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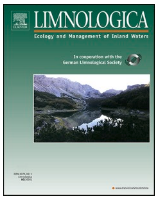

Land-use influence on the functional organization of Afrotropical macroinvertebrate assemblages

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ABSTRACT

Studies investigating the effects of human activities on the functional organization of macroinvertebrate communities in tropical streams and rivers are very limited, despite these areas witnessing the greatest loss of natural forests globally. We investigated changes in taxon richness, numerical abundance and biomass of macroinvertebrate functional feeding groups (FFGs) in streams draining different land-use types in the Sosiani-Kipkaren River in western Kenya. Twenty-one sites in river reaches categorized as forested, mixed, urban or agricultural were sampled during the dry and wet seasons. Collected macroinvertebrates were identified to the lowest taxon possible (mainly genus) and classified into five major FFGs; collector-gatherers, collector-filterers, scrapers, predators and shredders. There were significant ($p < 0.05$) spatial variation in habitat quality, organic matter standing stocks, total suspended solids, electrical conductivity, dissolved oxygen, temperature and nutrient concentrations across land-uses, with forested sites recording lowest values in mean water temperature, electrical conductivity and nutrients while recording highest levels in dissolved oxygen concentrations. Responses in macroinvertebrates to changes in land-use varied with richness, abundance and biomass showing differences within FFGs. Biomass-based metrics responded more strongly to change in land-use while taxon richness was the least predictive, indicating replacement of taxa within FFGs across land-use types. Higher shredder abundance, biomass and richness were recorded in forested streams which were cooler with protected riparian areas and high biomass of coarse particulate organic matter. Collector-gatherers dominated agricultural and urban streams owing to an abundance of particulate organic matter and nutrients, while scrapers responded positively to increased nutrient levels and open canopy in mixed and agricultural streams where primary production and algal biomass was likely increased. Overall, this study provides further evidence of the effects of agricultural and urban land-uses on tropical streams and rivers and contributes to the use of macroinvertebrate FFGs as indicators of ecological health.

1. Introduction

Land-use changes from forestry to agriculture or settlement is a subject of major concern worldwide because they are associated with soil erosion, sedimentation, nutrient enrichment, and input of toxic substances to aquatic habitats and alteration of biological communities (Allan, 2004; Dudgeon et al., 2006; Reid et al., 2019). As opposed to previous decades when the land transformation was mainly for industry and infrastructural development, land-use change is increasingly being driven by cropland farming and livestock grazing, with about 6 million km^2 of forests and grasslands being converted yearly (FAO, 2013). Agricultural activities can degrade streams by causing nutrient enrichment through fertilizer or manure use (McDowell and Sharpley, 2001), increase sediment input from farmlands (Burdon et al., 2013), increase mean water temperature (Benstead and Pringle, 2004), alter hydrologic regimes (O'Brien et al., 2018), and increase pesticide inputs (Osano et al., 2003) into streams. Similarly, urban development and its associated impervious surfaces can degrade streams through the release of excess nutrients, sediments and toxicants (Beasley and Kneale, 2002; Walsh et al., 2005), cause shifts in temperature regimes and significantly alter basal resources for food webs (Walsh et al., 2005; Imberger et al., 2011).

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Macroinvertebrates are the most common bioindicators in aquatic ecosystems because of their valuable characteristics such as; broad diversity of species with varying levels of tolerance to disturbance, high abundance, low mobility (good indicators of localized conditions), long lifespans which offer the ability to provide information about cumulative and synergistic effects of pollution, ease of collection and identification to the family level, and the considerable amount of background information that is available (Barbour et al., 1999; Resh, 2008). To ease their use in bioindication, macroinvertebrates have been divided into functional feeding groups (FFGs) based on behavioural and physiological mechanisms for food acquisition and habitat use (Cummins and Klug, 1979; Merritt and Cummins, 1996). This classification method is useful in that a small number of individuals from the community can be studied collectively based on behaviour and adaptations for feeding in the stream environment (Merritt and Cummins, 1996). Because of the varied environmental and food requirements, macroinvertebrate FFGs have been used as both indicators of ecological status and ecosystem functioning (Vannote et al., 1980; Merritt and Cummins, 1996). However, the use of FFGs for biomonitoring aquatic ecosystems in the tropics has received many challenges, notably limited keys and schema for classifications (Masese et al., 2014a; Buss et al., 2015). As a result, most studies have used temperate keys and guides to identify and classify macroinvertebrates into FFGs, sometimes with misleading outcomes (Camacho et al., 2009; Dobson et al., 2002; Masese et al., 2014a).

Despite the challenges of using macroinvertebrates as indicators of ecological condition and ecosystem functioning in tropical streams, many studies have used structural responses of communities to develop indices for bioindication (e.g., Dickens and Graham, 2002; Aschalew and Moog, 2015; Kaaya et al., 2015). Some of the factors that influence macroinvertebrate community composition in streams and rivers include fluctuations in water levels and land-use change or human-induced disturbances (Collier and Quinn, 2003; Cooper et al., 2013; Masese et al., 2020). The diversity, abundance and biomass of FFGs reflect a combination of seasonally varying factors including water quantity (flow velocity and discharge) and quality, habitat of biotope suitability and availability for different taxa, and the relative abundance of autochthonous and allochthonous food resources (Junker and Cross, 2014; Entrekin et al., 2020). Seasonal variation in taxon richness, abundance and biomass largely relies on biological traits, such as reproductive timing, longevity, and feeding habits (Beche et al., 2006). Collector-gatherers (generalist feeders) tend to be abundant both during the wet and dry seasons (Masese et al., 2014a), whereas more specialised feeders such as shredders are dependent upon seasonal availability of coarse particulate organic matter (litter fall), and thus may exhibit strong seasonality in abundance (Bogan and Lytle, 2007). Similarly, collector-filterers distribution can vary with season (Bogan et al., 2013), as they require specific flow conditions to acquire food from the water column, both of which can vary seasonally.

Land-use change has a strong influence on the diversity of macroinvertebrate FFGs because it influences water and habitat quality, and basal food resources through disruption of allochthonous resource subsidies decreased stream shading and increased sedimentation and water temperature (Lorion and Kennedy, 2009; García et al., 2017; Masese et al., 2018; Mwaijengo et al., 2020). Studies have shown that some shredder taxa are restricted to cooler and shaded forested streams, while FFGs that are tolerant to poorer water quality and habitat degradation (Yule et al., 2009; Masese et al., 2014a), such as collectors, can be more widespread (Masese et al., 2009a; Buss et al., 2015). Comparatively, forested streams have a higher taxon richness of macroinvertebrates compared to adjacent streams under other uses, such as agriculture or grazing (Minaya et al., 2013; García et al., 2017; Fugère et al., 2018). Watershed urbanization also negatively affects macroinvertebrate biomass and community structure, through changes in water quality and basal food resources (Lawrence and Gresens, 2004; Sterling et al., 2016; Alberts et al., 2018).

Understanding the effects of land-use and land cover changes on streams and rivers is an overarching objective for the management and conservation of riverine ecosystems. Effects of land-use change on the structure and functioning of freshwater ecosystems are of particular interest because freshwater ecosystems have conservation, economic, and cultural importance (Dudgeon et al., 2006; Vörösmarty et al., 2010). In concert with the increasing rate of land-use and land cover changes and human population growth on tropical catchments (López-Carr and Burgdorfer, 2013), there is a need for a concomitant increase in knowledge on the impacts of these developments on biodiversity, water resources and ecosystem functioning (Dudgeon et al., 2006; Ramírez et al., 2008). Data on the functional organization of macroinvertebrates in Afrotropical streams and rivers will help better understand organic-matter processing, trophic relationships, and the management actions needed to minimize impairment of ecosystem functioning (Dudgeon, 2010; Boyero et al., 2011; Ferreira et al., 2012; Fugère et al., 2018).

In this study, we set out to investigate how different land-use types ranging from forestry to urbanization and agricultural activities influence water and habitat quality in streams and rivers and the ensuing responses in the functional organization of macroinvertebrate assemblages. We hypothesized that the composition of macroinvertebrate FFGs would vary as a result of changes in land-use and seasonal variations in flow, water quality and habitat characteristics. We further hypothesized differences in abundance and biomass of macroinvertebrate FFGs, with biomass hypothesized to respond more strongly to change in land-use types because of the presence of large-bodied macro-consumers (freshwater crabs), which are very sensitive to deforestation and deterioration of habitat and water quality.

2. Materials and methods

2.1. study area

We studied 1st to 5th order streams in the Sosiani- Kipkaren River, a tributary of the Nzoia River in the Lake Victoria basin, Kenya (Fig. 1). The river originates in the Kaptagat Forest, which is part of the larger Mau Forest Complex in the Kenyan Rift Valley. The climate of the area is mainly tropical humid, with mean annual rainfall ranging from 900 to 2200 mm and temperature ranging from13 °C to 25 °C which varies strongly with elevation. The annual rainfall pattern is bimodal, with long rains between March to June, and short rains from August to October (Jaetzold. and Schmidt, 1983). The river traverses a land-use gradient with varying human population densities and pressures (Nyadawa and Mwangi, 2010). The catchment area is characterised by forest cover in its headwaters, but transitions into small- and large-scale agriculture, settlements (rural and urban), grazing, urbanization and agro-industrial activities (Fig. 1). Both commercial and subsistence agriculture are major livelihood sources for a large proportion of people in the catchment.

Study sites were grouped into four categories characterized by catchment or riparian land-use, and reach-scale human influences: forested, agricultural, mixed and urban. Based on the Digital Elevation Model of Kenya (90 m by 90 m) produced using data from the Shuttle Radar Topography Mission, catchments were delineated and the area of each land-use category upstream of each sampling site was calculated. Forested sites, had a riparian zone that was >60 % forest and the catchment area upstream of the site had >60 % forest, shrub lands or grasslands cover. Agricultural sites had a riparian zone with >60 % agriculture and the catchment area upstream of the site with <60 % crop cover. Urban sites were located in urban areas within Eldoret City and its outskirts, with >60 % human settlements and other developments along the riparian zone. Mixed sites were those with riparian zone and catchment areas comprising different proportions of the two main land-uses, forestry and agriculture, but none exceeding 60 % areal coverage (Masese et al., 2014b). A total of 21 sites [Forested (n = 5), Mixed (n = 6), Agricultural (n = 6) and Urban (n = 4)] were sampled during

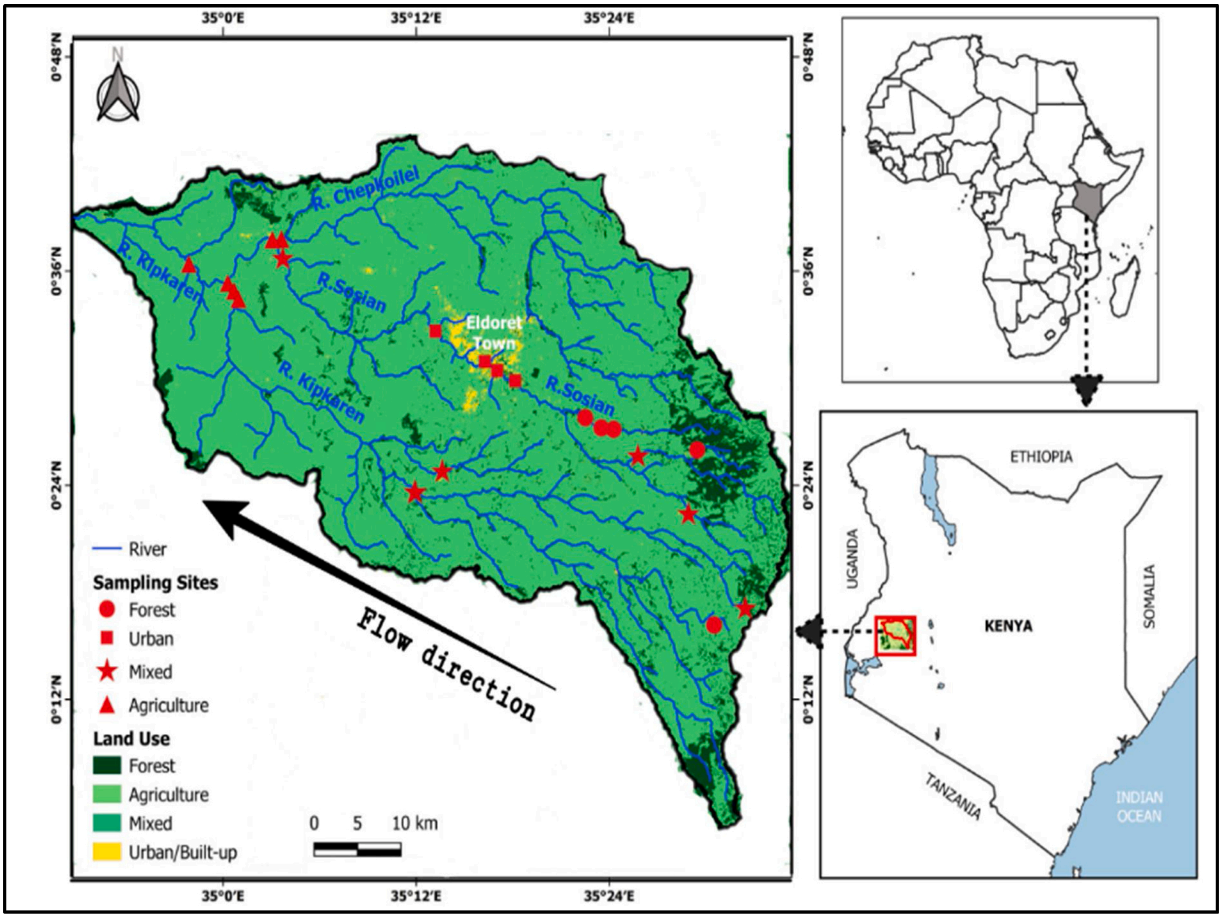

Fig. 1. Location of sampling sites along the Sosiani-Kipkaren River, Kenya.

the wet season. Due to logistical constraints, only 14 of the same sites [Forested (n = 3), Mixed (n = 5), Agriculture (n = 2) and Urban (n = 4)] were sampled during the dry season (Fig. 1). These sites traverse stream-size and land-use gradient from the forested upper reaches, through the mixed, agricultural and urban middle reaches to the lower reaches that were largely agricultural. The downstream agricultural sites were 45 km from the urban sites; a distance that was long enough for "self-cleansing" to have taken place so as to have distinct stream characteristics and influences of the urban and agricultural sites.

2.2. Field sampling

Sampling was done during both the wet (July-August 2018) and dry (February-March 2019) seasons. Sampling was done monthly with the wet season being sampled during the short-light rains. At each sampling site, before sampling of macroinvertebrates, water temperature, dissolved oxygen concentration (DO), pH and electric conductivity (EC) were measured *in situ* by directly inserting a YSI multi-probe water quality meter (556 MPS, Yellow Springs Instruments, Ohio, USA) into the stream over a 100-m stretch. At each sampling site, known volumes of water samples were filtered in replicate through pre-combusted and pre-weighed Whatman GF/F filters (0.7 μm pore size, 47 mm diameter) for the analysis of total suspended solids (TSS) and particulate organic matter (POM). The GF/F filters holding suspended matter were kept in aluminium envelopes and stored in a cooler at 4 °C for transport to the laboratory for analysis. In addition, the filtered water samples were collected from the thalweg using acid-washed HDPE bottles for analysis of nutrients. The water samples were kept in a cooler at 4 °C for transport to the laboratory where they were kept frozen until analysis.

At each sampling site, reach characterization was done by measuring stream width, water depth, water velocity and discharge over a 100-m stretch. Stream width was measured with a measuring tape at several points along 11 transects placed at 10-m intervals along the reach. On each transect, water depth was measured with a 1-m ruler at many points determined by channel shape and width. Velocity was measured at the same points as depth using a mechanical flow meter (General Oceanics; 2030 Flowmeter, Miami, Florida). Stream discharge was calculated by the velocity–area method (Wetzel and Likens, 2000).

Riparian and in-stream habitat assessment was also done at each site qualitatively to determine habitat quality and diversity using methods developed for the Lake Victoria Basin (Masese et al., 2009b; Raburu and Masese, 2012). Habitat quality variables assessed included substrate type and quality, instream cover, channel morphology, riparian zone and bank erosion, and pool/glide and riffle/run quality. For each site, the percentage of streambed covered by different substrate types was estimated for each biotope sampled for invertebrates – see details below. Data on water depth and velocity were also collected for each sampled biotope. A biotope was divided into nine sub-sampling units of similar size and counting the number of units occupied by various types of substrates. The dominant substratum was the particle size (boulders, cobbles, pebbles, gravel, sand and mud) that made up 50 % or more of the streambed surface within the quadrat when classified according to a modified Wentworth scale into one of the size classes (Mykrä et al., 2007). In addition to substrate types, the biomass (standing stock) of coarse particulate organic matter (CPOM), was estimated by collecting CPOM samples in triplicates from each sampling site using a quadrat ($0.5*0.5\ m^2$) and placed in zip lock bags for transportation to the laboratory for processing. The CPOM collected was mainly composed of sticks, leaves, seeds, fruits and flowers. Percentage coarse particulate organic matter (% CPOM) was determined as the % coverage of the

CPOM in the stream bed.

Macroinvertebrate sampling was conducted using a semi-quantitative kick-net sampling method (Dickens and Graham, 2002). The following biotopes were delineated and sampled within each site: 1) GSM: gravel, sand and mud; (2) STONES: bedrock, boulders, cobbles and pebbles, either under flowing or non-flowing conditions; (3) VEG: submerged and marginal vegetation (Masese et al., 2020). The sampling process involved disturbing / kicking the bottom upstream of the net (500-μm mesh size), so that dislodged invertebrates are washed into the net by water currents. Kicking was carried out on an area of approximately 1 m^2 for a standard 1 min per biotope. Large substrate types such as boulders and cobbles were disturbed by hand and washed into the net. Macroinvertebrate samples per biotope were preserved in 75 % ethyl ethanol for further processing in the laboratory.

2.3. Laboratory analyses

Analyses for NO_2^-, NO_3^-, SRP, and NH_4^+ in water samples was done using standard colourimetric methods (APHA, 2005). SRP was analyzed following the ascorbic method, NH_4^+ following the hypochlorite method while NO_2- and NO_3^- were analyzed following the salicylate method (APHA, 2005). The concentration of Na and K were also determined in water samples using flame atomic absorption spectrometry (FAAS).

For TSS and POM, GF/F filters with embedded sediments were dried at 60 °C for 72 h to attain constant weight. The filters were then reweighed using an analytical balance (Sartorius, Secura 124−1S, 0.0001 g) for TSS determination gravimetrically. The filters were then ashed at 450 °C for 5 h in a muffle furnace and re-weighed for the determination of POM as the difference between TSS and ash-free-dry mass (APHA, 2005). Coarse Particulate Organic matter (CPOM) standing stock biomass was determined as the summation of the dry weight of the various fractions collected (sticks, leaves, seeds, fruits and flowers) (Masese et al., 2014a).

Macroinvertebrates samples were washed in running water in sieves and transferred into sorting trays where they were counted and identified to the lowest taxon level possible, mainly genus, with the aid of keys and schema in several guides (Day and de Moor, 2002a,2002b; de Moor et al., 2003a, b; Merritt et al., 2008). Allocation of FFGs was done using the literature (Merritt and Cummins, 1996; Graça et al., 2001; Dobson et al., 2002; Polegatto and Froehlich, 2003; Molina Arzabe, 2004; Masese et al., 2014a; Supplementary Table 1).

Macroinvertebrates FFGs richness was obtained as the number of/ count of species belonging to the different FFGs in the different land-use types while numerical abundance was determined as the number of individuals per species in the different FFGs. Macroinvertebrates biomass was determined by oven drying the macroinvertebrates at 103 °C for four hours and thereafter weighed using an analytical balance (Sartorius, Secura 124−1S, 0.0001 g) (Mason et al., 1983).

2.4. Data analysis

We used two-way analysis of variance (ANOVA) to test for differences in water physico-chemical parameters and habitat variables among land-uses (forested, mixed, agricultural and urban) and seasons (dry and wet) with land-use and seasons as main factors and land-use × season interaction term. Two-way ANOVA was also used to compare total abundance, biomass, and taxon richness of all taxa between seasons (dry and wet) and the four land-use categories (forested, mixed, agricultural and urban) with season and land-use as the main factors and a season × land-use interaction. 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. Prior to analysis count data were log (x+1) transformed while the rest of the response variables were log-transformed to meet normality assumptions. Because of the interactions between land-use and seasonality (PERMANOVA) in both water and macroinvertebrate communities, we chose to analyze the data separately for the dry and wet seasons so as to ensure that the land-use differences we were interested in are not overshadowed by this interaction.

Principal Component Analysis (PCA) was used to reduce the dimensionality of the physico-chemistry and habitat variables data. To remove confoundment by seasonality, we did separate PCAs for all water and habitat quality data for the wet and dry seasons. We included two PCs to describe water and habitat quality variables separately. PCAs were statistically assessed using PERMANOVA (permutational analysis of variance), based on Bray-Curtis similarity matrices (McArdle and Anderson, 2001). All variables were scaled to zero mean and unit s.d. prior to PCA analysis.

Two-way nested analysis of similarities (ANOSIM) was used to compare average rank similarities of macroinvertebrate FFGs between the wet and dry seasons, with replicate land-uses nested within seasons. ANOSIM calculates a test statistic, the R-statistic, which varies between 0 and 1; higher values indicate greater differences between factors. Non-metric multidimensional scaling (NMDS) was then used to visualize the functional composition of macroinvertebrates in different land-uses and seasons (Clarke and Gorley, 2006) and confirm the differences in ANOSIM. Dissimilarity matrices based on the Bray–Curtis coefficients (Bray and Curtis, 1957) were derived for 2 data sets: un-transformed abundances data and presence-absence data for the FFGs. The 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).

To determine which key macroinvertebrate FFGs were responsible for the differences observed between land-uses, and hence indicator FFGs for changes in land-use, habitat and water quality, similarity percentages analysis (SIMPER) was used. The percentage contribution of each FFG to the overall dissimilarity between land-uses per season was quantified. SIMPER is a strictly pairwise analysis between two-factor levels (Clarke and Warwick, 2001), and in this case, comparisons were made between forested and mixed, forested and agricultural and lastly forested and urban site categories.

Redundancy analysis (RDA) was used to elucidate relationships between the functional composition of macroinvertebrates and environmental variables. The output was displayed as triplots, in which the plotted points for FFGs and land-use categories could be related to physico-chemical and habitat variables that were represented as rays. Before RDA was performed the gradient length in standard deviation (SD) units was estimated using Detrended Correspondence Analysis to test the suitability of a Canonical Correspondence Analysis (Ter Braak and Smilauer, 1998). Since gradient length was <3 SD, RDA was used instead of CCA to determine which factors were responsible for the structure or groupings of FFGs among sites (Ter Braak and Smilauer, 2004).

Statistical analyses were performed with R version 3.3.3. (R Development Core Team, 2017), using the *vegan* package (Oksanen et al., 2013). Figures were created in MS Office Excel (2016) and R version 3.3.3 (R-Development-Core-Team, 2017).

3. Results

3.1. Water physico-chemistry and nutrients

Both season and land-use change played significant roles in influencing water quality and habitat variables in our study. There was a significant decline in habitat quality, mainly riparian zone quality and instream cover from forested to urban land-uses (Table 1). Significant differences were recorded across the variables with higher values being recorded during the dry season than the wet season in all the physico-chemical and nutrient variables except for dissolved oxygen (DO), TSS, POM and depth. The Percentage of CPOM coverage and its standing stock biomass also declined among land-uses though did not differ

Table 1
Means (± SE) variation of physico-chemical variables, nutrient concentrations, habitat quality and stream size variables in the different land-use sites. EC = electrical conductivity, SRP = soluble reactive phosphorus, TSS = total suspended solids, POM = particulate organic matter and CPOM = coarse particulate organic matter.

Variable	Season	Forest	Mixed	Agriculture	Urban	F-Value	*p-value*
Seasonal variation							
Temperature (°C)	Wet	14.6 ± 0.4^{b}	18.3 ± 0.6^{a}	19.5 ± 0.3^{a}	18.7 ± 0.4^{a}	19.3	*0.001**
	Dry	15.6 ± 1^{c}	17.8 ± 0.4^{b}	22.6 ± 0.4^{a}	21.5 ± 0.3^{a}	29.7	*0.001**
EC (μS/cm)	Wet	32 ± 2.1^{b}	82 ± 7.5^{a}	101 ± 4.1^{a}	96 ± 7.2^{a}	25.99	*0.001**
	Dry	58 ± 7.7^{c}	102 ± 12.9^{c}	241 ± 25.9^{a}	165 ± 12.3^{b}	23.61	*0.001**
Dissolved oxygen (mg/L)	Wet	7.1 ± 0.4^{a}	6.3 ± 0.1^{ab}	6.4 ± 0.1^{ab}	5.9 ± 0.2^{b}	4.25	*0.008**
	Dry	6.5 ± 0.9^{a}	5.9 ± 0.2^{a}	4.5 ± 0.5^{b}	4.6 ± 0.4^{b}	3.86	*0.042**
pH	Wet	6.7 ± 0.1^{a}	6.4 ± 0.133^{ab}	6.7 ± 0.147^{a}	5.9 ± 0.2^{b}	5.87	*0.001**
	Dry	7.1 ± 0.04^{b}	7.1 ± 0.047^{b}	7.3 ± 0.031^{a}	7.2 ± 0.02^{a}	8.33	*0.001**
Nitrites (mg/L)	Wet	0.1 ± 0.01^{a}	0.1 ± 0.01^{a}	0.1 ± 0.01^{a}	0.1 ± 0.02^{a}	4.49	*0.208*
	Dry	0.2 ± 0.1^{a}	0.6 ± 0.3^{b}	0.1 ± 0.11^{a}	0.1 ± 0.03^{a}	1.63	*0.008**
Nitrates (mg/L)	Wet	0.1 ± 0.02^{c}	0.2 ± 0.02^{bc}	0.3 ± 0.1^{a}	0.3 ± 0.1^{ab}	6.88	*0.001**
	Dry	1.3 ± 0.4^{a}	1.9 ± 0.7^{a}	3.8 ± 0.9^{b}	2.7 ± 0.6^{c}	1.89	*0.001**
SRP (mg/L)	Wet	0.04 ± 0.02^{b}	0.05 ± 0.04^{b}	0.1 ± 0.01^{a}	0.1 ± 0.01^{ab}	9.44	*0.001**
	Dry	0.02 ± 0.01^{b}	0.02 ± 0.01^{b}	2.2 ± 1.2^{a}	0.2 ± 0.1^{b}	6.79	*0.002**
Ammonia (mg/L)	Wet	0.01 ± 0.01^{a}	0.01 ± 0.04^{a}	0.03 ± 0.02^{a}	0.01 ± 0.01^{a}	0.86	*0.47*
	Dry	0.2 ± 0.1^{a}	0.3 ± 0.1^{b}	0.4 ± 0.1^{b}	0.4 ± 0.1^{b}	6.68	*0.002**
TSS (mg/L)	Wet	20.4 ± 7.5^{b}	33.9 ± 19^{ab}	43.1 ± 6.1^{a}	27.3 ± 7.4^{ab}	3.63	*0.034**
	Dry	7.0 ± 0.3^{a}	12.2 ± 11.7^{a}	26.3 ± 0.9^{a}	17.0 ± 7.1^{a}	1.79	*0.212*
POM (mg/L)	Wet	8.4 ± 4.9^{a}	13.5 ± 4.6^{a}	13.7 ± 3.9^{a}	10.8 ± 5.2^{a}	1.55	*0.238*
	Dry	3.1 ± 0.1^{a}	3.6 ± 3.2^{a}	6.6 ± 1.4^{a}	4.6 ± 2.2^{a}	0.86	*0.492*
Depth (m)	Wet	0.3 ± 0.03^{b}	0.2 ± 0.03^{b}	0.7 ± 0.12^{a}	0.3 ± 0.08^{b}	7.43	*0.02**
	Dry	0.3 ± 0.13^{a}	0.2 ± 0.04^{a}	0.2 ± 0.03^{a}	0.2 ± 0.04^{a}	0.69	*0.58*
No seasonal variation							
Width (m)		5.4 ± 0.9^{b}	4.9 ± 0.6^{b}	15.7 ± 1.8^{a}	10.4 ± 2.7^{ab}	10.41	*0.001**
Discharge (m^3/s)		0.4 ± 0.01^{a}	0.1 ± 0.03^{a}	0.1 ± 0.01^{a}	0.3 ± 0.08^{a}	2.72	*0.061*
Substrate type (score)		13.2 ± 0.8^{a}	13.8 ± 1.0^{a}	13.2 ± 1.1^{a}	13.3 ± 1.1^{a}	0.06	*0.979*
Instream cover (score)		14.2 ± 0.5^{a}	9.8 ± 1.2^{b}	9.0 ± 0.9^{b}	6.8 ± 0.7^{b}	8.56	*0.001**
Channel morphology (score)		7.4 ± 0.3^{a}	6.8 ± 0.3^{a}	6.8 ± 0.3^{a}	6.5 ± 0.2^{a}	0.93	*0.449*
Riparian zone and bank erosion (score)		15.4 ± 1.2^{a}	13.8 ± 1.1^{ab}	9.3 ± 1.3^{b}	9.3 ± 1.1^{ab}	4.69	*0.015**
Pool/Glide Riffle/Run Quality (score)		5.8 ± 0.5^{a}	5.5 ± 0.3^{a}	7.2 ± 0.8^{a}	6.8 ± 0.5^{a}	2.96	*0.061*
Total Habitat Quality score (max score)		56.0 ± 2.8^{a}	49.8 ± 1.0^{ab}	45.5 ± 2.0^{b}	42.5 ± 2.3^{b}	7.55	*0.002**
%CPOM		52.5 ± 6.4^{a}	48.6 ± 6.3^{a}	41.3 ± 5.7^{a}	37.7 ± 5.5^{a}	0.55	*0.652*
CPOM standing stock (g/m^2)		60.2 ± 13.9^{a}	45.7 ± 7.3^{a}	28.7 ± 6.5^{a}	35.3 ± 8.9^{a}	2.1	*0.108*

*Means that do not share a letter are significantly different; Tukey *post hoc* tests.
**p*-values marked with asterisks are significantly different among land-uses at $p < 0.05$.

significantly (Table 1).

Highest temperature levels were recorded in agricultural sites (19.5 ± 0.3 °C) and (22.6 ± 0.4 °C) while forested sites recorded the lowest (14.6 ± 0.4 °C) and (15.6 ± 1.0 °C) during the wet and dry seasons, respectively. Forested sites recorded significantly higher DO concentrations during both wet (7.1 ± 0.4) and dry (6.5 ± 0.9) seasons. Highest conductivity was recorded in the agricultural sites during the dry season (241 ± 25.9 μS/cm) while the lowest was recorded in the forested sites (32 ± 2.1 μS/cm) during the wet season (Table 1). The concentrations of nutrients were lowest in forested sites in both the dry and wet seasons while agricultural and urban sites recorded highest levels of nitrates and SRP during both seasons.

The PCA biplot combining physico-chemistry and habitat quality data collected during both the dry and wets seasons indicated clear seasonal gradients (Supplementary Fig. 1 and 2), and hence further analysis was done for each season separately. Ordination of habitat quality and stream size variables indicated that forested and some mixed sites had protected riparian areas with stable instream substrate. Principal component 1 (PC 1) of the PCA explained 29.3–38.6 % of the total variation in habitat and stream size data, while PC 2 explained 21.2–25.5 % of the total association (Fig. 2a, b). During both seasons % CPOM, substrate quality, instream cover, riparian zone and bank erosion and morphology were associated with the forested and mixed land-use types, while POM (read TSS), discharge and river width were associated with agriculture and urban sites. Ordination of water quality physico-chemistry data indicated that principal component 1 (PC 1) of the PCA explained 38.7–44.2 % with PC 2 explaining 19.4–24.9 % of the total variation. During the dry season, high levels of DO were associated with forested and mixed sites, while higher levels of nutrients (SRP and nitrate), conductivity, TSS, temperature were associated agricultural and urban sites. During the wet season, similar trends were noted but with increased levels of electrical TSS, conductivity and nutrients in agricultural and urban sites (Fig. 2c, d).

Habitat quality and organic matter characteristics had significant differences between seasons (PERMANOVA, $F = 2.1$, $df = 1$, $p = 0.05$), among land-uses (PERMANOVA, $F = 4.3$, $df = 3$, $p = 0.001$), but without a significant season*land-use interaction (PERMANOVA, $F = 1.3$, $df = 3$, $p = 0.21$). For water quality physico-chemical variables, stronger seasonal (PERMANOVA, $F = 18.1$, $df = 3$, $p = 0.001$) and among land-uses (PERMANOVA, $F = 7.9$, $df = 3$, $p = 0.001$) differences were obtained, with a significant significant season*land-use interaction (PERMANOVA, $F = 3.4$, $df = 3$, $p = 0.001$).

3.2. Macroinvertebrate functional composition

A total of 43,479 macroinvertebrate individuals were collected in the study area. Total abundance was much higher during the wet season (35,827) compared with the dry season (7652). A total of 15 orders, 68 families and 98 genera were collected during the wet season while 13 orders, 53 families and 67 genera were collected during the dry season. During the wet season, order Ephemeroptera was the most abundant with 38.2 %, followed by Diptera 15.6 % then Tricladida 13.8 %. The least abundant orders were Arachnida, Lepidoptera and Collembola with 0.09 %, 0.08 % and 0.003 %, respectively. During the dry season, order Diptera was the most abundant with 47.2 % followed by Ephemeroptera with 17.8 %, then Mollusca with 12.1 %. The least abundant orders were Tricladida, Lepidoptera, and Arhynchobdellida with 0.2 %, 0.1 % and 0.09 %, respectively.

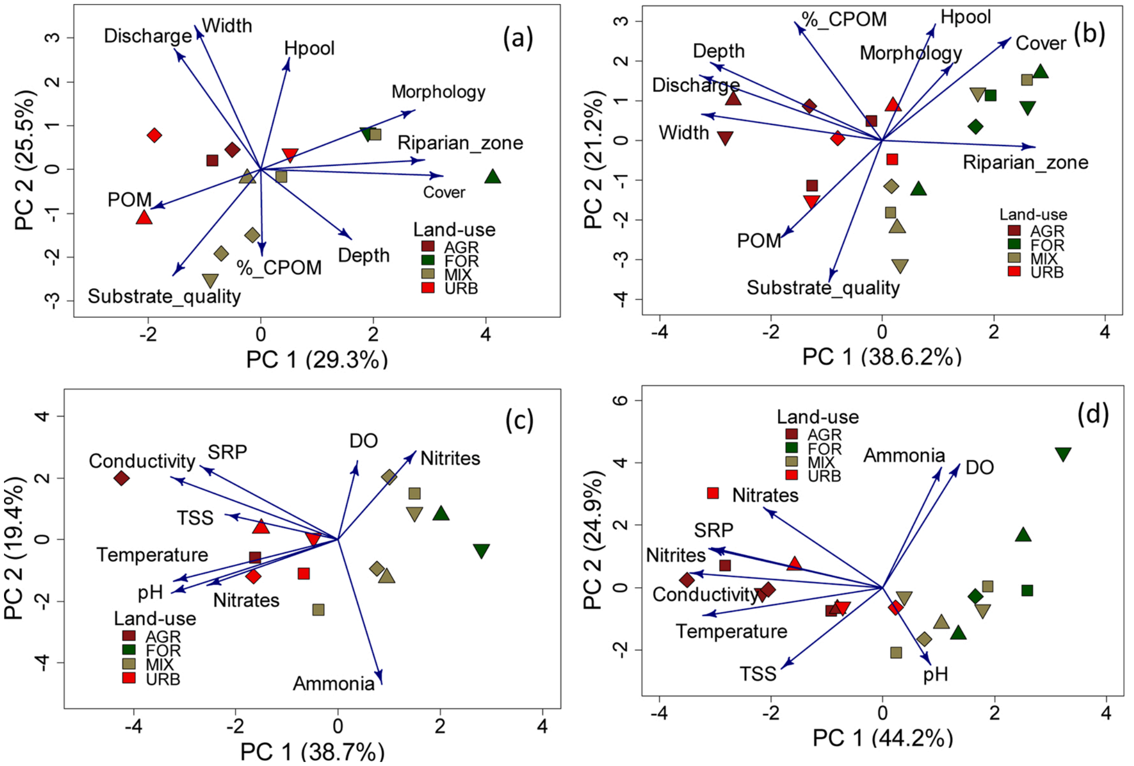

Fig. 2. PCA biplot for habitat quality (a, b) and water quality physico-chemical variables (c, d) during the dry (a, c) and wet (b, d) seasons in the Sosiani-Kipkaren River, western Kenya.

Seasonality strongly influenced the abundance of FFGs with higher numerical abundance during the wet season (2-way ANOVA, $F_{1,3} = 9.08$, $p < 0.05$). Shredder abundance (6.1 % and 8.9 %) was highest in forested sites while predators' numerical abundance increased with increase in disturbance from the forested sites (9.7 % and 8.9 %) to urban sites (40.1 % and 62.3 %) during the wet and dry seasons, respectively (Fig. 3A). During the wet season, scrapers were more abundant in mixed (29.5 %) and agricultural (30.5 %) sites while during the dry season, they were more abundant in forested (26.8 %) and mixed (22.9 %) sites. During the wet season, collector-filterers were more abundant in forested (30.2 %) and mixed (27.3 %) sites, while during the dry season, they displayed a decreasing trend from forested (26.8 %) to urban (11 %) sites (Fig. 3A).

Total macroinvertebrate biomass differed among the land-uses (One-way ANOVA, $F_3 = 1.74$, $p < 0.05$), but did not significantly differ between seasons (One-way ANOVA, $F_1 = 2.69$, $p = 0.11$). Shredder biomass was highest in forested sites (90.5 % and 80.7 %) and decreased gradually along the degradation gradient with the lowest biomass being recorded in the urban sites (23 % and 28.8 %) during wet and dry seasons respectively (Fig. 3B). During the wet season, predators (32 %) had the highest biomass in the agricultural sites while collector-filterers (33.7 %) were dominant at the urban sites. There was a gradual increase in the biomass of scrapers along the degradation gradient with the highest biomass recorded in urban sites (13.7 % and 38.6 %) and the least biomass recorded in forested sites (1.3 % and 5.6 %) during both wet and dry seasons respectively (Fig. 3B).

Taxon richness did not differ among land-uses and between seasons (2-way ANOVA, $F_{1,1} = 22.96$, $p > 0.05$). Taxon richness was dominated by predators in all land-uses during both the wet and dry seasons (Fig. 3C). During the wet season collector-filterers had the lowest taxon richness across all land-uses.

3.3. *Relationships between environmental variables and macroinvertebrate FFGs*

ANOSIM indicated significant differences in functional organization of macroinvertebrates for un-transformed abundance data of FFGs among land-uses (R-statistic = 0.14, $p < 0.028$), and between seasons (R-statistic = 0.66, $p < 0.001$). These findings suggest a stronger effect of "seasons" across land-uses as compared to "land-use" effect across seasons. Both the abundance and presence-absence data-based NMDS had good ordination with stress values <0.2 (Fig. 4). Both abundance and presence-absence data of FFGs grouped land-uses similarly, although there were some overlaps. Predators (Pred) and scrapers (Scr) clustered among agricultural sites (AGR) and Urban (URB) sites, collector-gatherers (Colg) clustered among mixed (MIX) sites, while shredders (Shr) clustered among forested (FOR) sites. Collector-filterers (Colf) were more associated with agricultural sites but overlapped across the different land-uses.

Abundance-based SIMPER's pair-wise comparison of forested sites with agricultural sites during the wet season identified collector-filterers (20.6 %) and collector-gatherers (17.2 %) to contribute the greatest dissimilarity between forested and agricultural sites, with higher abundance in forest sites (Table 2). Collector-filterers (13.8 %) and collector-gatherers (14.7 %) still contributed the greatest dissimilarity between forested and mixed streams, with higher abundance in forest sites, while collector-filterers (20.7 %) and predators (19.1 %) contributing the greatest dissimilarity between forested and urban sites, with higher abundance in urban sites. During the dry season, predators (25.0 %) and scrapers (16.6 %) accounted for the greatest dissimilarity between forested and agricultural sites, with higher abundance in the agricultural sites. Collector-filterers (19.7 %) and scrapers (18.7 %) were identified to contribute the dissimilarity between forested and mixed streams, with higher abundance in forested sites, while predators (29.8 %) and scrapers (17.0 %) contributed to the greatest dissimilarity between forested and urban sites, with higher abundance in urban sites

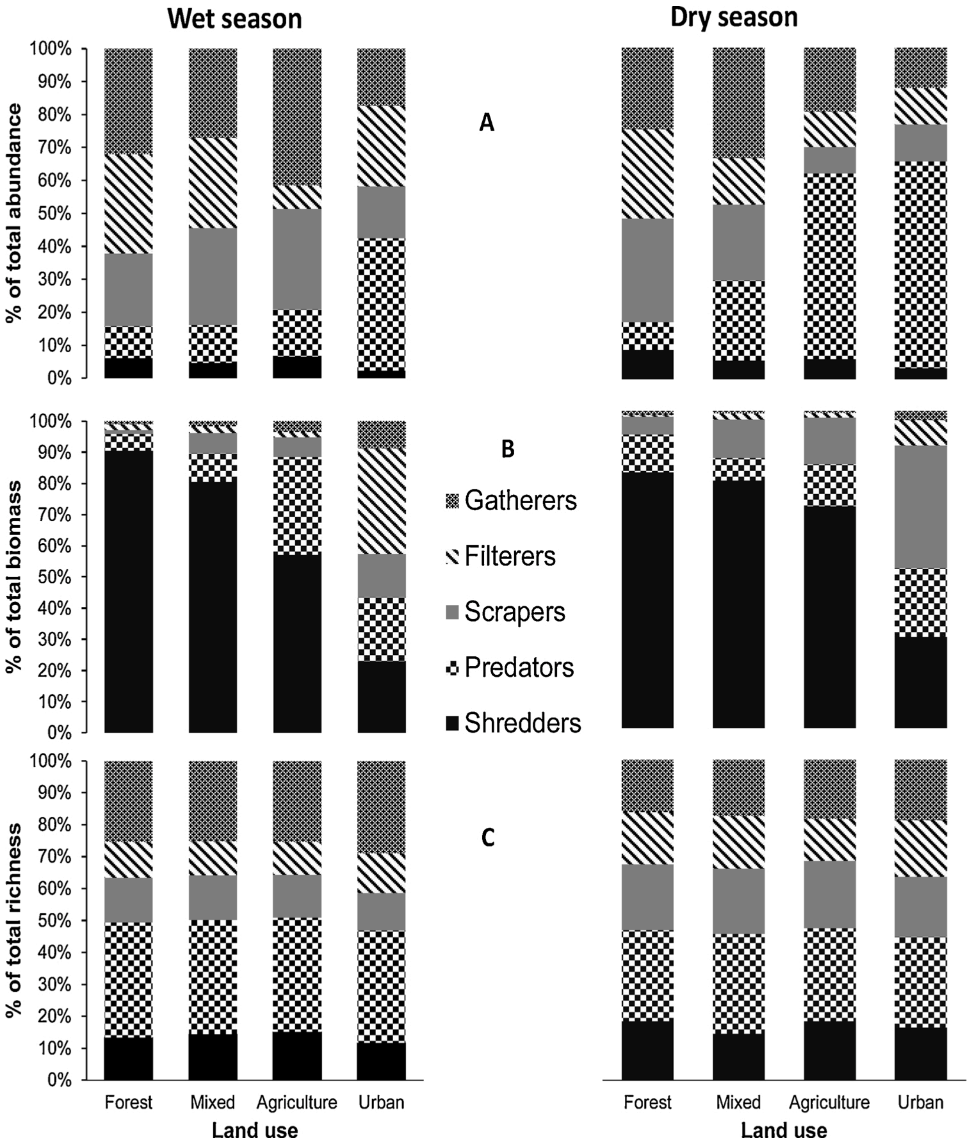

Fig. 3. Percentage composition of functional feeding groups in terms of total abundance (A), biomass (B), and taxon richness (C) in the different land-uses during the wet and dry seasons.

(Table 2).

Unlike the abundance data, biomass-based SIMPER's pair-wise comparison indicated that during the wet season, shredders and predators contributed the greatest dissimilarity among all the land-uses. Shredder biomass differentiated among the land-uses with more than 70 % total contribution to dissimilarity with higher biomass in the forested land-use while predators accounted for 11–14 % with higher biomass in the agricultural, mixed and urban sites during the wet season (Table 2). During the dry season, the forested sites were differentiated from agricultural sites by shredders (69.1 %) and predators (20.0 %), with higher biomass in the agricultural sites. Shredders (55.8 %) with higher biomass in the forested sites and scrapers (19.6 %) with higher biomass in the urban sites contributed the greatest dissimilarity between forested and urban sites, while shredders (70.5 %) and predators (15.7 %) differentiated forested from mixed sites, with higher biomass in the forest sites (Table 2).

RDA indicated distinct spatial patterns in macroinvertebrate community composition associated with water quality variables (Fig. 5) and stream size, organic matter and habitat variables (Fig. 6) for both dry and wet seasons. During the wet season, RDA Axis 1 accounted for the greatest variance (% explained variance, range 20.5–28.8 %) in the data. Both presence-absence and abundance data showed similar trends to water quality and nutrients during both wet and dry seasons. The first RDA axis (RDA 1) explained between 23.8 %–29.8 % of the association for both abundance and presence/absence data. The second RDA axis (RDA 2) explained between 16.3 % and 23.2 % of the association. Nutrients (SRP and nitrates), temperature, electrical conductivity and TSS were associated with predators and scrapers in urban and agricultural sites while high DO levels occurred in forested sites and were associated with shredders and collector-gatherers (Fig. 5).

Similarly, macroinvertebrate FFGs showed similar trends in habitat and stream size variables as those for water quality variables for both abundance and presence/absence data in both dry and wet seasons. Riparian zone quality, %_CPOM, cover and substrate quality were associated with shredders in forested and mixed sites while scrapers and predators were influenced by discharge, pool quality and stream morphology in agricultural and urban sites. The association were explained by (22.6 %–26.1 %) in axis 1 while axis 2 explained between (18.4 %–21.5 %) of the association (Fig. 6).

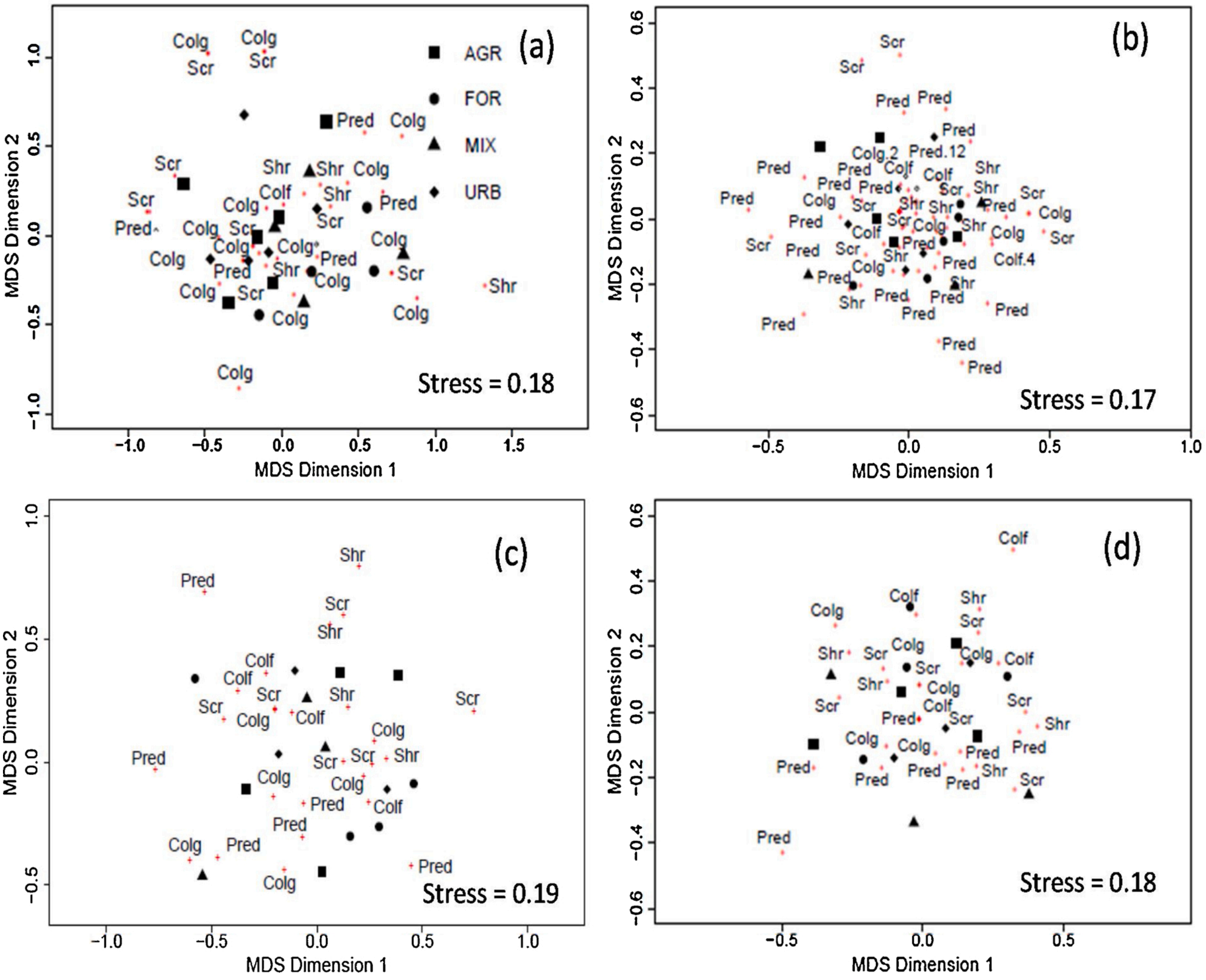

Fig. 4. NMDS based on abundance (a, c) and presence-absence (b, d) data of the various macroinvertebrate FFGs during the wet season (a, b) and dry season (c, d). Pred = predators, Shr = shredders, Scr = scrapers, Colf = collector-filterers, Colg = collector-gatherers.

4. Discussion

This study shows that macroinvertebrate FFGs (scrapers, shredders, predators, collector-filterers and collector-gatherers) displayed both spatial and temporal variability in abundance, biomass and taxon richness in response to land-use driven changes in water quality, organic matter and habitat characteristics. Seasonality amplified the land-use effects on water quality, with low dissolved oxygen and increased concentrations of nutrients and suspended solids, and higher electrical conductivity associated with agricultural and urban sites during the wet season. Macroinvertebrates FFGs responded to these changes with higher shredder abundance, biomass and taxon richness being recorded in forested sites, irrespective of the season, while predators and scrapers increased in agricultural and urban sites where conductivity, mean water temperature and nutrient concentrations and suspended sediments were higher. Biomass of FFGs responded more strongly to changes in land-use than abundance measures. For shredders, decrease in biomass along the land-use gradient was attributed to the presence of macro-consumers (freshwater crabs) which are very sensitive to deforestation and deterioration of habitat and water quality (Lancaster et al., 2008; Masese et al., 2014a).

4.1. Land-use effects on water quality

Both season and land-use played significant roles in influencing water quality, organic matter and habitat variables in our study. Changes in water quality across the land-use sites were indicated by decreasing DO levels, increasing temperature, conductivity, nutrients and TSS (Table 1). The higher mean temperature in the agricultural and urban streams can be attributed to open canopy cover along the riparian zones, while the lower mean temperature at forested sites was due to dense vegetation cover. Vegetation cover on river margins limits solar radiation reaching the water thus reducing fluctuations in water temperature in forested streams (Mathooko and Kariuki, 2000; Aura et al., 2010; López-Carr and Burgdorfer, 2013; Masese et al., 2017). The lower conductivity recorded in forested sites than other site categories during both seasons can be attributed to the fact that undisturbed catchments are characterized by very low in-stream ionic concentrations. On the contrary, higher conductivity was recorded in agricultural and urban streams during the wet season, probably due to runoff from farmlands and urban areas (Minaya et al., 2013; Mwaijengo et al., 2020). The high levels of nitrates in agricultural sites could be attributed to nitrogenous fertilizers used in farmlands used for maize and wheat production. Increase in dissolved fractions of nitrogen and electrical conductivity are indicators of disturbance that have been attributed to change in land-use type from forestry to agriculture in the region (Minaya et al., 2013; Masese et al., 2017; Jacobs et al., 2017). High levels of nutrients in urban sites are attributed to runoff and leakages from sewerage facilities and waste disposal from agro-industrial activities (Aura et al., 2010). It is also notable that many residents in the town of Eldoret and surrounding settlements do not have adequate sewerage facilities, heightening the potential for wastewater and sewage input to surface waters during the

Table 2
FFGs-ranked abundance- and biomass-based SIMPER contributors to % dissimilarity in the composition of macroinvertebrates between forest and agriculture, forest and mixed and forest and urban sites during the wet and dry seasons, for mean abundance and mean biomass for all sites per land-use.

FFG	Wet season									Dry Season								
	Forest vs Agric			Forest vs Mixed			Forest vs Urban			Forest vs Agric			Forest vs Mixed			Forest vs Urban		
	Forest	Agriculture	Contrib. %	Forest	Mixed	Contrib. %	Forest	Urban	Contrib. %	Forest	Agriculture	Contrib. %	Forest	Mixed	Contrib. %	Forest	Urban	Contrib. %
Abundance																		
Filterers	448	41	**20.6**	448	416	**13.8**	448	865	**20.7**	82	92	10.4	82	113	**19.7**	82	123	12.4
Gatherers	476	240	**17.2**	476	412	**14.7**	476	615	13.4	83	58	11.1	83	37	13.7	83	111	11.2
Scrapers	328	176	10.6	328	449	12.7	328	553	9.2	120	55	**16.6**	120	50	**18.7**	120	112	**17**
Predators	145	83	8.7	145	175	7.5	145	1419	**19.1**	56	225	**25**	56	67	15.5	56	629	**29.8**
Shredders	90	38	3.8	90	71	3	90	84	2.7	25	30	4.7	25	18	4.5	25	34	4.8
Biomass																		
Shredders	34.2	3.3	**81.9**	34.2	17.8	**77.9**	**34.2**	2.1	**73.7**	9.7	11.6	**69.1**	9.7	6.6	**70.5**	9.7	2	**55.8**
Predators	2	1.8	**12.9**	2	2.8	**13.8**	**1.9**	2	**10.8**	1.5	1.9	**20**	1.5	0.6	**15.7**	1.5	1.5	19.3
Filterers	0.7	0.1	2.2	0.7	0.5	2.2	0.7	3.1	8.8	0.04	0.2	1.7	0.04	0.2	1.3	0.04	0.6	3.6
Gatherers	0.4	0.2	1.5	0.4	0.4	2	0.4	0.8	2.8	0.2	0.1	1.3	0.2	0.1	1.5	0.2	0.2	1.7
Scrapers	0.5	0.4	1.4	0.5	1.5	4.1	0.5	1.2	3.8	0.7	0.7	7.9	0.7	0.8	**11**	0.7	2.7	**19.6**

wet season.

Habitat quality and organic matter characteristics had significant differences among land-uses, without significant interactions with seasonality. Forested sites had good riparian zone quality, instream cover and a higher percentage coverage and biomass of CPOM whose quality declined among agricultural and urban sites. This can be ascribed to the fact that forest streams are less interfered with, therefore still maintaining in-stream vegetation and riparian zones. It was evident from the study that water and habitat quality worsened with the change in land-use from the natural forest through mixed to agricultural and urban land-use.

4.2. *Patterns in macroinvertebrates functional composition*

Shredder biomass and abundance dominated in forested sites compared to sites in the other land-uses. This is in agreement with earlier studies in the tropics, including Dobson et al. (2002); Cheshire et al. (2005); Uwadiae (2009) and Masese et al. (2014a). Shredders (most of them being Trichoptera) and scrapers (mostly Ephemeroptera) are more sensitive to environmental changes, while collectors and predators are more tolerant to disturbance and organic pollution (Boyero et al., 2009; Masese et al., 2014a; Masese and Raburu, 2017). Abundance based SIMPER identified collectors (filterers and gathers) during the wet season and predators during the dry season in terms of numerical abundance as the major FFGs contributing to the dissimilarity among the land-uses. Shredders and predators co-dominated the biomass and contributed to differences among the land-uses. There was dominance in terms of richness and abundance of predators in urban streams, which can be attributed to tolerant taxa, among Odonata and Hemiptera (Masese et al., 2020). The dominance of these taxa in urban sites was made possible by the presence of other tolerant prey taxa such as Oligochaeta (Barbee, 2005).

Seasonality was a major driver of the functional organization of macroinvertebrates in the study area. There was high abundance, biomass and richness of FFGs during the wet season than the dry season, which can be attributed to the increase in habitats as marginal vegetation are flooded and a broad diversity of flow velocities are available for the flow velocities are maintained for both rheophilic taxa and pool taxa (Dallas, 2007; Muñoz-Mas et al., 2019; Masese et al., 2020). Food resources are also abundant and diverse during the wet season from run-off from terrestrial sources (Masese et al., 2009a). Flow reduction during the dry season contributes to seasonal variability in physico-chemical conditions that influences macroinvertebrate communities. For instance, we recorded the lowest DO concentration and highest nutrient levels and electrical conductivity during the dry season, indicative of point sources of pollution, which in urban areas emanates from wastewater treatment facilities and outfalls from agro-industrial facilities (Walsh et al., 2005).

There were distinct spatial patterns in macroinvertebrate community composition associated with water quality variables and stream size characteristics, organic matter and habitat variables for both dry and wet seasons (Figs. 5 and 6). For instance, predator abundance and richness dominated the dry season whose proportion increased with increase in disturbance from the forested sites to the degraded urban sites and were positively correlated with increased levels of nutrients and electrical conductivity. Anthropogenic activities influence on the riparian land of urban sites created conditions that could only accommodate a narrow range of macroinvertebrates (mainly tolerant FFG taxa) that can withstand and are opportunistic in the degraded water and habitat conditions. Shredders were the least abundant and diverse but had the highest biomass that was >80 % of all taxa in forested and mixed sites. Earlier studies by Pearson et al. (1989); Cheshire et al. (2005) and Camacho et al. (2009) had noted that the abundance and distribution of shredders in tropical streams can be temporally and spatially variable. The low numbers of shredders in agricultural and urban sites was probably due to the deforestation and clearance of

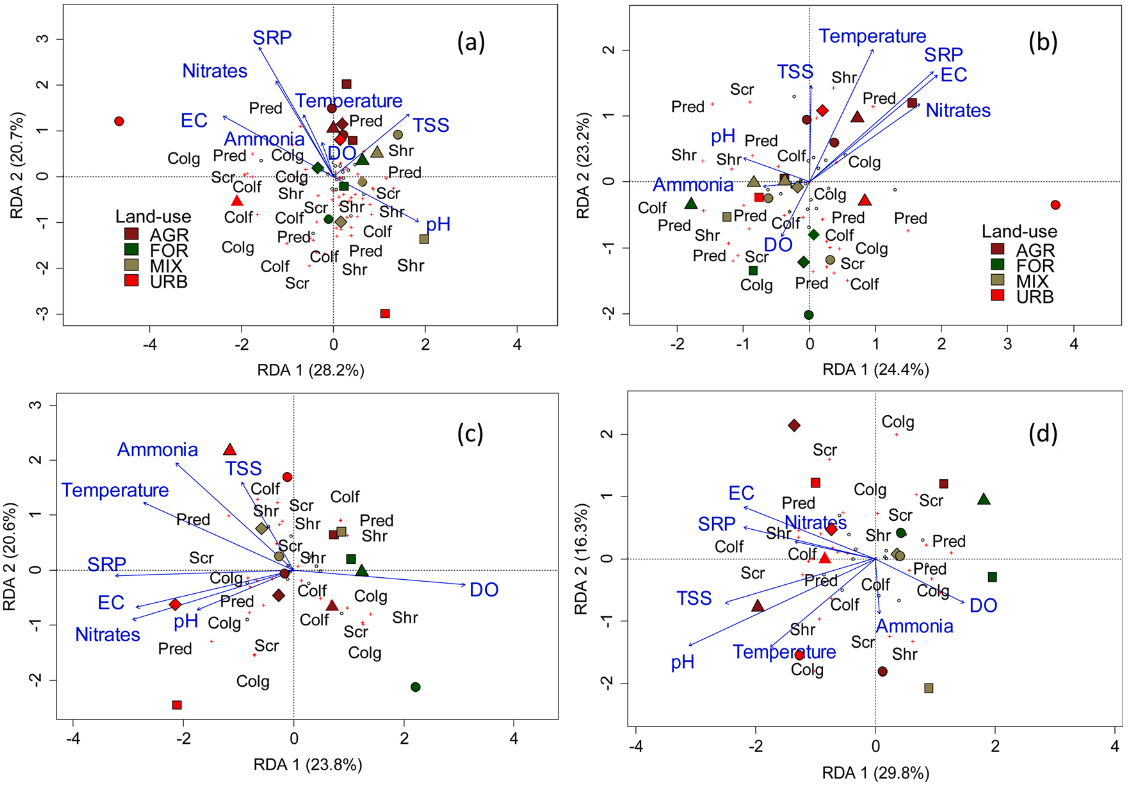

Fig. 5. Redundancy analysis (RDA) triplot of macroinvertebrate FFGs based on abundance (a, c) and presence-absence (b, d) data in relation to water quality variables during the wet (a, b) and dry (c, d) seasons in Sosiani-Kipkaren River. Pred = predators, Shr = shredders, Scr = scrapers, Colf = collector-filterers, Colg = collector-gatherers, EC = electrical conductivity, DO = dissolved oxygen, SRP = soluble reactive phosphorus, TSS-total suspended solids.

indigenous riparian vegetation, water pollution and habitat disturbance caused by farming activities and urbanization in the region (Masese et al., 2009a; Raburu et al., 2009; Aura et al., 2010). Furthermore, the remaining riparian vegetation is mainly dominated by exotic vegetation (mainly Eucalyptus, cypress and Pine cover). The insufficient quality and quantity of leaf litter input may jointly cause the paucity of shredders (Cummins et al., 1989; Tiegs and Peter, 2008; Jiang et al., 2011; Masese et al., 2014a).

The longitudinal distribution of FFGs at Sosiani-Kipkaren River varied widely among abundance, biomass and taxon richness of the various FFGs, and did not meet the expectations of the River Continuum Concept (RCC) (Vannote et al., 1980). While the abundance data showed a mixed trend in the distribution of shredders from upstream sites (forested) to downstream sites (agricultural and urban), biomass data had a clear distribution that noticeably matched the RCC predictions. The richness-based metric didn't show any systematic longitudinal patterns and was less responsive to change in land-use type. This can be attributed to the replacement of intolerant by tolerant taxa across FFGs (Masese et al., 2020). Abundance data indicated that collector-gatherers and collector-filterers co-dominated the upper reaches while predators dominated the mid and lower reaches. The biomass-based metric showed a clear trend in the distribution of shredders conforming to the RCC prediction. Although in low numbers, shredders numerical abundance was highest at the upper forested reaches and decreased from upstream to downstream sites. The biomass of total collectors (filtering and gathering collectors) and scrapers increased from upstream to downstream, results that conform to similar studies within the region by Dobson et al. (2002) and Masese et al. (2014a). The predominance of scrapers and collectors throughout the river has been reported in other studies in tropical streams (Tomanova et al., 2006; Jiang et al., 2011). The shredder biomass which differed significantly ($p < 0.05$) from the other functional feeding groups was contributed significantly by crabs of the genus *Potamonautes,* tipulids, and trichopterans (*Pisulia* sp., *Triaenodes* sp., *Adicella* sp., and *Lepidostoma* sp.) which are large-bodied and have been reported to be highly abundant in East African streams (Dobson et al., 2002; Masese et al., 2014a).

5. Conclusions

Our study shows that the functional organization of macroinvertebrates in headwater streams is subject to deterministic processes through the occurrence of gradients caused by changes in environmental conditions, such as organic matter, water and habitat quality. These differences are then amplified or ameliorated by variations in water levels (discharge) caused by seasonality in tropical streams. Changes in land-use type from forestry to agricultural and urbanization resulted in deterioration of water and habitat quality, which subsequently affected the different macroinvertebrate FFGs differently. Shredder biomass was most negatively responsive to change in land-use type, while the rest of the FFGs seemed to thrive in modified stream conditions. Overall, this study provides further evidence of the potential use of macroinvertebrate FFGs as indicators or surrogates on ecosystem health in headwater streams, and specifically the effects of agricultural and urban land-use on water and habitat and potential sources of nutrition in rivers. This study also shows that protection of riparian corridors along streams can play a major role in minimizing the effects of land-use on streams and rivers.

CRediT authorship contribution statement

Augustine Sitati: Conceptualized the study, designed the methods and study design, performed fieldwork and sample analysis, performed data, drafted the original manuscript. **Phillip Raburu:** Contributed to the study design and commented on the manuscript. **Mourine Yegon:** Performed fieldwork, sample analysis, commented and edited the manuscript. **Frank Masese:** Conceived the study, designed the methods

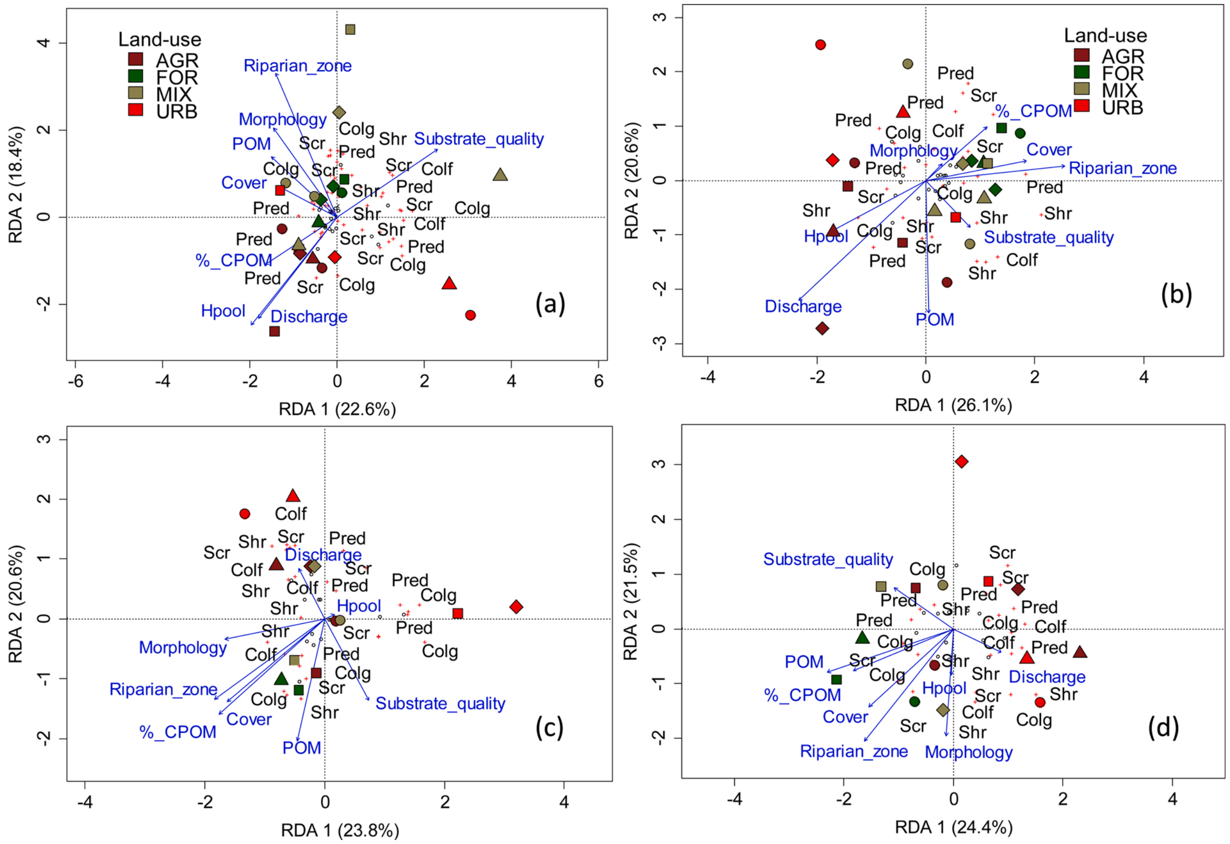

Fig. 6. Redundancy analysis (RDA) triplot of macroinvertebrate FFGs based on abundance (a, c) and presence-absence (b, d) data in relation to stream size, habitat quality variables during the wet (a, b) and dry (c, d) seasons in the Sosiani-Kipkaren River. Pred = predators, Shr = shredders, Scr = scrapers, Colf = collector-filterers, Colg = collector-gatherer, POM = particulate organic matter, Hpool = Habitat pool quality, CPOM = coarse particulate organic matter.

and study design, performed fieldwork, data analysis, edited and commented on the manuscript.

Declaration of Competing Interest

The authors declare no conflict of interest

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.limno.2021.125875.

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