



## Impacts of land-use intensification on litter decomposition in western Kenya

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**Abstract.** Tropical forests are faced with a substantial loss of forest cover due to human activities. The various forms of land use influence habitat structure, microclimate, and co-occurring species, with possible effects on ecosystem processes. The forests of western Kenya are the most eastern parts of the Congolian rainforests. Due to the high human population density only few remnants of these rainforests remained. Even protected areas are influenced by human disturbances, with unknown effects on ecosystem processes. Therefore, we quantified the mass loss of leaf litter with and without access of soil invertebrates within forest fragments and sites affected by increasing levels of agricultural land-use intensity in the Kakamega area (western Kenya; 1500 m a.s.l.). Mass loss of litter as an estimate of decomposition rate increased with rainfall during the annual cycle. Furthermore, mass loss increased with the area of forest fragments and decreased with land-use intensification. We found that soil invertebrates had only small effects on mass loss (< 10 %), and this effect decreased with land-use intensification. Our data showed that forest fragmentation has negative effects on litter decomposition. However, the magnitude of this negative effect was not as large as expected.

### 1 Introduction

Decomposition of plant litter is an important driver for the cycling of carbon as well as nutrients and therefore plays a significant role in the structure and function of ecosystems (Swift et al., 1979). Decomposition is mainly regulated by climate, litter quality, and the decomposer community (Swift et al., 1979; Knoepp et al., 2000). In the tropics litter decomposition is particularly important for ecosystem productivity because soils are highly weathered and therefore sometimes nutrient-poor (Martius et al., 2004).

Forest disturbance and land-use intensification continue at an unprecedented rate in tropical ecosystems worldwide, causing loss of biodiversity and associated ecosystem processes (Pimm and Raven, 2000). Although recently the tropical biodiversity crisis has been questioned (Wright and Muller-Landau, 2006; but see also Bihn et al., 2008), the dwindling of tropical forests may threaten ecosystem functions and services (e.g. Matson et al., 1997). In tropical ecosystems, decomposition rates have been reported to be higher in primary forests compared to disturbed forest types

or areas dominated by agriculture (e.g. Höfer et al., 2001; Attignon et al., 2004; Martius et al., 2004). The canopy of forests protects the soil biota from variations in temperature and drought stress (Dibog et al., 1999). Thus, clearing of forests increases variations in soil temperature and decreases soil moisture. These abiotic changes affect the abundance, composition, and activity of decomposers (Lavelle and Pashanasi, 1989; Martius et al., 2004), with consequences for ecosystem processes mediated by these organisms (Höfer et al., 2001; Kagezi et al., 2011). The contribution of the invertebrate fauna to decomposition is higher in the tropics compared to many other biomes of the world (Wall et al., 2008; Yang and Chen, 2009). Therefore, changes in the contribution of invertebrates to decomposition rates should be a sensitive indicator of the influence of forest disturbance on ecosystem processes.

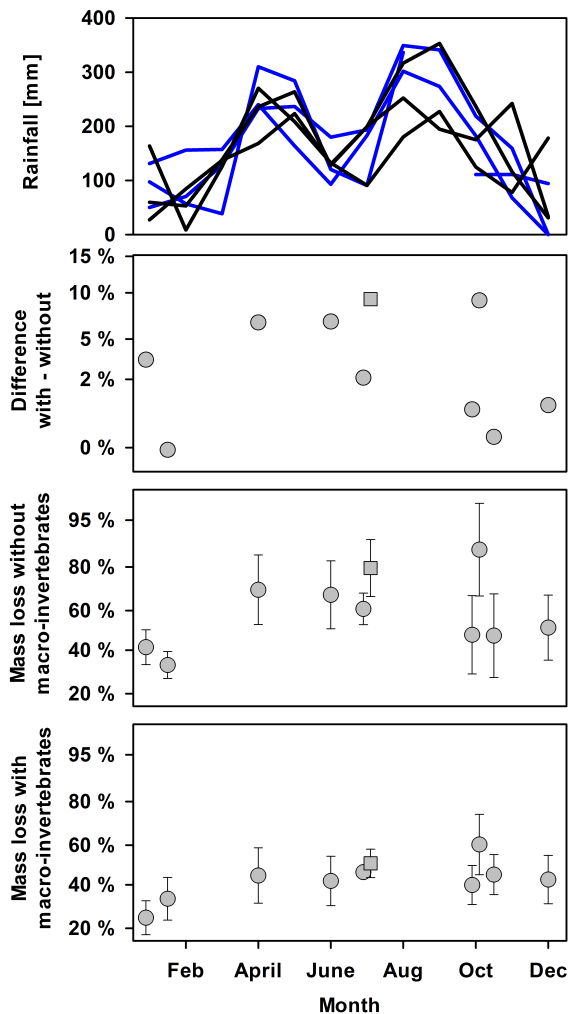
Kakamega Forest in western Kenya is an example of a tropical rainforest that was and is heavily affected by anthropogenic disturbances that resulted in considerable fragmentation of the original forest area (Lung and Schaab, 2006; Schleuning et al., 2011). In this area we examined the temporal and spatial variation of decomposition of standard leaf litter across forest fragments as well as land-use systems differing in land-use intensity (for other ecosystem functions see Schleuning et al., 2011). Specifically, we aim to answer the following questions:

1. Does forest fragmentation affect rates of leaf litter decomposition? In particular we explored whether decomposition increased with the area of forest fragments.
2. Does land-use intensification decrease rates of leaf litter decomposition?
3. Does the contribution of soil invertebrates change depending on fragmentation and land use?

## 2 Material and methods

### 2.1 Study area

The experiments were conducted in the Kakamega area (western Kenya) between September 2007 and April 2009 (for a map of the study area see Schleuning et al., 2011). Kakamega Forest is located northeast of Lake Victoria ( $0^{\circ}10'–0^{\circ}21' N$ ;  $34^{\circ}47'–34^{\circ}58' E$ ; 1500–1700 m a.s.l.). The area receives 1500–2300 mm of rain annually with two rainy seasons: one in April and one in September (Mitchell, 2004; see also Fig. 1). The soils are mostly infertile acrisoles, which are well-drained, deep, and heavily leached ( $pH < 5.5$ ). For comparative purposes, we also conducted a decomposition experiment in the Budongo Forest (Uganda) in June–July 2009. The Budongo Forest is located at the top of the Albertine Rift ( $1^{\circ}37'–2^{\circ}3' N$ ;  $31^{\circ}22'–31^{\circ}46' E$ ; average elevation: 1100 m). Annual rainfall varies between about 1200 and 2200 mm with a seasonal pattern similar to Kakamega Forest.



**Figure 1.** Mass loss (in % after 5 weeks) of litter in bags, with small mesh size (without access of invertebrates) and large mesh size (with access of invertebrates). We present means across all bags with standard errors calculated for arcsine-transformed values. The square indicates the decomposition rate measured in the Budongo Forest, Uganda. We also present the difference of the mass loss with and without invertebrates as well as the monthly rainfall data for two stations in 2007, 2008, and 2009 (blue: Kakamega Forest Station; black: Kakamega Meteorological Station).

### 2.2 Litter bag experiments

We conducted various litter bag experiments to study variation of mass loss of leaf litter. These experiments and their intentions are summarized in the Supplement (Table S1). Furthermore, sample sizes differed between experiments (Table S1). We attempted here a synoptic analysis of all results, although it was not possible to feed all data into a single analysis. Nevertheless, all experiments follow the same general protocol. To estimate decomposition rate, we measured mass loss of leaf litter from two plant species (except experiment 8; Table S1) common in the Kakamega area: *Croton*

**Table 1.** Land-use systems in and around Kakamega Forest, western Kenya, as described by Lung and Schaab (2006).

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 due 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 <i>Maesopsis eminii</i> 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 due to clearings, partly used as meadows, grass used for roof hatching.

(*Croton macrostachyus*, Euphorbiaceae) and sweet potatoes (*Ipomoea batatas*, Convolvulaceae). *Croton* is a forest tree, whereas sweet potatoes are a common crop planted throughout the area. Newly fallen leaves of “*Croton*” with no signs of herbivory and microbial activity were hand-picked from the ground. In contrast, mature leaves were harvested from the *Ipomoea* plants. *Croton* material had a higher initial *C/N* ratio (20.5) than *Ipomoea* leaf litter (14.9; measured with an Elementar Vario EL element analyser). This lower *C/N* ratio of *Ipomoea* leaves may have two reasons. First, *Ipomoea* plants may have been fertilized by farmers. Second, we used senescent leaves for *Croton*, whilst for *Ipomoea* fresh leaves had to be used. Although *Ipomoea* material was no leaf litter in the strict sense, we call all material used during the experiment for simplicity “litter”.

The importance of invertebrates for the mass loss of litter was estimated in all 10 experiments by using litter bags with two different mesh sizes. Large mesh size bags ( $5 \times 5 \text{ mm}^2$ ) allow the passage of most soil invertebrates, and small mesh bags ( $20 \times 20 \mu\text{m}^2$ ) allow access of bacteria, fungal hyphae, and small invertebrates, while restricting access of larger invertebrates (Schädler and Brandl, 2005).

Particularly important for our analyses is an experiment (experiment 8 in Table S1) where we analysed the mass loss of litter in forest fragments of the Kakamega area (see Schleuning et al., 2011) as well two experiments (2 and 3 in Table S1) where we analysed the variation of litter mass loss during decomposition with land-use intensity. For the latter experiments we selected five land-use systems (Table 1). These land-use systems represent a gradient of land-use intensification from (nearly) undisturbed primary forest to farmlands (Table 1; Kagezi et al., 2011). We additionally measured mass loss of litter in natural patches of grasslands.

However, these patches are not easily ranked within our land-use gradient (see also Lung and Schaab, 2006; Table 1).

As already noted, mass loss of leaf litter across different land-use types (five types; see Table 1) was done twice on the same plots (Table S1). For each land-use type we established five experimental plots ( $\approx 1 \times 1 \text{ m}^2$ ). The distribution of land-use types did not allow us to randomize location of plots across land-use types, and therefore plots are somewhat clustered, introducing spatial autocorrelation (Fig. S2 in the Supplement). In the first experiment (experiment 2 in Table S1) four litter bags of each mesh size (two *Croton* and two *Ipomoea*) and in the second experiment (experiment 3 in Table S1) eight litter bags of each mesh size (four *Croton* and four *Ipomoea*) were used on each plot. We removed the petioles and cleaned the leaves by washing them in water, sun-dried them, and stored them at room temperature. We established litter bags using  $3.0 \pm 0.1 \text{ g}$  of sun-dried litter of each plant species. Litter bags were individually labelled and initial litter mass was recorded. Before placing the litter bags on the soil surface at the plot, any litter or debris present was removed to ensure that the bags were in contact with the soil surface (Attignon et al., 2004). We covered the plots with a chicken mesh net, securing the net with wire hooks (Attignon et al., 2004) to prevent disturbance by animals (Fig. S1).

Based on a preliminary experiment (experiment 1 in Table S1), we decided to retrieve the litter bags from the field after 5 weeks. The large mesh size litter bags were put individually in labelled paper bags to prevent loss of any material. We cleaned the remaining litter by brushing off the soil particles. After experiment 3 (Table S1), the leaves were cleaned by floating in water. In one supplementary experiment in June/July 2008 (experiment 6 in Table S1), we tested the influence of the different cleaning techniques. This experiment showed that the impact of the experimental procedure

**Table 2.** Statistical analysis of the arcsine-transformed means of litter mass loss within 5 weeks as a measure of decompositions rates in five systems of land use with different types of land use (see Table 1). Within each type of land use we established five plots, and we treated plots as a random factor within land use. Therefore, we give for each test the  $df$  and MS for the numerator of the F-test (subscript 1) as well as for the denominator (subscript 2).

	Effect	SS	$df_1$	$MS_1$	$df_2$	$MS_2$	F	P
land use	Fixed	0.382	4	0.0954	20	0.00507	18.8	<0.001
plot (land use)	Random	0.101	20	0.00507	23.7	0.00267	1.90	<0.068
Leaf type	Fixed	0.0499	1	0.0499	20	0.00121	41.3	<0.001
Mesh	Fixed	0.550	1	0.550	20	0.00205	267	<0.001
Land-use*leaf type	Fixed	0.0161	4	0.00403	20	0.00121	3.34	0.030
Land-use*mesh	Fixed	0.0258	4	0.00646	20	0.00205	3.15	0.037
Plot (land-use*leaf type)	Random	0.0241	20	0.00121	20	0.000587	2.05	0.058
Plot (land-use*mesh)	Random	0.0411	20	0.00205	20	0.000587	3.49	0.004
Land-use*leaf*mesh	Fixed	0.0331	5	0.00661	20	0.000587	11.3	<0.001

on mass loss of litter was much lower than the effects of forest fragmentation and land-use intensity. We put the cleaned leaf material in labelled paper bags and sun-dried them. After re-weighing the dried remaining material, we calculated the percentage mass loss. Preliminary graphical and statistical analyses showed that the general patterns of the variation of mass loss with land-use, mesh size, and litter types including interactions were the same for the two experiments testing for the effects of land-use on mass loss. Furthermore as noted above, the bags were exposed on the same plots, and therefore the two experiments were repeated measures for the same plots. We were not interested in variation of mass loss with season in these two particular experiments, and therefore we averaged the estimates of the two experiments for analysis of the effects of land-use type, litter type, and mesh size (Table 2).

The decomposition experiments in the 11 plots within the seven fragments (Schleuning et al., 2011) were done in January and February 2009 (experiment 8 in Table S1) and followed the same experimental protocol as described above. However, in this particular experiment we used only *Croton* litter. During this experiment climate was particularly dry. This experiment was used to test for the relationship between mass loss and fragment size.

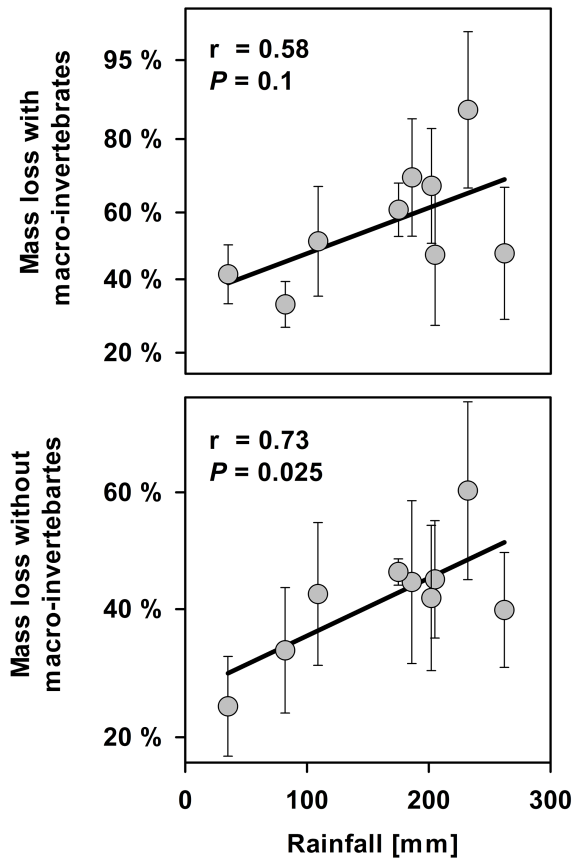
The experiments described above (experiments 1, 2, 3, 6, 8 in Table S1) as well as all other five experiments listed in Table S1 were used to explore the variation of mass loss throughout the year, calculating the mean for bags with large and small mesh size using arcsine-transformed values of each bag. The difference between both means indicates the contribution of invertebrates to decomposition. We correlated mass loss of litter with rainfall, using the mean monthly rainfall of the 2 months during which the bags were in the field (Table S1). The rainfall data are from two rainfall stations (Kakamega Forest Station and Kakamega Meteorological Station) and were provided by the Kenya Meteorological Department. We used the mean of the two stations.

### 2.3 Data analysis

The litter mass loss (in %) was arcsine-transformed to approach normality and to reduce heterogeneity of variances. We used simple regression analyses to test for the relationship of litter mass loss with rainfall (all experiments) or area of the forest fragments (area  $\log_{10}$ -transformed; experiment 8 in Table S1). We analysed the experiment, evaluating litter mass loss on plots affected by different levels of land-use intensification (experiments 2, 3; Table S1) using a general linear model to test for the effects of land-use system, mesh size, and litter type on decomposition. Plots were treated as a random factor within land-use. Autocorrelation refers to a correlation between observations induced by omitting one or more variables of major importance from the statistical model. Using plots as a random factor accounts for such omitted variables. Land-use, mesh size of the bags, and litter type were classified as fixed effects (see Table 2). As noted above, location of plots shows spatial autocorrelation. We ordered the land use systems with land-use intensification (excluding grasslands; see above) and calculated a simple correlation coefficient between land-use intensification and the average mass loss across all plots within a land-use system. This correlation coefficient has only two degrees of freedom and provides a very conservative estimate of the relationship of decomposition with land-use intensification. Because all our correlation coefficients are based on few values (low power), we accepted significance with  $P \leq 0.1$  to reduce the probability of type I errors.

### 2.4 Results

Averaging between the two leaf types, we found a clear correlation between mass loss and rainfall for both mesh sizes (Figs. 1 and 2), although there was more scatter between the experiments with large mesh size. In contrast to the expectation from the literature, the difference between mass loss in litter bags with large and small mesh sizes was low. The contribution of soil fauna to the mass loss varied between 0

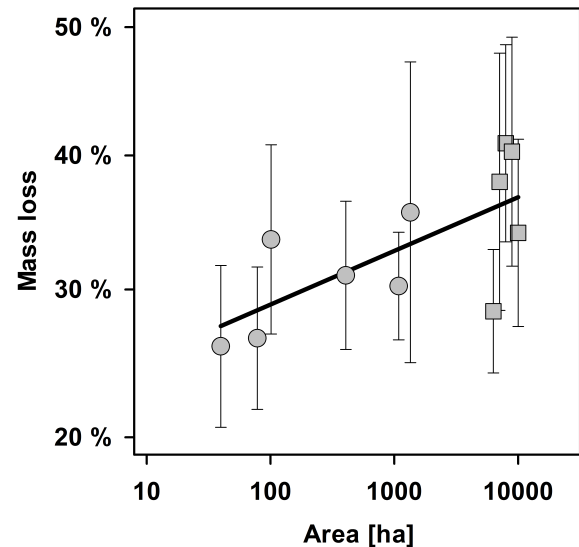


**Figure 2.** Relationship between rainfall during the decomposition experiments (mean across the months in which the experiment was run) and mass loss (mean  $\pm$  standard deviation of arcsine-transformed values; see Fig. 1; excluding the value for the Budongo Forest;  $n = 9$ ).

and 10%. Although the impact of soil animals on mass loss seemed to be low during the long dry season (Fig. 1), we did not find a correlation of rainfall on the influence of invertebrates ( $r = 0.23$ ;  $P = 0.5$ ).

As we found little influence of invertebrates on mass loss particularly during dry periods, we decided to average mass loss across mesh sizes for the analyses of the forest fragments. Using all the 11 plots, the scatter plot suggests an increase of mass loss with fragment area (Fig. 3). Four plots are only repeated measures for the largest fragment. After averaging these four values, the increase of mass loss with rainfall was significant ( $r = 0.77$ ;  $n = 7$ ;  $P = 0.04$ ).

We found that all the three main factors (land-use, leave type, mesh size) had a significant influence on mass loss (see Table 2). Mass loss in litter bags with small mesh sizes was lower compared to bags with large mesh sizes (Fig. 4). However, the difference of bags with large and small mesh size was small, as already noted for Fig. 1. *Ipomoea* showed a higher mass loss than *Croton* leaf litter except in grasslands (Fig. 4), leading to the interaction land-use\*leaf type. Fur-



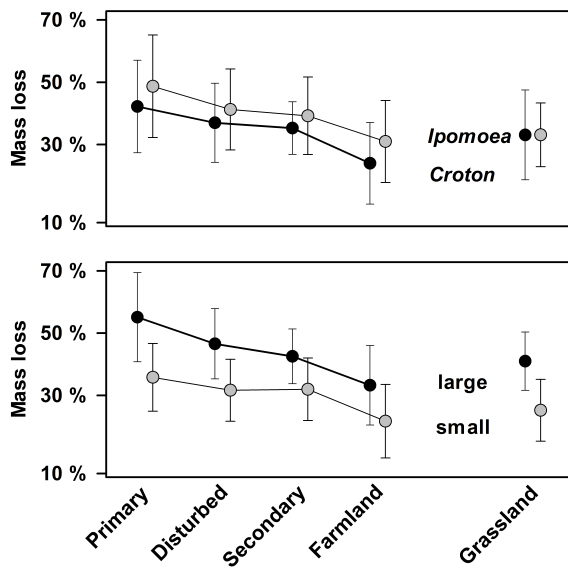
**Figure 3.** Relationship between mass loss over 5 weeks (mean  $\pm$  standard deviation of arcsine-transformed values) for 11 plots within 7 forest fragments in the Kakamega area, western Kenya. Mass loss was measured at all sites during January and February 2009. The squares indicate the four observatories in the largest forest fragment (values jittered to reduce the overlap of symbols)

thermore, we found a land-use\*mesh size interaction, indicating that the effect of invertebrates on mass loss differed between land-use types. As indicated in Fig. 4, the importance of invertebrates for mass loss is higher in primary forests than in farmland. Excluding grasslands, we ordered land-use systems along a land-use gradient from 1 (little anthropogenic influence) to 4 (large anthropogenic influence). Mass loss decreased along this gradient (Table 1;  $r = -0.95$ ;  $n = 4$ ;  $P = 0.032$ ; using overall means across sites). This pattern was similar irrespective of mesh size and litter type. The difference of mass loss with and without access of invertebrates decreased with land-use intensification using differences between means across all plots ( $r = -0.90$ ;  $n = 4$ ;  $P = 0.095$ ), which supported the results presented in Table 2.

## 2.5 Discussion

Summarizing our results, we found, as expected, a clear correlation between rainfall and decomposition measured by the mass loss of litter over 5 weeks. More important are the results suggesting that a decrease of forest fragments in area has a negative effect on decomposition. In line with this finding the experiments at sites affected by different levels of land-use intensity showed a decrease of decomposition with land-use intensification. Finally, we found that soil invertebrates had only small effects on decomposition and that this effect decreases with land-use intensification.





**Figure 4.** Mass loss of organic material (in % after 5 weeks) within five land-use systems affected by different levels of land-use intensity from (nearly) undisturbed primary forest to farmlands. We present a breakdown for *Ipomoea* leaves and *Croton* leaf litter in litter bags with large and small mesh sizes (with and without access of macro-invertebrates) in the Kakamega area, western Kenya. The graph shows raw means and associated standard deviations across all plots averaging across two experiments (see Table S1; sample size of each mean: 60; 5 plots  $\times$  4 bags during the first experiment and 5 plots  $\times$  8 bags during the second; the two experiments were kept separate in Fig. 1 and 2; for statistical tests see Table 2).

Our results are in agreement with earlier studies that have reported higher decomposition rates in undisturbed forests than in disturbed systems (e.g. Lavelle and Pashanasi, 1989; Didham, 1998; Höfer et al., 2001; Attignon et al., 2004; Martius et al., 2004; O'Neill et al., 2006; but see Vasconcelos and Laurance, 2005). In contrast, Schleuning et al. (2011) used part of our data and reported in their analysis of various ecosystem processes in correlation with fragment size and logging that the contribution of invertebrates to decomposition even increased with decreasing fragment size. This study included only the *Croton* leaves and forest sites in their analysis. Given the interactions between leaf type and land-use type in their effect on decomposition (see Table 1), the subtle differences in the analyses of the data as well as the limited number of replicates makes interpretations difficult. Nevertheless, overall mass loss of leaf litter is supposed to be a good indicator for the functioning of the decomposer community (Martius et al., 2004). Schleuning et al. (2011) reported in their analysis a clear correlation between the composition of the decomposer fauna and the contribution of these animals to the decomposition process. The vegetation cover accompanied by the diversity of plant species in near-primary forests provides diverse habitat structures with more buffered microclimate that protects the soil biota from varia-

tions in temperature and associated moisture stress (Mesquita et al., 1998; Dibog et al., 1999). Accordingly, soil invertebrates have been reported to be more numerous and diverse in primary forests than in disturbed systems (Giller et al., 1997; Barros et al., 2002).

The importance of sufficient moisture for decomposition is indicated by the correlation between decomposition and rainfall (see also Pandey and Singh, 1982; Hutson and Veitch, 2006; but see Deshmukh, 1985), probably due to the increased activity of the microorganisms and small invertebrates. For larger invertebrates, the relationship between rainfall and activity may be less simple. During periods with very low and very high rainfall animals may shift into deeper soil layers (Legakis and Adamopoulou, 2005). This behaviour may preclude any meaningful analysis of the contribution of soil invertebrates with rainfall with the available data. Nevertheless, a visual inspection of our data suggests that the influence of invertebrates is highest during the rainy season (see also Attignon et al., 2004).

Mesh size of litter bags is known to influence decomposition dynamics by controlling different size classes of the decomposer community (Schädler and Brandl, 2005). Mesh size, however, influences also the microclimate (Bradford et al., 2002; Hunter et al., 2003). This effect should be less important in forest ecosystems with less direct solar radiation and low evaporation. In our study, we always observed higher mass loss in litter bags with a large than small mesh size, irrespective of the land-use system or the litter type (Figs. 1 and 4). This demonstrates the importance of invertebrates for decomposition (e.g. González and Seastedt, 2001; Bradford et al., 2002; Schädler and Brandl, 2005; Vasconcelos and Laurance, 2005; O'Neill et al., 2006; but see Ribas et al., 2006). However, compared to other studies, this influence was low in all our experiments ( $< 10\%$ ; Fig. 1; but see also Whitford et al., 1986). Our findings contradict some of the earlier studies reporting the influence of invertebrates on leaf litter decomposition to be more pronounced in tropical compared to temperate ecosystems (e.g. Heneghan et al., 1999; González and Seastedt, 2001). This discrepancy may probably be in part due to the environmental context of the studies. Heneghan et al. (1999) and González and Seastedt (2001) measured decomposition rates in tropical systems at elevations of about 500 m a.s.l.. Decomposition rates are known to decrease with increasing elevation (Coûteaux et al., 2002), due to a decrease in abundance and activity of decomposer communities at higher elevations (e.g. Schinner, 1982; Olson, 1994; Gathorne-Hardy et al., 2001). Our study sites were located at about 1500 m a.s.l. (Mitchell, 2004).

In disturbed habitats the contribution of soil fauna to the decomposition processes was less pronounced than in near-primary forests. The clear correlation of mass loss with rainfall for bags with small mesh size shows that moisture is limiting. Therefore it is tempting to speculate that the interaction between land-use and mesh size is due to the reduced density and activity of invertebrates. In fact we found a decrease

of the contribution of invertebrates with land-use intensification. Clearing or disturbing forests affects assemblages and activities of the larger soil invertebrates (Radford et al., 2001; Vasconcelos and Laurance, 2005) and consequently should also affect decomposition (Mesquita et al., 1998; Höfer et al., 2001; Martius et al., 2004). Overall, our data are consistent with the hypothesis that the contribution of invertebrates to decomposition processes decreases with human disturbance (also see Höfer et al., 2001; Martius et al., 2004).

Our results suggest that forest fragmentation and land-use intensification lead to a decrease of leaf litter mass loss and that in the Kakamega area decomposition is mainly driven by microbiota and small invertebrates (body size < 20 µm). Soil moisture may be a limiting factor for decomposition. Therefore, all land-use practices that affect microclimate will also influence decomposition. However, it is worth noting that decomposition at disturbed sites is still at a level which may be sufficient to maintain ecosystem services for sustainable use (Höfer et al., 2001; Barros et al., 2002; Martius et al., 2004). Assemblages of small soil organisms may show a greater resistance to moderate levels of forest disturbance than previously thought (see also Eggleton et al., 1995; Quintero and Roslin, 2005). Nevertheless, in order to protect and enhance the biological activity responsible for decomposition, management practices should maintain as much canopy cover as possible (e.g. by using agroforestry practices) to achieve sustainable agricultural production (see also Dibog et al., 1999).

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