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# Macroinvertebrate functional responses to human disturbance and flow cessation in Afromontane-savannah rivers

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ABSTRACT

Wildlife, people, and livestock rely on riverine ecosystems in arid and semi-arid areas as primary water sources. Studies on the influence of human activities and livestock on the ecological health of these seasonal systems are thus necessary. This is more relevant given the increasing demand for water as human populations grow, which leads to over-abstractions and, sometimes, cessation of flows in streams and rivers during the dry periods. Although the structural composition of macroinvertebrate communities has been utilized to indicate the ecological integrity of streams and rivers, macroinvertebrate functional feeding groups (FFGs) are less studied, especially in intermittent Afrotropical streams. We used macroinvertebrate FFGs as indicators of water quality and ecological integrity of streams influenced by different levels of human disturbance and flow variability in the Afromontane-savanna Bura and Wundanyi rivers in Taita Taveta County, Kenya. A total of 18 sampling sites were identified for sampling and grouped into three (3) disturbance categories (low– $n = 7$, moderate - $n = 4$, and disturbed - $n = 7$) and two categories of flow permanence (permanent – $n = 9$, and seasonal – $n = 9$). At each site, sampling of physicochemical water quality parameters and macroinvertebrates was done twice during the wet and dry seasons. Ratios of five FFGs (collector-gatherers, collector-filterers, scrapers/grazers, predators, and shredders) were used to derive five metrics that are surrogates of ecosystem attributes in the rivers. There was a significant difference ($p < 0.05$) in the concentrations of dissolved organic carbon, total phosphorus, pH, and electrical conductivity between the three site categories. Seasonal sites recorded higher electrical conductivity and total dissolved solids compared to permanent streams. Total suspended solids and particulate organic matter were higher during the dry season. FFGs responded to the disturbance gradient, seasonality, and flow variability in the study area with high numbers of predators and scrapers during dry season, suggesting that the human disturbance influenced the functional composition of macroinvertebrates in the rivers. The findings also show that flow variability (seasonal vs flow permanence) played a important role in structuring communities and determining ecosystem functioning. Therefore, in addition to general human disturbance, there is also a need to study the impact of excessive water withdrawals or changes in natural flow regimes of streams and rivers on aquatic communities and the development of indices to assess their effects.

## 1. Introduction

The condition of a river can range from pristine to substantially degraded along a continuous gradient of impairment. According to Young et al. (2008), one of the most fundamental steps in restoring the condition of rivers is to assess their ecological state accurately. This allows for determining the factors that lead to the degradation of the river's environment as well as the degree to which rehabilitation efforts

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are successful. When evaluating or monitoring the health of a river, resource managers can use various metrics (Barbour, et al., 1999; Boulton and Lake, 2008). Traditional methods of assessing river health in different types of disturbances have relied on measures that focus on water quality variables, the physical habitat, and community composition of aquatic communities. Community composition measures include diversity, taxonomic richness, species richness, traits, and compositional metrics (Fierro et al., 2017; Gutiérrez-Cánovas et al., 2013; Moyo and Richoux, 2017; Masese et al., 2023).

Aquatic macroinvertebrate communities display spatial and temporal dynamics in response to changes in abiotic and biotic conditions due to the variation in behavior and structural adaptation among different taxa for food acquisition and habitat (Masese et al., 2025a; Sitati et al., 2021). As bioindicators of ecological integrity and ecosystem functioning (O'Brien et al., 2016; Palmer et al., 2005; Masese et al., 2025b), aquatic macroinvertebrates have been used as they are important in transferring energy between low and high trophic levels in food webs. Additionally, they contribute to the balance between heterotrophs, which rely on organic matter from land, and autotrophs which depend on primary production from periphyton and macrophytes in downstream river areas (Hanson et al., 2015; Palmer et al., 2005). A growing number of studies have examined aquatic ecosystem health in streams and rivers by using functional indicators, but the majority have relied on taxonomic composition to assess the condition (Cummins et al., 2005; Dolédec et al., 2006; Jiang et al., 2010; Savić et al., 2018; Stone et al., 2005). Many studies have utilized functional indicators, but there have been limited studies that have examined the relationship between functional diversity and environmental variables in Afrotropical streams and rivers (Makaka et al., 2018; Mangadze et al., 2019; Masese et al., 2014). Human activities like agriculture, grazing, and water abstractions at the catchment level as well as at the riparian zone or reach scale can significantly influence the structural and functional composition of macroinvertebrate communities in streams and rivers, as well as habitat conditions, water quality and biotic characteristics (Allan, 2004; Masese et al., 2014; Yegon et al., 2021; Wanderi et al., 2022). Forest clearance in stream catchments and riparian areas, which is still prevalent in Afrotropical regions, can alter the availability of allochthonous food resources, flow permanence and channel features, sediment regimes, and habitat complexity (Graziano et al., 2022). Similarly, animal activities such as in or near streams and rivers such as watering, crossing, and grazing influence in-stream habitat quality, channel geomorphology, and water quality (Fierro et al., 2017; Masese et al., 2023; Iteba et al., 2021). These human and animal activities are significant contributors to the degradation of streams and rivers in the Afrotropics (Mathooko, 2001; Akamagwuna and Odume, 2020; Minaya et al., 2013). Undisturbed streams typically exhibit a natural flow regime defined by the climate, geomorphology, and vegetation type of an area (Blythe and Schmidt, 2018; Bower et al., 2022). Therefore, human activities, such as agriculture, irrigation, sand harvesting in streams, and excessive water withdrawals, can alter the natural flow regimes of streams and rivers. Streams and rivers with modified flow regimes experience flooding during the rainy or wet season and cessation of flows during the dry season (Allan et al., 2021; Sobti, 2023). A dry riverbed is one of the most distinctive characteristics of seasonal rivers, but it is difficult to attribute changes to dry conditions in invertebrate communities because all river communities vary in time (Bêche and Resh, 2007; Palmer and Poff, 1997; Resh and Rosenberg, 1989). There is often a lack of temporal stability in the abundances of invertebrate communities in seasonal rivers, as well as a lack of persistence of presences and absences (Bêche and Resh, 2007; Blanchette and Pearson, 2013). As seasonal rivers alternate between wet and dry phases, and as flow conditions vary, invertebrate communities fluctuate similarly (Datry, 2012; Leigh, 2013; Sponseller et al., 2010). Flow variability has significant implications for instream habitat conditions, such as the movement of fine sediment in the channel and the levels of suspended solids in the water column (Bond and Downes, 2003; Knight, 1996). Consequently, due to the fluctuations in flow and the composition of species over time, it becomes essential to consider the long-term effects of flow cessation on aquatic communities (Banad et al., 2023; Schneider and Petrin, 2017). While research into the responses of aquatic communities to various stressors in streams and rivers has advanced, the Afrotropics lag behind other parts of the world in the development of biomonitoring tools and programs for streams and rivers, especially for temporary streams and rivers (Dalu and Masese, 2025).

Seasonality, which in the tropics is determined by the amount and availability of rain, also has an important role in defining water quality, establishing a strong energetic link between terrestrial and aquatic ecosystems, and determining food availability and diversity, which ultimately influence the structural and functional composition of macroinvertebrate communities (Bunn and Arthington, 2002; Leigh, 2013). According to some studies, there is an increase in macroinvertebrate abundance during the wet season (Camacho et al., 2009; Masese et al., 2014), while others have found the abundance and richness is higher during the dry season (Makaka et al., 2018; Jiang et al., 2010). There is evidence that the reduced abundance of macroinvertebrates during the wet season is due to increased turbidity, which limits primary production in rivers and streams, and this reduces the ability of aquatic consumers to assimilate algal resources (Junk et al., 1989). Compared to the dry season, when algae are more abundant, terrestrial organic matter is more important during the wet season (Masese et al., 2015; Roach and Winemiller, 2015; Zeug and Winemiller, 2008). While earlier research, as outlined in the river continuum concept (Vannote et al., 1980), acknowledged the usefulness of using macroinvertebrate functional feeding groups (FFGs) as indicators for ecosystem attributes and functioning, the last three decades have witnessed a significant increase in the adoption of species or community functional metrics and traits as substitutes for assessing community or ecosystem function in response to various disturbances (Fierro et al., 2017; Petchey et al., 2004; Verberk et al., 2013). Such disturbances include changes in land use, the loss of riparian vegetation, elevated levels of fine sediments, and the evaluation of ecological conditions (Sitati et al., 2021). This shift is evident in the works of (Merritt et al., 2017; Petchey et al., 2004; Verberk et al., 2013; Mathers et al., 2017 and Wagenhoff et al., 2012). Hence, the functional composition of macroinvertebrates offers a valuable means to assess trophic dynamics and the ecological state of aquatic environments, obviating the necessity to separately evaluate these characteristics (Makaka, et al., 2018 and Cummins, et al., 2005). Ecosystem features that can be investigated through the relative abundance of FFGs encompass trophic status (autotrophy or heterotrophy), the proportions of coarse particulate organic matter (CPOM) as opposed to fine particulate organic matter (FPOM) within the water column and streambed, top-down predator regulation, channel stability, and the integrity of riparian zones (Merritt et al., 2017).

Research in tropical streams has utilized FFG ratios as proxies for ecosystem attributes, drawing from metrics originally developed for temperate streams (Cummins et al., 2005). The use of FFG ratios has been preferred because there is a lack of classification guides at the species level and a lack of information on the feeding and functional habits of most species/taxa (Masese et al., 2025). However, variations exist in the composition of macroinvertebrate FFGs both within and between regions (Boyero et al., 2009; Adedapo et al., 2023), emphasizing the need for rigorous testing and validation of these metrics before their application in regions beyond the temperate zones where they were initially developed. The development of biotic indices for the biomonitoring of streams and rivers in various countries is the result of the increased understanding of these metrics (Dickens and Graham, 2002; Kaaya et al., 2015; L and Moog, 2015; Masese et al., 2025a). However, more data are still required to improve current biomonitoring indices and support the creation of new ones for bioindication, particularly on the impacts of human disturbance from rural agriculture and human settlements on water quality and aquatic communities.

Like many other tropical river catchments, the Taita Hills region

(Kenya) faces threats from encroachment on protected forests and other delicate ecosystems for human settlements, animal grazing, and agricultural activities (Government of Kenya, 2017; MoALF, 2016). The Wundanyi and Bura rivers in which this study was done are typical Afromontane-savannah rivers draining a gradient of land use, elevation, and rainfall with the more mesic forested upper reaches, and the semi-arid savannah lowlands. While the upper reaches are more protected and minimally disturbed, the middle and lower reaches are under different human activities ranging from mixed farming to agro-pastoral activities (Hohenthal et al., 2015). These upstream-downstream changes to natural conditions caused by human activities, terrestrial vegetation, and rainfall regimes have potential effects on the river and the structure and composition of aquatic communities, necessitating frequent biomonitoring. We investigated variations in the functional composition of macroinvertebrates in response to different levels of human disturbance, seasonality (wet vs dry), and stream flow permanence (permanent vs seasonal) in the Wundanyi-Bura catchment, Kenya. The objectives of the study were to test whether (1) water and habitat quality degraded with increasing levels of human disturbance in the basin; (2) macroinvertebrate communities responded functionally to human disturbance, seasonality, and flow permanence and (3) the ecosystem attributes of Afromontane-savannah rivers are influenced by human disturbance, seasonality, and flow permanence. The hypotheses tested were that (1) the ratios of FFGs can be used as surrogates of ecosystem attributes and at the same time serve as useful indicators of the ecological health of streams influenced by different levels of human disturbances, seasonality, and flow permanence, (2) low-disturbed sites with intact riparian zones would have a higher diversity and abundance of shredders than disturbed sites devoid of riparian zones and inputs of terrestrial organic matter, (3) flow variability will be a major variable structuring the functional organization of macroinvertebrates with seasonal river reaches dominated by predators and collector-gatherers, and permanent river reaches dominated by scrapers and collector-filterers.

## 2. Materials and methods

### 2.1. Study area and sampling design

South-eastern Kenya's Taita Taveta County is home to the rugged Taita Hills region (Fig. 1). The savannah grasslands, which are a part of the Tsavo National Park, surround the region, which has a surface area of about 1000 km$^2$. According to (Hohenthal et al., 2015; Pellikka et al., 2013), the region has an average elevation of 1500 meters above sea level (m.a.s.l.), with the lowest point in the surrounding low-lying plains (600 m.a.s.l.) and the highest point in Vuria (2208 m.a.s.l.).

The intertropical convergence zone influences the region's bimodal rainfall pattern, with the first rainy season (long rains) from March to June and the second rainy season (short rains) from October to December (Hohenthal et al., 2015; Pellikka et al., 2009). The low-lying plains in the region receive an average rainfall of 500 mm per year, whereas the mountainous area receives 1500 mm annually (Pellikka et al., 2013). Even though it is under increasing strain and only has around 1 % of the original forest cover left, the Wundanyi and Bura river catchments form an important natural conservation area with native rainforest and a high diversity of fauna and flora (Hohenthal et al., 2015). Given that it is the source of several important springs and river systems, including the Voi and Mwatate rivers, the Taita Hills region is also a significant source of water in Taita Taveta and other coastal Counties in Kenya (Pellikka et al., 2013)

The population of the County is estimated at 340,671 persons according to the 2019 national census (KNBS, 2019), with population densities ranging from 14 persons per km$^2$ in the lowlands to >117 persons per km$^2$ in the uplands. The lowland areas of the County outside the national parks are occupied by farms, ranches, estates, and wildlife sanctuaries. The County has approximately 25 ranches. The major land uses in the ranches are cattle grazing and mixed crop farming, intensive cultivation of crops such as maize and bananas is practiced in the highlands. Free-range livestock grazing regime is commonly practiced in the lowlands with animals watering directly from the rivers and artificially constructed water pans (Thornton et al., 2002; Waiswa, 2020). The foothill and lowland zones are dominated by shrubs, sisal plantations, and acacia tree species with dryland agriculture and livestock

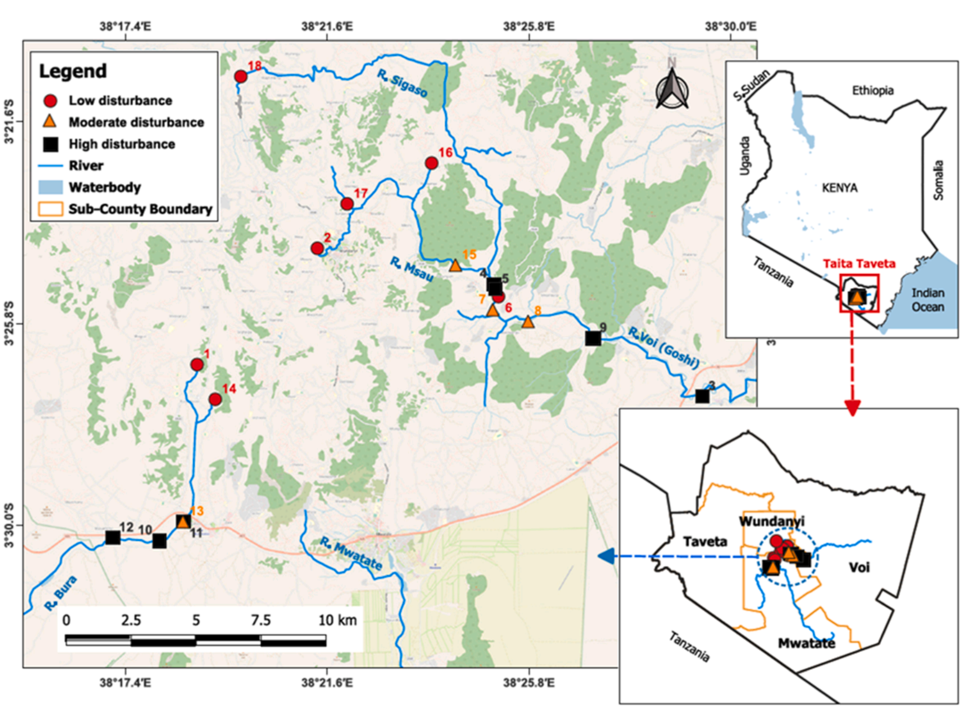


**Fig. 1.** Location of sampling sites along the Bura and Wundanyi Catchment, Kenya.

grazing (Pellikka et al., 2018).

The Wundanyi-Bura rivers are a typical Afromontane rivers arising in forested uplands where human activity is minimal and livestock do not access the watering points as zero-grazing is the most practiced form of a livestock production system. However, human activity increases in the middle and lower reaches. Because of the high human population and that of their livestock, the river is influenced by various human activities along its reach, including farming, human settlements and small urban centers, sand mining, water abstraction for irrigation and domestic use, animal grazing and watering, bathing and laundry washing (Waiswa, 2020). Changes in the rainfall amount between the uplands and lowlands, coupled with excessive water withdrawals have converted once permanent river reaches into seasonal ones that experience cessation of flows during periods of prolonged droughts.

To analyze the effects of human disturbance (disturbance category) caused by mixed crop farming, water abstraction, sand harvesting, livestock grazing, and climate-driven changes in seasonality, and flow variability (permanence) on macroinvertebrate communities, sampling sites were categorized into three levels of disturbance (low, moderate and high disturbance) based on catchment land use, and reach scale, human influences. Sites were further categorized into those with permanent flows throughout the year (permanent) and those whose flows ceased during the dry months (intermittent/seasonal). All sites were sampled during the dry and wet months. In total, 18 sites were selected for sampling: low disturbance ($n = 7$), moderate disturbance ($n = 4$) and high disturbance ($n = 7$) (Table 8). Regarding flow permanence, sites with permanent and seasonal flows were nine each ($n = 9$). All 18 sites were sampled for macroinvertebrates and associated physical habitat conditions during the wet and dry. These sites traverse stream size and land use gradients from the forested (low disturbance) upper reaches, through the moderately disturbed and highly disturbed middle and lower reaches that were largely influenced by crop farming and livestock grazing.

### 2.2. Analysis of catchment land-use

Land-use classification and catchment maps were generated using QGIS 3.14. The semi-automatic classification plugin was used to download sentinel-2 images for the six catchments of the streams used in this study according to Congedo (2020a, b). The satellite images were pre-processed for four categories of predominating land use in the study area (forest, grassland, cropland, and built-up areas or bare). For all sampling sites, catchments were delineated as the entire landscape contributing surface water to the site. The area of each land use category in the catchments of each sampling site was calculated and used to determine the percentage of each land use per sampling site.

### 2.3. Measurement of physicochemical parameters and laboratory analyses

Sampling was done during the wet and dry seasons (December-January 2021/2022) and dry seasons (June-August 2022). Both macroinvertebrates and environmental variables were sampled within a 100-m representative reach at the sampling sites. Physicochemical water quality variables were measured in situ using a YSI multiprobe water quality meter (556 MPS; Yellow Springs Instruments, Yellow Springs, OHIO, USA) including dissolved oxygen concentration (DO; mg/L), temperature (°C), electrical conductivity (EC, µS/cm), salinity mg/L, total dissolved solids (TDS, mg/L), and pH. For nutrient analyses, duplicate filtered water samples through pre-weighed and pre-combusted Whatman GF/F; Glassfiber filters (0.42 mm thickness, 0.7 µm pore size, and 47 mm diameter) were taken per site in acid-washed HDPE bottles, and instantly fixed with sulphuric acid. The filtered water samples were used for the analysis of nitrite (mg/L), nitrates (mg/L), ammonium (mg/L), soluble reactive phosphorus (SRP, mg/L), and dissolved organic carbon (DOC, mg/L). Known volumes of filtered water samples though the GFF filters were recorded, and the filters with attached sediments were retained for determination of total suspended solids (TSS, mg/L) and particulate organic matter (POM, mg/L) Unfiltered water samples were collected in HDPE bottles (500 ml) and transported to the laboratory for determination of total phosphorus (mg/L). All water samples and filters were stored in a cooler box in the field before being transported to the laboratory, where they were stored in the refrigerator at 4 °C before analysis.

At each sampling site, measurements of water depth (m), velocity ($m^3/s$), and river width (m) were done. Cross-sectional width measurements were made using a measuring tape, whereas velocity and depth were measured using a meter rule and velocity plank. Stream discharge ($m^3/s$)was calculated by the velocity area method (Wetzel and Likens, 2000). According to Lakew and Moog (2015), the substrate in the sampling sites was characterized by identifying the substrate types that constituted >5 % coverage at each sampling site.

Riparian and in-stream habitat assessment was also done at each site qualitatively to determine habitat quality and diversity using the Qualitative Habitat Evaluation Index by Rankin, (1995) which has been modified for the Lake Victoria Basin (Raburu and Masese, 2012). Habitat quality variables included: substrate type and quality, instream cover, channel morphology, riparian zone and bank erosion, and pool/glide and riffle/run quality. In addition, all animal (livestock) and human activities at the vicinity of the sampling sites were recorded and used in the calculation of habitat quality. These include livestock grazing or watering, sand harvesting, water withdrawals, channelization, laundry washing and washing of vehicles, etc. For each site, the percentage of streambed covered by different substrate types was estimated for each biotope sampled for invertebrates. 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 the number of units occupied by various types of substrates were counted. The dominant substratum was defined by 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).

Standard colorimetric procedures (APHA, 2005) were used in the laboratory to analyze the water samples for nutrients. The data were divided into two categories or datasets: physicochemical variables, and nutrients. The data on physicochemical measures included pH, DO (mg/L), temperature (°C), salinity (mg/L), EC (µS/cm), TDS (mg/L), TSS (mg/L), and POM (mg/L). The second dataset was on nutrients and included ammonium $NH_4{}^+$ (mg/L), nitrates ($NO_3^-$) (mg/L), nitrite ($NO_2^-$) (mg/L), SRB (mg/L), total phosphorus (mg/L), and DOC (mg/L). These variables have demonstrated their sensitivity to broader catchment-scale influences, such as agricultural or urban land use, as well as local-scale disruptions like wastewater disposal, removal of riparian zones, livestock disturbances, and other stressors, as evidenced by previous studies (Hwang et al., 2016; Iteba et al., 2021; Li et al., 2022; Minaya et al., 2013; Wanderi et al., 2022)

### 2.4. TSS, POM, and DOC determination

GF/F filters with embedded sediments were dried at 60 °C for 72 h to attain constant weight. The filters were then re-weighed using an analytical balance and subtracting the filters weight for TSS determination.

$$TSS\ (mgL-1) = ((A \;-\; - \;B)\,/\,V) \ast 106 \tag{1}$$

Where: A = mass of filter + dried residue (g), B = dry mass of filter (g), and V = volume of sample filtered (L).

The filters were then ashed at 450 °C for 4 h in a muffle furnace and re-weighed for the determination of POM as the difference between TSS and ash-free-dry mass/weight.

$$Equation: \ POM\ (mgL-1) = ((C-B)/V) * 106 \quad (2)$$

Where: B = dry mass of filter (g), C = Weight of ashed filter (g) and V = volume of sample filtered (L).

For DOC analysis, the water samples were filtered in situ using GF/F filters stored in new or acid-washed 60 mL HDPE bottles and stored in the cold at freezing temperatures. Measurements for DOC concentrations were done using the Shimadzu total dissolved nitrogen analyzer unit (TNM-1) at the International Llivestock Research Institute (ILRI) Nairobi, which is also equipped with a total dissolved organic carbon analyzer (TOC-V CPN). The autosampler for the Shimadzu instrument utilizes chemo luminescence for TDN oxidative combustion for DOC.

### *2.5. Macroinvertebrate sampling and identification*

Macroinvertebrate sampling was conducted using a SASS net (1000-µm mesh size), which is a semi-quantitative 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 in the stony substrate under flowing or non-flowing conditions; (3) VEG: submerged and marginal vegetation (Masese et al., 2021). The sampling process involved disturbing and kicking the bottom upstream of the net so that water currents could wash the dislodged invertebrates into the net. Larger substrates such as boulders and cobbles were disturbed by hand and washed into the net. Three replicates per biotope (9 kick samples per site) were collected where kicking was carried out for about 1 minute per biotope. A total of 398 macroinvertebrate kick samples from the biotopes were collected, sorted in the field, and preserved in 75 % ethyl ethanol for further processing in the laboratory.

In the laboratory, macroinvertebrate samples were transferred into sorting trays, counted, and identified to the lowest taxon level possible, mainly genus. Identifications were done with the aid of keys and schema in several guides (Day, 2002a,b; de Moor et al., 2003a,b; Merritt et al., 2008).

Allocation of FFGs was done based on (Fry, 2021; Dobson et al., 2002; Masese et al., 2014; Merritt et al., 2008). Macroinvertebrate functional composition was described in terms of numerical abundance of the 5 FFGs (collector–gatherers {gatherers}, collector–filterers {filterers}, predators, scrapers, and shredders). Five surrogates of ecosystem attributes were determined using various ratios of macroinvertebrate FFGs based on numerical abundance according to Cummins et al. (2005):

## 3. Data analysis

Statistical analyses were performed with R version 4.3.0 (R Development Core Team, 2017), using the packages vegan (Oksanen et al., 2013), sem (Fox, 2006), and deSolve (Soetaert et al., 2010). Figures were created in Sigma Plot (Version 12), MS Office Excel (2016), and R version 4.3.0 (R Development Core Team 2017). Descriptive statistics (means ± standard deviation) and plots were used to present spatial and temporal variation in water and habitat quality variables at different site categories (disturbance gradients- High, Moderate, and Low), seasonality, and flow permanence.

Two-way analysis of variance (ANOVA) was used to test for differences in physicochemical and habitat variables among disturbance gradients (low, moderate, and high), seasons (dry and wet), and flow permanence (permanent vs seasonal) with disturbance gradients and seasons as main factors and disturbance gradients × season interaction term. Where there were no significant seasonal differences, data were pooled, and one-way ANOVA was used to test for differences among disturbance categories followed by Tukey's multiple post-hoc comparisons of means. Before analysis, count data were log $(x+1)$-transformed while the rest of the response variables were log-transformed to meet normality assumptions. Principal Component Analysis (PCA) was used to reduce the dimensionality of the physicochemical and habitat variables data. Two PCs were included to describe water quality physicochemical and habitat quality variables separately. PCAs were statistically assessed using permutational analysis of variance (PERMANOVA), based on Bray-Curtis dissimilarity matrices (McArdle and Anderson, 2001). The average rank similarities of macroinvertebrate FFGs were compared between the disturbance gradients, seasons, and flow permanence using two-way nested analysis of similarities (ANOSIM), with replicate disturbance gradients nested within seasons. ANOSIM calculates the R-statistic, which is a test statistic that varies between 0 and 1; higher values indicate bigger differences between factors. Non-metric multidimensional scaling (NMDS) was then used to visualize the functional composition of macroinvertebrates in different disturbance gradients, seasons, and flow permanence (Clarke and Gorley, 2006). Using Bray–Curtis (Bray and Curtis, 1957), Coefficients and dissimilarity matrices were derived for 2 sets of data: un-transformed abundances data and presence-absence data for the FFGs. The magnitude of the associated stress value ($<$ 0.2 corresponding to a good ordination) was used to determine the ordination's fit (Kashian et al., 2007). Similarity percentages analysis (SIMPER) was performed to establish which key macroinvertebrates were accountable for the variations observed between disturbance gradients (indicator macroinvertebrates for changes in disturbance gradient, habitat and water quality) and flow permanence (permanent vs seasonal). The % contribution of FFGs to the overall dissimilarity was quantified between disturbance gradient and flow permanence per season. SIMPER is a restrictive pairwise analysis between two-factor levels (Clarke and Warwick, 2001) and in this case, comparisons were done between high and moderate, high and low, and finally moderate and low disturbance levels. On flow permanence, comparisons were between seasonal and permanent sites per season.

Redundancy analysis (RDA) was used to elucidate relationships between macroinvertebrate assemblages and environmental variables. The output was displayed as triplots, in which the plotted points for taxa and FFGs and disturbance categories could be related to physicochemical 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). Because the gradient length was $<$3 SD, RDA was employed instead of CCA to determine which factors were responsible for the structure or groupings of FFGs among site categories (Ter Braak, and Smilauer, 2004)

## 4. Results

### *4.1. Water quality physicochemical variables and habitat quality*

There was a significant difference ($p < 0.05$) in discharge, water velocity, riparian zone, and bank erosion, and pool and riffle quality were recorded along the disturbance gradient (Table 2). Discharge (5.3 ± 2.0m$^3$/s), velocity (0.5 ± 0.03$^{-1}$m/s), and riparian zone and bank erosion (7.2 ± 0.2), pool and riffle quality (6.7 ± 0.5) were significantly higher at high disturbance sites, whereas and substrate type or diversity (13.98±1.0) was significantly higher in low-disturbance sites. Moderate disturbance sites recorded the lowest values of discharge and velocity and low-disturbance sites recorded the highest values on stream substrate and channel morphology (Table 2).

There were significant differences in physicochemical variables ($p <$ 0.05) for DOC, total phosphorus, pH, and EC between site categories (high-, moderate-, and low-disturbance). The highest values of DOC (27.93±8.14 mg/l) were recorded at moderate disturbance sites, total phosphorus (1.1 ± 0.34 mg/l), and EC (718.81±22.46 µS/cm) recorded the highest values at high disturbed sites whereas pH (8.16±0.1) had the highest values at low disturbance sites. The low disturbance category recorded the lowest values for DOC and EC while total phosphorus and pH recorded the lowest values at moderate disturbance and high disturbance sites, respectively, whereas TSS, POM, nitrite, and nitrate were higher during the dry season (Table 2).

There were significant variations in water quality parameters between permanent and seasonal sites during both dry and wet seasons. Among the physicochemical parameters, only temperature (°C), DOC (mg/L), and ammonia (mg/L) significantly differed between the two site categories during the dry season. Permanent sites had a lower temperature (23.9 ± 0.9 °C) than seasonal/intermittent sites (28.0 ± 1.1 °C). A similar trend was observed for DOC and ammonia, with permanent sites having significantly lower levels (DOC: 8.6 ± 1.8mg/L; ammonia: 2.1 ± 0.6mg/L) than seasonal sites (DOC: 24.3mg/L ± 7.3; ammonia: 4.7 ± 1.1mg/L). In the wet season, significant differences ($p < 0.001$), were observed in temperature, EC and total phosphorus, with seasonal streams exhibiting higher temperatures (26.5 ± 0.91), TDS (88.0 ± 11.91), and EC (698.2 ± 2.69). In contrast, permanent sites had lower TP (0.3 + 0.13) than seasonal sites (0.9 + 0.23). Conversely, levels of TDS (mg/L), salinity (mg/L), DO (mg/L), pH, TSS (mg/L), POM (mg/L), and DOC (mg/L), were not significantly different between the two flow permanence categories in the wet season (Table 3).

The PCA biplot for habitat quality and water quality data collected during the dry and wet seasons identified variables that were associated with the different disturbance categories (Fig. 2). The principal component 1 (PC 1) for habitat quality explained (29.9 %), while that for water quality explained (23.3 %) of the total variation in the study area during the dry and wet seasons (Fig. 2I). The principal component 2 (PC 2) for habitat quality explained (23.1 %), while that for water quality explained 15.7 % of the total variation for the disturbance category (Fig. 2I). Consequently, the PCA biplots for habitat quality and water quality data collected during both the dry and wet seasons identified variables that differed between the seasons. The principal component 1 (PC 1) for habitat quality explained (29.9 %), while that for water quality explained (23.3 %) for the total variation in the study area during sampling seasons. The principal component 2 (PC 2) for habitat quality explained (23.1 %), while that for water quality explained (15.7 %) of the total variation for sampling seasons (Fig. 2 II). Similarly, the PCA biplot for habitat quality and water quality data sampled during both wet and dry seasons identified variables that differed between the flow permanence category (Fig. 2II). The principal component 1 (PC1) for habitat quality explained (25.3 %), while that of water quality explained (25.8 %) for the total variation in the study area. The principal component 2 (PC2) for habitat quality explained (20.8 %), while that for water quality explained (19.3 %) of the total variation in flow permanence (Fig. 2C).

For habitat quality and stream size variables, water velocity (0.5 ± 0.05$m^3$/s), discharge (10.5 ± 2.87 $m^3$/s), and river width (8.3 ± 1.64 m) were higher during the wet seasons (Table 3), while for water quality, TSS (95.1 ± 54.59 mg/L), POM (95± 57.41 mg/L), and nutrient (0.6 ± 0.12 mg/L) concentrations were higher during the dry season (Table 3). There were significant differences in physico-chemical variables between seasonal and permanent sites (PERMANOVA, $F = 3.38$, d. f. = 1, $p = 0.001$). Among the disturbance categories (PERMANOVA, $F = 1.9$, d. f. = 2, $p = 0.02$), no interaction effect was observed between river permanence and disturbance levels (PERMANOVA, $F = 1.03$, d. $f = 2$, $p = 0.52$). There were significant differences in habitat quality variables among the disturbance categories (PERMANOVA, $F = 4.86$, df = 2, $p =$ 0. 001), as well as with river permanence (PERMANOVA, $F = 2.62$, df =1, $p = 0.004$), with no significant river type × disturbance interaction (PERMANOVA $F = 0.56$, $df = 2$, $p =$ 0. 3).

### 4.2. Composition of macroinvertebrate functional feeding groups

Five functional feeding groups (FFGs) collected in the Bura and Wundanyi catchment were scrapers, collector-gatherers (gatherers), collector-filterers (filterers), predators, and shredders. For the disturbance categories (low, moderate, high) there was a shift in the abundance of the macroinvertebrate FFGs. Predators were the most abundant at low disturbance (1829 individuals), followed by shredders and scrapers (870 individuals). Filterers were the least abundant (409 individuals). At moderate disturbance, again, predators were the most abundant (2865 individuals), followed by scrapers (2377 individuals) and shredders (507 individuals). Filterers were the least abundant (225 individuals). At high disturbance, predators were the most abundant (4447 individuals), followed by scrapers (3212 individuals) and gatherers (1221 individuals), while filterers were the least abundant in this category (72 individuals).

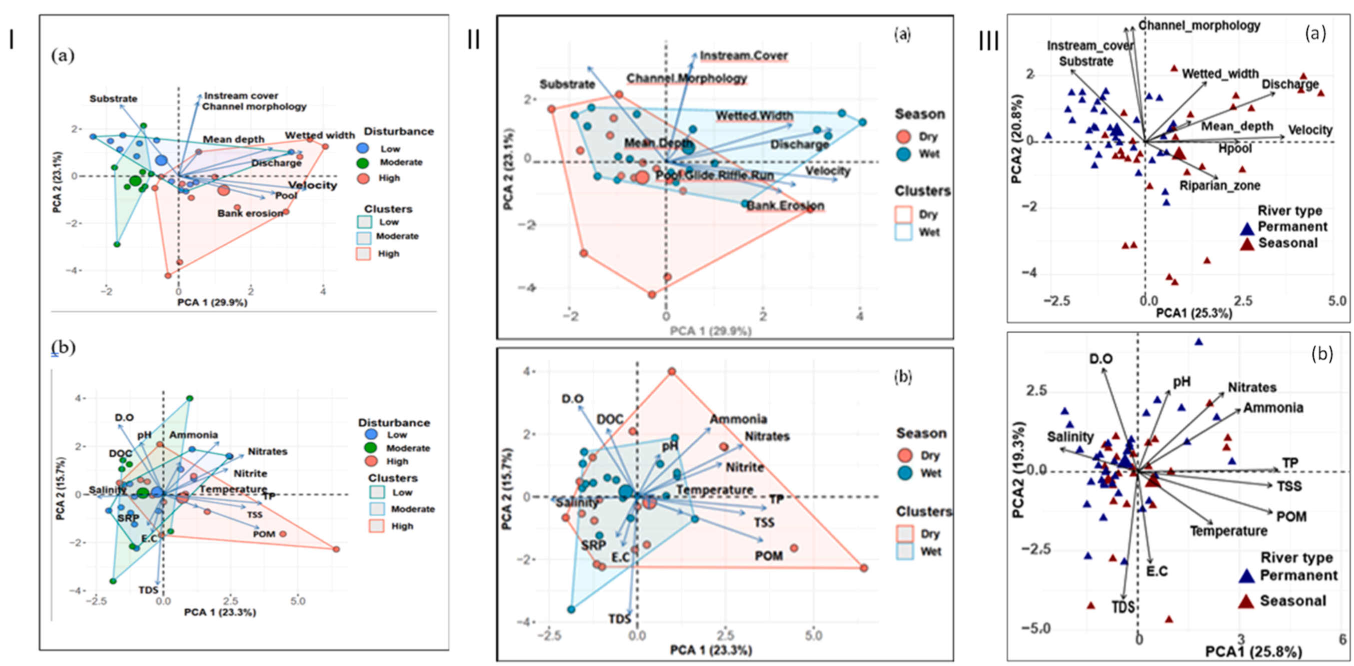


**Fig. 2.** PCA biplot for habitat quality (a), water quality (b) variables between disturbance categories (I), seasons (II), and flow permanence (III) in the Wundanyi and Bura rivers.

During the dry season, predators (5224 individuals) were the most abundant, followed by scrapers (2762 individuals) and shredders (1021 individuals). Filterers were the least abundant (104 individuals). During the wet season, predators (4801 individuals) were the most abundant followed by scrapers (4117 individuals) and gatherers (1545), again, filterers being the least abundant with 636 individuals.

For flow permanence (permanent vs seasonal), again, predators were the most abundant (4231 individuals) at permanent sites, followed by scrapers at (3040 individuals) and shredders (3040 individuals). Gatherers were the least abundant (563 individuals). At seasonal sites, predators also recorded the highest abundance (5794 individuals), followed by scrapers (3839 individuals), and gatherers (1459 individuals), while filterers were the least abundant (171 individuals). Predator abundance was highest in the high disturbance sites during the dry season, but this decreased in low- and moderate-disturbance sites during the dry season (Fig. 3a), a similar pattern that was observed in the wet season (Fig. 3b). Similarly, scrapers were abundant in the high disturbance sites during dry and wet seasons. They decreased in moderate and low disturbance (Fig. 3a, b). Shredders' numerical abundance increased in low disturbance sites and decreased in high disturbance during the wet and dry seasons (Fig. 3a, b). In flow permanence, predators were the most abundant in both the categories (permanent and seasonal) (Fig. 3c). Scraper's abundance was high in seasonal rivers but decreased in permanent rivers a pattern that was observed in both predators and gatherers (Fig. 3c). Shredder abundance was low in seasonal rivers but increased in permanent rivers, a pattern that was also observed in filterers (Fig. 3c).

### 4.3. *Relationships between water quality and macroinvertebrate functional feeding groups*

The ANOSIM indicated significant differences in the functional organization of macroinvertebrates for untransformed abundance data of FFGs among the river disturbance categories (*R-statistic*=0.26, $p = 0.001$), seasons (*R-statistic*=*0.15,* $p = 0.001$), and between river type categories (*R-statistic*= 0.18, $p = 0.002$).The NMDS ordination of FFGs abundance data identified and grouped the macroinvertebrates similarly, although there were some overlaps between wet and dry seasons and between disturbance site categories (Fig. 4). Shredders were associated with low disturbance sites which are dominated by sensitive taxa belonging to Decapoda, Diptera, Ephemeroptera, and Lepidoptera. Predators were associated with highly disturbed site categories which mainly consisted of Coleoptera, Diptera, Hemiptera, Odonata, and Trichoptera. Moderately disturbed categories had all the FFGs present. In the dry season, there was a high abundance of predators which mainly consisted of Hemiptera, Odonata, Coleoptera, and some Trichoptera. During the wet season, all groups of the FFGs were present. There was a high dominance of predators in temporary (seasonal) sites that experienced flow cessation. Predators were dominated by Odonata (e.g., Gomphidae, Lestidae, Libellullidae, and Cordulegastridae families), Hemiptera (e.g., Naucoridae, Corixidae, Pleidae, Notonectidae) and Diptera (e.g., Tabanidae). Permanent sites had all the groups of FFGs which were dominated by Odonata (Gomphidae), Ephemeroptera (Baetidae), Decapoda (Potamonautidae), Diptera (Chironomidae), and Trichoptera (Hyropsychidae).

Pairwise SIMPER comparison of macroinvertebrate FFGs between low-disturbance site categories and high-disturbance site categories identified scrapers (34.8 %) and predators (31.2 %) as contributing the greatest dissimilarity between the two site categories during the wet season with a high abundance of scrapers in high-disturbance sites (Table 4). Predators (29.8 %) and scrapers (28.8 %) contributed the greatest dissimilarity between moderate- and high-disturbance sites during the wet season with a higher abundance of predators in moderate disturbance sites (Table 4). Comparison between low- and moderate-

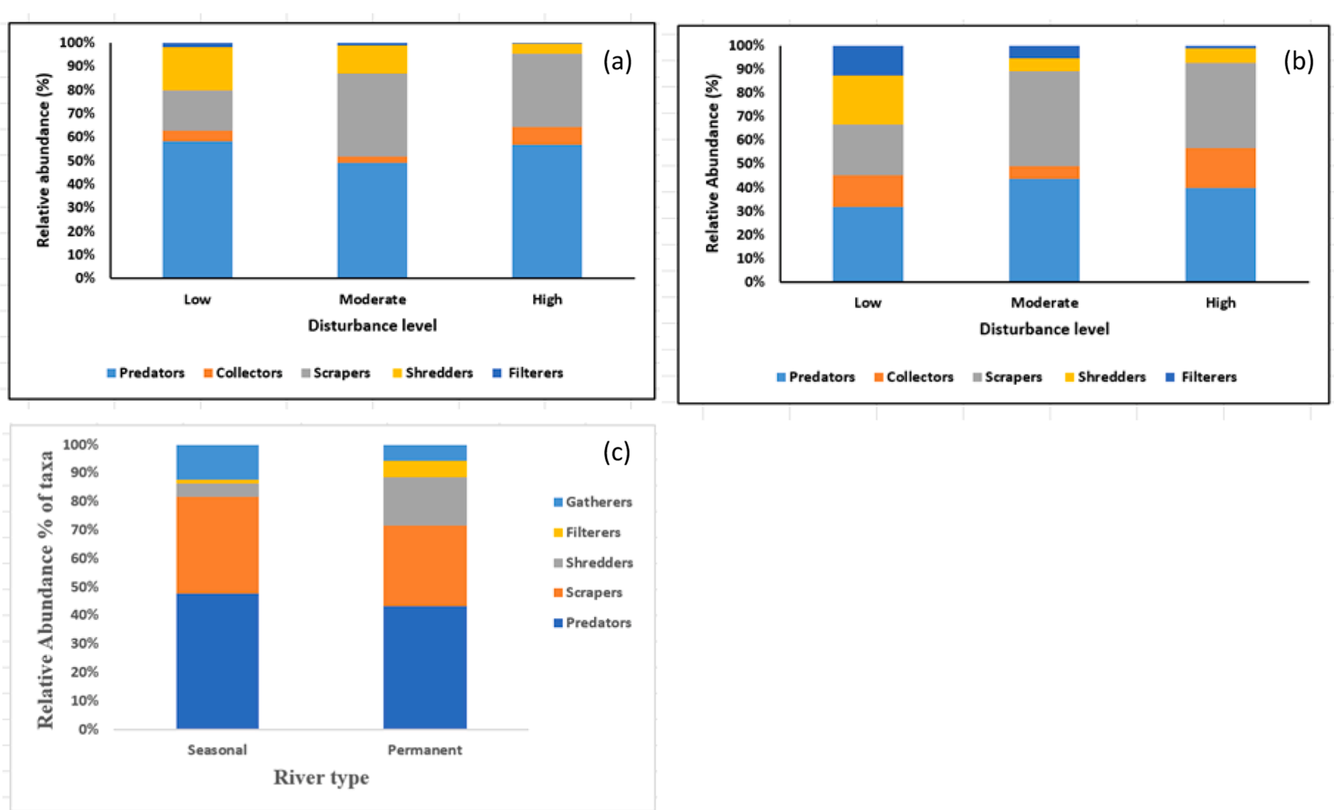


**Fig. 3.** Changes in the relative abundance of macroinvertebrate FFGs in different sites grouped according to the levels of disturbance seasonally (dry (a), wet (b)) (low, moderate and high) and flow permanence (permanent and seasonal).

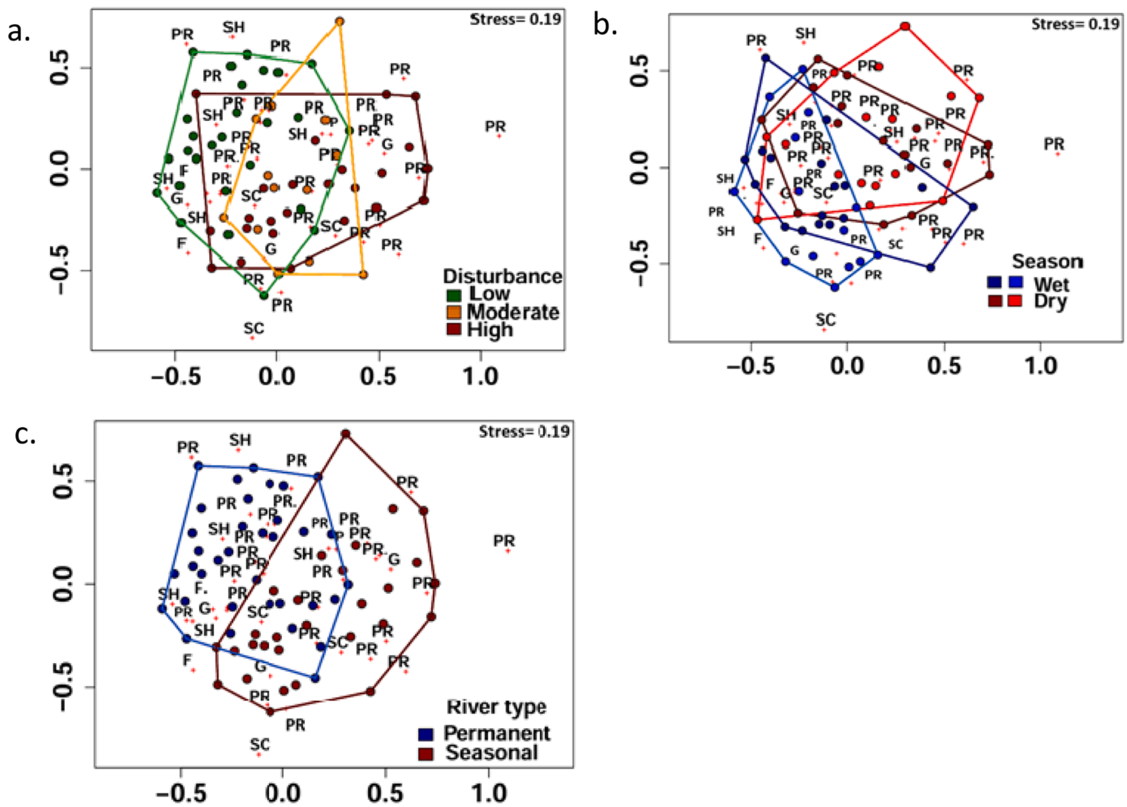


**Fig. 4.** Plots of nMDS based on abundance data of macroinvertebrate FFGs in Wundanyi and Bura rivers according to (a) disturbance gradient (low, moderate and high), (b) seasons (wet and dry) And, (c) river type or flow permanence (permanent and seasonal). Pr = predators, Sh = shredders, Sc =scrapers, F = collector-filterers, G = collector-gatherers.

disturbance sites identified scrapers (34.9 %) and predators (30.4 %) as contributing the greatest dissimilarity between two site categories with higher abundance of scrapers in moderate-disturbance sites in the wet season (Table 4).

During the dry season, scrapers (34.9 %) and predators (33.6 %) accounted for the greatest dissimilarity between low- and moderate-disturbance sites with both scrapers and predators having a higher abundance in the low-disturbance sites (Table 4). In comparison between moderate- and high-disturbance sites, again scrapers (41.7 %) and predators (34.8 %) were identified as having the greatest dissimilarity between the two disturbance sites with both (scrapers and predators) having a higher abundance in moderate-disturbance sites (Table 4).

Predators (51.6 %) and scrapers (15.4 %) were identified as having the greatest dissimilarity between permanent and seasonal rivers with predators having a higher abundance in seasonal rivers during the dry season (Table 5). During the wet season, again predators (46.1 %) and scrapers (23.4 %) were identified as having the greatest dissimilarity between permanent and seasonal rivers with higher abundance of predators in seasonal rivers (Table 5).

The RDA ordination showed spatial patterns in macroinvertebrate functional composition associated with water quality and POM with respect to the disturbance sites (Fig. 5a), seasonality (Fig. 5b) and flow permanence (Fig. 5c). RDA axes 1 and 2 explained 27.2 % on axis 1 and 21.1 % on axis 2 of the associations between water quality and macroinvertebrate FFGs in the study area. The RDA ordination showed that shredders were associated with dry season and seasonal rivers with higher particulate organic matter (Fig. 5b, c), whereas predators, scrapers, and filterers were associated with increased levels of pH, nitrite, and ammonia in high disturbance sites (Fig. 5a). Gatherers had the highest abundance at high disturbance sites and were associated with seasonal sites 0 and more occurred during the dry seasons (Fig. 5a, c).

### *4.4. Macroinvertebrates FFGs as surrogates of ecosystem attributes*

Disturbance and seasonality had strong influences on the functional composition of macroinvertebrates in the study area, and the metrics used as surrogates of ecosystem attributes responded similarly (Table 6). Metrics used for disturbance site categories, and seasons showed opposite results for the CPOM/FPOM index and TFPOM/BFPOM, with moderate disturbed sites indicating a weak shredder linkage with the riparian zone and with limited fine particulate organic matter (FPOM) in the water column at high-disturbance sites during dry and wet seasons, but agreed in terms of the channel stability (stable substrate abundance) indices.

Seasonality influenced metrics of ecosystem functioning, with more disagreements during the wet than the dry season. For instance, the metrices indicated that low-disturbance were heterotrophic ($P < R$) during the wet season but differed on the rest of the sites categories and seasons with data showing that they were autotrophic ($P > R$). During both seasons, the top-down control index indicated that all the site categories had an overabundance of predators, implying that there was a strong top-down control of the system. Irrespective of the level of disturbance, all sites had a stable channel and adequate FPOM in transport (TFPOM) than deposited in the benthos (TFBOM) during both the dry and wet seasons as indicated by the TFPOM/BFPOM index. However, at the high-and moderate- disturbance sites, the TFPOM/BFPOM index showed 0.06 and 0.42 during the wet and dry sampling seasons, respectively (Table 6).

With respect to flow permanence or river type, the P/R metrics were higher than the threshold value ($P/R = 0.75$), meaning that both the permanent ($P/R = 1.08$) and seasonal ($P/R = 1.78$) rivers were autotrophic. The surrogates for CPOM/FPOM index for the two river types indicated strong shredder linkage with the riparian zone. In terms of the predominating FPOM, the permanent sites had more FPOM in transport

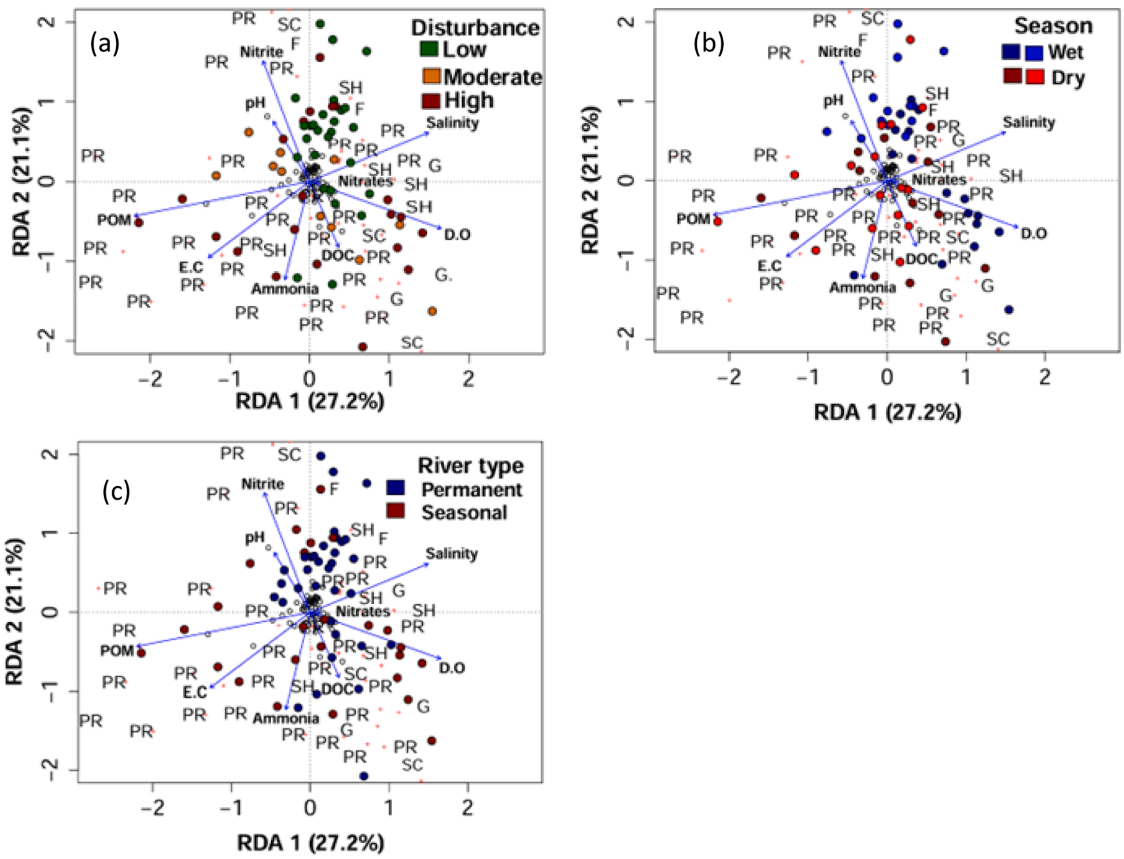


**Fig. 5.** Redundancy analysis (RDA) triplot of macroinvertebrate FFGs abundance data in relation to water quality variables in the Wundanyi and Bura rivers. Plots are for a) disturbance categories (low, moderate and high), b) seasons (wet and dry) and c) flow permanence (permanent and seasonal). Pr = predators, Sh = shredders, Sc = scrapers, F = collector-filterers, C = collector-gatherers, E.C = electrical conductivity, DO = dissolved oxygen, POM-particulate organic matter, DOC-dissolved organic carbon.

(TFPOM) than in the benthos (BFPOM), while this was not the case for seasonal rivers as the ratio was below the threshold value (TFPOM/BFPOM = 0.50). In both river types, there were stable channels and strong top-down controls of the macroinvertebrate community by predators (Table 7).

## 5. Discussion

Our primary objective was to empirically examine the impact of disturbances caused by both human activities and livestock grazing, alongside the factors of stream flow permanence and seasonality on the diversity and composition of macroinvertebrate FFGs in the Bura and Wundanyi rivers. There were significant seasonal and spatial differences in stream size, habitat, and water quality physicochemical variables in the study area caused by human disturbance and flow variability. Macroinvertebrate assemblages responded to these changes with various ratios and metrics of FFGs used as surrogates of ecosystem attributes and ecological conditions. However, the majority of these metrics did not conform to the expected threshold ratios (Table 1). Disturbance, seasonality, and flow permanence all emerged as significant factors shaping the composition of macroinvertebrate FFGs in the study area. During the wet season, there was an increase in the diversity and abundance of macroinvertebrate FFGs compared to the dry season.

### *5.1. Variation in water and habitat quality*

Disturbance, seasonality, and flow permanence exerted significant influences on water and habitat quality variables. Alterations in water quality among different disturbance categories were evidenced by declining DO levels, high temperature, increased EC, and higher levels of POM, TSS, nutrient concentrations, and TDS. The higher temperature observed in the high-disturbance sites and seasonal rivers can be

**Table 1**
Ratios of macroinvertebrate functional feeding groups (FFGs) as indicators of ecosystem attributes (Cummins et al., 2005).

| Ecosystem Parameter/Attribute | Symbols | Functional Feeding Group Ratios | Threshold Ratio |
|---|---|---|---|
| Autotrophy to Heterotrophy | P/R | Scrappers to (Shredders +Total Collectors) | Autotrophic>0.75 |
| Coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) | CPOM/FPOM | Shredders to Total Collectors | Normal shredder linkage with functioning riparian >0.25 |
| FPOM in transport (Suspended) to FPOM in storage (Deposited in Benthos) | TFPOM/BFPOM | Filtering collectors to Gathering collectors | FPOM Transport greater than normal FPOM loading in suspension>0.50 |
| Substrate (Channel) Stability | Stable Channel | (Scrappers + Filterers) to (shredders + Gatherers) | Stable Substrate Plentiful>0.50 |
| Top-Down Predator Control | Top-Down Control | Predators to Total of all other groups. | Normal Predator Prey Balance 0.10–0.20 |

NB: P=Primary production, R=Respiration

**Table 2**
Means (± SE) of habitat quality, water quality physico-chemical variables, and stream size variables in the different disturbance categories in the Wundanyi and Bura rivers. SRP= soluble reactive phosphorus, TSS= total suspended solids, POM= particulate organic matter, TDS= total dissolved solids, TP= total phosphorus, TSS= total suspended solids, DOC=dissolved organic carbon, DO=Dissolved Oxygen *P-values marked with asterisks are significantly different among site categories at $p < 0.05$.

| Parameter | Level of disturbance Low | Moderate | High | ANOVA test F | P value |
|---|---|---|---|---|---|
| **Habitat quality** | | | | | |
| Wetted width (m) | 5.2 ± 1.1 a | 2.9 ± 0.8a | 6.0 ± 1.23 a | 3.88 | 0.14 |
| Mean depth (m) | 0.1 ± 0.02 a | 0.1 ± 0.01 a | 0.1 ± 0.01 a | 2.12 | 0.35 |
| Discharge (m³/s) | 2.0 ± 1.42c | 0.3 ± 0.1b | 5.3 ± 2.0a | 6.77 | 0.03 * |
| Velocity (m³/s) | 0.3 ± 0.04b | 0.3 ± 0.03b | 0.5 ± 0.03a | 12.23 | 0.002 * |
| Substrate | 13.98±1.0 a | 12.4 ± 1.2 a | 11.4 ± 0.8 a | 2.84 | 0.24 |
| Instream cover | 10.3 ± 0.4 a | 9.6 ± 0.7 a | 9.5 ± 0.5 a | 1.14 | 0.57 |
| Channel morphology | 7.9 ± 0.1 a | 7.0 ± 1.01 a | 6.6 ± 0.8 a | 3.7 | 0.16 |
| Riparian zone and bank erosion | 5.9 ± 0.2b | 5.8 ± 0.3b | 7.2 ± 0.2a | 13.46 | 0.001 * |
| Pool and riffle quality | 5.2 ± 0.4a | 4.6 ± 0.2b | 6.7 ± 0.5a | 7.35 | 0.03 * |
| **Water quality** | | | | | |
| Ammonium (mg/L) | 1.8 ± 0.52 a | 4.0 ± 2.06 a | 3.8 ± 0.38 a | 1.89 | 0.17 |
| SRP (mg/L) | 0.1 ± 0.03 a | 0.1 ± 0.04 a | 0.2 ± 0.02 a | 0.52 | 0.6 |
| Nitrates (mg/L) | 0.6 ± 0.11 | 0.3 ± 0.06 a | 0.6 ± 0.06 a | 1.6 | 0.22 |
| Nitrite (mg/L) | 0.5 ± 0.09 a | 0.3 ± 0.1 a | 0.5 ± 0.07 a | 1.13 | 0.34 |
| DOC (mg/L) | 7.0 ± 0.71b | 27.9 ± 8.14a | 23.1 ± 4.87a | 6.01 | 0.01* |
| TP (mg/L) | 0.4 ± 0.15b | 0.2 ± 0.05b | 1.1 ± 0.34a | 3.96 | 0.03* |
| POM (mg/L) | 20.6 ± 3.66 a | 26.9 ± 11.14 a | 81.3 ± 45.11 a | 1.37 | 0.27 |
| TSS (mg/L) | 70.5 ± 11.34 a | 57.4 ± 15.91 a | 96.3 ± 30.89 a | 0.73 | 0.49 |
| pH | 8.2 ± 0.1b | 7.9 ± 0.19a | 7.8 ± 0.06a | 3.21 | 0.05 |
| DO (mg/L) | 5.7 ± 0.13 a | 6.3 ± 0.38 a | 6.0 ± 0.28 a | 1.28 | 0.29 |
| Salinity (mg/L) | 0.4 ± 0.04 a | 0.3 ± 0.05 a | 0.3 ± 0.04 a | 2.08 | 0.14 |
| TDS (mg/L) | 82.7 ± 11.1 a | 111.5 ± 24.26 a | 96.7 ± 8.82 a | 1.02 | 0.37 |
| Electrical conductivity (µS/cm) | 657.8 ± 11.91b | 687.7 ± 5.24b | 718.8 ± 22.46a | 3.78 | 0.03* |
| Temperature (°C) | 23.6 ± 0.78 a | 25.6 ± 1.46 a | 26.5 ± 0.93 a | 2.62 | 0.09 |
| **Landcover/ Land use** | | | | | |
| Bare ground | 0.86±0.83 | 0.01±0.01 | 0.02 ±0.01 | 2.24 | 0.15 |
| Built | 0.93±0.38 | 2.84±1.92 | 0.64 ±0.05 | 1.85 | 0.21 |
| Cropland | 68.35 ±17.42 | 73.27 ±6.09 | 62.16 ±7.2 | 0.19 | 0.83 |
| Grassland | 6.93±5.64 | 7.05±2.84 | 13.8 ± 3.83 | 0.78 | 0.48 |
| Shrubs | 18.03 ±16.57 | 9.05±3.93 | 13.61 ±2.87 | 0.15 | 0.87 |
| Tree cover | 5.39±1.29 | 7.76±3.66 | 9.85 ±2.27 | 1.11 | 0.36 |

**Table 3**
Means (± SE) of habitat quality, and water quality physico-chemical variables and stream size variables in the two flow permanence categories (seasonal and permanent) in the Wundanyi and Bura rivers (For abbreviations and acronyms refer to Table 2).

| Parameter | Season | Permanent | Seasonal | t | *P value* |
|---|---|---|---|---|---|
| Wetted width (m) | Dry | 5.0 ± 1.5 | 3.8 ± 0.7 | 0.666 | 0.511 |
| | Wet | 3.7 ± 1.3 | 8.3 ± 1.64 | 2.253 | 0.032* |
| Mean depth (m) | Dry | 0.1 ± 0.01 | 0.1 ± 0.02 | 1.458 | 0.155 |
| | Wet | 0.2 ± 0.04 | 0.1 ± 0.02 | 0.426 | 0.673 |
| Discharge (m³/s) | Dry | 0.9 ± 0.6 | 0.8 ± 0.41 | 0.12 | 0.905 |
| | Wet | 0.5 ± 0.24 | 10.5 ± 2.87 | 3.706 | 0.001* |
| Velocity (m³/s) | Dry | 0.3 ± 0.04 | 0.4 ± 0.03 | 1.542 | 0.134 |
| | Wet | 0.3 ± 0.03 | 0.5 ± 0.05 | 4.314 | 0.000* |
| Substrate | Dry | 14.3 ± 1.01 | 10.9 ± 0.82 | 2.474 | 0.019* |
| | Wet | 13.9 ± 1.08 | 12.0 ± 0.62 | 1.353 | 0.186 |
| Instream cover | Dry | 10.3 ± 0.39 | 8.0 ± 0.51 | 3.647 | 0.001* |
| | Wet | 10.2 ± 0.52 | 10.9 ± 0.39 | 1.026 | 0.313 |
| Channel morphology | Dry | 8.0 ± 0.14 | 4.9 ± 1.02 | 3.486 | 0.002* |
| | Wet | 7.9 ± 0.17 | 7.9 ± 0.18 | 0.183 | 0.856 |
| Riparian zone | Dry | 5.8 ± 0.22 | 6.9 ± 0.29 | 3.288 | 0.003* |
| | Wet | 6.1 ± 0.31 | 6.7 ± 0.23 | 1.692 | 0.101 |
| Pool and riffle quality | Dry | 5.0 ± 0.38 | 5.8 ± 0.6 | 1.209 | 0.236 |
| | Wet | 5.1 ± 0.4 | 6.3 ± 0.5 | 1.876 | 0.07 |
| Temperature (°C) | Dry | 23.9 ± 0.89 | 28.0 ± 1.11 | 2.82 | 0.007* |
| | wet | 22.4 ± 0.54 | 26.5 ± 0.91 | 4.07 | 0.001* |
| Electrical conductivity (µS/cm) | Dry | 655.2 ± 19.7 | 735.7 ± 41.2 | 1.89 | 0.068 |
| | wet | 669.0 ± 5.11 | 698.2 ± 2.69 | 4.86 | 0.001* |
| TDS (mg/L) | Dry | 93.3 ± 10.86 | 108.3 ± 22.92 | 0.63 | 0.531 |
| | wet | 84.1 ± 13.1 | 88.0 ± 11.91 | 0.21 | 0.832 |
| Salinity (mg/L) | Dry | 0.3 ± 0.04 | 0.2 ± 0.04 | 1.73 | 0.094 |
| | wet | 0.3 ± 0.04 | 0.4 ± 0.03 | 0.22 | 0.83 |
| DO (mg/L) | Dry | 5.9 ± 0.24 | 5.7 ± 0.37 | 0.52 | 0.609 |
| | wet | 6.0 ± 0.24 | 6.4 ± 0.27 | 1.11 | 0.274 |
| pH | Dry | 8.1 ± 0.13 | 8.0 ± 0.13 | 0.70 | 0.491 |
| | wet | 8.1 ± 0.13 | 7.7 ± 0.12 | 1.82 | 0.079 |
| TSS (mg/L) | Dry | 89.8 ± 15.55 | 95.1 ± 54.59 | 0.10 | 0.919 |
| | wet | 72.6 ± 14.75 | 62.0 ± 15.82 | 0.41 | 0.628 |
| POM (mg/L) | Dry | 25.3 ± 7.17 | 95.3 ± 57.41 | 1.37 | 0.18 |
| | wet | 27.1 ± 6.23 | 19.7 ± 2.78 | 1.04 | 0.305 |
| TP (mg/L) | Dry | 0.4 ± 0.2 | 0.7 ± 0.35 | 0.71 | 0.483 |
| | wet | 0.3 ± 0.13 | 0.9 ± 0.23 | 2.62 | 0.014* |

(*continued on next page*)

**Table 3** (*continued*)

| Parameter | Season | Permanent | Seasonal | t | *P value* |
|---|---|---|---|---|---|
| DOC (mg/L) | Dry | 8.6 ± 1.79 | 24.3 ± 7.34 | 2.32 | 0.027* |
| | wet | 9.8 ± 2.2 | 27.0 ± 7.3 | 2.38 | 0.024* |
| Nitrite (mg/L) | Dry | 0.3 ± 0.08 | 0.3 ± 0.06 | 0.04 | 0.972 |
| | wet | 0.6 ± 0.14 | 0.6 ± 0.11 | 0.3 | 0.766 |
| Nitrates (mg/L) | Dry | 0.6 ± 0.12 | 0.5 ± 0.06 | 0.82 | 0.417 |
| | wet | 0.5 ± 0.15 | 0.5 ± 0.06 | 0.03 | 0.975 |
| SRP (mg/L) | Dry | 0.1 ± 0.05 | 0.1 ± 0.05 | 0.24 | 0.812 |
| | wet | 0.1 ± 0.02 | 0.2 ± 0.03 | 2.59 | 0.015* |
| Ammonium (mg/L) | Dry | 2.1 ± 0.58 | 4.7 ± 1.1 | 2.21 | 0.035* |
| | wet | 1.6 ± 0.66 | 3.0 ± 0.65 | 1.54 | 0.133 |

ascribed to the relatively open canopy cover in the riparian zones, whereas the comparatively lower mean water temperature is in low-disturbance sites in forested areas. Riparian vegetation acts as a buffer against solar radiation, limiting its penetration to the water's surface, thus mitigating temperature fluctuations within forested streams. This ecological phenomenon is in line with the existing literature (Aura et al., 2011; López-Carr and Burgdorfer, 2013; Mathooko and Kariuki, 2000).

The TSS, POM, and nutrients were higher during the dry season. We expected these variables to be higher during the wet season due to surface runoff from agricultural farms and fertilizers leaching into the rivers. These contrary results can be attributed to livestock disturbance and input of nutrients and organic matter during the dry season when livestock access to streams and rivers is increased as other sources of water become limited (Iteba et al., 2021; Yillia et al., 2008). On the other hand, seasonal sites (those that recorded flow cessation) recorded higher EC and TDS, and this was attributed to increased evaporation of water and water abstractions in the lower reaches of these rivers.

Seasonality further exacerbated the effects of disturbances on water quality. Moderate-disturbance sites had highest levels of DOC concentration, whereas high-disturbance sites had the highest values of TP and EC. Seasonality amplified the disturbance effects on water quality, with high DOC recorded in moderate-disturbance sites, while TP and EC had high values in high disturbance, whereas pH recorded higher values in minimally disturbed sites. Therefore, seasonal changes worsened the impact of disturbances on water quality, with different types of disturbances affecting specific water quality parameters (DOC, TP, EC) differently depending on the disturbance level.

### *5.2. Patterns in structural and functional composition of macroinvertebrates*

In comparison to previous studies on the functional composition of macroinvertebrates in Afromontane rivers, interesting patterns were obtained in this study. An overall increase in the abundance of all FFGs in the Bura-Wundanyi streams was observed during the wet season. This can be attributed to the increased diversity and complexity of habitats caused by the inundation of marginal vegetation, resulting in a broader diversity of flow velocities available to both rheophilic and pool taxa (Dallas, 2007; Masese et al., 2021; Muñoz-Mas et al., 2019). Additionally, during the wet season, there was a rich and varied supply of food resources originating from terrestrial runoff (Masese et al., 2009a). These findings agree with prior investigations conducted in different geographical locations. For instance, in their study on habitat diversity and macroinvertebrate FFGs conducted in Serra Do Cipo, Brazil, Callisto et al. (2001) documented a substantial rise of 3000 more individuals per square meter of collector filterers, shredders, and collector-gatherers during the wet season compared to the dry season. This surge in individuals was attributed to the heightened presence of organic matter, a factor that can also be applied to the collectors in our study. This is because rainwater carries organic materials from terrestrial regions and deposits them into the river, thereby acting as allochthonous sources of food for the macroinvertebrate community (Chakraborty, 2021a, 2021b).

The reduced abundance and diversity of FFGs during the dry season can be attributed to constraints imposed by the physico-chemical conditions of the environment. Notably, seasonal sites characterized by the cessation of flows during this period had elevated levels of EC, TDS, and water temperature. These parameters negatively influence both the diversity and abundance of macroinvertebrates (Buss et al., 2002; Masese and Raburu, 2017; Minaya et al., 2013). Diminished flow conditions leading to the exposure of riffles or stable substrate are expected to undermine the growth and accrual of algae and periphyton, which constitute a significant nutritional resource for scrapers. Additionally, the absence of stable substrate and reduced flow velocities pose adverse consequences for rheophilic species, including Hydropsychidae and Simuliidae, which depend on water flow for procuring food from the water column (Masese et al., 2021; Thirion, 2016). Dry season declines in the abundance of collectors can also be linked to limited food supply from the terrestrial environment as hydrologic connectivity is minimized during this period (Benson and Pearson, 2020; Callisto et al., 2001).

Shredders, primarily comprising Trichoptera species, and scrapers, predominantly represented by Ephemeroptera, have shown high sensitivity to alterations in their environment. In contrast, collectors and predators exhibit a relatively higher tolerance to disturbances and organic pollution (Boyero et al., 2009; Masese et al., 2014 and Masese and Raburu, 2017). Using an abundance-based similarity percentage (SIMPER) analysis, we identified scrapers and predators as the major FFGs contributing to dissimilarities among disturbance and flow permanence site categories, both during the wet and dry seasons. Numerical dominance was consistently observed for predators across all sites, regardless of the nature of disturbance or flow permanence. This dominance can be attributed to the presence of tolerant taxa among the predators, such as Coleoptera, Odonata, and Hemiptera, that are fast colonizers and contain terrestrial adult forms that can survive desiccation or flow cessation (Masese et al., 2021). The availability of other tolerant collector taxa, such as Oligochaeta, facilitated the dominance of collectors, particularly in highly disturbed sites exposed to substantial disturbances stemming from human activities, and inputs of organic matter and nutrients from livestock (Barbee, 2005; Mathooko et al., 2005; Masese et al., 2021).

### *5.3. Macroinvertebrate FFGs as surrogates of ecosystem attributes*

The functional structure of macroinvertebrate communities was significantly altered by the interplay of disturbance, seasonality, and flow permanence (Tables 4 and 5). The temporal and spatial dynamics exhibited by macroinvertebrate

FFGs in response to disturbance and flow permanence position them as valuable indicators of both ecosystems functioning and the ecological state of the river. The diverse FFG ratios and metrics employed proved effective in monitoring variations in ecosystem integrity and performance resulting from human disturbance, and seasonal flow fluctuations.

Most streams were autotrophic ($P/R > 1$), an observation that conforms to earlier studies in Kenyan streams (Masese et al., 2014, 2017) except for sites located at minimally disturbed sites which were mostly heterotrophic ($P/R < 1$). The streams in the study area had low abundances of collectors (Oligochaeta and Chironomidae), which likely shifted the P/R ratios in the potentially heterotrophic streams toward autotrophy. Thus, autotrophy at most of the sites during both the wet

**Table 4**
FFG-ranked SIMPER contributors to percentage dissimilarity (Contrib.%) in the composition between disturbance site categories: Values other than Contrib.% indicate mean abundance. Site categories were defined as (high, moderate, and low disturbance, respectively).

| | Dry season | | | | Wet season | | |
|---|---|---|---|---|---|---|---|
| FFGs | Contrib. % | Mean Low | Mean High | FFGs | Contrib. % | Mean Low | Mean high |
| Scrapers | 34.9 | 149 | 121 | Scrapers | 34.8 | 174 | 239 |
| Predators | 33.6 | 285 | 285 | Predators | 31.2 | 267 | 253 |
| Shredders | 20.5 | 41 | 89 | Filterers | 12.3 | 17 | 67 |
| Gatherers | 8.8 | 45 | 13 | Shredders | 12 | 32 | 77 |
| Filterers | 2.3 | 8 | 6 | Gatherers | 9.7 | 59 | 69 |
| **FFGs** | **Contrib. %** | **Mean Moderate** | **Mean High** | **FFGs** | **Contrib. %** | **Mean Moderate** | **Mean High** |
| Scrapers | 41.7 | 221 | 121 | Predators | 29.76 | 304 | 253 |
| Predators | 34.8 | 385 | 285 | Scrapers | 28.8 | 324 | 239 |
| Shredders | 18.4 | 50 | 89 | Gatherers | 19.14 | 169 | 69 |
| Gatherers | 3.8 | 28 | 13 | Shredders | 11.97 | 106 | 77 |
| Filterers | 1.2 | 4 | 6 | Filterers | 10.33 | 13 | 67 |
| **FFGs** | **Contrib. %** | **Mean Low** | **Mean Moderate** | **FFGs** | **Contrib. %** | **Mean Low** | **Mean Moderate** |
| Scrapers | 44.6 | 149 | 221 | Scrapers | 34.9 | 174 | 324 |
| Predators | 35 | 285 | 385 | Predators | 30.4 | 267 | 304 |
| Shredders | 10.4 | 41 | 50 | Gatherers | 18.5 | 59 | 169 |
| Gatherers | 8.3 | 45 | 28 | Shredders | 13.5 | 32 | 106 |
| Filterers | 1.7 | 8 | 4 | Filterers | 2.8 | 17 | 13 |

**Table 5**
FFGs-ranked SIMPER contributors to percentage dissimilarity (Contrib.%) in the composition between flow permanence or river type site categories (permanent and seasonal). Values other than Contrib.% indicate mean abundance.

| FFGs | Contrib. % | Mean Permanent | Mean Seasonal |
|---|---|---|---|
| Dry season | | | |
| Predators | 51.6 | 17.1 | 20.8 |
| Scrapers | 15.4 | 1.67 | 2.8 |
| Shredders | 13.3 | 2.78 | 2.5 |
| Gatherers | 10.0 | 2.0 | 2.5 |
| Filterers | 9.8 | 1.4 | 0.9 |
| Wet season | | | |
| FFGs | Contrib. % | Mean Permanent | Mean Seasonal |
| Predators | 46.1 | 17.2 | 20.0 |
| Scrapers | 23.4 | 2.2 | 4.8 |
| Collectors | 14.8 | 2.1 | 3.4 |
| Shredders | 10.5 | 2.7 | 3.2 |
| Filterers | 5.2 | 1.6 | 2.0 |

**Table 6**
Mean values of stream ecosystem attributes derived from FFG ratios along Wundanyi and Bura rivers in the different disturbance categories during the dry and wet seasons.

| Disturbance level | Low disturbance | | Moderate disturbance | | High disturbance | |
|---|---|---|---|---|---|---|
| Season | Wet | Dry | Wet | Dry | Wet | Dry |
| PR | 0.47 | **0.88** | **2.52** | **2.21** | **1.49** | **2.58** |
| CPOM/FPOM | **0.84** | **2.56** | **0.50** | **2.82** | **0.35** | **0.52** |
| TFPOM/BFPOM | **0.96** | 0.39 | **1.02** | 0.42 | 0.06 | 0.06 |
| Channel stability | **1.02** | **1.03** | **4.29** | **2.48** | **1.59** | **2.72** |
| T/Down control | **0.47** | **1.26** | **0.77** | **0.96** | **0.67** | **0.43** |

**N: B** Ratios are based on numerical abundance. Boldface indicates very strong autotrophic, strong shredder linkage with the riparian zone, heavy suspended of loading FPOM, or good quality of FPOM, stable substrate abundance, and an overabundance of predators with strong top-down control. Boldface identifies those values above the thresholds for that metric. Threshold values for the attributes are: P/R> 0.75, CPOM/FPOM>0.25, TFPOM/BFPOM>0.50, Channel Stability>0.50, Top-Down control>0.20.

and dry seasons is a significant departure from expectations based on other measures of ecosystem functioning. There was a strong linkage between food webs and the riparian zone (CPOM > FPOM) at all site

**Table 7**
Mean values of stream ecosystem attributes derived from FFG ratios along Wundanyi and Bura rivers between the flow permanence or river type categories (permanent and seasonal).

| Flow Permanence | Seasonal | Permanent |
|---|---|---|
| P/R | **1.78** | **1.08** |
| CPOM/FPOM | **0.32** | **1.49** |
| TFPOM/BFPOM | 0.11 | **1.01** |
| Channel Stability | **2.02** | **1.6** |
| Top/Down Control | **0.97** | **0.72** |

**N:B** Ratios are based on numerical abundance. Boldface indicates very strong autotrophic, strong shredder linkage with the riparian zone, heavy suspended of loading FPOM, or good quality of FPOM, stable substrate abundance, and an overabundance of predators with strong top-down control. Boldface identifies those values above the thresholds for that metric. Threshold values for the attributes are: P/R> 0.75, CPOM/FPOM>0.25, TFPOM/BFPOM>0.50, Channel Stability>0.50, Top-Down control>0.20.

categories, seasons, and flow permanence. This better performance of this metric, which implies a well preserved riparian zone, can be attributed to the presence of shredders, especially the freshwater crabs (*Potamonautes* sp.) and Tipulidae (Diptera), whose large bodies, even in small numbers, can disproportionately shift the P/R ratio toward greater heterotrophy when biomass is used, and the CPOM/FPOM ratio metric to identify sites as having a well-protected and functioning riparian zone, when in essence they may not (Masese et al., 2014; Sitati et al., 2021).

The findings on the use of the ratios of FFGs as surrogates of ecosystem attributes underscore potential concerns regarding the bias that may be introduced into metrics assessing ecosystem functioning in the presence of large-bodied macroconsumers, such as freshwater crabs. Although macroconsumers, including crabs, crayfish, and shrimps, are frequently categorized as shredders and are recognized for their significant contributions to organic matter decomposition in tropical streams (Crowl et al., 2001; Masese et al., 2014; Yang et al., 2021), it is important to acknowledge their omnivorous nature and diverse dietary preferences. This characteristic implies that classifying them as shredders when calculating ecosystem functioning metrics could be potentially misleading. Furthermore, macroconsumers can impose substantial top-down control on other invertebrate populations, as documented by (Lancaster et al., 2008). This aspect introduces complexities that could potentially diminish their suitability as reliable indicators of ecosystem condition and functionality.

The findings of this study indicate a heightened influence of top-down control by predators in response to increased disturbances and flow variability. Across all site categories and variations in flow permanence, predators were abundant, such as Hemiptera, Coleoptera, and Odonata. Notably, there was an increased abundance of larger-bodied odonates, beetles, and bugs, which are known for their rapid colonization and tolerance to suboptimal water conditions, including in seasonal streams and rivers (Boulton and Lake, 2008). Some coleopterans (beetles) and hemipterans (bugs) can persist in drying pools and possess high mobility, allowing them to fly away and seek refuge in larger, more permanent water bodies (May, 2019; Meena and Kachhwaha, 2024). Certain Odonata species also exhibit resilience to fluctuations in flow and temperature (Hardersen, 2008; Stewart and Samways, 1998) contributing to their prevalence and high diversity across all study sites.

The findings of this study also showed a strong correlation between channel stability and fine particulate organic matter in transport or in the water column (TFPOM) versus benthic fine particulate organic matter (BFPOM) metrics as indicators of ecological condition. These metrics consistently indicated a higher presence of FPOM in transport than that deposited on the streambed, highlighting the importance of water movement for transporting organic matter utilized by filter feeders in the study area. These findings suggest that the metric primarily relied on rheophilic taxa such as Hydropsychidae and Simuliidae, both of which are known to be sensitive to flow cessation and rely on water flow to feed. Simuliidae also serve as a primary food source for predatory Hydropsychidae such as *Cheumatopsyche* spp. (Masese and Raburu, 2017; Rivers-Moore et al., 2007).

## 6. Conclusions

This study contributes to the expanding pool of information regarding the functional arrangement of macroinvertebrates in Afrotropical streams and their efficacy as bioindicators for assessing ecosystem functionality across various disturbance levels, temporal scales, and flow permanence. The findings offer empirical support for the concept that the functional composition of macroinvertebrate communities in tropical streams is significantly influenced by seasonality, flow variability and habitat alterations caused by human disturbance. The impact of these factors is manifested through many proximal metrics, including flow permanence, organic matter standing stocks, water quality, and habitat quality. The results suggest that the presence of human-induced stressors throughout the rivers has impacted the structure and composition of macroinvertebrate FFGs. We suggest that including indicator taxa, and site-specific environmental variables in biomonitoring programs is crucial and warrants attention in subsequent investigations, given the limitations associated with drawing overarching conclusions from categorical responses across various altitudes and land use classifications. Hence, it is imperative to consider the site-specific environmental conditions while executing conservation and restoration projects in the Afromontane-savannah streams and rivers.

## CRediT authorship contribution statement

**Christine A.A. Owade:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Horst Kaiser:** Writing – review & editing, Supervision, Data curation. **Gelas M. Simiyu:** Writing – review & editing, Supervision. **Godfrey Owuor:** Writing – review & editing, Methodology, Data curation. **Evans Sicharani:** Writing – review & editing, Methodology, Investigation, Data curation. **Gretchen M. Gettel:** Writing – review & editing, Supervision, Funding acquisition, Methodology, Investigation, Conceptualization. **Frank O. Masese:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

We declare no conflict of interest.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecohyd.2025.100649.

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