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Elevation and land use as drivers of macroinvertebrate functional composition in Afromontane headwater streams

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Abstract. Macroinvertebrates play a unique role in aquatic ecosystems by acting as processors of nutrients and organic energy from allochthonous and autochthonous sources. Within East Africa, and especially Kenya, anthropogenic influences on streams and rivers as a result of deforestation and the expansion of agricultural lands are pervasive. This study investigated land use *v.* altitudinal shifts in the functional composition of macroinvertebrates within the Mount Elgon catchment in western Kenya. A total of 20 sampling sites in 12 streams, 10 sites each within forested and agricultural areas, located in 3 elevation categories were sampled for physicochemical water parameters and macroinvertebrates. Significant ($P < 0.05$) spatial variation was observed in total suspended solids, coarse particulate organic matter, temperature and electrical conductivity between forested and agricultural sites. Shredder biomass and abundance was higher in forested streams at higher elevations. There was a significant increase in the abundance (of shredders, predators, collector filterers and gatherers), taxon richness (of shredders, predators and scrapers) and biomass (of shredders, collector filterers and gatherers) of functional feeding groups with increasing elevation. Data of near-natural sites are urgently needed to disentangle altitude and land use influences on the diversity and composition of aquatic communities in high-elevation streams in the tropics.

Keywords: Afrotropical, altitude, benthic invertebrates, bioindication, functional feeding groups.

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Introduction

A recurring theme in freshwater ecology that has increasingly attracted scientific and management interests globally has been a focus on the effects of human activities on the structure and functioning of ecosystems (Allan 2004; Dubois *et al.* 2018). Human activities in the catchment and vicinity of freshwater ecosystems have resulted in unprecedented changes in the physical, chemical and biotic attributes of many ecosystems, with a resultant change or loss in biodiversity and ecosystem functioning (Dudgeon *et al.* 2006; Hecky *et al.* 2010; Cooper *et al.* 2013). Nowhere have these effects been more evident than in streams and rivers draining messic watersheds that have been subjected to changes in land use and land cover.

Land use change, defined as the conversion of natural indigenous forests to other uses, such as agriculture and urbanisation, represent the most vivid imprint of human activities in the catchments of streams and rivers. Many montane forests and agro-ecological zones have lost their extensive native vegetation to exotic plantations, crop farming, human settlements and livestock grazing lands (Kasangaki *et al.* 2008; Mati *et al.* 2008). In the East African region, only 28% of the original forest cover remains (White and Martin 2002), and the region is projected to lose up to 95% of its forest area by 2040 (Food and Agriculture Organization of the United Nations 2005, 2015). The accelerating rates of forest conversion and degradation have implications on surrounding catchments, including streams and rivers. This is because the extent of most freshwater systems is not confined to the wetted perimeter, but includes the catchment characteristics (Hynes 1975; Frissell *et al.* 1986; Dudgeon *et al.* 2006).

Tropical Afromontane streams are dynamic systems strongly influenced by factors operating at both local and catchment scales (Masese *et al.* 2017, 2018; Fugère *et al.* 2018). Catchment-scale influences are largely responsible for the characterisation of substrate composition, channel morphology, the input of nutrients, shading and water temperature, which affect the overall ecological status. The co-occurrence of catchment-scale activities, such as urbanisation, forestry and agriculture, with local-scale activities, such as riparian area management, affect habitat conditions in streams (Richards and Host 1994). The clearing of forests within stream catchments has led to changes in the supply of allochthonous resources, flow and channel characteristics and sediment regimes, as well as to the homogenisation of habitats. The associated increase in surface run-off and sediment loads has led to habitat alteration, such as the clogging of river bottoms and flood plain aggradation (Dudgeon *et al.* 2006).

Aquatic biodiversity plays a major role in the functioning of streams because of its roles in organic matter processing and facilitating food web interactions. The biodiversity in streams includes benthic macroinvertebrates, which play an important ecological role in aquatic–terrestrial systems by acting as subsidies of aquatic–terrestrial food chains (Richardson and Sato 2015). Because of this, benthic macroinvertebrates form an important link between basal resources and higher trophic levels. They act as processors of organic matter from both allochthonous and autochthonous sources in aquatic ecosystems and are themselves a resource for secondary consumers like fish or birds. As excellent indicators of stream processes, benthic macroinvertebrates are widely used in developing biotic and other indices used for biomonitoring the ecological condition of streams and rivers (Dickens and Graham 2002; Masese *et al.* 2009).

Land use changes in the catchment areas and riparian zones of riverine ecosystems can directly affect macroinvertebrate communities through changes in resource availability, habitat quality and hydrological conditions (Tanaka and Dos Santos 2017). Anthropogenic activities in the riparian corridor alter the quantity, quality and seasonality of allochthonous resources getting into streams, including light regimes and primary productivity (Sweeney *et al.* 2004; Richardson *et al.* 2005; Fugère *et al.* 2018), as well as altering environmental conditions, such as sediments, water temperature and chemistry (Masese *et al.* 2017; Fugère *et al.* 2018). Anthropogenic activities also affect the functional composition of macroinvertebrates by modifying the supply of food resources and the structure and quality of habitats (Dudgeon 2010; Masese and McClain 2012; Minaya *et al.* 2013).

Biodiversity in a substantial number of tropical montane cloud forests remains undocumented (Tomanova *et al.* 2006), despite these areas being ranked among the most important ecosystems for sustaining life in tropical regions (Bubb *et al.* 2004). Specifically, few studies exist on the functional composition of aquatic macroinvertebrates along land use and altitudinal gradients in Afromontane streams. Several studies have shown that physicochemical variables and geographical variables (altitude and longitude) affect macroinvertebrate community patterns in tropical river systems (Kasangaki *et al.* 2006; Dalu *et al.* 2017; Musonge *et al.* 2020). However, limited studies have analysed the combined effects of changes in water physicochemical and geographical variables (altitude) on macroinvertebrate communities (Suren 1994; Musonge *et al.* 2020). The present study fills an important knowledge gap about the combined effects of environmental (land use-driven) and geographical (elevation-driven) variables on macroinvertebrate assemblages in Afromontane streams. These studies are important for informing decisions regarding the conservation of endemic and threatened species and the sustainable management of high-elevation streams. In this study we examined the spatial variation in macroinvertebrate functional composition in relation to changes in both land use and altitude (elevation) in order to understand their responses to changes in water and habitat quality along these gradients and how the two gradients interact. To achieve this, we examined responses in three metrics (abundance, biomass and richness) of macroinvertebrate functional composition to land use change from forestry to agriculture along an altitudinal gradient in streams draining the southern slopes of Mount Elgon, western Kenya.

We hypothesised that: (1) the composition of macroinvertebrate functional feeding groups (FFGs) would change in response to changes in water and habitat variables along land use and altitudinal gradients; (2) the differences in macroinvertebrate functional composition between elevation categories would be minimal and exhibit similar relationships within similar land use categories; and (3) based on the river continuum concept (RCC), there would be more shredders upstream in forested streams due to higher allochthonous input and more scrapers in mid-elevation agricultural streams due to reduced shading and increased nutrient loads that support autochthonous resources.

Materials and methods

Study area and study sites

This study was conducted in Mount Elgon streams, which are part of the headwaters of the Nzoia River, Lake Victoria Basin, Kenya (Fig. 1). The Mount Elgon landscape in Kenya is partly in Trans-Nzoia and Bungoma counties in western Kenya, has a size of 72 874 ha and is located between latitudes 0°47′N and 0°54′N and longitudes 34°34′E and 34°45′E. The Nzoia River has a length of 257 km and flows south and west of Mount Elgon and into Lake Victoria, where it discharges at a rate of ~118 $m^3 s^{-1}$. The Nzoia River is the largest river in Kenya's Lake Victoria basin. It drains the Afromontane forests in the upper reaches of the Mount Elgon National Park (Musau *et al.* 2015), but extensive land use change from forestry to agriculture and overgrazing has significantly reduced native forest cover (Okeyo-Owuor *et al.* 2011; Petursson *et al.* 2013).

The Mount Elgon landscape is characterised by a high topographic relief with extensive areas of undulating hills and gentle slopes (Marchant *et al.* 2018). The elevation ranges from 878 to 4304 m above sea level (ASL) at its peak. The climate of the area is mainly tropical humid, with a mean annual rainfall of 1400–1800 mm and a mean air temperature of 14–24°C, although both climate parameters vary strongly with elevation. Mean temperature is lowest in June–September (Musau *et al.* 2015). The annual rainfall pattern is bimodal, with long rains between March and June and short rains from September to November (Musau *et al.* 2015)

The abundant rainfall makes the area highly productive, for both agriculture and natural ecosystem productivity. Approximately 3.5 million people live within the Nzoia River basin, and over 2 million people live on the Mount Elgon landscape in Kenya and Uganda. High population densities exist in the basin, with the mean population density being 190 people km^{-2} (Nyadawa and Mwangi 2010). Areas around the base of the

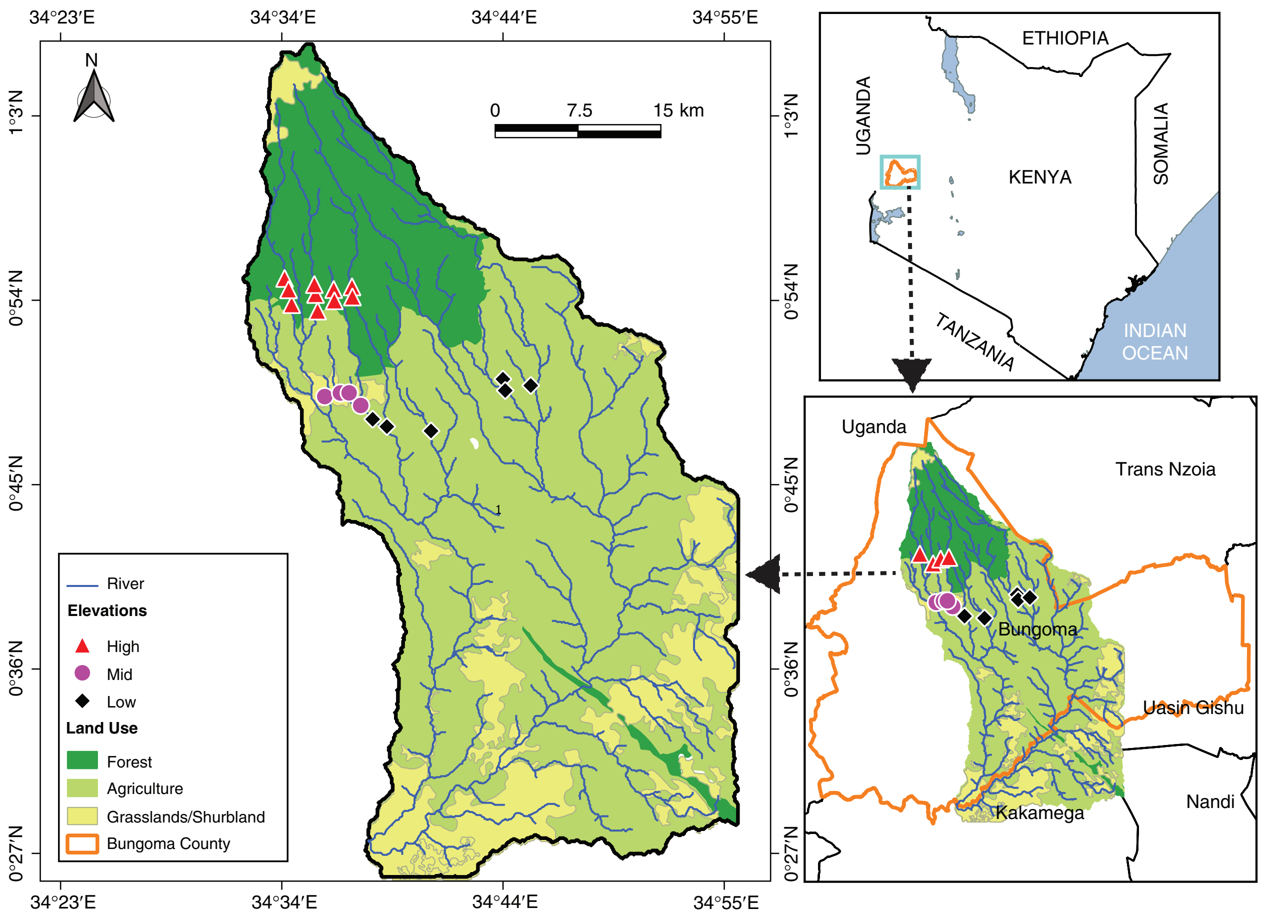

Fig. 1. Map of the study area showing the location of the sampling sites and the associated elevation and land use types.

mountain are densely populated, with communities using the deeply rich volcanic soils for agriculture, which is the livelihood for a large proportion of the basin's population. Communities farm maize, onions, cabbages, potatoes and beans, as well as keep livestock. The farmlands range between smallholder intensive farms to medium-scale semi-intensive holdings. Water from the basin plays an important economic role and serves many purposes, including for domestic use, watering animals, irrigation, industrial purposes, aquaculture and cultural and spiritual services.

Study design

To analyse land use and altitudinal effects on macroinvertebrate communities, streams were chosen in two major land uses (forested and agricultural) along an elevation gradient from 1624 to 2435 m ASL (Fig. S1 of the Supplementary material). The elevation gradient was further divided into three categories, namely high (2200–2500 m ASL), mid (1800–2200 m ASL) and low (1600–1800 m ASL; see Table S1 of the Supplementary material), based on vegetation type and the slope gradient in the area (Jiang *et al.* 2014). Sampling sites were targeted to be in forested (reference sites) and agricultural (disturbed sites) land use areas based on the riparian and catchment characterisation. In all, 20 sites in 12 streams were sampled for macroinvertebrates and associated physical habitat conditions (Table 1). Forested sites had a riparian and catchment zone that was >60% forested land, whereas agricultural sites had a riparian and catchment zone with >60% agricultural land. The proportion of forested and agricultural land in the riparian and catchment areas of sampling sites were determined using land cover satellite imagery (Digital Elevation Model of Kenya; 90 × 90 m) produced using data from the Shuttle 152 (Radar Topography Mission) within a 1500-m buffer of the sampled sites.

Field methods

Sampling was done during medium discharge between October and November 2019. Both macroinvertebrates and environmental variables were sampled within a 100-m representative reach at the sampling sites. Physicochemical water quality parameters of dissolved oxygen (DO; mg L^{-1}), temperature (°C), electrical conductivity (EC; μS cm^{-1}) and pH were measured *in situ* using a YSI multiprobe water quality meter (556 MPS; Yellow Springs Instruments, Yellow Springs, OH, USA). Known volumes of water samples for each sample were filtered through precombusted and preweighed GF/F filters (Whatman; pore size 0.7 μm, diameter 47 mm) and thereafter transported to the laboratory for determination of total suspended solids (TSS) and particulate organic matter (POM).

Table 1. Mann–Whitney *U*-test for significance of physicochemical parameters between the two land use types (agricultural and forested; *n* = 20) and Kuskal–Wallis test for significance of physicochemical variables among the three elevation categories

Data for the elevation categories are expressed as the mean ± s.d.

	Land use type		
	Agriculture	Forested	*P*-value
Physicochemical variables			
TSS (mg L^{-1})	197.5	30.6	0.005
EC (μS cm^{-1})	167.3	72.5	0.001
DO (mg L^{-1})	10.2	9.3	0.479
pH	7.1	7.3	0.082
Temperature (°C)	19.1	14.8	0.004
Organic matter			
CPOM standing stock (g m^{-2})	59.1	176.4	0.001
Stream characteristics			
Depth (m)	0.3	0.2	0.19
Width (m)	4.4	3.4	0.362
Velocity (m s^{-1})	0.8	0.6	0.092
Discharge (m^3 s^{-1})	0.6	0.4	0.825

	Elevation				
	High	Mid	Low	*H*	*P*-value
Physicochemical variables					
TSS (mg L^{-1})	29.3 ± 9.2	265.0 ± 108.5	199.6 ± 145.4	13.44	0.001
EC (μS cm^{-1})	72.1 ± 15.9	161.8 ± 27.9	171.0 ± 38.0	14.33	0.001
DO (mg L^{-1})	9.3 ± 2.6	9.2 ± 1.4	10.8 ± 0.3	3.27	0.195
pH	7.3 ± 0.4	7.07 ± 0.02	7.10 ± 0.04	0.29	0.864
Temperature (°C)	14.9 ± 1.0	18.9 ± 1.4	18.8 ± 1.5	14.29	0.001
Organic matter					
CPOM standing stock (g m^{-2})	176.4 ± 79.5	75.7 ± 68.5	72.8 ± 29.5	9.15	0.011
Stream characteristics					
Depth (m)	0.2 ± 0.1	0.19 ± 0.04	0.3 ± 0.2	2.86	0.239
Width (m)	3 ± 4	3.6 ± 1.6	4.4 ± 2.0	0.19	0.912
Velocity (m s^{-1})	0.6 ± 0.3	0.7 ± 0.3	0.9 ± 0.3	4.52	0.104
Discharge (m^3 s^{-1})	0.6 ± 0.6	0.4 ± 0.3	0.8 ± 0.6	1.16	0.561

At each sampling site, measurements of water depth, velocity and width were taken. Transectoral width measurements were made using a measuring tape, whereas velocity and depth were measured using a metre rule and velocity plank. Stream discharge was calculated by the velocity–area method (Wetzel and Likens 2000). Substrate in the sampling sites was characterised by identifying the substrate types that constituted more than 5% coverage at each site according to Lakew and Moog (2015).

A multihabitat sampling technique was used during macroinvertebrate sampling following the AQEM Consortium (2002) sampling manual. Accordingly, habitats were sampled in proportion to their presence or coverage within a sampling reach. At each site, 20 sampling units were collected from substrate types with more than 5% coverage within a 100-m representative study reach, with these 20 sampling units from different substrate types constituting one multihabitat sample (MHS). This sampling design is based on the principle that each habitat is colonised by a unique assemblage of macroinvertebrates (Resh and Rosenberg 1993). The proportion or coverage of each substrate type per site determined the number of units among the 20 MHS that were collected from that particular habitat type. Therefore, the substrate types and percentage coverage of the streambed were initially documented.

Sampling of macroinvertebrates was done by disturbing the substrates using a hand brush and collecting the dislodged organisms using a multihabitat sampling net (mesh size 100 μm). An area of 0.0625 m^2 was sampled for each sampling unit. Organisms attached to the substrates were inspected by scrubbing the substrate with the brush and washing the organisms into the net. Sampling was performed from downstream to upstream within a reach to minimise drift. Macroinvertebrate samples were preserved in 98% ethyl ethanol, labelled and stored in cool boxes for transportation to the laboratory for further processing. In addition, the biomass of course POM (CPOM) was estimated by collecting CPOM samples in triplicate from each sampling site using a quadrat (0.5 × 0.5 m^2), which were placed in zip-lock bags for transportation to the laboratory for processing. The CPOM collected was composed of sticks, leaves, seeds, fruits and flowers.

Laboratory analyses

TSS and POM were determined by drying the GF/F filters with embedded sediments at 60°C for 72 h to attain constant weight. The filters were then reweighed using an analytical balance (Secura 124-1S; Sartorius; 0.0001 g) for gravimetric determination of TSS. The filters were then ashed at 450°C for 5 h in a muffle furnace and reweighed for the determination of POM as the difference between thee TSS and ash-free dry mass (American Public Health Association and Water Pollution Control Federation 2005). The CPOM fractions were dried in an oven at 60°C until a constant weight was attained and weighed for biomass estimation.

Macroinvertebrate samples were rinsed in a series of sieves under flowing water to remove the preservative and to make the sorting procedures easier. Sorting was done with different taxa, divided in separate Petri dishes for ease of identification, counting and weighing. Complex and large samples were subsampled into smaller fractions for easier and thorough sorting. The samples were then preserved in 75% ethyl ethanol for archiving. Macroinvertebrates were identified under a dissecting microscope to family or genus level with the aid of keys in several guides (Gerber and Gabriel 2002; Day and de Moor 2002*a*, 2002*b*; de Moor *et al.* 2003*a*, 2003*b*; Merritt *et al.* 2008). Macroinvertebrate biomass was determined by oven drying the macroinvertebrates at 103°C for 4 h, after which they were weighed using an analytical balance (Secura 124-1S; Sartorius; 0.0001 g; Mason *et al.* 1983). FFGs were then assigned to the identified taxa basing on the work of Merritt *et al.* (2017) and Masese *et al.* (2014) and references therein. For families Baetidae, Caenidae, Leptophlebiidae and Chironomidae, which have not been distinctly functionally classified in the tropics, abundance and biomass were split into the FFGs they fall into according to Fugère *et al.* (2018) and Masese *et al.* (2014) (Table S2 of the Supplementary material). Five major FFGs were identified: shredders, scrapers, predators, collector-filterers (hereafter 'filterers') and collector-gatherers (hereafter 'gatherers').

Statistical analysis

The Mann–Whitney *U*-test was used to test the significance of differences in physicochemical water variables, stream size variables and organic matter fractions between agricultural and forested land use types. The Kruskal–Wallis test was used to test the significance of differences in physicochemical variables among elevation categories.

Principal component analysis (PCA) was used to reduce the dimensionality of the physicochemical data. We included two principal components (PCs) to describe water quality and stream size variables for both land use and elevation. The PCAs were statistically assessed using permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity matrices (McArdle and Anderson 2001).

The structure and composition of macroinvertebrate FFGs across land use categories and among elevation categories were described using abundance, biomass and richness metrics. Independent *t*-tests were used to test the significance of differences in the log- transformed macroinvertebrate abundance, biomass and richness data between land use types, whereas the Kruskal–Wallis test was used to test the significance of differences in abundance, biomass and richness among elevation categories.

One-way analysis of similitude (ANOSIM; randomisation procedure with 999 permutations) was used to compare average rank similarities of macroinvertebrate FFGs between the forested and agricultural land uses, as well as among elevation categories. This analysis was performed to confirm whether the grouping of samples based on *a priori* defined levels of the factors 'land use' and 'elevation' could account for the variability in the FFG data obtained by non-metric multidimensional scaling (nMDS) plots (Clarke and Gorley 2006). ANOSIM calculates the *R*-test statistic, which varies between 0 and 1, with higher values indicating greater differences between factors. This method was implemented in PAST software (ver. 3.21, see https://www.nhm.uio.no/english/research/infrastructure/past/; Hammer *et al.* 2001).

nMDS was used to visualise FFG composition in the two land use types and elevations. Dissimilarity matrices based on the Bray–Curtis coefficients (Bray and Curtis 1957) were derived from arcsine transformed data using the R function 'vegdist' of the vegan package in R (ver. 2.5-7, J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner, see https://cran.r-project.org/web/packages/vegan/index.html). 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). PERMANOVA was used as implemented in the 'adonis' function of the vegan package in R (ver. 2.5-7) to test for significant differences in FFG composition between land uses and among elevation categories. Pairwise differences in FFG composition between land uses and among elevation categories were run for all pairs of land use and elevation categories using the 'adonis.pair' function of the EcolUtils package in R (ver. 3.2.1, G. Salazar, see https://github.com/GuillemSalazar/EcolUtils), and Bonferroni correction was used to set significance levels for *P*-values. The statistical significance was determined by 999 permutations.

Both abundance- and biomass-based similarity percentage analysis (SIMPER) pairwise comparison tests were performed to identify the most discriminant FFGs for land use and elevation categories. The percentage contribution of each FFG to the overall dissimilarity between land use and elevation categories was quantified and presented for each pairwise comparison between levels (forested and agricultural; high *v.* mid elevation; high *v.* low elevation; and mid *v.* low elevation).

Canonical correspondence analysis (CCA) was used to elucidate relationships between the functional composition of macroinvertebrates and environmental variables. The output was displayed as a triplot, in which the plotted points for FFGs and land use and elevation categories could be related to physicochemical and habitat variables that were represented as rays (Ter Braak and Smilauer 1998).

To assess longitudinal trends in numerical abundance, taxon richness and the biomass of individual macroinvertebrate FFGs with changes in altitude (elevation), we used generalised additive models (GAMs; Wood 2017), which incorporate smooth functions that are more flexible in modelling non-linear relationships (Hastie and Tibshirani 1990). GAMs were built using penalised cubic regression splines with degrees of freedom automatically identified based on the generalised cross-validation (GCV) score. GAMs were fitted using the R package mgcv (ver. 1.8-36, see https://cran.r-project.org/web/packages/mgcv/index.html; Wood 2017). GAMs were used further to investigate the influence of land use and stream size (stream order) on altitudinal and longitudinal patterns in FFGs, including potential interactions. GAMs included altitude, land use and stream order as fixed effects, and individual streams as a random effect. Models were fitted using the mgcv package (ver. 1.8-36; Wood 2017) in R.

Statistical analyses were performed with PAST (ver. 3.21; Hammer *et al.* 2001) and R (ver. 3.3.3, R Foundation for Statistical Computing, Vienna, Austria, see http://www.R-project.org/). Figures were created in MS Office Excel (ver. 2105, Microsoft Corporation) and R (ver. 3.3.3, R Foundation for Statistical Computing).

Unless indicated otherwise, data are presented as the mean ± s.d.

Results

Water physicochemistry

There were significant ($P < 0.05$) differences in temperature, TSS, EC and CPOM standing stock between agricultural and forested sites. Agricultural land use sites recorded the highest values for TSS (225.8 ± 30.7 mg L^{-1}), temperature (19.0 ± 1.2°C) and EC (167.3 ± 32.9 µS cm^{-1}), which were lowest in forested land use sites. These agricultural sites however had lower CPOM standing stock (59.1 ± 33.1 g m^{-2}) than forested land use sites (Table 1).

Significant differences ($P < 0.05$) in temperature, TSS, EC and CPOM standing stock along the elevation gradient were recorded. Temperature (18.9 ± 1.5°C) and EC (171.0 ± 38.0 µS cm^{-1}) were significantly higher at low-elevation sites, whereas and CPOM standing stock (176.4 ± 59.5 g m^{-2}) was significantly higher in high-elevation sites. TSS (265.0 ± 108.5 mg L^{-1}) was highest in mid-elevation sites. The high-elevation sites had the lowest recorded values of temperature, EC and TSS (Table 1).

There were significant differences in physicochemical and stream size variables between land use sites (PERMANOVA, $F = 6.9$, d.f. = 1, $P = 0.01$), but not with elevation (PERMANOVA, $F = 1.7$, d.f. = 2, $P = 0.09$; Fig. 2). However, there was a significant land use × elevation interaction (PERMANOVA, $F = 2.7$, d.f. = 1, $P = 0.01$). The first (PC1) axis in PCA explained 39.3% and 37.3% of the total dataset variance, whereas the second (PC2) axis explained 24.0% and 24.1% of the total variance in water physicochemistry among elevations (Fig. 2*a*) and between land uses (Fig. 2*b*) respectively. Low elevation sites recorded high EC, TSS, temperature, POM and TDS, whereas high-elevation sites were characterised by high discharge, velocity, depth and width (Fig. 2*a*). Land use categorisation grouped the agricultural sites with high levels of temperature, TDS, EC, POM and TSS, whereas those in forested areas were categorised by high CPOM levels (Fig. 2*b*).

Functional composition of macroinvertebrates

The numeric abundance of FFGs did not differ between the two land use types ($t_{20} = 2.1098$, $P = 0.08$). Filterers (mainly Simuliidae and Hydropsychidae) dominated in numeric abundance in both land uses, but were highest in the agricultural land use (Fig. 3*a*). The highest abundance of gatherers (33.4%; mainly Baetidae and Caenidae) and shredders (5%; mainly Potamonautidae, Lepidostomatidae, Tipulidae and Triaenodes) was recorded in forested sites.

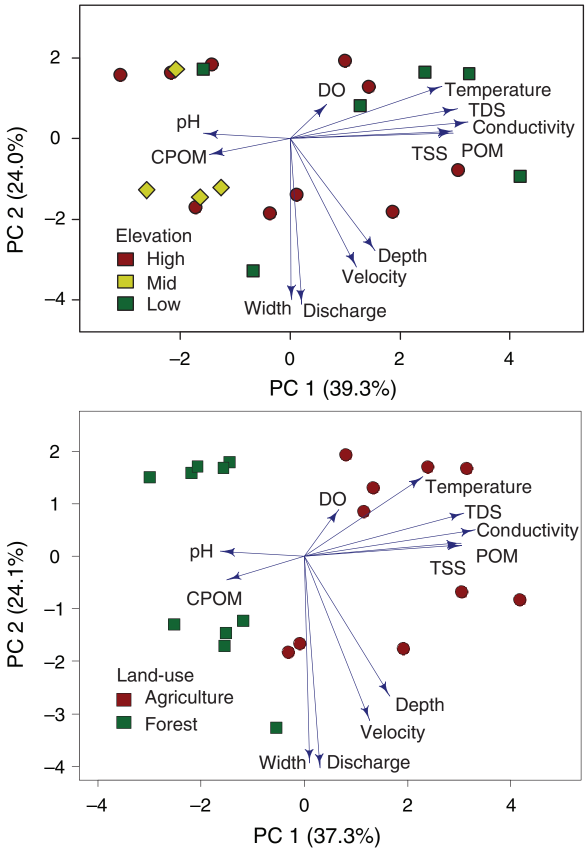

Fig. 2. PCA biplot for physicochemical and stream variables for Mount Elgon streams. (*a*) Loadings for streams defined by elevation categories; (*b*) loadings for land use categories.

The biomass of FFGs in the two land uses differed significantly ($t_{20} = 2.1098$, $P = 0.009$). Shredder biomass dominated (74%) in forested land use, whereas the biomass of filterers dominated (42.3%) in the agricultural land use. The biomass of predators was highest in the agricultural sites (3.7%).

The number of taxa of the different FFGs differed significantly ($t_{20} = 2.1098$, $P = 0.0001$) between agricultural and forested land uses, with the forested land use having a higher number of taxa of the different FFGs. Gatherers dominated in both land uses (forested = 24.1%; agricultural = 26.4%), whereas scrapers recorded the least number of taxa of the different FFGs in both land uses (forested = 13%; agricultural = 13.6%; Fig. 3).

There was no significant difference in abundance ($H_2 = 1.6$, $P = 0.23$) and in biomass ($H_2 = 3.47$, $P = 0.055$) between the elevation categories. However, the number of taxa of the different FFGs between elevation categories was significantly different ($H_2 = 8.88$, $P = 0.002$), with a significantly higher number of taxa at high than mid and low elevations. Filterers dominated in numerical abundance across all three elevation categories. Shredder abundance was higher in the high-elevation category (5%), whereas scraper abundance was higher in the low-elevation category (10.1%). Shredder biomass decreased downstream, with higher biomass in the high-elevation category (73.5%) and lowest biomass in the

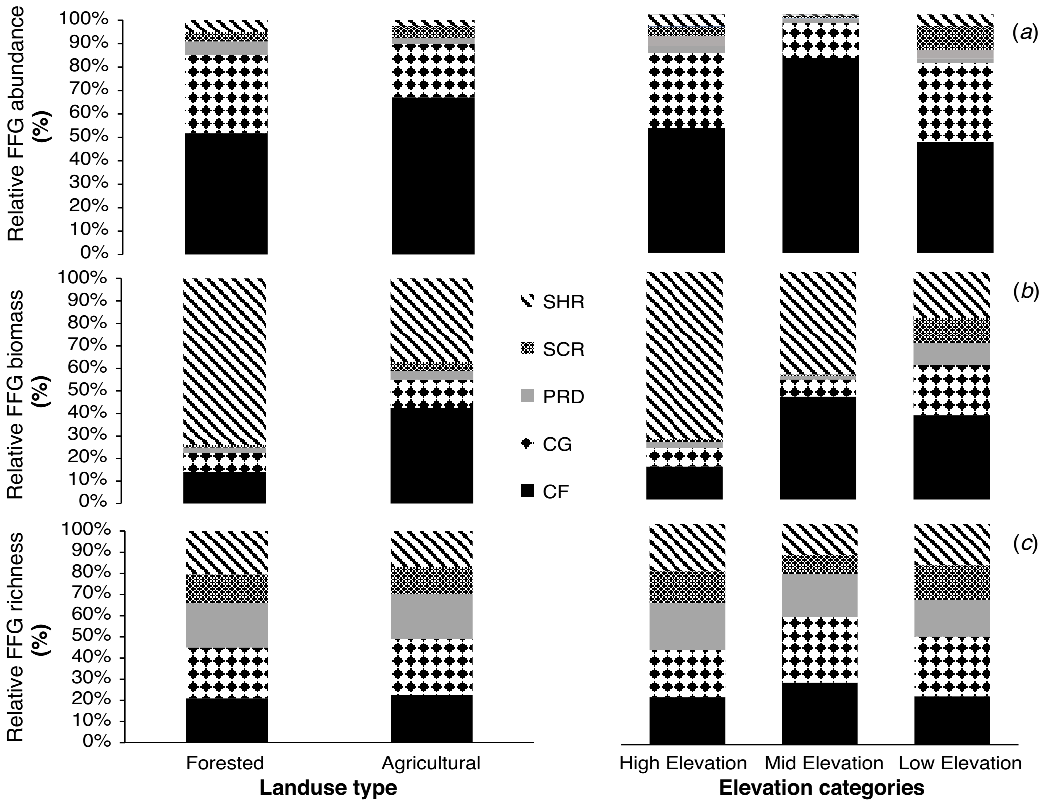

Fig. 3. Land use and elevation of FFGs in terms of (*a*) relative abundance, (*b*) biomass and (*c*) species richness. CF, collecting filterers; CG, collecting gatherers; SCR, scrapers; SHR, shredders.

low-elevation category (20.4%). Gatherers increased downstream, with highest biomass (22.2%) at low elevations and lowest biomass (8.2%) at high elevations. The biomass of scrapers and predators was higher in the low-elevation sites (10.9 and 8.9% respectively) than in the high- and mid-elevation sites. The taxa richness of the different FFGs was dominated by gatherers across the three elevation categories, whereas the richness of scrapers was the lowest (Fig. 3*c*).

Relationships between physicochemical parameters, habitat variables and macroinvertebrate FFGs

ANOSIM indicated significant differences in the functional organisation of macroinvertebrates for untransformed abundance data of FFGs between land uses ($R = 0.35$, $P < 0.002$) and among elevation categories ($R = 0.20$, $P < 0.021$). Similarly, the biomass data of FFG taxa indicated significant differences between forested and agricultural sites ($R = 0.46$, $P < 0.0003$) and among the three elevation categories ($R = 0.38$, $P < 0.002$).

nMDS based on the functional composition of macroinvertebrates showed a clear differentiation among elevations (PERMANOVA, $F = 3.4$, d.f. $= 2$, $P = 0.001$; Fig. 4*a*, *c*, *e*). Further differences were obtained between land uses (PERMANOVA, $F = 4.7$, d.f. $= 1$, $P = 0.001$; Fig. 4*b*, *d*, *f*). There was an effect of land use on functional composition among the elevations (land use × elevations combinations: PERMANOVA, $F = 4.9$, d.f. $= 1$, $P = 0.001$). Both abundance- and biomass-based nMDS clustered scrapers in the low-elevation sites and shredders and gatherers in forested sites. Filterers clustered in the mid-elevation sites using all three metrics (abundance, biomass and presence–absence). Shredders clustered in high-elevation sites and in the forested sites. The presence–absence metric clustered predators and scrapers in the agricultural sites and filterers, gatherers, scrapers and predators in the low-elevation sites (Fig. 4).

To test for significant differences in the observed patterns in the nMDS, PERMANOVA (with 999 permutations) was used. There were significant differences between forest and agricultural land uses, between high and mid elevations and between high and low elevations. There were also significant differences in high-elevation forest *v.* low-elevation agriculture and in high-elevation forest *v.* mid-elevation agriculture (Table 2).

Abundance-based SIMPER pairwise comparison of forested with agricultural sites identified filterers (52.2%) and gatherers (32.4%) as contributing the greatest dissimilarity between the forested and agricultural sites, with a higher abundance in forested sites. Filterers (55.2%) and gatherers (31.0%) contributed the greatest dissimilarity between high- and mid-elevation sites, with a higher abundance for filterers at mid-elevation sites and higher abundance of gatherers at the high-elevation sites. Similarly, filterers (50.3%) and gatherers (33.4%) contributed the greatest dissimilarity between high- and low-elevation sites, with the abundance of both groups being higher in the high-elevation sites. In addition, filterers (55.7%) and gatherers (26.8%) differentiated mid- from low-elevation sites, with both

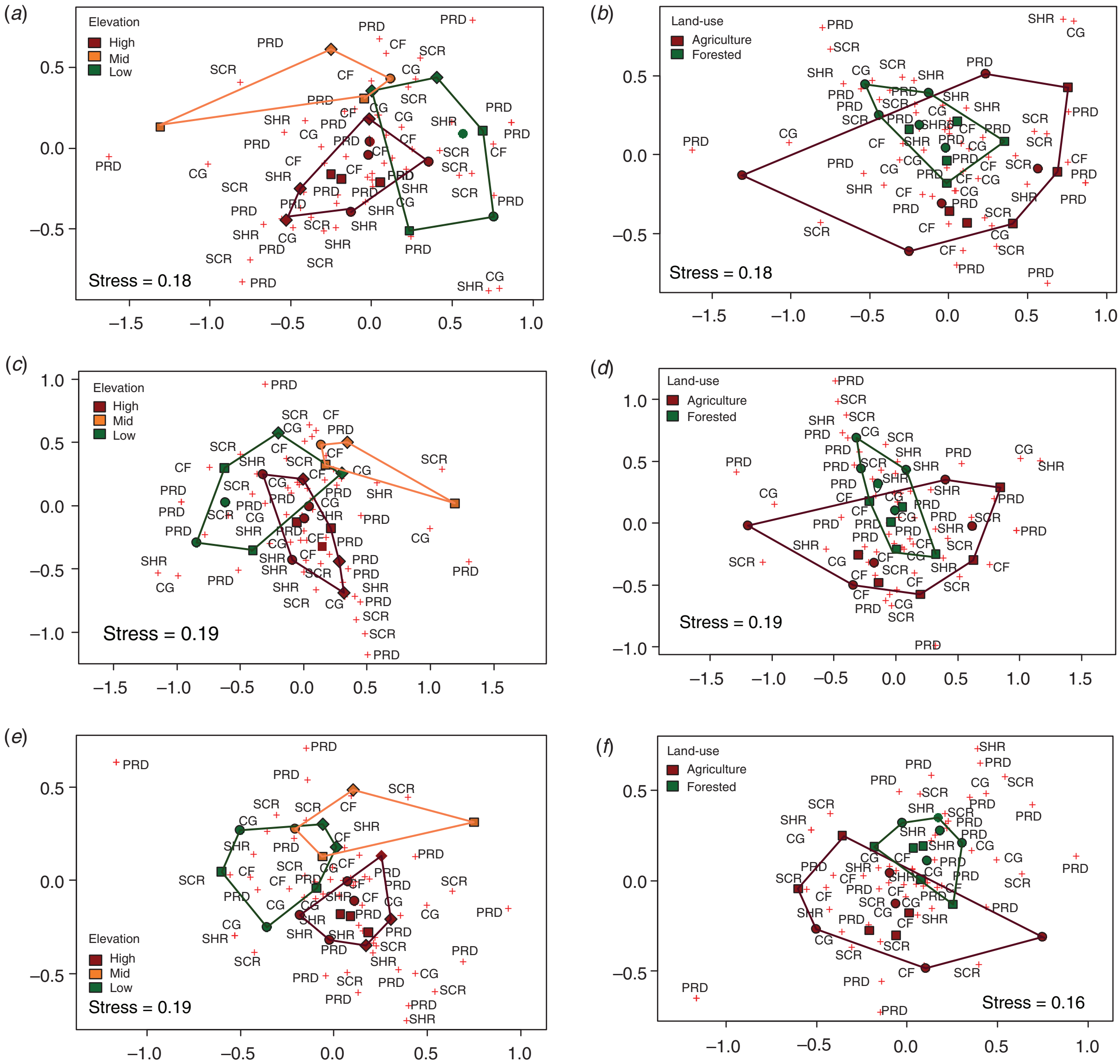

Fig. 4. nMDS based on (*a*, *b*) abundance, (*c*, *d*) biomass and (*e*, *f*) presence–absence data of macroinvertebrate FFGs in Mount Elgon streams, across land use categories (*a*, *c*, *e*) and elevation classes (*b*, *d*, *f*).

Table 2. Pairwise PERMANOVA for functional composition of macroinvertebrates between forest and agricultural land uses, elevations and combinations of land uses and elevations

Comparisons	*F* model	R^2	Corrected *P*-value
Land uses and elevations			
Forest *v.* agriculture	6.6	0.27	<0.001
High *v.* mid elevation	4.3	0.26	0.007
High *v.* low elevation	5.7	0.29	0.006
Mid *v.* low elevation	0.7	0.08	0.62
Land uses × elevations combinations			
High–forest *v.* low–agriculture	5.7	0.29	0.003
High–forest *v.* mid–agriculture	4.3	0.26	0.013
Low–agriculture *v.* mid–agriculture	0.7	0.08	0.60

Table 3. FFG-ranked SIMPER contributors to percentage dissimilarity (Contrib.%) in the composition between forest and agriculture land uses and among elevation categories

Values other than Contrib.% indicate mean abundance and mean biomass. High, mid and low elevations were defined as 2200–2500, 1800–2200 and 1600–1800 m above sea level (ASL) respectively

FFG	Land use			Elevation								
	Forest *v.* agriculture			High *v.* mid			High *v.* low			Mid *v.* low		
	Forest	Agriculture	Contrib.%	High	Mid	Contrib.%	High	Low	Contrib. %	Mid	Low	Contrib. %
Abundance												
Filterers	604	396	52.2	604	690	55.2	604	200	50.3	690	200	55.7
Gatherers	403	123	32.4	403	133	31	403	117	33.4	133	117	26.8
Predators	49	10	5.1	49	6	4.1	49	13	5.7	6	13	3.9
Scrapers	47	24	5.1	47	9	5	47	35	5.2	9	35	9.8
Shredders	58	11	5.1	58	4	4.6	58	15	5.4	4	15	3.8
Biomass												
Shredders	19.9	2.6	59	19.9	5.2	59.5	19.9	0.8	58.7	5.2	0.8	32.6
Filterers	3.9	2.9	24.4	3.9	5.2	26.7	3.9	1.5	23	5.2	1.5	35.6
Gatherers	2.3	0.9	9.7	2.3	0.9	9	2.3	0.9	10.2	0.9	0.9	17.4
Predators	0.6	0.3	4.3	0.6	0.1	3.1	0.6	0.3	5	0.1	0.3	6.7
Scrapers	0.3	0.3	2.6	0.3	0.1	1.7	0.3	0.4	3.1	0.1	0.4	7.7

FFGs having a higher abundance in the mid-elevation sites (Table 3).

Biomass-based SIMPER had different FFGs contributing to differences between land uses and among elevation categories. Shredders were identified as the main FFG differentiating the site categories, accounting for more than 50% of the dissimilarity, whereas filterers accounted for 24–36% of the dissimilarity, with a higher biomass in the forested sites and in high-elevation sites (Table 3). Forested sites were differentiated from agricultural sites by shredders (59.0%) and filterers (24.0%), with higher biomass in forested sites. Shredders (59.5%) and filterers (26.7%) contributed the greatest dissimilarity between the high- and mid-elevation categories, with a higher biomass of shredders in the high-elevation sites, whereas filterers were more prevalent in the mid-elevation sites. Similarly, shredders (58.7%) and filterers (23.0%) differentiated high- from low-elevation sites, with the biomass of both being higher at higher elevations. Mid- and low-elevation sites were differentiated by filterers (35.6%) and shredders (32.6), with both groups having a higher abundance in the mid-elevation sites (Table 3).

CCA showed spatial patterns in macroinvertebrate functional composition associated with water quality, stream size, organic matter and habitat variables for both elevation (Fig. 5*a*, *c*) and land use (Fig. 5*b*, *d*). CCA Axis 1 accounted for the greatest variance, between 32.5 and 39.2%, whereas the second CCA axis accounted for between 20.8 and 28.1% of the variation. The two CCA axes explained between 53.3 and 67.3% of the association. CCA ordination for both numerical abundance and biomass showed that shredders were associated with forested sites with higher CPOM standing stocks, whereas predators, scrapers and filterers were associated with increased levels of TSS, temperature and conductivity in agricultural sites. Shredders grouped in high-elevation sites and were associated with high altitude and CPOM standing stock for both abundance- and biomass-based metrics. High conductivity, TSS and temperature were associated scrapers, filterers and predators in low-elevation sites. Mid-elevation sites grouped filterers and predators associated with high discharge levels.

Using the elevation gradient in GAMs with a smoother for altitude interacting with land use, we found a significant increase in the abundance, taxon richness and biomass of many FFGs with increasing elevation, except in the taxon richness of filterers and gatherers and the biomass of scrapers and predators (Table 4; Fig. S2 of the Supplementary material). The independent effects of land use and stream size (stream order) in GAMs were limited. Similarly, GAMs did not identify significant interactions between the elevation smoother and land use and stream order, indicating that the elevation gradient played an overriding role in affecting the composition of FFGs in these streams.

Discussion

Physicochemical water variables

Deforestation in the catchment areas of streams, as well as in the riparian zone, alters their integrity by increasing mean water temperature, erosion and sedimentation, resulting in the degradation of physical habitats and water quality (Chapman and Chapman 2003; Leal *et al.* 2016; Masese *et al.* 2017). These activities have detrimental effects on the aquatic biodiversity in streams, which depends on these streams for habitat, food and shelter. Higher EC, temperature, TSS, total dissolved solids (TDS) and lower pH were recorded in streams within agricultural areas. These variables were positively correlated with agricultural land use and negatively correlated with altitude. Similar findings were reported by Kasangaki *et al.* (2008), Minaya *et al.* (2013) and Kibichii *et al.* (2007), who documented that, despite the narrow temperature range in the tropics, agricultural streams are warmer and have higher EC, suspended sediments and dissolved nutrients than forested streams.

Temperature difference is a factor of both land use and altitude. There is a decrease in temperature with increasing altitude as a result of decreasing air pressure (Mani 1962;

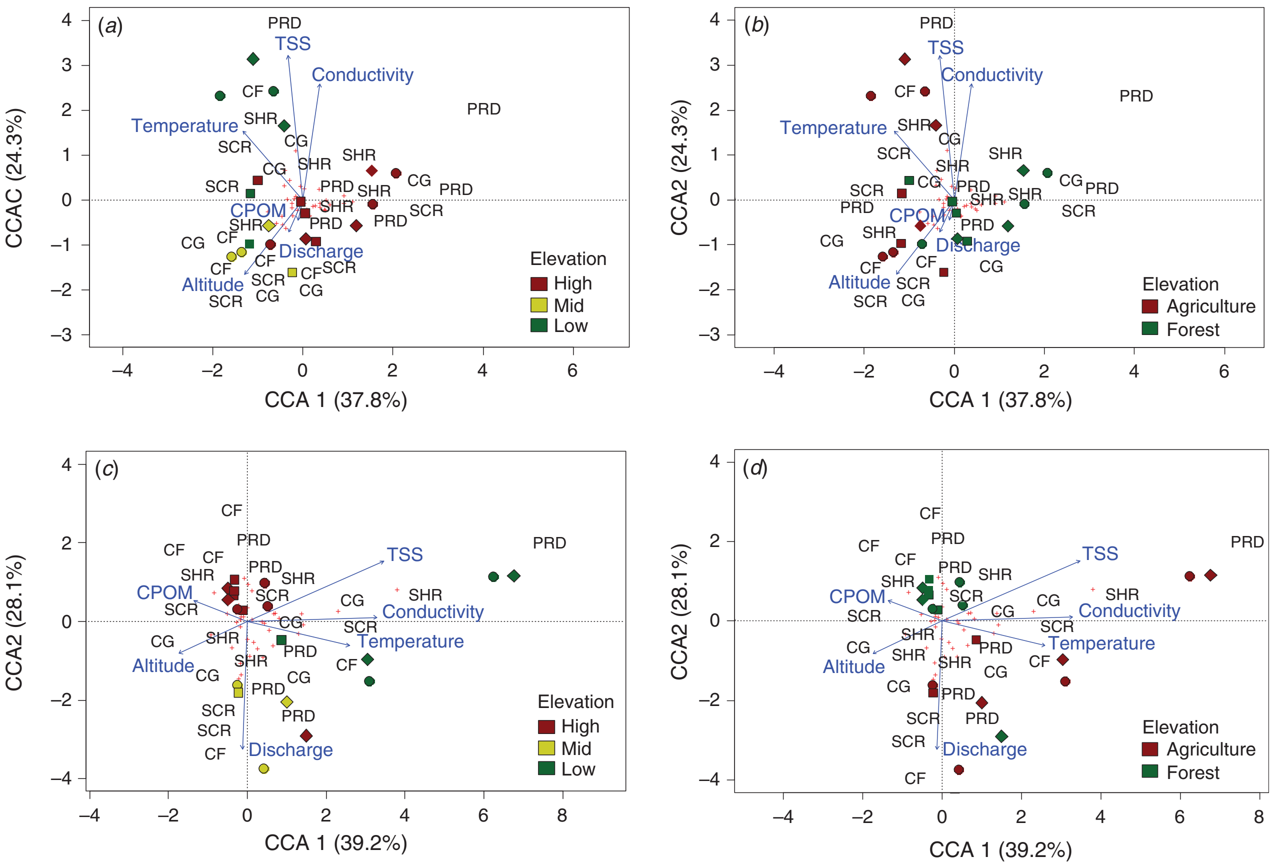

Fig. 5. CCA triplot of macroinvertebrate FFGs based on abundance data in relation to physicochemical water variables, stream size and habitat variables across (*a*, *c*) elevation classes and (*b*, *d*) land use categories for numerical abundance (*a*, *b*) and biomass metrics (*c*, *d*).

Nebeker 1971), as seen by the cooler temperatures in the higher-altitude streams. Similarly, the opening of the canopy in the agricultural streams enabled light penetration and accompanying warming effects on the stream, explaining the higher temperatures in agricultural low-altitude streams. The lower temperatures in the forested streams are attributed to shading provided by the riparian vegetation, which was lacking for most streams in the agricultural areas.

Masese *et al.* (2009) documented the importance of forest cover in limiting solar radiation reaching the water and therefore contributing to minimal fluctuations in forested areas. The altitudinal drop, rapids and falls characterising the streams allowed reoxygenation of the water and could explain the lack of variation in DO levels with both altitude and land use change from forestry to agriculture. Similar studies, including that of Jacobsen (2008), showed decreasing DO saturation and temperature levels with increasing altitude. This is corroborated by the findings of Minaya *et al.* (2013), and captures the dynamic nature of tropical streams and rivers affected by both land use change and riparian and in-stream activities.

Conductivity responded strongly to land use change from forestry to agriculture and showed an increasing trend downstream. High conductivity recorded in agricultural streams could be a factor of fertiliser and nutrient enrichment from the farms draining the catchment. Sediments transported from the farms to the streams in the event of run-off have low pH and are rich in exchangeable Ca^{2+}, Mg^{2+}, Na^{2+}, K^{-}, $SO4^{2-}$ and Cl^{-} ions found in fertilisers used on the agricultural farms (Tittonell *et al.* 2013). In addition, soil tillage mobilises major ions and increases their leaching into waterbodies, where they elevate conductivity levels, as discussed by Masese *et al.* (2017). High TSS and TDS values recorded in agricultural streams most probably resulted from the erosion of unprotected banks and siltation. Because samples were collected in the rainy season, the run-off was deposited in these agricultural streams, and the water was murky and laden with sediments. Kilonzo *et al.* (2014) conducted a similar study and documented elevated concentrations of nutrients and sediments in streams draining agricultural catchments during the wet season due to run-off from unpaved roads, footpaths and farmlands.

Patterns of macroinvertebrate FFG composition and distribution

This study identified Simuliidae, *Cheumatopsyche*, Oligochaeta, Sphaeriidae, Chironomidae, Lepidostomatidae, *Diplectrona, Baetis*, Tipulidae, Caenidae and *Afronurus* as the most commonly occurring taxa in most of the sites. Mean abundance, biomass and richness of FFGs were higher in forested than agricultural sites. Similarly, high-elevation sites recorded significantly higher abundance, biomass and richness of FFG taxa with a clear and

Table 4. Summary of GAM of the effects of altitude, land use and stream order (stream size) on longitudinal patterns in numerical abundance, taxon richness and biomass of the five macroinvertebrate FFG (collector-filterers, collector-gatherers, scrapers, predators and shredders) and their combined totals in Mount Elgon streams

Altitude, land use and stream order were treated as fixed factors, whereas each study stream was used a random factor. In all cases, d.f. = 1

Variables	Macroinvertebrate FFGs										Total abundance	
	Collector-filterers		Collector-gatherers		Scrapers		Predators		Shredders			
	F	*P*-value	*F*	*P*-value	*F*	*P*-value	*F*	*P*-value	*F*	*P*-value	*F*	*P*-value
Abundance												
Altitude	13.52	0.003	9.08	0.011	2.27	0.157	7.57	0.017	11.57	0.005	7.47	0.018
Land use	0.16	0.698	1.43	0.255	11.93	0.005	3.02	0.108	5.21	0.042	0.81	0.385
Stream order	0.28	0.01	0.35	0.568	0.72	0.413	1.6	0.229	0.68	0.426	3.78	0.076
Altitude × land use	0.03	0.857	0.0002	0.99	2.47	0.142	0.12	0.733	2.35	0.151	0.19	0.666
Altitude × stream order	2.28	0.517	0.55	0.474	0.85	0.374	0.61	0.452	0.09	0.774	0.06	0.809
Land use × stream order	5.15	0.042	3.71	0.078	1.91	0.192	0.03	0.869	0.32	0.583	7.14	0.02
Altitude × land use × stream order	0.37	0.555	0.0003	0.986	0.025	0.877	0.17	0.686	0.07	0.801	0.15	0.71
Adjusted R^2	0.52		0.36		0.3		0.15		0.41		0.43	
Scale estimate	0.006		0.003		0.003		0.019		0.007		0.002	
Residual deviance	0.99		0.52		0.43		2.64		1.27		0.38	
Taxon richness												
Altitude	3.44	0.089	2.11	0.172	6.44	0.026	4.87	0.049	7.94	0.015	11.76	0.005
Land use	0.1	0.753	7.05	0.021	4.35	0.059	0.44	0.52	9.75	0.009	7.02	0.021
Stream order	2.28	0.158	5.91	0.032	2.96	0.111	0.45	0.515	2.08	0.175	1.61	0.228
Altitude × land use	0.44	0.522	2.36	0.15	1.34	0.269	0.42	0.536	0.26	0.617	0.03	0.871
Altitude × stream order	0.66	0.434	3.07	0.105	0.63	0.443	0.18	0.675	2.48	0.141	0.0001	0.993
Land use × stream order	2.02	0.18	8.1	0.015	0.72	0.414	0.23	0.642	2.82	0.118	4.33	0.06
Altitude × land use × stream order	0.09	0.771	0.22	0.646	0.11	0.75	2.84	0.118	2.07	0.175	1.67	0.22
Adjusted R^2	0.13		0.3		0.32		0.05		0.45		0.37	
Scale estimate	0.031		0.004		0.022		0.041		0.037		0.005	
Residual deviance	0.51		0.05		0.43		0.71		0.53		0.06	
Biomass												
Altitude	6.47	0.026	6.91	0.023	0.19	0.672	1.58	0.233	12.7	0.004	12.28	0.004
Land use	0.82	0.384	0.55	0.472	8.221	0.014	4.47	0.056	0.75	0.411	0.48	0.5
Stream order	6.98	0.022	0.13	0.72	0.47	0.506	0.11	0.746	2.58	0.134	5.19	0.042
Altitude × land use	0.05	0.829	0.31	0.585	0.96	0.347	0.9	0. 362	0.32	0.581	0.01	0.91
Altitude × stream order	0.33	0.578	2.23	0.161	1.27	0.282	0.08	0.785	0.9	0.361	0.61	0.449
Land use × stream order	6.38	0.027	1.44	0.255	0.002	0.962	0.24	0.629	0.4	0.54	2.17	0.167
Altitude × land use × stream order	0.63	0.444	0.73	0.409	0.005	0.943	0.95	0.349	41	0.536	0.12	0.735
Adjusted R^2	0.23		0.21		0.29		0.12		0.42		0.41	
Scale estimate	0.427		0.133		0.014		0.055		0.762		0.596	
Residual deviance	5.4		2.25		0.27			1	14.28		10.01	

distinct separation from mid- and low-elevation sites. The higher diversity of macroinvertebrate FFGs in forested compared with agricultural areas could be attributed to habitat diversity and complexity in these sites. Streams with minimally disturbed riparian forest are known to contribute branches and large wood to channels, increasing habitat complexity and producing habitats that favour an increased abundance and diversity of macroinvertebrates (Kaufmann and Faustini 2012). Sites in forested areas also contained more stable substrate (cobbles, pebbles and boulders) that acted as refuge sites for the macroinvertebrates compared with the less stable substrate types of sand and fine sediments in agricultural areas (Masese *et al.* 2021). Allan (1995) conceptualised that in constantly disturbed streambeds, even larger particles are less attractive for colonisation because their surfaces are covered by silt. Kibichii *et al.* (2007) and Wood *et al.* (2005) stated that the frequently disturbed streambeds meant that only a few taxa tolerant to constantly shifting sediments and bedrock can proliferate in large numbers, whereas a majority of the taxa occur only rarely. Our results corroborate those of Musonge *et al.* (2020), who, while working in Rwenzori highlands, recorded more taxa at higher altitudes. Other studies on macroinvertebrate distribution along an altitude gradient in other regions (Suren 1994; Jacobsen *et al.* 2003, Jacobsen 2008) found less richness and a lower abundance of taxa at higher altitudes (>4000 m ASL), which the authors attributed to lower oxygen saturation at higher altitudes, which could limit aquatic biodiversity.

Forested sites were differentiated from agricultural sites mainly by shredders, with a higher biomass in forested and high-elevation sites. Shredder biomass was largely contributed by freshwater crabs *Potamonautes elegonensis*, which are endemic to Mount Elgon streams. In similar studies, Masese *et al.* (2014) and Dobson *et al.* (2002) reported a high abundance of *Potamonautes* sp. in East African highland streams.

Cumberlidge and Clark (2010) reported the occurrence and endemicity of *P. elegonensis* in the upper reaches of rivers on the highlands of western Kenya and eastern Uganda. The role of *P. elegonensis* in the utilisation of detritus and CPOM components places them in an important niche in Afrotropical streams (Boyero *et al.* 2020). Simuliidae, the most abundant taxa in our study, have been reported to have short regeneration times with rapid colonisation rates, enabling them to cope with fluctuating environments and to build up large populations opportunistically (Williams and Hynes 1971; Williams 1991). The higher abundance of filterers in the forested upstream reaches was contributed to mainly by this taxa, which prefers a stable substrate (the major substrate in the forested sites) for attachment and tends to be present in fast-flowing waters (Chapman *et al.* 2004). Another prominent example of filterers is *Oligoneuriopsis dobbsi*, an endemic Kenyan ephemeropteran (Barber-James *et al.* 2020), that was primarily found in forested streams with a high current.

Relationship between instream and physicochemical water variables and macroinvertebrate functional organisation

The changing physicochemistry of water quality variables with changes in land use and altitude, as noted for TSS, temperature, EC, TDS and CPOM standing stocks, played a significant role in describing the patterns observed in macroinvertebrate assemblages. CCA indicated that CPOM was the predictor variable affecting invertebrate assemblages in the forested land use sites. This corresponds to the high biomass levels of shredders recorded in these streams. Agricultural sites at lower elevations were characterised by the replacement of native vegetation by pasture and intensive agriculture, which, in turn, strips the shredder guild of their riparian litter trophic resource and accounts for their low numbers in these sites. Shifts in land use from forested to agricultural typically reduce habitat complexity and affect organic matter dynamics (Mbaka *et al.* 2015; Masese *et al.* 2017). This was reflected in the reduction in the richness, abundance and biomass of shredder communities and subsequent increases in the abundance and biomass of filtering collectors in agricultural areas. Consequently, temperature and discharge also greatly affected the occurrence of macroinvertebrate taxa in forested, higher-elevation streams. Increased water temperature was associated with changes in macroinvertebrate community structure, with generalist shifts along the river continuum, and reduced resilience of community states (Jacobsen 2008).

Our study shows that higher temperature levels, conductivity and TSS were the main variables that influenced the distribution of scrapers and predators mainly in mid- and low-elevation sites (agricultural sites). The availability, quality and quantity of CPOM and lower temperature levels were the major variables that affected the shredder guild. The presence of shredders was also a key factor in the distribution of collectors (gatherers and filterers) as they break down CPOM into fine POM used by the collectors. This was evident in this study, in which shredder biomass was strongly correlated with the biomass of gatherers in upstream (forested) sites. Even though land use and altitudinal changes resulted in distinct patterns in FFG distribution, the patterns observed were interconnected with the trophic food resources and physicochemical characteristics of the stream.

To further analyse the comparability between the (upstream) forest sites and (downstream) agricultural sites, natural and forested streams have to be investigated along their altitudinal gradient from mountainous areas to the lowlands, but reference systems are very rare and limited in Kenya, and East Africa in general, and large-scale degradation is pervasive. Nevertheless, without these kinds of data, sound assessment systems cannot be calibrated and developed. From a conservation point of view, the identified species turnover from forested to agricultural streams indicates a severe loss of specific taxa and biodiversity in general within our case study catchment, a process that is likely to be similar in many other parts of East Africa and one that should be addressed quickly through management measures.

Altitudinal shifts and longitudinal zonation in macroinvertebrate functional composition

There were notable altitudinal and longitudinal trends in the composition of macroinvertebrate FFGs in this study. Of the three elevation categories, sites at high elevations had the highest abundance, biomass and richness. *Adicella*, Trycorythidae, Libellulidae or Cordulidae and Empididae were limited to mid- and low-elevation sites. Leptophlebiidae, *Afrocaenis*, Physidae, Dixidae, Pisuliidae, *Wormaldia*, Glossiphoniidae, Gomphidae, *Trichosetodes*, *Prosopistoma*, *Neoperla* and *Dipletrona* were limited to high-elevation sites. The occurrence of Scirtidae, Limoniidae, *Triaenodes* and *Potamonautes* was high in high-elevation forested sites, although these macroinvertebrates were not restricted to these sites. Although changes in elevation or altitude can structure invertebrate communities in streams (Jacobsen 2008; Musonge *et al.* 2020), the findings of this study are preliminary because most of the high-elevation streams were in forested areas and the low-elevation streams were in agricultural areas. Thus, the low taxa abundance, biomass and richness of macroinvertebrate FFGs in mid- and low-elevation sites, with a significant increase with elevation, can probably be attributed to the high and moderate levels of anthropogenic disturbance from agricultural activities such as farming and livestock husbandry, as well as water abstraction in the low-elevation sites. Previous studies have shown that anthropogenic pressures in high-altitude streams can reduce macroinvertebrate abundance and diversity (Jacobsen 2008; Masese *et al.* 2014; Musonge *et al.* 2020).

This study documented interesting longitudinal trends in FFGs. Whereas abundance data did not show any trend in the distribution of shredders, biomass data presented a clear longitudinal trend. Shredder biomass decreased from upstream to downstream sites, whereas the biomass of total collectors (filtering and gathering collectors) increased from upstream to downstream. Both scraper biomass and abundance were higher in the mid-elevation and downstream sites. These sites were characterised by agriculture as the main land use and had an open canopy, which allows the light penetration required for the establishment of algae and periphyton, which supports the scraper functional guild. Predators (Hemiptera), which are tolerant taxa that can withstand anthropogenic disturbance, were more abundant in low-elevation sites in agricultural areas.

Although the spatial and longitudinal trends in this study are interesting, there has been a lot of discussion as to whether tropical streams fit into existing models of river function, such as the RCC (Vannote *et al.* 1980). The RCC address changes in the relative abundance of macroinvertebrate FFGs along the longitudinal gradient of streams. Although it has been noted that the relative abundance and biomass of shredders do not show similar trends (Masese *et al.* 2014), the present study had mixed results, with abundance and richness exhibiting no clear trends but biomass data showing a clear and distinct pattern whereby shredder biomass decreased from upstream (high-elevation) to downstream (low-elevation) sites. Tomanova *et al.* (2007) offer plausible reasons why the distribution in their work did not 'fit' the RCC concept that they attributed to the influence of working with relative abundances, which was addressed in the present study by the use of all three (abundance, biomass, richness) metrics. Masese *et al.* (2014) further pointed out that assignment of FFGs to family level, as opposed to species level, can cause misclassifications because different species within a family can be classified into different FFGs. It is important to note that, in this study, the assignment of FFGs was done at either morphospecies or genus level (Table S3 of the Supplementary material).

Data on altitudinal and longitudinal zonation of aquatic communities are very limited in tropical streams (Araújo *et al.* 2009; Brasil *et al.* 2014; Dalu *et al.* 2017; Englmaier *et al.* 2020). Moreover, reference or near-natural systems along an altitudinal gradient are largely non-existent because human activities (settlements, agriculture and grazing) can extend to relatively high altitudes in the tropics, which, in turn, subjects these high-altitude streams to deforestation, organic pollution, agrochemicals and sedimentation (Kasangaki *et al.* 2006; Masese *et al.* 2009; Englmaier *et al.* 2020). This means that forested streams are very limited in low-elevations areas, making it difficult to control for both high-elevation agricultural sites and low-elevation forested sites. Nevertheless, data on the altitudinal and longitudinal distribution of organisms in tropical mountain regions are urgently needed to initiate management and conservation actions. Despite this challenge in our study, we recorded endemic species (*P. elegonensis* and *O. dobbsi*) that were restricted to high-elevation streams. This shows that these species are dependent on near-natural mountainous areas, as has been noted in other studies of high-elevation streams in Kenya (Dobson *et al.* 2007; Masese *et al.* 2014). Further studies are needed to disentangle altitude and land use influences on the diversity and composition of aquatic communities in high-elevation streams in the tropics, especially in the Afrotropics, where the process of land cover changing from natural forest to other uses, such as agriculture and settlements, is occurring rapidly.

Conclusion

Even though macroinvertebrate FFGs were expected to exhibit a natural distribution upstream–downstream, anthropogenic stressors along the river continuum shaped the outcomes of this study and highlighted the significance of these stressors in determining macroinvertebrate distribution. As hypothesised, shredder abundance, biomass and richness were greater in the forested, higher-elevation streams. The mid- and low-elevation sites, both within the agricultural land use, exhibited similar patterns in macroinvertebrate assemblages. These results show that both elevation and land use change from forest to agriculture were major drivers of changes in water physicochemistry and habitat quality variables, which significantly affected the diversity and distribution of macroinvertebrate taxa. From this work, it can be deduced that the conversion of stream catchments from forested to agricultural has adverse effects on a stream ecosystem's integrity. The study findings indicate that biomonitoring programs, indicator taxa and site-specific environmental variables are important and, in future, should be taken into account given the limitations associated with generalising categorical responses, along both altitudinal and land use categories. Thus, site-specific environmental variables are integral when carrying out conservation and restoration programs in these Afrotropical montane streams and rivers.

Conflicts of interest

The authors declare that they have no conflicts of interest to disclose.

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