest Reserve 1993.

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Discussion

Both the richness and composition of the canopy ant fauna at Mbalmayo were affected by silvicultural treatment; the number of ant species was up to 87% greater in plantation plots established after partial manual clearance than plantation plots established after complete clearance of existing vegetation (Fig. 3), and cluster analysis suggested that the species composition of complete clearance plantations differed from that of partial clearance plantations (Fig. 4a). However, the canopy ant fauna of only two 'sites' within the Reserve was studied and not only did species composition vary from site to site (Fig. 4a), but the effect of silvicultural treatment on species richness was only significant at one site (Fig. 3). The latter finding may relate to the large difference in abundance of ants in the two forest sites (Watt *et al.* 1997b). Ants were 20 times more abundant in the partial manual clearance plot in Ebogo than the partial manual clearance plot in Bilik. This difference was due to the large number of a *Technomyrmex* species in the partial manual clearance plot in Ebogo, and the numerical dominance of this species may have had a negative impact on the number of ant species in this plot.

The species richness of leaf-litter ants, like that of canopy ants, tended to be greater in plantation plots established after partial forest clearance than in plantation plots established after complete forest clearance. However, silvicultural treatment had no consistent effect on leaf-litter ant species composition (Fig. 4b). There was some evidence to suggest that intermediate forest disturbance in the form of plantation establishment after partial forest clearance resulted in an increase in species richness in comparison to uncleared forest (Fig. 6). This part of the study was less intensive than the canopy part of the study, and further research on the possible impact of silvicultural treatment on leaf-litter ants is needed.

Published research on the impact of tropical forest management practices on arthropods is currently limited to studies on termites, moths, dung and carrion beetles and leaf-litter ants. Most previous studies have compared natural forest with plantations of exotic tree species such as *Acacia mangium Eucalyptus deglupta*, *Gmelina arborea*, *Pinus caribaea* and cocoa (Holloway, Kirk-Spriggs & Chey 1992; Chey 1994).

In Ghana, Belshaw & Bolton (1993) surveyed the leaf-litter ant fauna in 14 primary forest sites, 10 secondary forest sites and 10 cocoa sites. A total of 176 ant species was recorded, but there was no difference between the number of species found in the three site types, on average 26–28 species in each site. They concluded that forest clearance and the establishment of cocoa farms in Ghana had little or no effect on either the species richness or the species composition of the leaf-litter ant fauna (Belshaw & Bolton 1993). In Columbia, Estrad & Fernandez (1999) failed to find any difference in ant species richness along a transect from primary forest to pasture. Similarly, the diversity of dung and carrion beetles has been found to be unaffected by forest clearance and the establishment of plantations (Hanski & Krikken 1991). However, in central Amazonia, Vasconcelos, Vilhena & Caliri (2000) found that although logging did not affect species richness and abundance, it did affect species composition, and Davis *et al.* (2001) found that dung beetle species composition did respond to logging in northern Borneo.

A number of studies have investigated spatial variation in ant diversity within unmanaged forests in the tropics (Kaspari 1996a; Samson, Rickart & Gonzales 1997). Feener & Schupp (1998), for example, found that species richness and composition did not differ between treefall gaps and forest understorey. In contrast, Basu (1997) found more ant species in closed canopy forest than treefall gaps in the Western Ghats, India.

In their study in the same part of Cameroon as this study, Eggleton *et al.* (1995, 1996) showed that complete forest clearance reduces the number of termite species by approximately 50%. However, they found that slight disturbance, such as the establishment of a plantation after partial manual clearance, did not have a detrimental effect on termites species richness. As decomposers, termites require dead plant material, and do not appear to be critically limited by the number and type of tree species in an area (Eggleton *et al.* 1996). Indeed, there is some evidence that termites benefit from some forest disturbance, the heterogeneous habitat in an old secondary forest or a partially cleared plantation with a rich supply of dead wood providing a diversity of microhabitats for a wide range of termite species. Eggleton *et al.* (1995, 1996) suggest that habitats, such as 'enrichment' plantations with lines of forest cleared prior to tree planting, contain the equivalent of natural tree-fall gaps in primary forest. In contrast to Eggleton *et al.* (1995, 1996), who found that the nesting- and feeding-group composition of termites was affected by forest disturbance, we found no evidence that either the nesting habit of canopy ants or the feeding specialization of litter ants was affected by forest clearance or silvicultural treatment (Fig. 5). However, the relative lack of knowledge of the ecology of ants in tropical forests (in contrast to elsewhere, Andersen 1997; but see recent research by Dejean, Durand & Bolton 1996; Dejean *et al.* 2000) in comparison to termites may have meant that differences in the 'guild' composition of the ant fauna went undetected in this study.

The problems associated with this and similar studies are discussed elsewhere (Watt *et al.* 1997a). One of the major concerns expressed is that the scale of this type of study is too small to be relevant to large-scale forest clearance or establishment of forest plantations. While this is undoubtedly true, it is probably only true quantitatively; the differences reported here are likely to be magnified at larger scales. However, research at larger scales is clearly needed to give accurate estimates of changes in species numbers and composition after deforestation and plantation establishment.

This study, and several others (Eggleton *et al*. 1995, 1996; Watt *et al*. 1997a; Lawton *et al*. 1998), provide evidence to support the view that deforestation can cause a reduction in arthropod species richness. There is, however, a need for further studies on other taxa and in other parts of the tropical forest zone. We argue that estimates of the impact of deforestation on arthropod diversity, and biodiversity generally, should not be based on extrapolations derived from island biogeography theory (Lugo 1988; Reid 1992), but on direct measurement of species richness and composition.

Studies have shown that changes in land use and management have an impact on ant diversity and behaviour (Perfecto & Snelling 1995; Perfecto & Vandermeer 1996; Perfecto *et al*. 1997; Whitford 1999; Dunn 2000). Previous studies in temperate and tropical forests have demonstrated that deforestation has a dramatic impact on ant diversity (Punttila *et al*. 1991; Quirozrobledo & Valenzuelagonzalez 1995; Ewuim, Badejo & Ajayi 1997; Vasconcelos 1999; Carvalho & Vasconcelos 1999). However, this study is unique in showing that the way in which reforestation (using a single tree species) is carried out can have a marked effect on arthropod species richness and composition. The immediate implication of this study for forest management and arthropod diversity, therefore, is that ant species richness is greater in plantations established after partial manual clearance than complete clearance. Indeed, leaf-litter ant species richness, like termite species richness (Eggleton *et al*. 1995, 1996), was not reduced by conversion of intact forest to partial manual clearance plantation. Thus, as pointed out by Lugo (1988) for other taxa, there is the potential to manage previously forested areas in such a way as to achieve high levels of arthropod diversity. However, although termites and ants are numerically dominant in tropical forests, they are much less diverse than other taxa such as beetles, flies and parasitic Hymenoptera (Stork 1991), and the impact of different forest management practices on such taxa needs to be quantified before the value of different reforestation techniques can be properly understood.

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Appendix 1

Ant species (and morpho-species) recorded from the canopy of *Terminalia ivorensis* plantation plots in the Mbalmayo Forest Reserve in 1992 and 1993 (listed in terms of overall abundance).

Technomyrmex 2; *Crematogaster stadelmanni* Mayr; *Crematogaster striatula* Emery; *Crematogaster clariventris* Mayr; *Oecophylla longinoda* (Latreille); *Crematogaster africana* Mayr; *Pheidole* 3; *Paratrechina* 1; *Crematogaster* 2; *Atopomyrmex cryptoceroides* Emery; *Cataulacus guineensis* Smith; *Crematogaster gabonensis* Emery; *Myrmicaria exigua* André; *Technomyrmex* 1; *Crematogaster buchneri* Forel; *Polyrhachis decemdentata* André; *Cataulacus kohli* Mayr; *Crematogaster wellmani* Forel; *Crematogaster* 3; *Polyrhachis laboriosa* Smith; *Crematogaster depressa* (Latreille); *Crematogaster* 1; *Paratrechina* 2; *Tetraponera mocquerysi* (André); *Camponotus* 4; *Crematogaster* 5; *Camponotus* 2; *Polyrhachis alexisi* Forel; *Camponotus* 1; *Cataulacus egenus* Santschi; *Lepisiota* 1; *Tetraponera ophthalmica* (Emery); *Polyrhachis fissa* Mayr; *Cataulacus pullus* Santschi; *Camponotus* 5; *Crematogaster* 9; *Monomorium egens* Forel; *Pheidole* 1; *Polyrhachis n.sp nr. Lanuginosa* Santschi; *Tetramorium aculeatum* (Mayr); *Cataulacus* 4; *Melissotarsus weissi* Santschi; *Pheidole* 4; *Cataulacus mocquerysi* André; *Axinidris ghanensis* Shattuck; *Camponotus* 7; *Camponotus* 8; *Crematogaster* 15; *Plagiolepis* 2; *Technomyrmex* 6; Plagiolepis 1; *Polyrhachis lestoni* Bolton; *Axinidris* 5; *Tetramorium quadridentatum* Stitz; *Crematogaster* 6; *Axinidris* 1; *Camponotus* 3; *Crematogaster* 12; *Lepisiota* 2; *Polyrhachis militaris* (Fabricius); *Tetramorium dumezi* Menozzi; *Atopomyrmex mocquerysi* André; *Cataulacus* 6; *Pyramica maynei* (Forel); *Cataulacus tardus* Santschi; *Cataulacus pilosus* Santschi; *Polyrhachis otleti* Forel; *Cataulacus* 7; Cataulacus taylori *Bolton*; *Crematogaster* 11; *Monomorium exiguum* Forel; *Tapinoma* 2; *Camponotus brutus* Forel; *Crematogaster* 13; *Crematogaster* 8; *Paratrechina longicornis* (Latreille); *Crematogaster* 10; *Crematogaster* 7; *Platythyrea conradti* Emery; *Tapinoma melanocephalum* (Fabricius); *Axinidris* 3; *Axinidris* 4; *Cataulacus centrurus* Bolton; *Cataulacus lujae* Forel; *Cataulacus vorticus* Bolton; *Monomorium pharaonis* (Linnaeus); *Monomorium strangulatum* Santschi; *Pyramica serrula* (Santschi); *Strumigenys sp. queen*; *Tapinoma* 3; *Tetramarium n.sp nr. Psymanum* Bolton; *Tetramorium gegaimi* Forel; *Axinidris* 2; *Polyrhachis n.sp nr. braxa* Bolton; *Phasmomyrmex buchneri* (Forel); *Phasmomyrmex wolfi* (Emery); *Tetramorium n.sp nr dumezi* Menozzi.

Appendix 2

Ant species (and morpho-species) recorded from the leaf litter in the Mbalmayo Forest Reserve in 1993 (listed in terms of overall abundance).

Pheidole 6; *Technomyrmex* 3; *Tetramorium rhetidum* Bolton; *Oligomyrmex* 2; *Oligomyrmex* 3; *Pyramica serrula* (Santschi); *Crematogaster striatula* Emery; *Strumigenys petiolata* Bernard; *Tetramorium furtivum* (Arnold); *Monomorium invidium* Bolton; *Dorylus* 1; *Tetramorium antrema* (Bolton); *Tetramorium zambezium* Santschi; *Hypoponera* 1; *Strumigenys bernardi* Brown; *Pyramica ludovici* (Forel); *Monomorium bicolor* Emery; *Oligomyrmex* 1; *Oligomyrmex* 6; *Monomorium cryptobium* (Santschi); *Hypoponera* 4; *Pachycondyla ambigua* André; *Pristomyrmex orbiceps* (Santschi); *Paratrechina* 5; *Tetramorium capillosum* Bolton; *Technomyrmex* 4; *Paratrechina* 4; *Pheidole* 8; *Tetramorium muscorum* Arnold; *Tetramorium geminatum* Bolton; *Acropyga* 1; *Oligomyrmex* 4; *Technomyrmex* 5; *Pachycondyla caffraria* (Smith); *Anochetus katonae* Forel; *Phrynoponera bequaerti* Wheeler; *Technomyrmex* 2; *Tetramorium n.sp.*; *Monomorium floricola* (Jerdon); *Pyramica concolor* (Santschi); *Hypoponera* 3; *Anoplolepis tenella* (Santschi); *Discothyrea mixta* Brown; *Oligomyrmex* 7; *Pyramica sistrura* (Bolton); *Monomorium exiguum* Forel; *Cerapachys nitidulus* Brown; *Decamorium decem* (Forel); *Odontomachus troglodytes* Santschi; *Pachycondyla brunoi* Forel; *Pheidole* 5; *Tetramorium coloureum* Mayr; *Cerapachys foreli* (Santschi); *Pachycondyla fugax* Forel; *Pheidole* 7; *Pyramica lujae* (Forel); *Strumigenys rogeri* Emery; *Odontomachus assiniensis* Emery; *Pyramica tetragnatha* (Taylor); *Leptogenys n.sp.*; *Pyramica dotaja* (Bolton); *Pyramica ravidura* (Bolton); *Probolomyrmex guineensis* Taylor; *Pyramica depilosa* Bolton; *Anochetus bequaerti* Forel; *Cardiocondyla emeryi* Forel; *Pyramica africana* (Bolton); *Pachycondyla tarsata* (Fabricius); *Pheidole* 1; *Sphinctomyrmex rufiventris* Santschi; *Tetramorium muralti* Forel; *Anochetus traegaordhi* Mayr; *Camponotus brutus* Forel; *Hypoponera* 5; *Pachycondyla pachyderma* Emery; *Pachycondyla soror* (Emery); *Paratrechina* 1; *Strumigenys tetraphanes* Brown; *Tetramorium weitzeckeri* Emery; *Anochetus africanus* Mayr; *Cataulacus* *kohli* Mayr; *Centromyrmex sellaris* Mayr; *Crematogaster clariventris* Mayr; *Oligomyrmex* 8; *Paratrechina* 3; *Phrynoponera gabonensis* (André); *Prionopelta amieti* Terron; *Pyramica cavinasis* (Brown); *Technomyrmex* 1; *Tetramorium camerunense* Mayr; *Tetramorium gabonense* (André); *Asphinctopone silvestrii* Santschi; *Calyptomyrmex nummuliticus* Santschi; *Cerapachys sp*; *Crematogaster buchneri* Forel; *Pyramica roomi* (Bolton); *Hypoponera* 2; *Leptogenys bubastis* Bolton; *Monomorium spectrum* Bolton; *Oligomyrmex* 5; *Paedalgus rarus* Bolton & Belshaw; *Pheidole* 9; *Polyrhachis rufipalpis* Santschi; *Pristomyrmex africanus* Karavaiev; *Pyramica arahana* (Bolton); *Pyramica enkara* (Bolton); *Pyramica malaplax* (Bolton); *Strumigenys ettillax* Bolton; *Tetramorium pinnipilum* Bolton; *Tetramorium quadridentatum* Stitz; *Tetramorium zapyrum* Bolton.