African Journal of Ecology

Decomposition of tissue baits and termite density along a gradient of human land-use intensification in Western Kenya

Godfrey H. Kagezi[1], Manfred Kaib[2]*, Philip Nyeko[3], Christopher Bakuneeta[4], Martin Schädler[5] and Roland Brandl[5]

[1]Department of Ecology, Faculty of Biology, Philipps-Universität Marburg, Germany, C/o National Research Organization, Coffee Center, PO Box 158, Mukoko, Kampala, Uganda, [2]Department of Animal Physiology, University of Bayreuth, 95440 Bayreuth, Germany, [3]Department of Forest Biology and Ecosystems Management, Faculty of Forestry and Nature Conservation, Makerere University, PO Box 7062 Kampala, Uganda, [4]Department of Zoology, Faculty of Science, Makerere University, PO Box 7062 Kampala, Uganda and [5]Department of Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch Strasse 8, 35032 Marburg, Germany

Abstract

Termites are important decomposers and 'ecosystem engineers' in tropical ecosystems. Furthermore, termite assemblages are sensitive to human land-use intensification and often termite density and the importance of soil-feeding termites decrease with land-use intensification. These changes in termite assemblages may also lead to a decrease in termite-mediated ecosystem processes (e.g. soil formation, cellulose decomposition). We compared density and functional composition of termites with cellulose removal from undisturbed primary forests to farmlands (Kakamega Forest, Western Kenya). In contrast to the expectation, we found no response of termite abundance along the gradient of land-use intensification. However, as expected, the relative abundance of soil-feeders decreased from primary forests to farmlands. In contrast, frequency of attack on tissue paper baits and removal of tissue showed a clear hump-shaped relationship to land-use intensification with high values in secondary forests. These nonconcordant patterns of density and functional composition of termite assemblages with cellulose removal by termites suggest that it may be misleading to infer changes in a process by the characteristics of the assemblage of organisms that mediate that process.

Key words: cellulose removal, fungus-growing termites, Kakamega, soil-feeders, termite abundance

Résumé

Les termites sont des décomposeurs et des 'ingénieurs paysagers' très importants dans les écosystèmes tropicaux. De plus, les assemblages de termites sont sensibles à l'intensification de l'aménagement humain du territoire, et souvent la densité de termites et l'importance des termites qui se nourrissent du sol diminuent avec l'intensification de l'utilisation des terres. Ces changements qui touchent les assemblages de termites peuvent aussi entraîner une réduction des processus écosystémiques induits par les termites (ex. formation des sols, décomposition de la cellulose). Nous avons comparé la densité et la composition fonctionnelle des termites avec la disparition de la cellulose de forêts primaires intactes jusqu'aux terres exploitées de fermes (Forêt de Kakamega, dans l'ouest du Kenya). Contre toute attente, nous n'avons trouvé aucune réponse de l'abondance des termites tout le long du gradient d'intensification de l'utilisation des terres. Cependant, comme prévu, l'abondance relative des espèces se nourrissant du sol diminuait de la forêt primaire jusqu'aux fermes. Par contre, la fréquence des attaques sur les pièges appâtés avec du papier de soie et la disparition du papier présentaient une relation nette en forme de bosse (*hump-shaped relationship*) avec l'intensification de l'utilisation des sols, avec des valeurs élevées dans les forêts secondaires. Ces schémas non concordants de la densité et de la composition fonctionnelle des assemblages de termites avec la disparition causée par les termites suggèrent qu'il peut être erroné de déduire des changements dans un processus à partir des caractéristiques de l'assemblage d'organismes qui interviennent dans le processus.

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*Correspondence: E-mail: manfred.kaib@uni-bayreuth.de

Introduction

Termites constitute often more than 90% of the insect biomass in the soils of tropical forests, and that biomass of these insects can reach values of 100 gm^{-3} (Watt *et al.*, 1997). As the dominant group of insect detritivores, they are important for decomposition processes (Collins, 1983; see also references by Holt & Lepage, 2000) and play a major role as mediators of nutrient and carbon fluxes (Bignell *et al.*, 1997). In tropical Africa, for example, fungus-growing termites can consume almost all dead wood and more than 50% of leaf and grass litter (Bignell & Eggleton, 2000). By their feeding and nesting activities, termites exert positive effects on soil properties and processes (Holt & Lepage, 2000). Therefore, termites are considered as major 'ecosystem engineers' (Bignell & Eggleton, 2000). Furthermore, termites exhibit a wide range of dietary habits, with a varying degree of resource specializations, and the influence of termites on termite-mediated decomposition processes is governed to a large extent by the functional composition of local assemblages (Davies, 2002; Schuurman, 2005): wood-feeders, fungus-growers or soil-feeders play different roles in the decomposition processes (Tayasu *et al.*, 1997).

Human land-use intensification is among the major causes of the loss of forest biodiversity (Turner, 1996). The functional groups of termites show contrasting responses to land-use intensification (e.g. Eggleton *et al.*, 1997, 2002; Okwakol, 2000; Jones *et al.*, 2003). This is accompanied by selective loss of some functional groups with intensification, chiefly the soil-feeders (de Souza & Brown, 1994; Eggleton *et al.*, 1997, 2002, Eggleton, Davies & Bignell, 1998). But there is also an increase in the relative abundance of fungus-growing termites (Eggleton *et al.*, 1997, 2002). Although the importance of termites for soil processes in tropical ecosystems is well documented (Wardle, 2002), few studies compare the effects of land-use intensification on termite-mediated ecological processes such as decomposition (e.g. Genet *et al.*, 2001; Davies, 2002; Okwakol & Sekamatte, 2007). Such studies are needed, given the importance of ecosystem responses to land-use in determining nutrient cycling and atmospheric gas exchange (Trumbore *et al.*, 1995). Ecological functions of wood-feeding and fungus-growing termites can be inferred using cellulose baits (LaFage, Nutting & Haverty, 1973; Nash, Anderson & Whitford, 1999). Furthermore, such baits yield abundance data consistent with results from other survey studies (Taylor *et al.*, 1998), suggesting that such baits are a surrogate for ecological processes associated with termites. Thus, the objective of our study was to infer termite-mediated decomposition processes using baits in relation to termite functional groups along a gradient of land-use intensification in the Kakamega area, Western Kenya. In particular, we evaluated the following questions:

1. Is there a decrease in termite density with human land-use intensification?
2. Is there a change in the composition of termite functional groups along the gradient?
3. How does termite-mediated decomposition process change with human land-use intensification?

Materials and methods

Study area

The study was conducted in and around Kakamega Forest, Western Kenya (for the map of the study area, see Farwig, Braun & Böhning-Gaese, 2008). The forest lies north-east of Lake Victoria (0°10–0°21′N; 34°47′–34°58′E), 1500–1700 m above sea level (Mitchell, 2004). It receives 1500–2300 mm of rain annually. Kakamega Forest is the easternmost remnant of the Guineo-Congolian rain forests. The forest area now consists of a number of fragments that differ in size and degree of human disturbance (Lung & Schaab, 2004). About 4000 ha of the northern part of the forest (Buyangu and Kisere) fragments is declared as National Reserves under management of Kenya Wildlife Services with conservation of biodiversity as the main dogma (Blackkett, 1994).

The soils of Kakamega are mostly ferralo-chromic acrisols (FAO-UNESCO, 1997), which are well drained, deep and heavily leached with pH < 5.5. Despite the infertile soils, Kakamega Forest harbours a considerable diversity of plants and animals (Blackkett, 1994). Even the farmlands show a diverse landscape characteristic, with trees and bushes along plot boundaries. Agriculture is mainly subsistence with sugarcane, maize, sweet potatoes and vegetables as the main crops grown (Lung & Schaab, 2004; Guthiga, Mburu & Holm-Mueller, 2008).

Termite sampling and bait experiments

We established transects and experimental plots (hereafter referred to as bait stations) in five land-use systems forming a gradient of land-use intensification from nearly undisturbed primary forest to farmlands (Lung & Schaab, 2004; Table 1 and Fig. 1). Furthermore, in the study area, grasslands occur that are not easily classified along the land-use intensification gradient from forests to farmland. To estimate density and functional composition of termite assemblages, we sampled between April and November 2007 in all the land-use systems five transects (100 × 2 m) following the protocol of Jones & Eggleton (2000). In order to standardize the sampling effort, we divided each transect into twenty continuous plots of 5 × 2 m, and we sampled each plot for one man-hour by searching in all microhabitats suitable for termites including twelve samples of surface soil (each about 12 × 12 cm to 10 cm depth; Jones *et al.*, 2003). In each plot, we also visually estimated tree canopy, bush as well as ground cover (all in percentage), and we measured litter depth (cm). We used a pragmatic way to define bush cover by defining bushes as the layer that lies between the trees and the forest floor. By a ruler, litter depth was measured at four randomly selected sites in a plot. We also noted the occurrence of dead wood material and the occurrence of termite mounds in a plot (presence/absence data). When termites were encountered, we estimated the number of individuals in such a foraging party and collected a sample in 95% ethanol.

Table 1 Land-use systems in and around Kakamega Forest, Western Kenya, as described by Lung & Schaab (2004)

Land-use system	Description
Near primary forest	Forest of lowest disturbance level, dense canopy with trees older than 50 years
Disturbed primary forest	Primary forest with some degree of disturbance owing to human activities such as logging and grazing, lighter canopy compared to primary forest
Secondary forest	Mid-aged secondary forest of 20–30 years as well as aged *Maesopsis eminii* plantations as well as with indigenous species
Farmlands	Cultivated land of diverse characteristics, highly devised land with trees, bushes along plot boundaries, mainly subsistence agriculture, high percentage of bare ground
Grasslands	Grasslands with scattered trees or even arrangements of successional stages, partially of natural origin, partially because of clearings, partly used as meadows, grass used for roof hatching

The number of termite encounters across the whole transect is a surrogate for the termite density (Jones, 2000). For this paper, we have not determined samples to species. In almost all studies of community composition, number of encounters and species richness is tightly correlated (Davies, 2002). Gathorne-Hardy, Syaukani & Eggleton (2001) report a correlation of 0.9 between encounters and species richness in termites, and therefore species richness and encounters show similar patterns. We classified the termites into two broad feeding categories: wood- and leaf litter-feeders (including fungus-growing species) and soil-feeders (Davies, 2002). To characterize the relative abundance of soil-feeders, we calculated the percentage of encounters (foraging parties) that were classified as soil-feeders.

We established five bait stations within each land-use system (Table 1). Owing to logistic problems, we were not able to locate the bait stations near transects. Therefore, the spatial spreading of the decomposition experiments is less than that of transects. Each bait station consisted of a 3 × 3 m grid of sixteen paper rolls on the soil surface positioned at intervals of 1 m (roll size of toilet paper: 10 × 12.5 × 250 cm long with 200 sheets, unscented and unbleached tissue; hereafter referred to as baits). We reinforced the baits at each end with a 19-mm strip of packing tape to prevent unravelling (LaFage, Nutting & Haverty, 1973), and we installed them upright at each bait station. Before placing the baits on the surface, we removed any litter/debris present to ensure that the uncovered bases were in contact with the soil surface. We placed polythene planter bags (2.5 l) over the baits to protect baits from heavy rains. The baits were held in position by U-shaped steel pins, with one half inserted centrally through the planter bag (Dawes-Gromadzki & Spain, 2003).

We inspected the baits regularly at 1, 2, 4, 6, 8, 12, 16 and 20 weeks after installation. During each sampling, baits were lifted and we recorded the presence of termites as indicated by the presence of live termites, termite damage or gallery material on the bait (Nash, Anderson & Whitford, 1999; Dawes-Gromadzki & Spain, 2003). Termite attack was characterized by using the percentage of baits (n = 16) with foraging termites or with termite damage. Termites forage within the tissue paper rolls and consume varying amounts of tissue leaving hollow areas within the rolls, which can be easily estimated visually

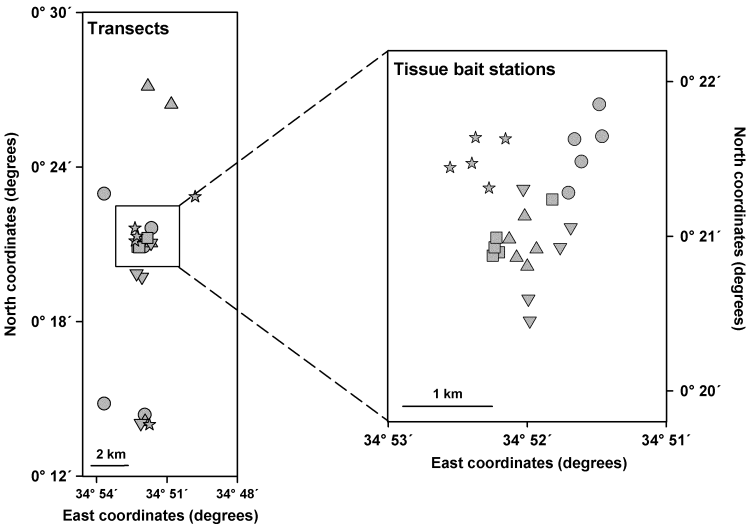

Fig 1 Spatial spreading of transects and experimental plots. ○, primary forest; △, disturbed primary forest; ▽, secondary forest; □, grassland; ☆, farmland

(Nash, Anderson & Whitford, 1999). Therefore, we estimated the percentage of tissue removal before rolls were put back in their original positions (Dawes-Gromadzki & Spain, 2003). The experiment was replicated five times in each land-use system and run from February to July 2007 and repeated from September 2007 to February 2008.

Data analysis

To analyse the transect data, we calculated means across the twenty plots of each transects, and these means were used for further analysis. We used simple ANOVA and regression analyses with appropriately transformed dependent variables. In particular, we arcsine-transformed all estimated percentages (e.g. percentage tree cover). For percentages of count data (e.g. percentage of encounters of soil-feeders), we used generalized linear models with a binomial error structure and a logit link-function. The bait experiments were run twice on the same plots. Furthermore, termite colonies are long-lived, and therefore, we considered the two experiments as repeated measures of cellulose removal by the same colonies and analysed them with a repeated-measures ANOVA. Finally, for significant ANOVA, we calculated homogeneous subgroups using Tukey's honestly significant difference test with $P = 0.05$. All calculations were made using STATISTICA (StatSoft, Inc., 2007) and/or the appropriate functions in R (Venables *et al.*, 2010).

Results

Our gradient of land-use from (near) primary forests to farmland (Table 1) is associated with steep decrease in the occurrence of dead wood (diameter > 5 cm), canopy cover, bush cover and also litter depth (Fig. 2). Canopy cover showed a sharp decrease from forest to farmlands as indicated by the *post hoc* tests (Fig. 2a). Depth of litter showed a clear decrease from the different types of forests to the farm- and grasslands (Fig. 2d). Ground cover showed an opposite trend with an increase from primary and disturbed forests to secondary forests and farmland (Fig. 2c; see *post hoc* tests). In 50–60% of the plots of a particular system, we recorded termites (Fig. 3a). We used the total number of termite encounters along each transect as a measure of termite density (Jones, 2000). Mean number of encounters across all transects was 26 ± 14 transect^{-1} (range 8–57). We found no difference in the density across the gradient of land-use intensification for all termite encounters (Fig. 3b). This was also true when we looked at the density of soil-feeders alone (soil-feeders: $F = 0.3$; df = 4 and 20; $P > 0.5$). However, we found a significant pattern in the number of individuals estimated during each encounter: party size was largest in secondary forests and grasslands (Fig. 2c).

The functional composition of the termite assemblages changed along the land-use gradient. During the transect

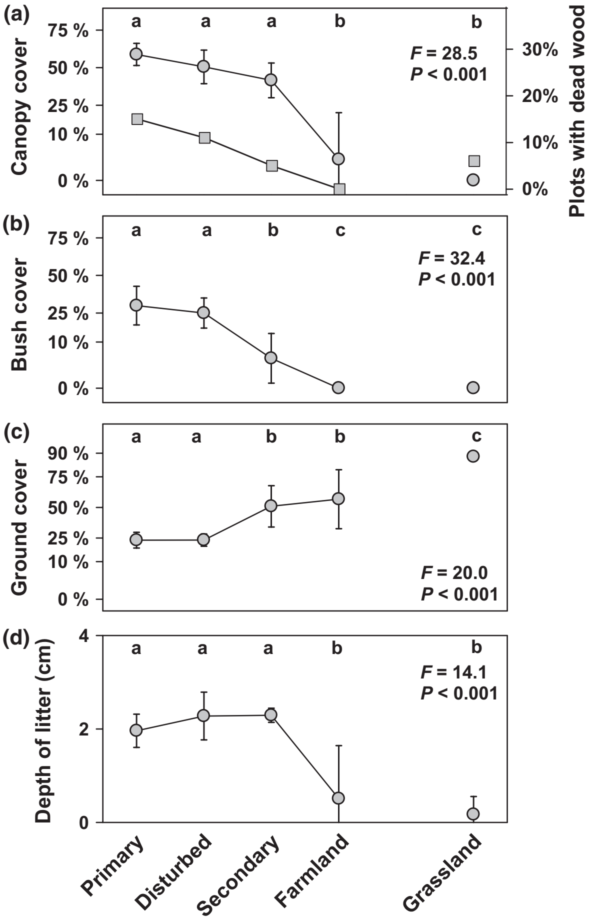

Fig 2 Change in environmental characteristics along the gradient of land-use intensification in Kakamega area, Western Kenya. (a) Mean percentage ± SD across estimated canopy (grey circles) as well as plots in the transects with dead wood (>5 cm; grey squares). (b, c) Mean percentage ± SD of bush and ground cover along the gradient. (d) Mean litter depth ± SD along the gradient. Litter depth was measured at four randomly selected sites in each plot. All statistical tests were on the level of transects (n = 25; df for *F*-Tests 4 and 20). The letter code above the graphs indicates homogeneous subgroups using Tukey's honestly significant difference test with $P = 0.05$

counts, termites building mound aboveground were found mainly in the grassland (deviance = 38.9; df = 4; $P < 0.001$; Fig. 3a). However, transects might not be adequate to sample species building large mounds, which are very common in the farmland (in particular *Macrotermes herus* and *Pseudacanthotermes spiniger*). The percentage of soil-feeders decreased from (near) primary forest to farmlands (deviance = 58.6; df = 4; $P < 0.01$; Fig. 4).

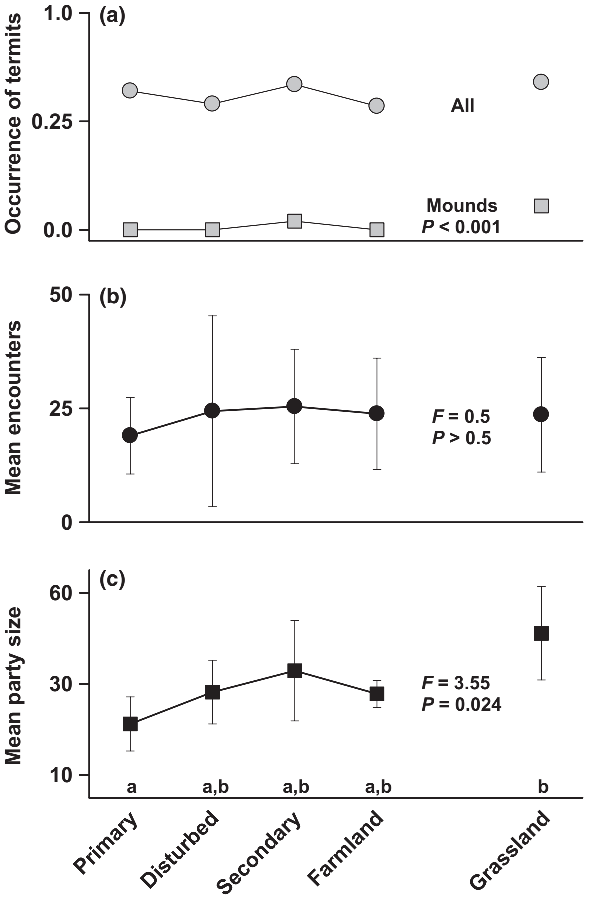

Fig 3 Change of several measures of termite density along a land-use gradient in Kakamega area, Western Kenya. (a) Percentage of plots across all transects (twenty plots along each transect; five transects for each land-use system) where we encountered termites in a plot (grey circles). Grey squares indicate the percentage of plots where we recorded aboveground mounds. (b) Mean number of encounters along the land-use gradient. For this analysis, we summed all encounters within a transect and calculated the mean (±SD) across the five transects of each land-use system. (c) Mean party size ± SD across the land-use gradient. Party size is defined as the mean number of individuals estimated during each encounter. All statistical tests were on the level of transects (n = 25; df for *F*-Tests 4 and 20). The letter code below the graph in (c) indicates homogeneous subgroups using Tukey's honestly significant difference test with $P = 0.05$

After a short lag of time, most bait stations were found by termites and termites started to consume the cellulose of the tissue with little differences between the two experiments. We found only a marginal significant interaction between experiment and land-use (Fig. 5; for statistical

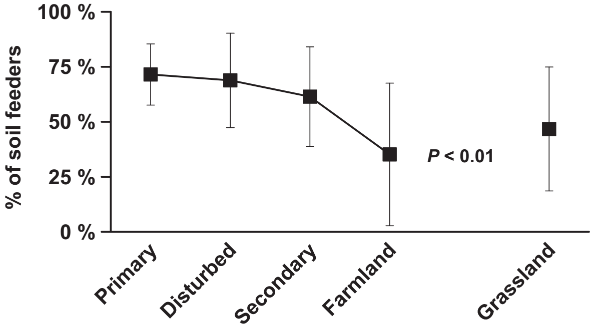

Fig 4 Change in relative abundance of soil-feeders (number of encounters of soil-feeders divided by the total number of encounters along each transect; arcsine-transformed for analyses and calculation of standard deviation across transects)

tests, see Table 2). Using the mean amount of removed tissue across all sixteen baits of each station after 20 weeks as an indicator of cellulose removal by termites (in percentage), we found a clear correlation between cellulose removal at the end of each experiment and mean termite activity at the bait station (Fig. 6; the mean activity was calculated across all eight inspection dates). Patterns were very similar during the two experiments. Termite activity and cellulose removal increased from primary to secondary forest and then dropped to low levels in farmlands (Fig. 7; for statistical tests, see Table 2). The *post hoc* tests indicate the peak of cellulose removal in disturbed and secondary forests. Termite activity and cellulose removal were also high in the grasslands (Figs 5 and 7). Note that the patterns of cellulose removal and termite activity at the bait stations correspond with the pattern of mean party size across the gradient of land-use intensification found on the transects (Figs 3 and 7).

Discussion

In our study, termite density showed no response to intensification in land-use. However, the proportion of soil-feeders decreased with land-use intensification. Furthermore, we found an increase in cellulose removal by termites with increasing disturbance within forest types with a sharp decrease to farmlands (see *post hoc* tests in Fig. 7a). Clearly, along the gradient of land-use intensification, our data showed contrasting patterns of functional composition of termite assemblages and termite-mediated ecosystem processes as inferred from cellulose removal.

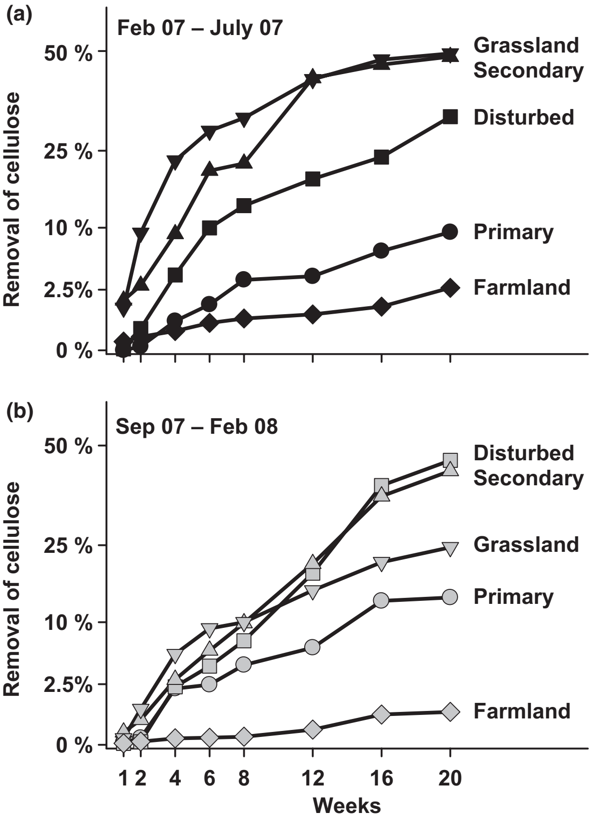

Fig 5 Mean removal of cellulose paper baits over time along a land-use gradient in Kakamega area, Western Kenya, for the two series experiments. Note the almost consistent ranking of land-use systems for the two experiments at different times of the year

In our study, termite density was low and independent of land-use intensity. Across all transects, we encountered only 0.13 parties m^{-2} (range 0.04–0.29). Assuming that each encounter is a colony, this estimate may be regarded as an upper estimate of the density of colonies in Kakamega. In contrast, Attignon *et al.* (2005) reported 0.5–1.1 encounters m^{-2} in semi-deciduous forests and plantations in Benin. We attribute our low values to the altitude of the Kakamega area (*c.* 1500 m asl.; Mitchell, 2004). Furthermore, other studies in tropical ecosystems also found little change in densities of termites along such gradients (Genet *et al.*, 2001; Davies, 2002). For example, Eggleton *et al.* (1995) reported densities of 2282–6967 individuals m^{-2} in near primary forest, 2328–6703 individuals m^{-2} in old secondary forest and 5170 individuals m^{-2} in *Terminalia ivorensis* plantations in Cameroon. In fact, low or moderate levels of disturbance (e.g. foraging and hunting

Table 2 Statistical analyses of the cellulose removal experiment using repeated-measurement ANOVA. Note the significant and marginal significant influence of the land-use system on cellulose removal and termite activity at the bait stations. We also found significant differences between the two experiments as well as interactions between the experiments and land-use system

	SS	df	Mean SS	*F*	*P*
Cellulose removal					
Land-use	2.77	4	0.694	4.51	0.00098
Error	3.08	20	0.154		
Experiment	0.0162	1	0.0162	0.656	0.43
Experiment*Land-use	0.235	4	0.0587	2.38	0.086
Error	0.494	20	0.0247		
Activity					
Land-use	0.909	4	0.227	2.26	0.098
Error	2.01	20	0.100		
Experiment	0.116	1	0.116	4.71	0.042
Experiment*Land-use	0.344	4	0.0860	3.49	0.026
Error	0.494	20	0.0247		

SS = Sum of square.
Mean SS = mean sum of square.

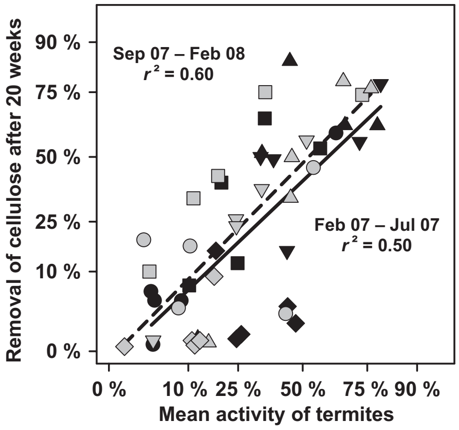

Fig 6 Scatter diagram of cellulose removal after 20 weeks (mean across sixteen baits of each baiting station) versus termite activity (mean percentage of baits with termites or termite damage across all inspection dates) in Kakamega area, Western Kenya. Filled symbol, solid line: experiment February to July 2007; Grey symbols, broken line: experiment September 2007 to February 2008. The types of symbols characterize the land-use systems (for symbols see Fig. 5)

by local people, selective logging, agroforestry) have little impact on species richness, abundance and biomass of termites (Eggleton *et al.*, 1995; Davies *et al.*, 1999). Interestingly, many of the studies reporting a decline of termite density along gradients of land-use intensification are from Asia and Amazonia (e.g. Bandeira & Vasconcelos, 2002; Jones *et al.*, 2003). In these biogeographical areas, Macrotermitinae either do not occur (Neotropics; Davies *et al.*, 2003) or are much less species-rich (Orientalis; Thakur, 1983). This suggests that the occurrence of a particular functional group of termites leads to the contrasting responses of overall termite density with land-use intensification (see also Eggleton *et al.*, 1995, 2002), which underlines that the properties of ecological systems depend on the biogeographical context in which the system is embedded.

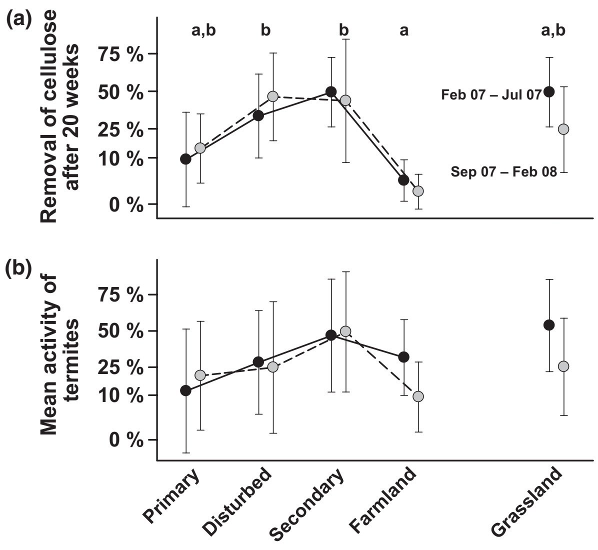

Fig 7 (a) Mean removal ± SD of cellulose after 20 weeks for each land-use system as well as (b) termite activity at the bait stations (mean and standard deviation across transect) in Kakamega area, Western Kenya. For statistical analyses, see Table 2. The letter code above the graph (a) indicates homogeneous subgroups using Tukey's honestly significant difference test with $P = 0.05$

Although we found no change in encounters of termites along the land-use intensification gradient (Fig. 2b), the relative abundance of soil-feeding termites declined from primary forests to farmlands (Fig. 4; also see Eggleton *et al.*, 1995, 2002; Davies, 2002; Jones *et al.*, 2003). This may have three mutually nonindependent reasons. First, tree and bush cover in primary forests create moist and buffered microhabitat (see Fig. 1; Dibog *et al.*, 1999), which facilitates the survival of these soft-bodied soil-feeding termites in primary and secondary forests (de Souza & Brown, 1994; Jones *et al.*, 2003). Secondly, feeding on low-quality diet like soil particles leads to energetic constraints (Eggleton, Davies & Bignell, 1998), which may increase for this functional group the vulnerability to changes in composition and quality of humus associated with land-use intensification. Thirdly, the available food as indicated by the low depth of litter as indicator for soil formation also decreases from forests to farmlands (Fig. 2d).

The close correlation of termite activity at a bait station and removal of cellulose suggest that this removal is caused by termites. In a study of tissue paper and wood-litter decomposition in the semi-arid Okavango Delta region of northern Botswana, variation in abundance of fungus-growing termites explained more than 80% of variation in decomposition rates (Schuurman, 2005). The difference between our study (60% explained variance) and the study of Schuurman (2005) may be attributed to differences in climate and altitude. Schuurman worked in a semi-arid region and at a lower altitude of *c.* 1000 m asl. (Ramberg *et al.*, 2006) compared with Kakamega at a higher altitude of *c.* 1500 m asl. (Mitchell, 2004). In Africa, increasing aridity is associated with increasing dominance of fungus-growers and the importance of this functional group for decomposition increases also (Bagine, 1984). We have at least indirect evidence that fungus-growers drive the general pattern of cellulose removal along the land-use intensification gradient. Fungus-growers form often large foraging parties (Bignell & Eggleton, 2000). We found a hump-shaped relationship of the mean party size with land-use intensification with its peak at secondary forests (Fig. 3c). In these secondary forests, removal of cellulose showed also its peak (Fig. 7a). This close correspondence in the patterns of cellulose removal and mean party size across the gradient of land-use intensification indicate that fungus-growers may be important for the removal of cellulose (see also Schuurman, 2005). Nevertheless, the low attack rate in the farmlands was surprising given the abundance of fungus-growers in these systems (in particular *Pseudacanthotermes spiniger*). One explanation may be the microclimate with fluctuating temperature and moisture levels owing to low vegetation cover after harvesting of the fields (see also LaFage, Nutting & Haverty, 1973; Abensperg-Traun & De Boer, 1990).

We found a clear pattern of inferred termite-mediated processes along the gradient of land-use intensification, which corresponded with termite activity but not with density: the highest cellulose removal was found in the secondary forests and grasslands. This discrepancy of termite density and inferred process along a land-use intensification gradient indicates that inferring ecosystem processes from estimates of the density or species richness of the organisms that mediate the considered process may be misleading (Genet *et al.*, 2001).

Acknowledgements

The authors would like to express their appreciation to the German Federal Ministry of Education and Research (BMBF) for providing funding for this study through the Biodiversity Analysis Transect for Africa-East (BIOTA-E) project. We thank Henry Mukhola and David Eichenberg for their valuable assistance with field work. Dr. Charles Masembe and Dr. Ann Akol provided technical advice. We are grateful to farmers of Buyangu village for permitting us to use their fields for this study. Permission to work in Kakamega Forest was granted by the National Museums of Kenya (NMK) and the Kenya Wildlife Service (KWS). Finally, we thank two anonymous referees for their helpful comments.

References

Abensperg-Traun, M. & De Boer, E.S. (1990) Species abundance and habitat differences in biomass of subterranean termites (Isoptera) in the wheatbelt of Western Australia. *Aust. J. Ecol.* **15**, 219–226.

Attignon, S.E., Lachat, T., Sinsin, B., Nagel, P. & Peveling, R. (2005) Termite assemblages in a West-African semi-deciduous forest and teak plantations. *Agric. Ecosyst. Environ.* **110**, 318–326.

Bagine, R.K.N. (1984) Soil translocation by termites of the genus *Odontotermes* (Holmgren) (Isoptera: Macrotermitinea) in an arid area of northern Kenya. *Oecologia* **64**, 263–266.

Bandeira, A.G. & Vasconcellos, A. (2002) A quantitative survey of termites in a gradient of disturbed highland forest in north-eastern Brazil (Isoptera). *Sociobiology* **39**, 429–439.

Bignell, D.E. & Eggleton, P. (2000) Termites in ecosystems. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (Eds T. Abe, D. E. Bignell and M. Higashi). Kluwer Academic Press, Dordrecht, The Netherlands.

Bignell, D.E., Eggleton, P., Nunes, L. & Thomas, K.L. (1997) Termites as mediators of carbon fluxes in tropical forest: budgets for carbon dioxide and methane emissions. In: *Forests and Insects* (Eds A. D. Watt, N. E. Stork and M. D. Hunter). Chapman and Hall, London, U.K.

Blackkett, H.L. (1994) *Forest Inventory Report No.3.* KIFCON, Kakamega.

Collins, N.M. (1983) Termite populations and their role in litter removal in Malaysian rain forests. In: *Tropical Rain Forest: Ecology and Management* (Eds S. L. Sutton, T. C. Whitmore and C. A. Chadwick). Blackwell Scientific Publications, Oxford, U.K.

DAVIES, R.G. (2002) Feeding group responses of a Neotropical termite assemblage to rain forest fragmentation. *Oecologia* **133,** 233–242.

DAVIES, R.G., EGGLETON, P., DIBOG, L., LAWTON, J.H., BIGNELL, D.E., BRAUMAN, A., HARTMANN, C., NUNES, L., HOLT, J. & ROULAND, C. (1999) Successional response of a forest termite assemblage to experimental habitat perturbation. *J. Appl. Ecol.* **36,** 946–962.

DAVIES, R.G., HERNÁNDEZ, L.M., EGGLETON, P., DIDHAM, R.K., FAGAN, L.L. & WINCHESTER, N.N. (2003) Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. *J. Trop. Ecol.* **19,** 509–524.

DAWES-GROMADZKI, T.Z. & SPAIN, A.V. (2003) Seasonal patterns in the activity and species richness of surface-foraging termites (Isoptera) at paper baits in a tropical Australian savanna. *J. Trop. Ecol.* **19,** 449–456.

DIBOG, L., EGGLETON, P., NORGROVE, L., BIGNELL, D.E. & HAUSER, S. (1999) Impacts of canopy cover on soil termite assemblages in an agrisilvicultural system in southern Cameroon. *Bull. Entomol. Res.* **89,** 125–132.

EGGLETON, P., DAVIES, R.G. & BIGNELL, D.E. (1998) Body size and energy use in termites (Isoptera): the responses of soil feeders and wood feeders differ in a tropical forest assemblage. *Oikos* **81,** 525–530.

EGGLETON, P., BIGNELL, D.E., SANDS, W.A., WAITE, B., WOOD, T.G. & LAWTON, J.H. (1995) The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *J. Trop. Ecol.* **11,** 85–98.

EGGLETON, P., HOMATHEVI, R., JEEVA, D., JONES, D.T., DAVIES, R.G. & MARYATI, M. (1997) The species richness and composition of termites (Isoptera) in primary and regenerating lowland dipterocarp forest in Sabah, East Malaysia. *Ecotropica* **3,** 119–128.

EGGLETON, P., BIGNELL, D.E., HAUSER, S., DIBOG, L., NORGROVE, L. & MADONG, B. (2002) Termite diversity across an anthropogenic gradient in the humid forest zone of West Africa. *Agric. Ecosyst. Environ.* **90,** 189–202.

FAO-UNESCO (1997) *Soil Map of the World.* Revised Legend. ISRIC, Wageningen.

FARWIG, N., BRAUN, C. & BÖHNING-GAESE, K. (2008) Human disturbance reduces genetic diversity of an endangered tropical tree, *Prunus africana* (Rosaceae). *Conserv. Genet.* **9,** 317–326.

GATHORNE-HARDY, F., SYAUKANI, A.N. & EGGLETON, P. (2001) The effects of altitude and rainfall on the composition of the termites (Isoptera) of the Leuser Ecosystem (Sumatra, Indonesia). *J. Trop. Ecol.* **17,** 379–393.

GENET, J.A., GENET, K.S., BURTON, T.M., MURPHY, P.G. & LUGO, A.E. (2001) Response of termite community and wood decomposition rates to habitat fragmentation in a subtropical dry forest. *Trop. Ecol.* **42,** 35–49.

GUTHIGA, P.M., MBURU, J. & HOLM-MUELLER, K. (2008) Factors influencing local communities' satisfaction levels with different forest management approaches of Kakamega Forest, Kenya. *Environ. Manag.* **41,** 696–706.

HOLT, J.A. & LEPAGE, M. (2000) Termites and soil properties. In: *Termites: Evolution, Sociality, Symbioses, Ecology* (Eds T. ABE, D. E. BIGNELL and M. HIGASHI). Kluwer Academic Press, Dordrecht, The Netherlands.

JONES, D.T. (2000) Termite assemblages in two distinct montane forest types at 1000m elevation in Maliau Basin, Sabah. *J. Trop. Ecol.*, **16,** 271–286.

JONES, D.T. & EGGLETON, P. (2000) Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *J. Appl. Ecol.* **37,** 191–203.

JONES, D.T., SUSILO, F.X., BIGNELL, D.E., HARDIWINOTO, S., GILLISON, A.N. & EGGLETON, P. (2003) Termite assemblage collapse along a land-use intensification gradient in lowland central Sumatra, Indonesia. *J. Appl. Ecol.* **40,** 380–391.

LAFAGE, J.P., NUTTING, W.L. & HAVERTY, M.I. (1973) Desert subterranean termites: a method for studying foraging behaviour. *Environ. Entomol.* **2,** 954–956.

LUNG, T. & SCHAAB, G. (2004) Change-detection in Western Kenya: the documentation of fragmentation and disturbance for Kakamega forest and associated forest areas by means of remotely-sensed imagery. In: *ISPRS Archives. Vol. 25. Part B (DVD)*, Proceedings of the ISPRS 20th congress, 12–23 July 2004, Istanbul, Turkey.

MITCHELL, N. (2004) The exploitation and disturbance history of Kakamega forest, Western Kenya. In: *BIOTA-East Report* (Eds B. BLEHER and H. DALITZ). Bielefelder Ökologische Beiträge Vol. 20.

NASH, M.S., ANDERSON, J.P. & WHITFORD, W.G. (1999) Spatial and temporal variability in relative abundance and foraging behaviour of subterranean termites in desertified and relatively intact Chihuahuan Desert ecosystems. *Appl. Soil Ecol.* **12,** 149–157.

OKWAKOL, M.J.N. (2000) Changes in termite (Isoptera) communities due to the clearance and cultivation of tropical forest in Uganda. *Afr. J. Ecol.* **38,** 1–7.

OKWAKOL, M.J.N. & SEKAMATTE, M.B. (2007) Soil macrofauna research in ecosystems in Uganda. *Afr. J. Ecol.* **45,** 2–8.

RAMBERG, L., HANCOCK, P., LINDHOLM, M., MEYER, T., RINGROSE, S., SILVA, J., VAN AS, J. & VANDERPOST, C. (2006) Species diversity of the Okavango Delta, Botswana. *Aquat. Sci.* **68,** 310–337.

SCHUURMAN, G. (2005) Decomposition rates and termite assemblage composition in semiarid Africa. *Ecology* **86,** 1236–1249.

DE SOUZA, O.F.F. & BROWN, V.K. (1994) Effects of habitat fragmentation on Amazonian termite communities. *J. Trop. Ecol.* **10,** 197–206.

STATSOFT, INC. (2007) *STATISTICA (Data Analysis Software System), Version 8.0.* http://www.statsoft.com [accessed on 8 November 2010].

TAYASU, I., ABE, T., EGGLETON, P. & BIGNELL, D.E. (1997) Nitrogen and carbon isotope ratios in termites: an indicator of trophic habit along the gradient from wood-feeding to soil-feeding. *Ecol. Entomol.* **22,** 343–351.

TAYLOR, H.S., MACKAY, W.P., HERRICK, J.E., GUERRERO, R.A. & WHITFORD, W.G. (1998) Comparison of field methods to detect termite activity in the Northern Chihuahuan Desert (Isoptera). *Sociobiology* **32,** 1–15.

Thakur, M.L. (1983) A review of the family Macrotermitidae (Isoptera) from the Oriental region. *Orient. Insects* **17**, 35–73.

Trumbore, S.E., Davidson, E.A., Barbosa de Camargo, P., Nepstad, D.C. & Martinelli, L.A. (1995) Belowground cycling of carbon in forests and pastures of eastern Amazonia. *Global Biogeochem. Cycles* **9**, 515–528.

Turner, I.M. (1996) Species loss in fragments of tropical rain forest: a review of the evidence. *J. Appl. Ecol.* **33**, 200–209.

Venables, W.N., Smith, D.M. & the R Development Core Team (2010) An introduction to R version. Available at: http:\\www.R-project.org. [accessed on 16 December 2010].

Wardle, D.A. (2002) *Communities and Ecosystems. Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton and Oxford.

Watt, A.D., Stork, N.E., Eggleton, P., Srivastava, D., Bolton, B., Larsen, T.B., Brendell, M.J.D. & Bignell, D.E. (1997) Impact of forest loss and regeneration on insect abundance and biodiversity. In: *Forests and Insects* (Eds A. D. Watt and M. D. Hunter). Chapman and Hall, London, U.K.

(*Manuscript accepted 13 January 2011*)

doi: 10.1111/j.1365-2028.2011.01263.x