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Litter processing and shredder distribution as indicators of riparian and catchment influences on ecological health of tropical streams

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ABSTRACT

Terrestrial plant litter is the main source of energy for food webs in forest headwater streams. Leaf litter quality often changes when native tree species are replaced by exotic ones and land use change in the watershed can alter physico-chemistry and functional composition of invertebrate communities, ultimately impairing associated ecosystem processes. We used the composition of invertebrate functional feeding groups (FFGs) and the ecosystem process of leaf breakdown as structural and functional indicators, respectively, of ecosystem health in upland Kenyan streams. During dry and wet conditions, invertebrates were sampled in 24 streams within forest (10), mixed (7) and agriculture (7) catchments. Five forest and five agriculture streams were subsequently used for leaf litter breakdown experiments using two native (*Croton macrostachyus* and *Syzygium cordatum*) and one exotic (*Eucalyptus globulus*) species differing in quality. Coarse- and fine-mesh litterbags were used to compare microbial (fine-mesh) with shredder + microbial (coarse-mesh) breakdown rates, and by extension, determine the role of shredders in litter processing in these streams. Seasonal influences on water quality were observed across catchment land uses. Total suspended sediments, turbidity and total dissolved nitrogen were consistently higher during the wet than dry season. However, seasonal influences on FFGs were inconsistent. Catchment land use influenced invertebrate functional composition: 21 taxa, including eight shredders, were restricted to forest streams, but abundance was a poor discriminator of disturbance. Breakdown rates were generally higher in coarse- compared with fine-mesh litterbags for the native leaf species and the relative differences in breakdown rates among leaf species remained unaltered in both agriculture and forest streams. Shredder and microbial breakdown of leaf litter displayed contrasting responses with shredders relatively more important at forest compared with agriculture streams. However, these patterns were inconsistent across leaf species over the dry and wet seasons. Overall, shredder mediated leaf litter breakdown was dependent on leaf species, and was highest for *C. macrostachyus* and lowest for *E. globulus*. This suggests that replacement of indigenous riparian vegetation with poorer quality *Eucalyptus* species has the potential to reduce nutrient cycling in streams, with foodwebs becoming more reliant on microbial processing of leaf litter, which cannot support diverse consumers and complex food webs.

1. Introduction

Developing landscapes to meet human needs has altered surface water hydrology, geomorphology and physico-chemistry, impacting the ecology of streams (Allan, 2004; Dudgeon et al., 2006; Vorosmarty et al., 2010). Land-use changes in catchments and along riparian corridors have replaced natural forests with agriculture, pastures and exotic forestry species (Ferreira et al., 2006a; Hladyz et al., 2011). Loss of natural riparian corridors alters stream light and temperature regimes and the timing, quality and quantity of inputs of leaf litter and dead wood (Elosegi and Johnson, 2003; Wantzen et al., 2008), in turn increasing nutrient inputs and primary production (Scarsbrook and Halliday, 1999; Baxter et al., 2005). These changes typically reduce habitat complexity and biodiversity, and affect organic matter dynamics, nutrient cycling, water purification and erosion processes (Palmer and Filoso, 2009; Acuña et al., 2013).

Riverine ecosystems exhibit extreme heterogeneity in environmental conditions at multiple temporal and spatial scales ranging from microhabitats to whole landscapes (Frissell et al., 1986; Poff,

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1997). Tropical streams and rivers are highly dynamic and water quality is influenced by both catchment land use, and riparian and in-stream activities (Jinggut et al., 2012; Minaya et al., 2013; Silva-Junior et al., 2014). For example, elevated concentrations of nutrients and sediments have been recorded in streams draining agricultural catchments during the wet season due to run-off from unpaved roads, footpaths and farmlands (Kilonzo et al., 2013). In rural catchments, in-stream human activities (water abstraction, bathing, washing and watering of livestock) are influenced by weather conditions, being more common during the dry season (Mathooko, 2001; Yillia et al., 2008). The quality and quantity of leaf litter inputs into these streams is also seasonally variable and dependent on catchment and riparian conditions (Wantzen et al., 2008).

Assessing anthropogenic disturbances on streams relies mostly on monitoring metrics of aquatic communities and physicochemistry (Barbour et al., 1999; Bonada et al., 2006). The relative abundances of various taxa and functional feeding groups (FFGs) of stream benthic invertebrates have been used as structural indicators (Rosenberg and Resh, 1993; Barbour et al., 1999), while functional components (Gessner and Chauvet, 2002; Young et al., 2008) have tended to be neglected. Structural and functional indicators are not necessarily concordant, highlighting the need to consider both during bioassessment (Gessner and Chauvet, 2002; Bonada et al., 2006). Breakdown of leaf litter is an important functional indicator that links riparian vegetation, environmental conditions, microbial and invertebrate activities (Vannote et al., 1980; Hladyz et al., 2010; Woodward et al., 2012). However, while the use of leaf litter breakdown as a measure of ecosystem functioning is receiving increased attention in temperate streams (Gessner and Chauvet, 2002; Young et al., 2008; Woodward et al., 2012), studies in the tropics are limited (Jinggut et al., 2012; Silva-Junior et al., 2014), and the influence of seasonality is not well understood. Moreover, variability of leaf litter decomposition is likely across climatic regions that differ in environmental factors and invertebrate functional composition (Pozo et al., 2011; Pérez et al., 2011).

Despite under-representation in the literature, the functioning of freshwater tropical ecosystems is highly impacted by human disturbance (Dudgeon et al., 2006). For Africa, balancing increased demands for economies, food production, clean water and environmental quality is an increasing challenge (McClain, 2013; McClain et al., 2014). Many catchments in East African montane forests and high potential agro-ecological zones have lost extensive areas of native vegetation to exotic forests, farming, settlement and grazing (Mati et al., 2008; Maitama et al., 2009). Many landscapes are crisscrossed with unpaved roads and footpaths with extensive areas under grazing and farmlands of mainly fast maturing crops. This risks increased soil erosion and sediment loading to streams and rivers; most notably during the rainy season. Indigenous vegetation along streams and rivers in agriculture catchments is increasingly replaced by exotic *Eucalyptus* species. Even though *Eucalyptus* spp. belong to the same group (Family: Myrtaceae) as *Syzygium cordatum* that is endemic and dominant along riparian areas (Mathooko and Kariuki, 2000), *Eucalyptus* leaves are highly sclerophyllous (Graça et al., 2002). As a result, most leaf litter that enters agriculture streams is refractory and high in polyphenolic compounds. This can significantly alter microbial, fungal and invertebrate communities that colonize leaves, leaf-litter breakdown rates, and the higher trophic levels supported by allochthonous resources (Graça et al., 2002; Ardón and Pringle, 2008). Partitioning effects of pressures on stream biota at different spatial and temporal scales is often lacking, but necessary to guide management and safeguard ecosystem services. With few exceptions, data on ecosystem functioning and the extent of anthropogenic influences on East African streams remain limited (Masese and McClain, 2012; Masese et al., 2014).

Leaf litter breakdown in streams is driven by resource quality, activity of consumers and environmental conditions (Tank et al., 2010; Kominoski and Rosemond, 2012). The chemical composition and physical structure of leaf litter influence preferences of shredders and microbial colonization rates (Graça et al., 2001; Ligeiro et al., 2010). Nutrient enrichment of streams can accelerate leaf litter breakdown by stimulating microbial activities and invertebrate consumption (Rosemond et al., 2002; Gulis and Suberkropp, 2003), but the stimulation effect is also dependent upon the quality of leaf litter (Ardón et al., 2006; Ferreira et al., 2006b; Gulis et al., 2006). However, land use influences on the diversity and abundance of shredders, which are more sensitive to nutrient pollution compared with microbes (Hieber and Gessner, 2002; Pascoal et al., 2003), imply that contrasting responses to resource quality among microbes and shredders might be expected. In the tropics, higher temperatures stimulate fast rates of microbial breakdown of litter and may reduce food availability for shredders (Irons et al., 1994; Boyero et al., 2011a). Despite the narrow temperature range in the tropics, agriculture streams are warmer and with higher electrical conductivity, suspended sediments and dissolved nutrients compared with forest streams (Kasangaki et al., 2008; Kilonzo et al., 2013; Minaya et al., 2013). Effects of these changes on ecosystem functioning are poorly understood in Afrotropical streams where land use change has been linked to terrestrial biodiversity loss and changes in the natural flow regimes of rivers (Maitama et al., 2009; Mango et al., 2011; McClain et al., 2014).

In this study, we compared the use of functional and structural indicators to detect changes in land use. We used leaf litter breakdown as a functional indicator and the composition of invertebrates FFGs as structural indicators to assess the influence of rural land use and riparian conditions on ecosystem functioning of Kenyan highland streams. Wet and dry season functional organization of benthic invertebrates were characterized in 24 streams distributed among forest, mixed and agriculture catchments. Leaf breakdown experiments were conducted using two native (*Croton macrostachyus* and *S. cordatum*) and one exotic (*Eucalyptus globulus*) leaf species in five forest and five agriculture streams. The two native species represent nearly the extremes of the litter quality range of native riparian trees in the study area, and the exotic species used has lower litter quality and is common along farm edges, and planted as woodlots in riparian areas as well as in commercial plantations. We hypothesize that: (1) the influence of land use and riparian disturbance on invertebrate structural and functional organization are accentuated by seasonality, (2) breakdown rates of all plant species will be higher in agriculture streams than in forest streams, (3) the relative importance of invertebrates shredders on litter breakdown will be lower in agricultural than in forest streams, and (4) breakdown rates will be species-specific with the nutrient poor species displaying the slowest response to land use.

2. Materials and methods

2.1. Study area

The study was conducted in mid-altitude (1900–2300 m a.s.l) first to third order streams draining the western slopes of the Mau Escarpment within the Kenyan Rift Valley. A total of 24 sites were selected in the headwaters of the Mara River, which flows to Lake Victoria. The river drains the extensive tropical moist broadleaf Mau Forest Complex (MFC) that is a source of rivers draining into Lakes Baringo, Nakuru and Victoria (Fig. 1). Vegetation in the MFC is diverse, with over 95 tree species (Blackett, 1994). Catchment and sub-catchments were delineated and land use categorized using a combined digital elevation model, remote-sensing images (Landsat 5 Thematic Mapper data of 2008, 30 m resolution) and topographic

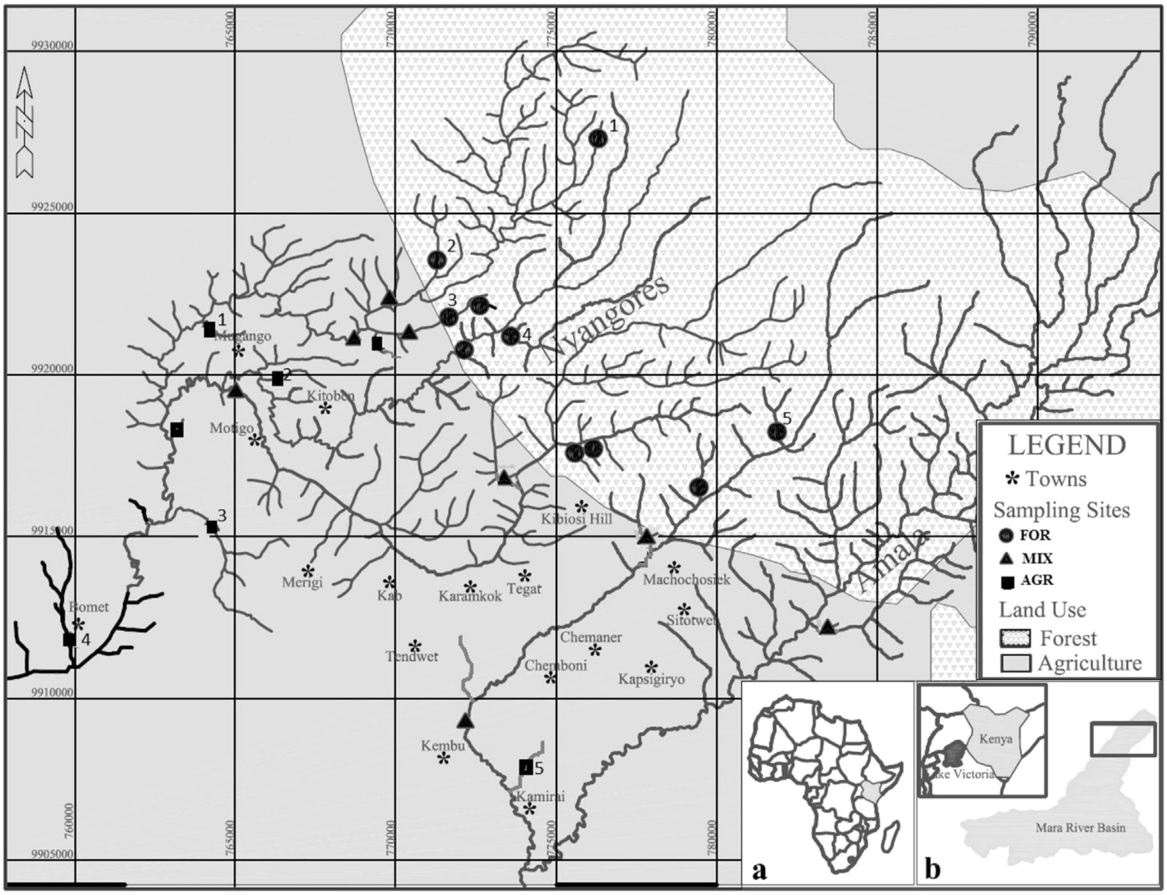

Fig. 1. Map of the upper Mara River basin showing position of study sites. All the 24 streams were kick-sampled for invertebrates while the numbered streams 1–5 in the agriculture (darker shading) and forest (lighter shading) land uses were used for leaf litter processing experiments.
Modified from Minaya et al. (2013).

maps (1:50,000 survey of Kenya 1971) (Minaya et al., 2013). The area of each land use type for each sub-catchment draining to a sampling site (point) was calculated. Sites were selected in one of 3 catchment-scale land uses that were defined as: (a) forest sites (FOR, $n = 10$) draining catchments with >60% forest; (b) agriculture sites (AGR, $n = 7$) draining catchments with >60% agriculture; and (c) mixed sites (MIX, $n = 7$) located in agricultural areas with the upstream catchments comprising different proportions of the two main land uses, forestry and agriculture, but none with >60%. FOR sites had a mean (±SD) value of 95.3 ± 13.4% of total catchment area under forestry with other land uses (grasslands, shrubland) comprising <10% (Table 1). All FOR sites did not have any proportion of agricultural land use. AGR sites had a mean (±SD) of 93.8 ± 3.4% of total catchment area under agriculture with the rest of the land uses (roads, bare ground, urban areas) comprising <10% of the land area. All AGR sites did not have any proportion of forest land use. MIX sites had means of 51.4 ± 11.4% and 44.0 ± 8.6% of land area under forestry and agriculture, respectively. Among the three land uses, sites were selected based on accessibility, stream size (discharge), in-stream gradient and physical habitat conditions.

Table 1
Mean (±SE) values for different proportions of land uses in the Agriculture, Mixed and Forest streams in the upper Mara River basin, Kenya; agriculture – $n = 7$, mixed – $n = 7$, forest – $n = 10$.

Land use proportions	Stream types		
	Agriculture	Mixed	Forest
% Forest	–	51.4 ± 11.4	95.3 ± 13.4
% Agriculture	93.8 ± 3.4	44.0 ± 8.6	–
% Other land uses	6.3 ± 4.2	4.6 ± 1.2	5.8 ± 3.3

The present coverage of the MFC is fragmented and reduced in size because of excisions for human settlement, coniferous forest plantations and large- and small-scale cultivation of tea (Lovett and Wasser, 1993). Some intact forest blocks are protected as part of forest reserves and national parks (Lovett and Wasser, 1993). People living in the adjoining areas are involved in semi-intensive smallholder agriculture, characterized by cash crops (mainly tea), food crops (mainly maize, beans and potatoes) and animal husbandry. This has also resulted in the loss of indigenous riparian vegetation along agriculture streams and rivers where exotic *Eucalyptus* dominate.

Climate of the MFC is characterized by low ambient temperatures, falling below 10 °C during the cold months of January–February. Annual precipitation ranges from 1000 to 2000 mm and is bimodal. Dry conditions occur during January–March and July and two wet conditions during April–June and October–November, which are periods for the long and short rains, respectively.

2.2. Physical and chemical variables

At each site, percent canopy cover, stream width, water depth, velocity and discharge were determined over a 100 m reach. Percent canopy cover above each stream was estimated visually. Stream width was measured at 10 transects located at mid-points of 10-m intervals. On each transect, water depth was measured at least at 5 points across the river using a 1-m ruler. Velocity was measured at the same points as depth using a mechanical flow metre (General Oceanic 2030). Stream discharge was estimated using the velocity-area method (Wetzel and Likens, 2000). Presence or absence of leaf litter was noted at each point where depth measurements were made and used to estimate percentage of substratum covered by leaf litter. The proportion of riffles and pools in the stream was determined by identifying whether each of the 10 transects crossed a pool or a riffle, and recorded as a percentage of the 100-m reach. Concurrent measurements of pH, dissolved oxygen (DO), temperature and electrical conductivity were measured *in situ* using a YSI multi-probe water quality metre (556 MPS, Yellow Springs Instruments, Ohio, USA), and turbidity was measured using a portable Hach turbidity metre (Hach Company, 2100P ISO Turbidimeter, USA). Water samples were collected from the thalweg using acid washed HDP bottles for analysis of nutrients, major anions and cations, dissolved organic carbon (DOC) and particulate organic matter (POM). For total suspended solids (TSS) and POM stream water samples were immediately filtered through pre-weighed glass-fibre filters (Whatman GF/F, pre-combusted at 450 °C, 4 h). GF/F filters holding suspended matter were carefully folded and wrapped in aluminium foil before transport in a cooler box at 4 °C to the laboratory. Both the filtered and unfiltered water samples were stored and transported in a cooler box and frozen within 10 h of sampling.

Water quality variables determined in the laboratory were alkalinity, TSS, POM, DOC, total dissolved nitrogen (TDN), total dissolved phosphorus (TDP), total phosphorus (TP), soluble reactive phosphorus (SRP) and total nitrogen (TN). Alkalinity (mmol l^{-1}) was determined by potentiometric titration of 200 ml of filtrate with 0.1 N HCl acid (3.65 g/l) to a pH of 4.3. GF/F filters holding suspended matter were dried (95 °C) to constant weight and TSS was determined by re-weighing on an analytical balance and subtracting the filter weight. Filters were ashed at 500 °C for 4 h and re-weighed for determination of POC as the difference between TSS and ash-free-dry weight. DOC and TDN concentrations were determined using a Shimadzu TOC-V-CPN with a coupled total nitrogen analyzer unit (TNM-1). TDP was determined using the ascorbic acid spectrophotometric method, while TP, SRP NH_4-N and TN were determined using standard calorimetric methods (APHA, 1998). Major anions, nitrate (NO_3^-), ortho-phosphate (PO_4^{3-}), chloride (Cl^-) and sulphate (SO_4^{2-}), were determined by Ion Chromatography (Dionex ICS-1000) and the major cations, sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), dissolved silicates (DSi), using an ICP-MS. Organic matter in kick samples was washed into a 100-μm-mesh sieve to remove inorganic materials. This size of organic matter that is >100 μm is collectively referred to as particulate organic matter (POM) in this study. POM was dried to a constant mass at 68 °C for at least 48 h, and the different fractions (leaves, sticks, seeds and flowers) weighed separately using a Sartorius balance.

2.3. Leaf litter breakdown

Leaf litter breakdown experiments were conducted during wet-(May–July 2011) and dry-(January–March 2012) seasons at five forest streams and five agriculture streams in rural agriculture catchments. These ten sites were part of the 24 sites for invertebrate kick sampling, and were a compromise between representativeness of environmental conditions and effort.

Three different leaf species were used to test the influence of litter quality on invertebrate colonization and breakdown. We chose two indigenous leaf species – Lace-leaf *C. macrostachyus* Hochst. ex Delile (Family Euphorbiaceae) [henceforth *Croton*] and *S. cordatum* Hochst ex Krauss (Family Myrtaceae) [henceforth *Syzygium*] – that are typical riparian trees along streams in the region and are among the ten most dominant species in the MFC (Blackett, 1994; Mathooko and Kariuki, 2000), and one exotic species – *E. globulus* Labill. (Family Myrtaceae) [henceforth *Eucalyptus*] – which is the most common replacement species along streams in agriculture catchments in the region (Kenya Forestry Service, 2009). *Croton* leaves are soft and fast decaying and thus were chosen to represent high quality leaf litter in the region. In contrast, *Syzygium* has tough and smooth leaves whose breakdown was hypothesized to be comparable with that of *Eucalyptus*. Syzygium has also been used in decomposition studies in the region and was chosen for comparison (Mathooko et al., 2000).

Abscised leaves were air dried at room temperature for two weeks to attain constant mass before weighing. Thereafter leaves were enclosed in either coarse-mesh (10 mm) or fine-mesh (0.5 mm) bags (~4 g of each species per bag). Unlike the coarse-mesh, the fine-mesh was meant to exclude shredders so that breakdown rates could be attributed to microbial processing only (Gessner and Chauvet, 2002). Before deployment 252 litterbags were arranged into sets of four replicates per litterbag type (2 types) per plant species (3 plant species) in each stream (10 streams = 240 litterbags) per season. The 12 extra litterbags were used to determine initial ash-free-dry mass (AFDM) for each leaf species. Litterbags were deployed at each site and secured by nylon lines sufficiently far apart to avoid overlap. Bags were retrieved after 56 days. Loss of invertebrates and leaf fragments was avoided by enclosing bags in 300-μm mesh net before removal. Individual bags were preserved in 75% ethanol.

2.4. Invertebrates

Stream invertebrate kick samples were collected once each during the dry (January–February 2011) and wet season (May–July 2011). Sample sites included ten least-disturbed forest (FOR) streams located in Transmara Forest, seven agriculture (AGR) streams in catchments draining agriculture lands and seven mixed (MIX) streams in catchments that were partly forest and partly agriculture (Fig. 1). At each site and occasion, and along a 100-m reach of stream, five random kick samples each were collected, respectively, from riffles and pools (total 10 samples) using a dip net of 300 μm mesh-size. An area covering approximately 30 cm × 50 cm was disturbed rapidly for 10 s and all contents from the net preserved in 75% ethanol and stored in polythene bags. The rapid sampling method was necessary to capture large invertebrates, especially fast moving crabs (Magana et al., 2012).

2.4.1. Community structure and functional composition

Kick samples: After sorting from debris, invertebrates were identified to the lowest possible taxonomic level or morphospecies with a series of guides (Day et al., 2002; de Moor et al., 2003a,b; Stals and de Moor, 2007; Merritt et al., 2008). All samples from pools and riffles were composited for each site per season. Invertebrates were assigned into four FFGs – collectors, predators, scrapers and shredders according to Masese et al. (2014). In summary, gut contents were removed under 40× magnification onto a glass slide before being mounted with polyvinyl lactophenol. Using a compound microscope, estimates were made of percent of different food items in guts, assumed to be 100% full. Food items identified included vascular plant material (VPM – particles >1 mm), coarse particulate organic matter (CPOM – particles from 50 μm to 1 mm), fine particulate organic matter (FPOM – particles <50 μm), algae and animal material. Shredders were invertebrates whose gut contents comprised mainly leaf and wood fragments >1 mm, while predators fed mainly on animal material. Collectors were assumed to consume CPOM and FPOM and scrapers FPOM and algae. For invertebrates whose guts were empty or food items indistinguishable, literature was used to determine FFG (Dobson et al., 2002; Merritt et al., 2008).

Litterbag samples: During retrieval, some litterbags were lost to sedimentation and this reduced the number of analyzed replicates to 3 per mesh size per leaf species. Invertebrates in litterbags were sorted under a stereo microscope and identified to the lowest possible taxonomic level. Leaves and leaf fragments from bags were rinsed and oven-dried at 105 °C for 24–48 h to yield dry mass and then ashed at 550 °C for 4 h and reweighed to calculate percent ash and AFDM.

2.5. Statistical analyses

Habitat conditions expressed as percentages were arcsin [$\sqrt{}(x/100)$] transformed while physico-chemical parameters, except pH, were Ln $(x+1)$ transformed before analysis to meet assumptions for parametric tests (Zar, 1999). Invertebrate count data were Ln $(x+1)$ transformed for parametric tests while un-transformed data were used for non-parametric tests. The arcsin ($\sqrt{}(x/100)$ transformation is appropriate for data expressed as a percentage while Ln$(x+1)$ transformation is appropriate for count data with values less than 10 (Zar, 1999). All statistical analyses were performed with Statistica (Version 7, 2004, StatSoft, Tulsa, Oklahoma), unless otherwise indicated. Two-way ANOVA was used to test for differences in physico-chemical parameters, riparian and organic matter variables among land uses (AGR, MIX, FOR) and seasons (dry and wet) with land use and seasons as main factors and a land use × season interaction term. Where there were no significant seasonal differences, data were pooled and one-way ANOVA tested for differences among land uses followed by Tukey multiple *post hoc* comparisons of the means. Principal Component Analysis (PCA) was used to summarize variation in physico-chemical parameters, riparian and organic matter characteristics among land uses and sites.

Community structure and functional composition of invertebrates in kick samples and coarse-mesh litterbags were described as abundance (number of individuals per sample or litterbag), taxa richness (number of taxa per sample or litterbag) and the four FFGs-collectors, predators, scrapers and shredders. General linear models (GLMs) were used to test differences in total abundance of all taxa, richness of all taxa (number of taxa), shredder and non-shredder richness and shredder abundance in kick samples between seasons (dry and wet) and among land uses, followed by *post hoc* Tukey tests to identify differences among land uses and land use × season interactions.

Non-metric multidimensional scaling (NMDS) was used to visualize invertebrate community structure and functional composition in the kick samples among land uses and seasons. Dissimilarity matrices based on the Bray–Curtis coefficients (Bray and Curtis, 1957) were derived for 4 data sets: taxa presence–absence data of taxa richness for all invertebrates, un-transformed abundances for all invertebrate taxa, un-transformed abundances for the four functional groups, and taxa presence–absence for the four functional groups. Goodness of fit of the ordination was assessed by the magnitude of the associated stress value; a value of <0.2 corresponds to a good ordination (Kashian et al., 2007). The percentage contribution of each taxon to the overall dissimilarity between agriculture and forest land use were quantified by the similarity percentages (SIMPER) routine in Paleontological Statistics (PAST) software package (Version 2.17; Hammer et al., 2001). SIMPER is a strictly pairwise analysis between two factor levels (Clarke and Warwick, 2001); in this case agriculture and forest.

Leaf breakdown rates were estimated using an exponential decay model $Wt = W_0e^{-kt}$ (Wt = remaining AFDM at time t (56 days); W_0 = initial AFDM; $-k$ = decay rate (Boulton and Boon, 1991). Breakdown rates for fine- (kf) and coarse-mesh (kc) litterbags were calculated separately. To determine the effect of excluding potential invertebrate shredders from fine-mesh litterbags on breakdown, kc/kf coefficients were calculated for each stream. Similarly, ki/kr coefficients (i for impacted [agriculture] and r for reference [forest] streams, respectively) were calculated for coarse- and fine-mesh litterbags (Gessner and Chauvet, 2002) to determine the effect of land use on shredder and microbial breakdown, respectively. GLMs were used to compare total taxa richness, shredder and non-shredder taxa richness, and shredder abundance in coarse-mesh litterbags for forest and agriculture streams. Four-way ANOVA explored variation in leaf breakdown rates ($-k$) with season (wet and dry), land use (forest and agriculture), leaf species (*Croton*, *Syzygium* and *Eucalyptus*) and treatment by mesh size (fine- or coarse-mesh litterbags) as the main factors, including interactions. Because of lack of season × land use × leaf species × treatment-by-mesh-size interactions and to partition seasonal influences on breakdown, three-way ANOVAs were re-run separately for the wet and dry seasons with land use, leaf species and treatment by mesh size as the main factors, including interactions.

3. Results

3.1. Environmental conditions

Streams in agriculture and forest catchments showed differences in physico-chemical and organic matter characteristics, with mixed streams being intermediate (Table 2). Factor 1 in the PCA ordinations accounted for most variation, distinguishing most forest from agriculture sites (Fig. 2a–d). Variables most related to Factor 1 were related to water quality (temperature, turbidity TSS) and stream size (discharge, width and depth), which increased towards agriculture and mixed streams. Riparian and organic matter characteristics (% canopy cover, % leaf litter and litter biomass) increased towards forest streams (Fig. 2a–d). Canopy cover was >80% in most forest streams with decomposing leaf litter and woody debris dominating in pools. In agriculture streams, canopy cover was less than 50% and discontinuous in stream reaches frequented by people and livestock. Area covered by decomposing litter (% leaf litter) did not differ between seasons but was higher in forest than in both agriculture and mixed streams (one-way ANOVA, $F_2 = 28.62$, $p < 0.001$). There were significant differences in POM standing stocks among the land uses (one-way ANOVA, $F_2 = 8.44$, $p < 0.05$), but not with season (Table 2).

Factor 2 was associated with nutrients (SRP and TDN) and DOC, which increased towards agriculture streams. Forest streams were cooler (mean temperature: 14.4 ± 0.58 °C) than agriculture streams (mean: 18.7 ± 2.88 °C). TSS, turbidity, TDN, DOC, Cl^-, $SO_4{}^{-2}$, $HCO_3{}^-$, DSi and NH_4-N had significantly ($p < 0.05$) higher values in agriculture streams than in forest streams (Table 2). TSS, turbidity, TDN, NH_4-N and DOC were consistently higher during the wet season while Cl^-, $SO_4{}^{-2}$, and $HCO_3{}^-$ were higher during the dry season across the three land uses. Fe^{++}, Na^+, K^+ and PO_4-P, NO_3-N and conductivity showed no seasonal variation but significantly ($p < 0.05$) higher values in agriculture streams compared with forest.

3.2. Community structure

The distribution and abundance of invertebrate taxa identified in the study area are presented in Appendix 1 (online supplementary material). A total of 25,887 individuals belonging to 109 taxa were collected. Of the 109 taxa, 81and 93 were collected during the dry and wet seasons, respectively. Total abundance was higher during the wet than dry season ($F_{1,2} = 7.03$, $p < 0.05$) but did not differ among land uses. Taxa richness was highest in forest streams (richness, $F_{1,2} = 3.02$, $p < 0.05$), but did not differ between seasons (Fig. 3). Ninety-six taxa were found in forest streams, 70 in mixed streams and 60 in agriculture streams. Fifty-four taxa occurred in

Table 2
Mean (±SE) values for physico-chemical parameters, riparian conditions and organic matter for streams within the three land use categories; agriculture, mixed and forest. Means for physico-chemical parameters that displayed significant differences (Two-way ANOVA) between the dry and wet seasons have been presented separately. Similar superscripts on means indicate no significant difference for parameters and organic matter among land use types – *post hoc* Tukey tests; agriculture – $n = 7$, mixed – $n = 7$, forest – $n = 10$ per season.

Physico-chemical parameters	Land use			*F*	*p*-Value
	Agriculture	Mixed	Forest		
Organic matter fractions					
Leaves (g/m^2)	100.1 ± 14.8^{a}	117.5 ± 14.0^{b}	162.9 ± 15.2^{b}	5.02	0.012*
Sticks/wood (g/m^2)	55.8 ± 7.4^{a}	62.1 ± 11.7^{a}	60.22 ± 7.4^{a}	0.14	0.870
Fruits and flowers (g/m^2)	15.9 ± 5.5^{a}	17.5 ± 4.8^{a}	24.2 ± 5.2^{b}	7.20	0.028*
Seeds (g/m^2)	7.4 ± 0.8^{a}	3.4 ± 0.2^{a}	5.3 ± 0.9^{a}	0.45	0.799
Standing stock (g/m^2)	145.6 ± 13.6^{a}	169.1 ± 19.2^{b}	233.0 ± 14.4^{b}	8.44	0.040*
% Litter	36.8 ± 4.5^{a}	45.2 ± 3.3^{a}	78.1 ± 4.4^{b}	28.62	<0.001*
% Canopy cover	45.4 ± 2.6^{a}	54.2 ± 2.9^{a}	80.7 ± 4.5^{b}	27.96	<0.001*
No seasonal variation					
Ca (mg/l)	5.2 ± 0.1^{a}	4.3 ± 0.1^{a}	$2.\ 7 \pm 0.5^{a}$	5.62	0.051
Mg (mg/l)	1.3 ± 0.1^{a}	1.4 ± 0.1^{a}	0.9 ± 0.2^{a}	4.10	0.128
K (mg/L)	9.2 ± 0.8^{a}	4.6 ± 0.3^{b}	4.3 ± 0.2^{b}	8.31	0.016*
Na (mg/L)	11.8 ± 1.3^{a}	$7.7 \pm 0.\ 5^{b}$	6.2 ± 0.5^{b}	16.00	<0.001*
Fe (mg/l)	2.0 ± 0.9^{a}	2.4 ± 1.2^{a}	0.9 ± 0.4^{b}	8.57	0.015*
NO$_3$-N (mg/l)	1.2 ± 0.3^{a}	1.2 ± 0.4^{a}	0.3 ± 0.1^{b}	11.62	0.003*
PO$_4$-P (mg/l)	0.2 ± 0.1^{a}	0.2 ± 0.2^{a}	0.1 ± 0.01^{b}	8.97	0.011*
pH	5.0 ± 0.8^{a}	6.5 ± 1.1^{a}	6.7 ± 0.4^{a}	0.54	0.764
DO (mg/l)	6.7 ± 0.7^{a}	5.7 ± 1.0^{a}	7.3 ± 0.2^{a}	3.42	0.181
Conductivity (μS/cm)	167.3 ± 29.6^{a}	$116.1 \pm 25.8^{a,b}$	87.3 ± 11.2^{b}	10.021	0.007*
Temperature (°C)	18.7 ± 2.9^{a}	16.4 ± 1.9^{ab}	14.4 ± 0.6^{b}	7.61	0.022*
TP (mg/l)	0.3 ± 0.1^{a}	0.3 ± 0.1^{a}	0.2 ± 0.1^{a}	2.94	0.231
TN (mg/l)	1.3 ± 0.25^{a}	1.6 ± 0.34^{a}	0.6 ± 0.1^{b}	9.61	0.008*
SRP (μg/l)	17.2 ± 7.6^{a}	18.7 ± 6.5^{a}	1.3 ± 0.9^{b}	9.61	0.008*
Seasonal variation					
TSS (mg/l)					
Dry	85.7 ± 24.6^{a}	73.3 ± 8.0^{a}	22.7 ± 7.6^{b}	26.17	<0.001*
Wet	254.9 ± 74.1^{a}	173.5 ± 14.6^{a}	36.6 ± 20.5^{b}	20.21	<0.001*
Turbidity (NTUs)					
Wet	122.8 ± 23.3^{a}	77.1 ± 9.2^{a}	21.1 ± 1.2^{b}	7.68	0.023*
Dry	64.5 ± 9.5^{a}	38.7 ± 6.1^{a}	7.8 ± 0.8^{b}	8.89	0.012*
TDN (mg/l)					
Dry	1.1 ± 0.3^{a}	1.2 ± 0.3^{a}	0.3 ± 0.2^{b}	6.78	0.041*
Wet	1.3 ± 0.4^{a}	2.8 ± 0.5^{ab}	1.0 ± 0.4^{b}	10.73	0.005*
POM (mg/l)					
Dry	25.0 ± 13.5^{a}	38.5 ± 14.6^{a}	10.6 ± 8.5^{a}	0.089	0.956
Wet	70.7 ± 17.1^{a}	84.6 ± 40.1^{ab}	21.9 ± 10.2^{b}	6.45	0.045*
DOC (mg/l)					
Dry	3.6 ± 0.9^{a}	3.9 ± 0.3^{a}	2.7 ± 0.4^{b}	8.07	0.016*
Wet	8.1 ± 0.92^{a}	4.2 ± 1.23^{a}	3.5 ± 0.6^{b}	14.11	0.001*
Cl (mg/l)					
Dry	5.6 ± 1.4^{a}	6.1 ± 1.2^{ab}	3.8 ± 0.4^{b}	6.38	0.046*
Wet	3.9 ± 0.6^{a}	5.1 ± 1.2^{a}	1.0 ± 0.8^{b}	6.72	0.035*
SO$_4$ (mg/l)					
Dry	3.8 ± 0.6^{a}	6.1 ± 1.8^{b}	3.2 ± 0.7^{a}	6.78	0.041*
Wet	2.7 ± 0.5^{a}	4.0 ± 2.1^{a}	0.5 ± 0.4^{b}	7.78	0.020*
HCO$_3$ (mg/l)					
Dry	59.3 ± 18.7^{a}	56.7 ± 6.3^{ab}	25.0 ± 5.6^{b}	10.73	0.00
Wet	23.3 ± 6.9^{a}	29.5 ± 2.1^{a}	13.1 ± 10.8^{a}	3.02	0.223
DSi (mg/l)					
Dry	25.9 ± 2.4^{a}	39.2 ± 2.8^{a}	27.7 ± 2.7^{b}	6.8	0.040*
Wet	38.5 ± 16.4^{a}	25.1 ± 9.3^{a}	9.0 ± 6.6^{b}	4.88	0.039*
NH$_4$-N (μg/l)					
Dry	28.2 ± 13.6	51.3 ± 32.4^{a}	11.2 ± 1.4^{b}	10.73	0.005*
Wet	11.6 ± 7.7^{a}	14.2 ± 8.6^{a}	2.5 ± 1.2^{b}	7.61	0.022*
% Riffle					
Wet	49.0 ± 2.3^{a}	48.6 ± 5.3^{a}	53.3 ± 5.4^{a}	0.36	0.702
Dry	53.6 ± 4.4^{a}	54.0 ± 5.8^{a}	43.6 ± 2.0^{a}	1.02	0.325
% Pool					
Wet	51.2 ± 4.3^{a}	47.9 ± 3.4^{a}	46.7 ± 4.5^{a}	0.40	0.678
Dry	52.0 ± 4.8^{a}	51.8 ± 2.3^{a}	62.9 ± 5.7^{a}	2.03	0.118
Depth (m)					
Wet	0.2 ± 0.1^{a}	0.2 ± 0.1^{a}	0.3 ± 0.1^{a}	0.10	0.906
Dry	0.2 ± 0.1^{a}	0.1 ± 0.02^{a}	0.1 ± 0.02^{a}	2.20	0.137
Width (m)					
Wet	2.8 ± 0.4^{a}	2.3 ± 0.3^{a}	2.1 ± 0.3^{a}	1.12	0.346
Dry	3.6 ± 0.9^{a}	3.1 ± 1.1^{a}	2.4 ± 0.9^{a}	0.44	0.651
Discharge (m^3 s^{-1})					
Wet	0.6 ± 0.1^{a}	0.5 ± 0.4^{a}	0.4 ± 0.3^{a}	1.56	0.233
Dry	0.2 ± 0.1^{a}	0.1 ± 0.1^{a}	0.1 ± 0.1^{a}	2.85	0.081

* Significant differences at $p < 0.05$.

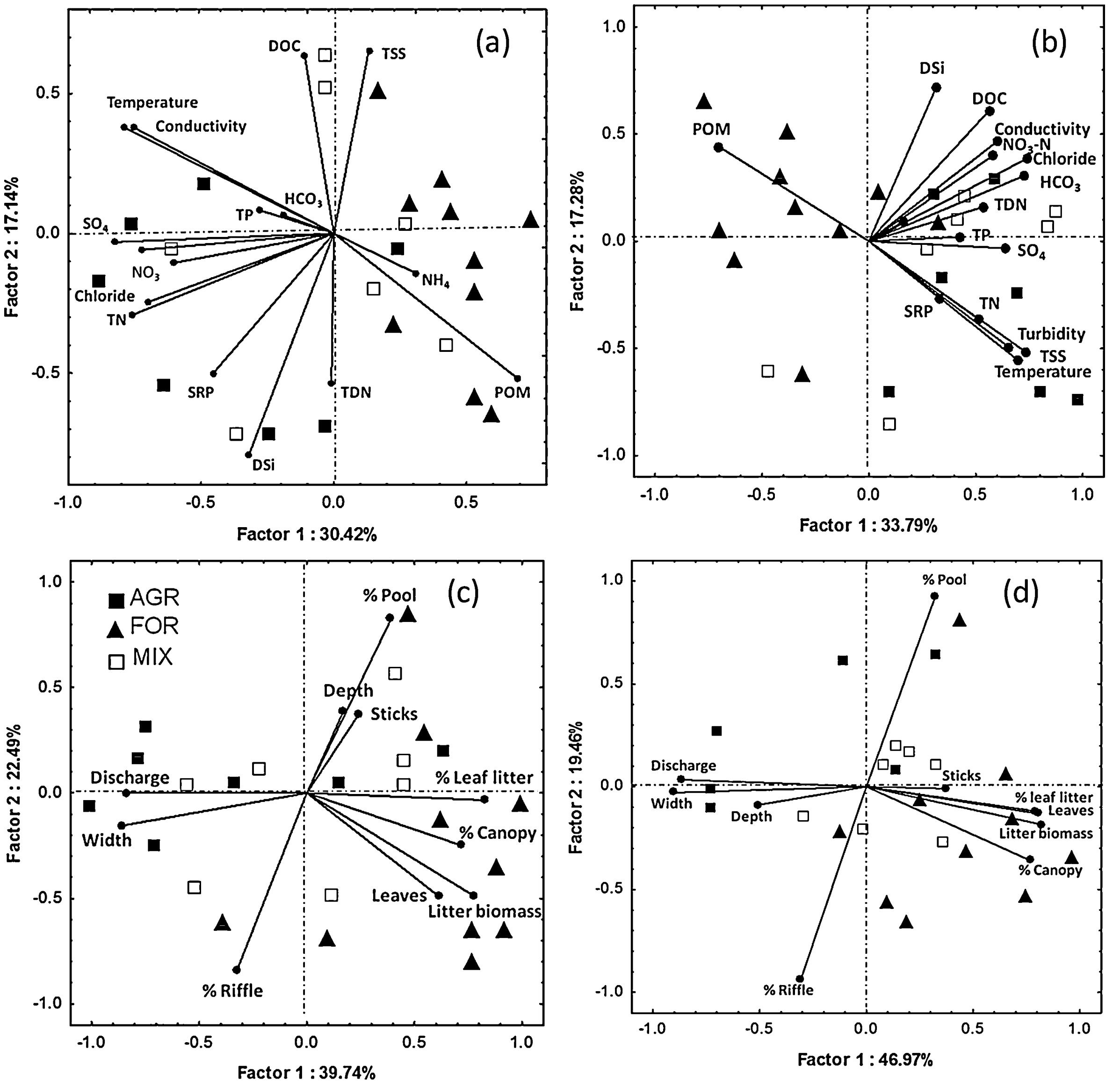

Fig. 2. Principal component analysis on physico-chemical parameters (a and b) and riparian and organic matter characteristics (c and d) during the wet (a and c) and dry (b and d) seasons. Variation explained by each axis (r^2, expressed as a percentage) is shown; FOR – $n = 10$, AGR – $n = 7$, MIX – $n = 7$ per season.

all land uses, 21 taxa were restricted only to forest streams, six to mixed streams and two to agriculture streams. NMDS ordinations of abundance data indicated separation of most FOR from AGR sites (Fig. 4a and b), and clear separation of FOR and AGR sites for presence–absence of taxa (Fig. 4c and d) indicating that the difference in invertebrate communities was not only as a result of differences in relative abundance, but was also caused by differences in taxa richness. SIMPER identified Simuliidae, *Tricorythus tinctus* and *Pseudocloeon* sp. as taxa most influencing the difference between FOR and AGR communities during the wet season (Table 3). Other important taxa included Chironominae, *Afronurus* sp., *Cheumatopsyche thomassetti*, *Tubifex* sp., *Hydropsyche* sp. and *Afrocaenis* sp. The same taxa were important during the dry season, except for a decrease in abundance of most taxa in both FOR and AGR streams.

3.3. Functional composition

The distribution and abundance of FFGs among sites and land uses are presented in Appendix 1. A total of 19 shredders, 26 collectors, 21 scrapers and 43 predator taxa were identified in the study area. All 19 shredder taxa occurred in forest streams, while none were restricted to the streams in mixed or agriculture catchments. Eight shredder taxa were restricted to forest streams and another eight widespread across all land uses, with a seasonal × land use interaction ($F_{1,1} = 3.94$, $p < 0.05$). In both seasons, total number of taxa and number of shredder taxa were higher in forest than in agriculture streams. Non-shredder richness did not vary among land uses during the dry and wet seasons (Fig. 3). Shredder abundance was higher in forest compared with agriculture and mixed streams only during the wet season (Fig. 3). *Potamonautes* sp.1 was the most abundant shredder in forest streams with a mean abundance per sample of (29.6 ± 5.0), followed by *Lepidostoma* sp. (14.6 ± 2.4) and *Acanthiops* sp. (8.3 ± 3.4). In agriculture streams, *Pyralidae* sp. 1 dominated abundance (9.3 ± 3.6) followed by *Lepidostoma* sp. (5.9 ± 1.6), then *Tipula* sp.1 (4.6 ± 1.3).

NMDS ordination plots for un-transformed abundances and un-transformed presence–absence (taxa richness) data for the four functional groups were similar during the wet and dry seasons and separated most forest streams from agriculture streams on

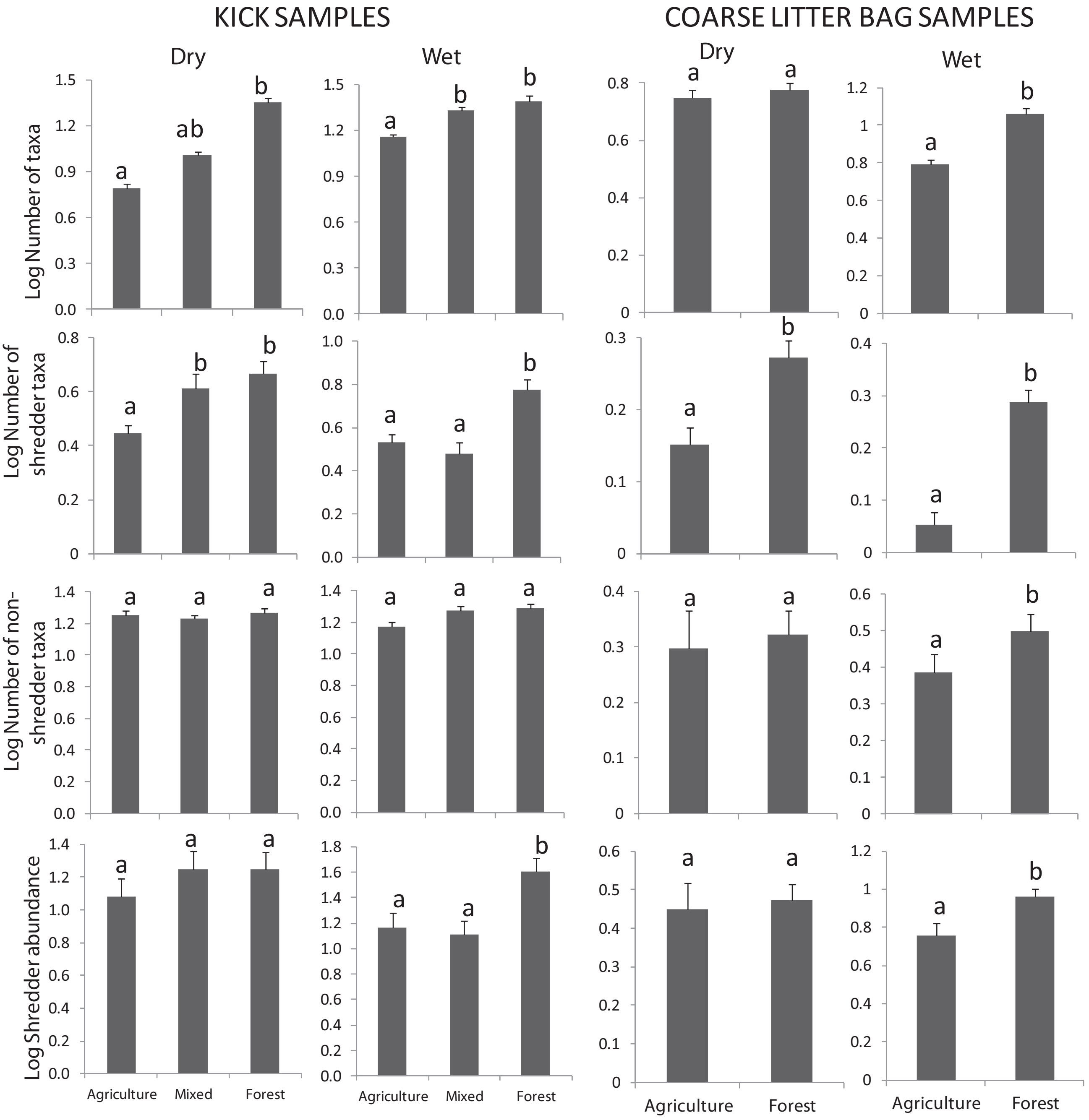

Fig. 3. Mean (±SE) number of taxa, number of shredder taxa, number of non-shredder taxa and shredder abundance (transformed to the log[$x+1$]) during the dry and wet seasons at agriculture, mixed and forest sites for kick samples and at agriculture and forest sites for colonized coarse-mesh bags (different letter indicates significant differences among land uses). Note the differing range in y-axes. For kick samples FOR – $n=10$, AGR – $n=7$, MIX – $n=7$ per season; for coarse litterbag samples, $n=15$ for all sites per season.

both axes (Fig. 5a–d). While the responses among the various FFGs were variable, abundance and taxa richness of each FFG responded similarly to land use influences.

3.4. *Leaf litter breakdown*

Across seasons and land use, breakdown rates were species-specific and generally displayed similar trends with *Croton* having the fastest decay rate followed by *Syzygium* then *Eucalyptus* (Fig. 6). Breakdown rates ($-k$) were higher in coarse- than in fine-mesh litterbags for the three species and in the two land uses, except for *Eucalyptus* during the wet season. Plant species and mesh-size influenced breakdown rates during the wet and dry seasons, but land use was only important during the wet season (Table 4). However, lack of interactions between and among the three factors implies that shredder and microbial contributions to litter breakdown were not consistent for all plant species across sites in the two land uses. During the wet season, there interaction between land use and treatment by mesh size was significant while that between land use and leaf species was marginally significant ($0.05 > p < 0.1$). This indicates that response of breakdown, by both shredders and microbes, to land use was dependent on leaf quality. For instance, *Croton* displayed the greatest response to microbial processing in agriculture streams during the dry and wet seasons.

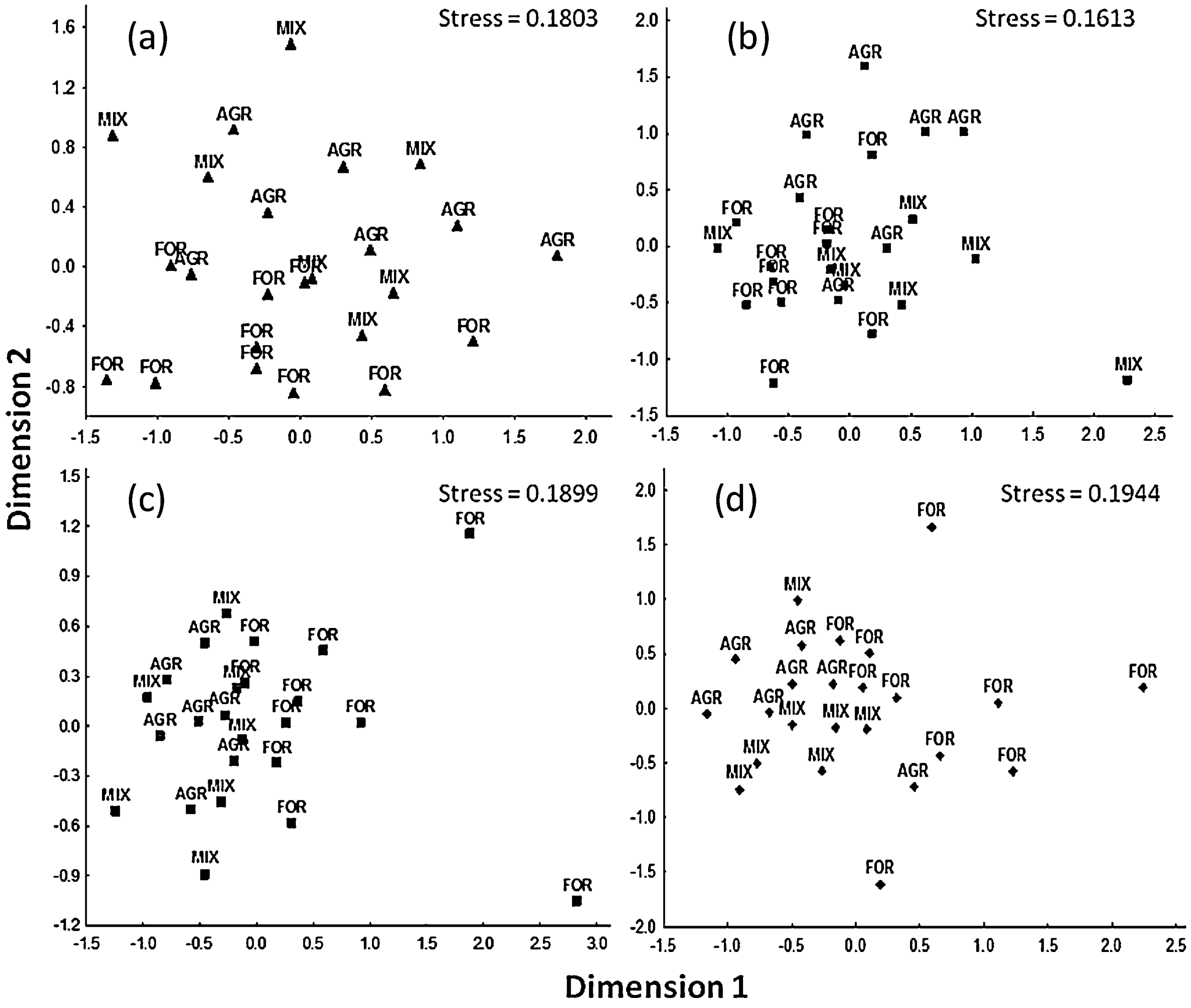

Fig. 4. Non-metric multidimensional scaling (NMDS) plots of invertebrate community composition based on abundance data of the various taxa during (a) wet season and (b) dry season, and species presence–absence data of various taxa during (c) wet season and (d) dry season in the three land uses: forest (FOR), agriculture (AGR) and mixed (MIX). Presence–absence data responded more strongly to land use compared with abundance data.

However, shredder processing were similar for *Croton* and *Syzygium* during both seasons and in the two land uses, except in agriculture streams during the wet season (Fig. 6). Total number of taxa, number of shredder taxa and shredder abundance in coarse-mesh litterbags were higher in forest than agriculture streams during the wet season (Fig. 3). During the dry season, land use effects were not evident; shredder abundance was not affected by land use, although shredder taxa richness was higher in forest streams.

The relative contribution of shredders to breakdown was higher in forest streams for the three leaf species and was highest for *Croton*, followed by *Syzygium* and then *Eucalyptus*, except in agriculture streams when the contribution was highest in *Syzygium* (Table 5). In coarse-mesh litterbags during the dry season the *ki*/*kr* coefficients showed that shredder breakdown of leaf litter was limited in agriculture streams for *Croton* (*ki*/*kr* = 0.84) but not for *Eucalyptus* (*ki*/*kr* = 1.39) or *Syzygium* (*ki*/*kr* = 0.99). During the wet season the effects on shredder breakdown were more evident for *Croton* (*ki*/*kr* = 0.82), and *Syzygium* (*ki*/*kr* = 0.43) (Fig. 6). Conversely, during the dry season microbial breakdown was enhanced in agriculture streams for *Croton* (*ki*/*kr* = 1.26) and *Eucalyptus* (*ki*/*kr* = 1.38). During the wet season microbial processing in forest and agriculture streams were similar for *Croton* (*ki*/*kr* = 1.08) and *Eucalyptus* (*ki*/*kr* = 1.01) and reduced in agriculture streams for *Syzygium* (*ki*/*kr* = 0.60).

4. Discussion

Assessing the influence of catchment land use, and riparian and in-stream disturbances (livestock activity, bathing and laundry washing) on ecological condition, while accounting for natural and seasonal variation, is essential for natural resource management. In this study, human-induced changes in physico-chemical variables, nutrient concentrations and organic matter (leaf litter) were propagated to consumers. This skewed the contribution of shredders to leaf litter breakdown in agriculture streams and that of microbes in forest streams.

There were increased concentrations of major ions, turbidity, TSS, conductivity, temperature and dissolved nitrogen in streams in agriculture landscapes compared with those in forest. Low temperature in forest streams was due to high canopy cover (above 80%) provided by natural riparian vegetation, which protected the streams from direct insolation. Most native riparian trees tend to grow over the stream whereas *Eucalyptus* spp. are more columnar to pyramidal in shape.

In streams that drain catchments of similar geology, variability in electrical conductivity is indicative of anthropogenic activities. Whereas turbidity, TSS and bioavailable nitrogen showed a relationship with catchment land use, they have been found to be more responsive to local human and animal activities in the study area

Table 3
Top-ranked SIMPER contributors to % dissimilarity in the composition of invertebrate taxa between forest (FOR) and agriculture (AGR) sites during the wet and dry seasons; FOR – $n = 10$, AGR – $n = 7$ per season.

Taxon	Mean abundance		% Contribution	% Cumulative
	FOR	AGR		
Wet season				
Simuliidae	412.0	148.0	17.5	17.5
Tricorythus tinctus	2.8	115.0	7.7	25.2
Pseudocloeon sp.	65.5	106.0	6.5	31.7
Chironominae	65.8	63.6	4.5	36.1
Afronurus sp.	11.3	78.4	4.4	40.5
Cheumatopsyche thomassetti	9.7	50.9	3.0	43.5
Tubifex sp.	5.4	30.6	2.5	46.0
Hydropsyche sp.	10.6	34.6	2.4	48.4
Afrocaenis sp.	36.3	10.0	2.4	50.8
Pisidium sp.	33.4	6.6	2.4	53.2
Orthocladinae	23.7	20.4	2.1	55.3
Elminae	6.8	15.0	1.3	56.6
Acanthiops sp.	14.6	9.9	1.2	57.8
Lestidae	0.0	9.4	1.2	59.0
Lepidostoma sp.	9.6	15.0	1.1	60.2
Dicercomyzon sp.	0.8	22.4	1.1	61.3
Cheumatopsyche sp. 1	10.4	12.6	1.1	62.3
Potamonautes sp.1	15.8	0.9	1.0	63.3
Wormalidia sp.	4.6	10.6	0.9	64.3
Neoperla spio	13.5	1.1	0.9	65.2
Tanypodinae	14.6	9.3	0.9	66.1
Dry season				
Simuliidae	240.5	83.3	8.0	8.0
Pseudocloeon sp.	46.5	83.5	7.8	15.8
Cheumatopsyche thomassetti	8.2	80.8	7.2	23.0
Tricorythus tinctus	4.0	98.0	6.9	29.9
Chironominae	44.0	63.5	5.9	35.9
Hydropsyche sp.	12.8	45.3	5.1	41.0
Tanypodinae	14.1	32.5	3.4	44.3
Afronurus sp.	4.5	33.0	3.1	47.4
Pisidium sp.	28.8	5.5	2.8	50.2
Caenis sp.	2.4	15.3	2.6	52.8
Cheumatopsyche sp.	19.0	8.8	1.8	54.6
Scirtidae	16.0	4.4	1.6	56.2
Afrocaenis sp.	10.8	5.8	1.3	57.5
Orthocladinae	8.3	8.8	1.3	58.8
Neoperla spio	12.6	1.8	1.1	59.9
Wormalidia sp.	10.4	4.5	1.1	61.0
Elminae	8.3	15.1	1.1	62.1
Propistomatidae	6.1	5.4	0.9	63.0
Dicercomyzon sp.	0.0	8.0	0.9	63.9
Lepidostoma sp.	9.5	4.9	0.9	64.7
Pyralidae sp.1	0.9	7.3	0.7	65.5
Acanthiops sp.	0.0	10.8	0.7	66.1
Potamonautes sp 1	6.9	0.8	0.6	66.7
Polycentropus sp.	5.3	0.6	0.5	67.2

(Minaya et al., 2013; Kilonzo et al., 2013), implying that even among agriculture streams variability is expected.

Seasonal influences on run-off and discharge emphasized differences among land uses in some of the variables such as nitrogen, turbidity and suspended sediments. Increased in-stream activities by livestock and people observed in streams in agriculture landscapes were major sources of sediments during the dry season (see also Mathooko, 2001 and Yillia et al., 2008), whereas unpaved roads and footpaths became major source of sediments during the wet season. Since human activities were irregular along agriculture streams, physico-chemical conditions were patchy resulting in greater inter-site differences during the dry season.

Reduced canopy cover due to removal of indigenous riparian vegetation and its replacement by *Eucalyptus* spp. in agriculture streams reduced the quality of litter. The allelopathy of *Eucalyptus* spp. reduce species diversity and alter structural attributes of native vegetation (May and Ash, 1990). This could further reduce the quality of leaf litter in agriculture streams. Compared with particulate fractions, dissolved organic matter was higher in agriculture streams, likely contributed by enhanced primary production and inputs of human and animal wastes.

4.1. Invertebrate assemblages

Numerical abundance of invertebrates was a poor measure of disturbance and the abundance of most taxa was considerably lower during the dry season. However, these results should be interpreted with caution given the short period of the study. Although natural conditions influence taxon richness and abundance, it is likely that human activities exacerbated the effects observed in this study. Land use activities relating to road building, agriculture and settlements have been found to influence the quantity of runoff and sediments that enter recipient water bodies during the rains (Wang and Lyons, 2003; Donohue and Irvine, 2004). However, during the peak of the dry season, conditions can worsen in streams and rivers because, as discharge declines

Table 4
Results of three-way ANOVA exploring variation in leaf breakdown rates ($-k$) with land use (forest and agriculture), leaf species (*Croton*, *Syzygium* and *Eucalyptus*) and treatment by mesh size (coarse and fine mesh) during the wet and dry season. Degrees of freedom (df), sums of squares (SS), *F*-statistic and *p*-values are shown (significant values at $p < 0.05$ level in bold).

Source of variation	df	SS	*F*	*p*
Wet season				
Land use (LU)	1	1.53×10^{-3}	6.35	**0.013**
Leaf species (LS)	2	7.83×10^{-3}	16.25	**<0.001**
Treatment by mesh size (Tr)	1	4.08×10^{-3}	16.93	**<0.001**
LU × LS	2	1.25×10^{-3}	2.59	0.079
LU × Tr	1	1.09×10^{-3}	4.53	**0.035**
LS × Tr	2	1.73×10^{-4}	0.36	0.699
LU × LS × Tr	2	3.00×10^{-4}	0.63	0.538
Error	168	4.05×10^{-2}		
Dry season				
Land use (LU)	1	3.88×10^{-6}	0.03	0.875
Leaf species (LS)	2	3.40×10^{-3}	10.95	**<0.001**
Treatment by mesh size (Tr)	1	1.01×10^{-2}	64.88	**<0.001**
LU × LS	2	2.80×10^{-4}	0.90	0.408
LU × Tr	1	1.34×10^{-4}	0.86	0.354
LS × Tr	2	4.11×10^{-3}	1.32	0.269
LU × LS × Tr	2	1.12×10^{-3}	0.36	0.699
Error	168	2.61×10^{-2}		

fines accumulate, temperatures rise and dissolved oxygen becomes limiting (Harrison and Hynes, 1988; Mathooko and Mavuti, 1992; Shivoga, 2001). Long-term studies are needed in these streams to elucidate temporal trends and to differentiate between natural variability arising from insect adult emergence and human-induced declines in water and habitat quality.

Taxa richness varied with land use and season with higher numbers in forest streams compared with agriculture streams. However, there was a decrease in land use related influences during the wet season and an increase in reach-scale influences during the dry season. During the wet season, spates and scouring make the stream substratum more uniform and reduces inter-site differences in community structure (Leung et al., 2012). Flow increases connectivity enabling taxa to colonize new areas. There is also a notable reduction in human and livestock disturbance during the wet season when harvested rainwater is the main source of water for domestic and livestock use, reducing the pressure on streams (Masese, pers. obser.). In contrast, human and livestock activities (bathing, laundry washing and livestock watering) in streams are higher during the dry season (Yillia et al., 2008). As this happens at select reaches, impacts are irregularly spaced, resulting in greater inter-site variability and among land use differences. Rheophilic taxa (e.g., Simuliidae, *T. tinctus*, *Cheumatopsyche* spp.) responded to land use influences, signifying the important role played by flow in structuring invertebrates in these streams. As flow remains interstitial and exposes riffles, rheophilic taxa are disadvantaged while burrowing and pool taxa such as Tubificidae and Chironomidae thrive (Mathooko et al., 2005; Masese et al., 2009). Studies that explore flow-ecology relationships in these highly hydrologically variable systems are needed to inform sustainable water resources development (McClain et al., 2014).

During the dry and wet seasons, abundance and taxa richness of FFGs responded similarly to land use influences. Shredders exhibited highest diversity in forest streams while collectors were dominant in agriculture streams. Changes in water quality and organic matter characteristics can explain the skewed distribution of shredder taxa in forest streams. Although shredder numbers are quite variable in the tropics, water temperature and leaf litter characteristics play important roles (Yule et al., 2009; Boyero et al., 2011a,b). In this study, agriculture streams were warmer and with higher nutrient concentrations and suspended sediments, and leaf litter was mainly of the exotic *Eucalyptus* species.

4.2. *Litter breakdown and ecosystem functioning*

The importance of microbes relative to shredders as agents of breakdown in agriculture streams compared with forest streams connects land use with stream processes, even though microbial breakdown was not measured directly but inferred from the exclusion of shredders in fine-mesh litterbags. Shredders, although important in agriculture streams during the dry season, were generally disadvantaged for *Eucalyptus*. Nevertheless, the combined effects of increased microbial activity and high abundance and widespread distribution of certain shredders such as *Tipula* sp.1 and *Lepidostoma* sp. are interpreted to have contributed to increased breakdown rates in some agriculture streams during the dry season. This also implies that both seasonal and reach-scale influences were highly relevant for invertebrate assemblage structure, and consequently litter decomposition as a metric of function. Microbial processing responded more to higher ambient nutrient concentrations in agriculture streams for the higher quality *Croton* than for *Syzygium* and *Eucalyptus*. These results conform to the hypothesis that leaf quality mediates the effects of

Table 5
Relationship between leaf litter breakdown rates between coarse- (kc) and fine-mesh (kf) sizes (kc/kf coefficient) across all streams used for the litterbag experiments. The coefficients show the contributions of shredders (coarse-mesh) relative to microbes (fine-mesh) to litter breakdown. Coefficients have been provided for each leaf species separately for the dry and wet seasons. Means are for each leaf species per land use and season; $n = 3$ for site means per leaf species per season. The site numbers correspond to litterbag experiments site numbers in Fig. 1.

Land use/site	Dry season			Wet season		
	Croton	*Eucalyptus*	*Syzygium*	*Croton*	*Eucalyptus*	*Syzygium*
Forest						
F1	1.89	1.56	1.23	2.95	0.98	1.91
F2	1.22	0.82	1.47	1.95	1.54	2.60
F3	1.73	1.53	1.11	1.21	0.90	1.28
F4	1.80	1.55	1.66	1.60	0.59	1.56
F5	1.63	1.94	2.15	2.98	1.67	2.50
Means	1.65	1.48	1.52	2.14	1.14	1.97
Agriculture						
A1	0.64	0.85	1.10	0.76	0.31	1.35
A2	1.28	1.44	2.38	1.45	1.39	2.46
A3	1.52	0.84	2.03	1.75	0.88	1.96
A4	1.34	1.16	0.61	1.88	0.26	2.07
A5	1.74	1.51	2.12	1.53	0.95	0.66
Means	1.30	1.16	1.64	1.48	0.76	1.70

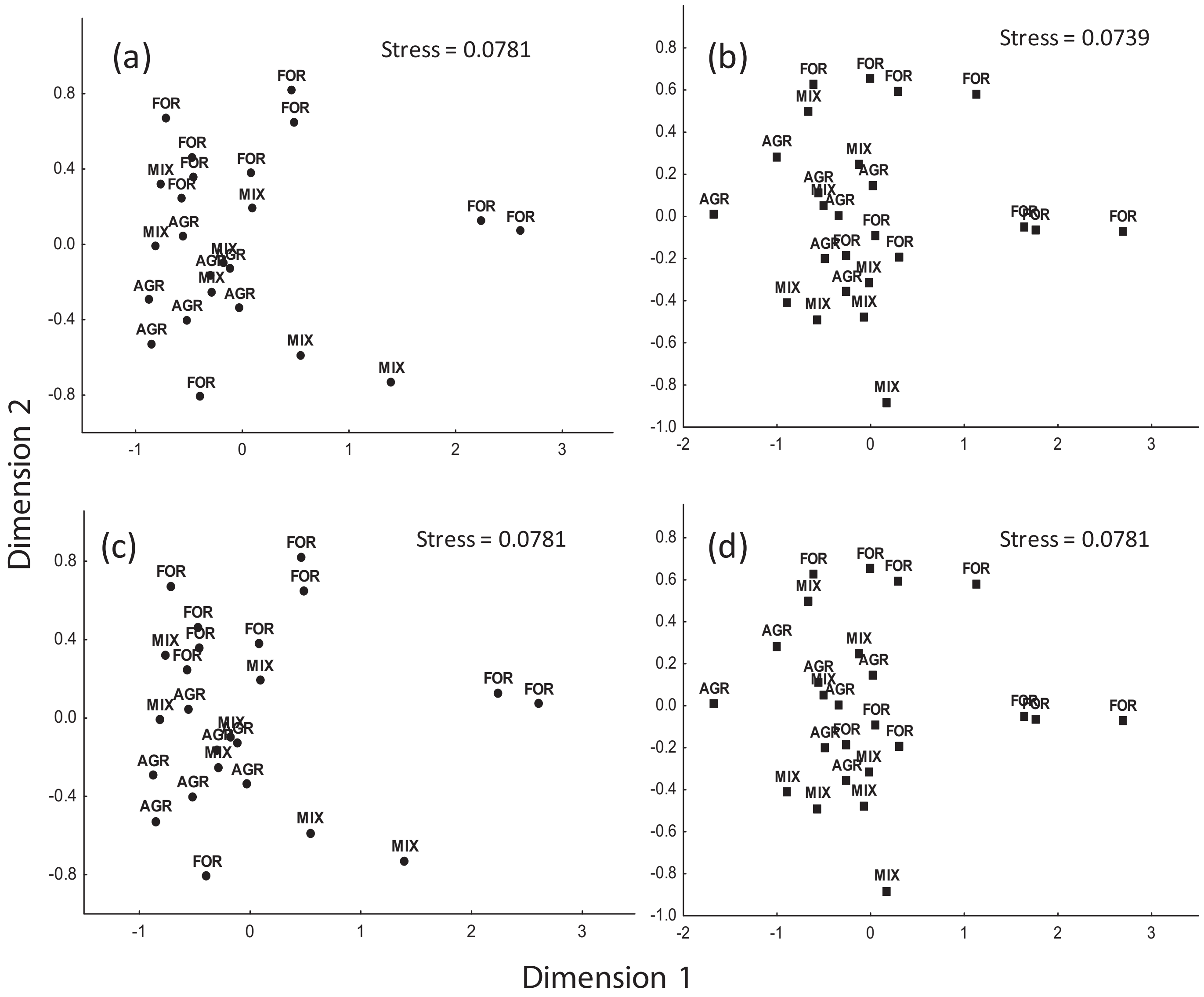

Fig. 5. Non-metric multidimensional scaling (NMDS) plots of invertebrate composition of the four functional groups based on abundance data during (a) wet season and (b) dry season, and based on presence–absence data during (c) wet season and (d) dry season in the three land uses: forest (FOR), agriculture (AGR) and mixed (MIX). Abundance and presence–absence of the functional feeding groups responded similarly to land use during the two seasons.

elevated nutrients on microbial processing (Ardón et al., 2006). The poorer quality (C:N ratio, 63.7–89.7) of *Eucalyptus* for shredders compared with *Croton* (10.6–16.2) and *Syzygium* (38.9–50.9) (FO Masese unpublished results) is supported by this study. In most sites, the *kc*/*kf* coefficients were highest in *Croton*, indicating that invertebrate – mediated breakdown was also affected by litter quality.

Even though reported for individual leaf species, the *kc*/*kf* coefficients for *Croton* and *Syzygium* incubated in forest streams are comparable with a value of 1.98 reported for a litter mixture in a forest stream in Borneo (Yule et al., 2009). The decomposition rates of *Syzygium* in coarse-mesh litterbags found in our agriculture streams during the wet season (0.010–0.043 d^{-1}) are also comparable to those found by Dobson et al. (2003, 0.022 d^{-1}). Like the Bornean forest stream (Yule et al., 2009), our forest streams contained diverse and abundant shredder taxa.

The results of this study have important implications on the management of riverine ecosystems in the region. First, catchment-scale pressures influence ecosystem functioning as can be inferred from the restricted occurrence of 21 taxa, including eight shredder taxa, in forest streams. The importance of reach-scale influences was illustrated by inter-site differences in some physico-chemical variables and assemblage characteristics among streams with similar catchment land uses. To maintain ecological integrity of these streams management actions addressing both catchment- and reach-scale are required (Minaya et al., 2013). Second, shredder diversity response to changes in allochthonous POM quality demonstrates the potential to affect nutrient cycling when indigenous vegetation is replaced by *Eucalyptus* species. Accumulation of significant amounts of slowly decomposing leaf litter reduces the capacity to support diverse consumers and complex food webs *via* detrital pathways. Replacing riparian forests with exotic tree species also increases available light, stimulating benthic algal production and overall ecology of shallow streams and a shift in the relative importance of allochthonous relative to autochthonous sources of carbon for food webs. Thirdly, through its controls on discharge, depth and material load (particulate and dissolved) seasonality accentuate differences in environmental conditions among

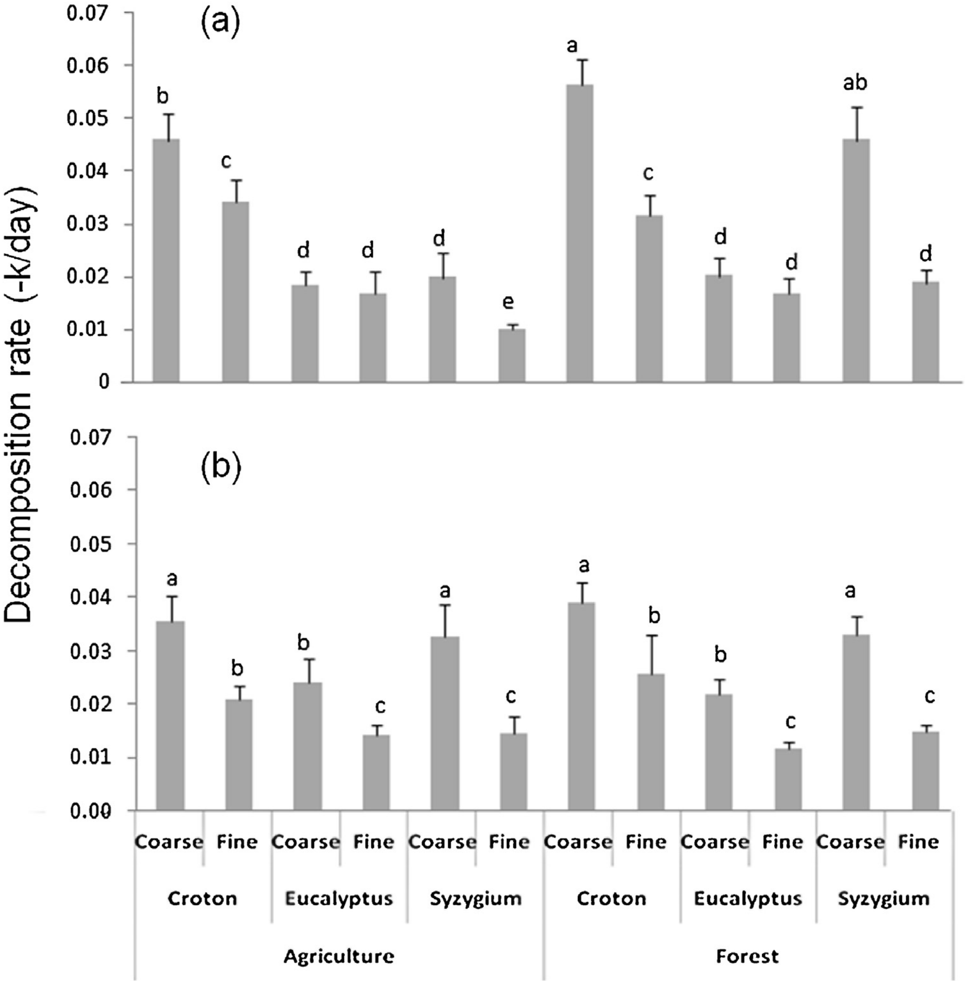

Fig. 6. Mean (±SE) showing the effects of land use, leaf species and treatment by mesh size on leaf decomposition rate ($-k\text{day}^{-1}$) for the (a) wet and (b) dry seasons. Similar trends are displayed for decomposition of the three leaf-types across land uses during the wet and dry seasons with *Croton* decomposing fastest followed by *Syzygium* and then *Eucalyptus*; $n = 15$ per leaf species, per land use, per season.

land uses and within sites among agriculture and mixed land uses.

5. Conclusions

In addition to highlighting the applicability of leaf litter processing and the composition of invertebrate FFGs as functional and structural indicators, respectively, of ecological health, this study highlights interactions among catchment land use, riparian activities and seasonality as drivers of ecosystem functioning in upland tropical streams. While catchment land use is an important determinant of temperature and litter biomass in our streams, reach-scale influences that affect leaf litter quality through exotic introductions and reduced water quality were equally important in structuring invertebrate communities, with effects propagating to consumers and processing of leaf litter. The relative differences in breakdown rates among the three plant species remained unaltered in both agriculture and forest streams irrespective of mesh-size; *Croton* was fastest followed by *Syzygium* while *Eucalyptus* was the slowest. The fast leaf breakdown in fine-mesh litterbags observed in this study has been observed in other tropical stream studies (Wantzen et al., 2008), but the comparatively higher rates in coarse- compared with fine-mesh litterbags in forest sites in this study ($kc/kf > 1.5$) indicate that shredders contributed to leaf breakdown. However, shredder contribution to leaf breakdown was dependent on leaf species suggesting that replacement of indigenous riparian vegetation with poorer quality *Eucalyptus* species has the potential to reduce nutrient cycling. If unchecked, riparian and watershed deforestation will shift the functioning of these streams with foodwebs becoming more reliant on autochthonous resources and microbial processing of leaf litter, which cannot support diverse consumers and complex food webs.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2014.05.032.

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