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Macroinvertebrate functional feeding groups in Kenyan highland streams: evidence for a diverse shredder guild

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Abstract: Data on the functional composition of invertebrates in tropical streams are needed to develop models of ecosystem functioning and to assess anthropogenic effects on ecological condition. We collected macroinvertebrates during dry and wet seasons from pools and riffles in 10 open- and 10 closed-canopy Kenyan highland streams. We classified macroinvertebrates into functional feeding groups (FFGs), which we used to assess effects of riparian condition and season on functional organization. We used cluster analysis of gut contents to classify 86 taxa as collectors, predators, scrapers, or shredders. We classified 23 taxa whose guts were empty or had indistinguishable contents based on literature. In total, we identified 43 predators, 26 collectors, 19 scrapers, and 19 shredders. Total abundance was higher in open-canopy agricultural streams, and species richness was higher in closed-canopy forested streams. Predators and shredders dominated richness and biomass, respectively, in the closed-canopy streams. The shredders, *Potamonautes* spp. (Brachyura:Potamonautidae) and *Tipula* spp. (Diptera:Tipulidae), made up >80% of total biomass in most samples containing both. Canopy cover and litter biomass strongly influenced shredder distribution. Seven shredder taxa occurred only in closed-canopy forested streams, and few shredder taxa occurred in areas of low litter input. Collectors dominated abundance at all sites. Richness and biomass of scrapers increased during the dry season, and more shredder taxa were collected during the rainy season. Temperate keys could not be used to assign some tropical invertebrates to FFGs, and examination of gut contents was needed to ascertain their FFGs. The Kenyan highland streams harbor a diverse shredder assemblage that plays an important role in organic matter processing and nutrient cycling.

Key words: detritivore shredders, stream invertebrates, ecosystem function, gut content analysis, omnivory, trophic relationships, *Potamonautes* spp., organic matter, riparian disturbance, Afrotropical streams

Macroinvertebrates are useful surrogates of ecosystem attributes, and the relative abundance of functional groups reflects anthropogenic impact (Merritt et al. 2002, Cummins et al. 2005, Merritt and Cummins 2006). However, this approach is difficult to apply in many tropical streams where information on the functional composition of macroinvertebrate communities is limited (Boyero et al. 2009). Taxonomic keys developed for temperate-zone invertebrates (e.g., Merritt et al. 2008) often are used to assign tropical macroinvertebrates to trophic and functional feeding groups (FFGs). This approach has been successful for some taxa, but evidence is increasing that related species occurring in different regions do not share the same diets (Dobson et al. 2002, Cheshire et al. 2005, Chará-Serna et al. 2012). Even within regions, some taxa can shift their feeding in response to changes in land use and riparian condi-

tions (Benstead and Pringle 2004, Li and Dudgeon 2008). Moreover, groups, such as the case-building Trichoptera, Plecoptera, and Gammaridae, that dominate the detritivorous shredder guild in temperate streams are represented by very few taxa in tropical streams.

A number of authors have reported low diversity of shredders in streams in some tropical regions (e.g., Brazil: Gonçalves et al. 2006; Colombia: Mathuriau and Chauvet 2002; Costa Rica: Irons et al. 1994; East Africa: Tumwesigye et al. 2000, Dobson et al. 2002, Masese et al. 2009b; Hong Kong: Li and Dudgeon 2008; Papua New Guinea: Yule 1996), but others have reported diverse shredder assemblages (Australia: Cheshire et al. 2005; Malaysia: Yule et al. 2009, Salmah et al. 2013; Panama: Camacho et al. 2009). Resource availability and quality and biogeography may explain the paucity of shredders (Irons et al. 1994,

Hallam and Read 2006, Boulton et al. 2008), but growing evidence indicates that many tropical shredders have been overlooked because investigators commonly use temperate keys to assign FFGs (Dobson et al. 2002, Cheshire et al. 2005, Camacho et al. 2009). Scale and sampling effort also could be affecting taxon counts, as evidenced by the many shredder taxa (31) identified from 10 kick samples (sampling time for each ~2 min) from each of 52 forested streams in 9 catchments distributed over the Malaysian peninsula (Salmah et al. 2013).

In many parts of the world, landuse change, particularly loss of riparian vegetation, has resulted in loss of diversity and major shifts in the structural and functional organization of macroinvertebrates in streams (Allan 2004, Benstead and Pringle 2004, Jinggut et al. 2012). Loss of riparian forests increases stream temperatures through loss of shade (Baxter et al. 2005), reduces inputs of leaf litter, and affects the relative differences between wet and dry seasons (Wantzen et al. 2008). Shredder taxa are particularly vulnerable to riparian deforestation because it eliminates their main source of food. Many shredder species are adapted to cold water and may be close to their thermal maxima in the tropics. Thus, they may be especially susceptible to increases in water temperatures (Irons et al. 1994, Boyero et al. 2011a, b).

Knowledge of the functional composition of invertebrates in tropical streams is important to understand organic-matter processing, energy flow, trophic relationships, and the management actions needed to minimize the impairment of ecosystem functioning (Benstead and Pringle 2004, Dudgeon 2010, Boyero et al. 2011a, b, Ferreira et al. 2012). Research in eastern African streams has increased over the last 2 decades (Tumwesigye et al. 2000, Kasangaki et al. 2008, Minaya et al. 2013), but understanding of the functional composition of aquatic invertebrates and consequence on ecosystem structure and function is limited. Moreover, paucity of taxonomic information on most aquatic invertebrates is a major hindrance to ecological research. The only detailed information on FFGs in eastern African streams and in Afrotropical streams was published by Dobson et al. (2002), who collected samples only during the dry season and analyzed gut contents and mouthparts of 11 and 44%, respectively, of macroinvertebrate taxa collected. They classified the rest of the taxa based on temperate-zone keys. They concluded that shredders were scarce but noted that allocation of taxa to FFGs might have been incorrect because of their use of temperate-zone keys. We used gut contents to classify macroinvertebrates from 20 Kenyan highland streams to FFGs and tested their responses to riparian conditions, availability of leaf litter, and season. We used ratios of the various FFGs as indicators of ecosystem attributes and to assess the ecological health of the streams (Merritt et al. 2002, Merritt and Cummins 2006). We hypothesize that:

1) analysis of gut contents of macroinvertebrates in these streams will help refine classification of FFGs, 2) functional groups are seasonally variable, 3) riparian conditions and availability of leaf litter play important roles in the distribution and abundance of shredders, and 4) the ratios of the various FFGs can be used as surrogates for ecosystem attributes to assess the ecological condition of the streams.

METHODS
Study area
We studied mid-altitude (1900–2300 m asl), 1st- to 3rd-order streams draining the western slopes of the Mau Escarpment, which forms part of the Kenyan Rift Valley. We selected 20 sites for study (Fig. 1). The streams form the headwaters of the Mara River, which drains the tropical moist-broadleaf Mau Forest Complex (MFC) that is a source of many rivers draining into Lakes Baringo, Nakuru, and Victoria. The Mara River flows to Lake Victoria.

The MFC has been fragmented and reduced in size because of excisions for human settlement, coniferous-forest plantations, and large-scale cultivation of tea (Lovett and Wasser 1993). This activity also has resulted in a loss of riparian vegetation along streams and rivers. However, some intact forest blocks remain in protected forest reserves and national parks (Lovett and Wasser 1993, Chapman and Chapman 1996). At their lower edges, the forest blocks are protected by tea plantations that were established in the 1980s to buffer against encroachment. People living in the adjoining areas are mainly involved in semi-intensive smallholder agriculture, characterized by cash crops (mainly tea), food crops (mainly maize, beans, and potatoes), and animal husbandry. A clear transition with a shift in vegetation cover and tree species composition exists between the protected forests and inhabited and farmed areas where exotic *Eucalyptus* species dominate riparian vegetation along the streams and rivers.

Climate of the area is relatively cool and seasonal because of the altitude. The area is characterized by distinct rainy seasons and low ambient temperature that falls <10°C during the cold months of January and February. Annual precipitation ranges from 1000 to 2000 mm with a bimodal regime. Dry conditions exist in January to March and wet conditions occur from March to July and October to November, periods with long and short rains, respectively.

Field methods
We sampled macroinvertebrates along 100-m reaches once during February 2011 (dry) and once during May to July 2011 (wet) at each site. We collected 5 benthic samples at random locations in riffles and pools (total of 10 samples) with a dip net (300-μm mesh size), following Cheshire et al. (2005) and Yule et al. (2009), but with a shorter sam-
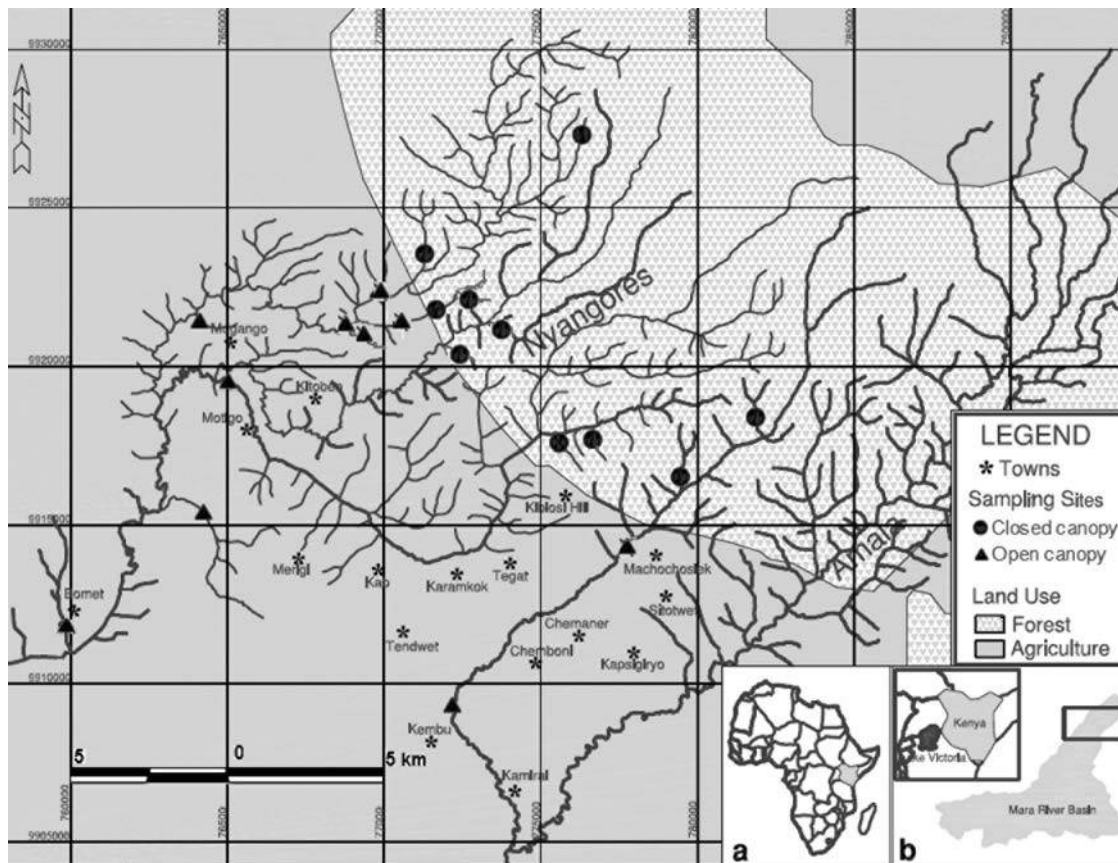
Figure 1. Map showing the study sites in the upper Mara River Basin, Kenya. The insets show the location of Kenya in Africa (a) and the location of the Mara River Basin in Kenya (b).

pling time. We disturbed an area covering ∼30 × 50 cm vigorously for 10 s, so as to avoid escape of large macro-invertebrates (Magana et al. 2012). We emptied all contents of the net into polythene bags, preserved them in 75% ethanol, and transported them to the laboratory for further processing.

At each site, we measured % in-stream canopy cover, stream width, water depth, velocity, and discharge over a 100-m reach. We measured stream width with a measuring tape on 10 transects at midpoints of 10-m intervals along the reach. On each transect, we measured water depth with a 1-m ruler at a minimum of 5 points. Velocity was measured at the same points as depth with a mechanical flow meter (General Oceanics; 2030 Flowmeter, Miami, Florida). We estimated stream discharge by the velocity–area method (Wetzel and Likens 2000). At each point, we also estimated the percentage of substratum covered by leaf litter (% leaf litter). We quantified the proportion of riffles and pools as the proportion of the 10 transects that crossed a pool or a riffle. We made concurrent measurements of pH, dissolved O_2 (DO), temperature, and electrical conductivity in situ with a YSI multiprobe water-quality meter (556 MPS; Yellow Springs Instruments, Yellow Springs, Ohio).

We used a portable Hach turbidity meter to measure turbidity (2100P ISO Turbidimeter, Hach Company, Loveland, Colorado). We washed all coarse particulate organic matter (CPOM) in dip-net samples through a 100-μm-mesh sieve to remove macroinvertebrates and inorganic materials. We dried CPOM to a constant mass at 68°C for ≥48 h, and weighed different fractions—leaves, sticks, seeds, and flowers—separately to the nearest 0.1 mg with a Sartorius balance (SECURA224-1ORU; Sartorius, Goettingen, Germany).

Laboratory analyses

After sorting macroinvertebrates from debris, we preserved them in 75% ethanol and identified them to the lowest-possible taxonomic level or morphospecies with the aid of keys in several guides (Day et al. 2002, de Moor et al. 2003a, b, Stals and de Moor 2007, Merritt et al. 2008). We measured wet mass of all macroinvertebrate individuals as an estimate of biomass. For most macroinvertebrates, we described diets from gut contents according to Cheshire et al. (2005). We analyzed gut contents of 3 (rare species) to 61 individuals per species. We squeezed

foregut contents onto a slide, mounted them in polyvinyl lactophenol, and examined them with the aid of a compound microscope equipped with a graticule with a 50 × 20 grid, which we used to estimate percentages of food types. Gut contents were divided into 6 food types: vascular plant material (VPM; particles >1 mm), CPOM (particles 50 μm–1 mm), fine particulate organic matter (FPOM; particles <50 μm), algae (ALG), animal material (AM; including whole prey and fragments of exoskeleton), and inorganic materials (IM; mainly sand and silt). For taxa for which no individual's stomach contained food items or when food items were indistinguishable, we used the literature to assign an FFG (Dobson et al. 2002, Day and de Moor 2002a, b, de Moor et al. 2003a, b, Merritt et al. 2008).

Community structure and functional composition

We described community structure and functional composition in terms of relative biomass, numerical abundance, and species richness of all taxa and 4 FFGs (collectors, predators, scrapers, and shredders) that were identified from cluster analysis and literature. We calculated ratios of the various FFGs based on numerical abundance and biomass and used them as surrogates for ecosystem attributes and for assessing the ecological health of the streams (Vannote et al. 1980, Merritt et al. 2002, Merritt and Cummins 2006): 1) balance between autotrophy and heterotrophy (production [P]/respiration [R]) index was calculated as the ratio of scrapers to (shredders + total collectors); 2) linkage between riparian inputs and stream food webs (CPOM/FPOM) was calculated as the ratio of shredders to total collectors; 3) top-down predator control was calculated as the ratio of predators to prey (total of all other groups). We did not calculate other common ratios, such as the relative dominance of FPOM in suspension compared with that deposited in the benthos and channel stability, because we did not examine mouthparts and, therefore, we could not separate collectors further into gatherers and filterers. No other investigators have published similar studies containing these ratios for Afrotropical streams, so we based our interpretations of these data on a study done in tropical southern Brazil (Cummins et al. 2005). P/R > 0.75 indicates autotrophy; CPOM/FPOM > 0.25 indicates normal shredder association linked to a functioning riparian zone; and predator/prey between 0.1 and 0.2 indicates a normal predator-to-prey balance, whereas a value >0.2 indicates an overabundance of predators.

Statistical analysis

We used 2-way analysis of variance (ANOVA) to test for differences in physical-habitat, riparian, and organic-matter variables between seasons (dry and wet) and 2 categories of canopy cover (open and closed) with canopy cover and seasons as main factors and a canopy cover × season interaction term. In cases where canopy cover and season did not influence the dependent variables, we ran 1-way ANOVAs with stream as the main factor. We arcsin ($\sqrt{[x/100]}$)-transformed habitat conditions expressed as percentages and $\ln(x + 1)$-transformed physicochemical variables, except pH, before analysis to meet assumptions for parametric tests. We calculated means for the physical-habitat measurements, including stream-size variables and water-quality variables for the 2 seasons. We allocated species/morphospecies whose gut contents were examined to a dietary group according to diet with the aid of cluster analysis (Ward's clustering method; Statistica version 7; StatSoft, Tulsa, Oklahoma) based on average percentages of each food type for all individuals examined (Cheshire et al. 2005). We confirmed differences among groups with a multivariate analysis of variance (MANOVA) with dietary group as the independent variable and the arcsin($\sqrt{[x/100]}$)-transformed percentages of each food type as the dependent variables. We then ran separate general linear models (GLMs) with single food types as independent variables, followed by Fisher's least significant difference (LSD) post hoc tests to identify groups that differed in gut contents for each food type.

We compared total abundance, biomass, and taxon richness of all taxa, shredders, and nonshredders in litter samples between seasons (dry and wet) and 2 categories of canopy cover (open and closed) with 2-way ANOVA with season and canopy cover as the main factors and a season × canopy cover interaction. We used 60% canopy cover as the threshold between open- and closed-canopy sites. We used Spearman's correlation analysis to test for correspondence among macroinvertebrate structural and functional attributes and physical-habitat conditions that represented availability of organic matter (% canopy cover, % leaf litter, litter biomass), water quality (turbidity), and stream size (discharge, stream width and depth). To assess how shredders responded to environmental characteristics in the streams, we used analysis of covariance (ANCOVA) with litter biomass, % canopy cover, % leaf litter, discharge, and stream width and depth as covariates to explore variation in shredder abundance, biomass, and taxon richness between seasons and canopy-cover categories and among streams. We regarded differences as significant at $p < 0.05$ and highly significant at $p < 0.01$ and $p < 0.001$.

RESULTS
Physical-habitat conditions

Season affected DO, discharge, and depth, whereas canopy cover affected temperature, % leaf litter, litter biomass, and turbidity (all $p < 0.05$). Both season and canopy cover influenced water-quality variables, but only canopy cover affected organic-matter characteristics. Closed-canopy sites were in forested catchments where human and livestock activities were limited, whereas open-canopy streams were in agricultural catchments. Most closed-canopy streams

were highly shaded (>70% canopy cover), whereas in most open-canopy streams, canopy cover was <50% and discontinuous in sections frequented by livestock and people. Closed-canopy streams were cooler (temperature < 15°C) and had lower turbidity (<60 NTU) than open-canopy sites (Table 1). Ranges of conductivity differed between cover types, and were 44.0 ± 3.9 to 97.4 ± 2.3 µS/cm in closed-canopy streams and 56.7 ± 2.1 to 148.0 ± 2.0 µS/cm in open-canopy streams. However, the means were not significantly different. Season and canopy cover had no interactive effect on any variable tested.

We observed considerable variability among streams. For instance, conductivity and turbidity were variable among individual streams regardless of whether the streams had closed or open canopies (Table 1). The lowest DO concentration (4.6 ± 2.1 mg/L) was recorded in an open-canopy stream in an agricultural catchment. The minimum DO in a closed-canopy forested stream was 5.7 ± 1.0 mg/L. pH was similar among streams and did not differ between canopy-cover categories (overall range: 6.5 ± 0.8–8.1 ± 0.6).

Dietary analysis

We identified 6 dietary groups (Fig. 2). Food items overlapped between groups III and IV and between groups V and VI, but groups differed in their use of food items (MANOVA, Wilk's $\lambda_{30,302}$ = 0.0002, p < 0.0001). FPOM and CPOM were eaten by 77 and 75 taxa, respectively (Appendix S1). Only 41 taxa included animals in their diets, whereas 51 and 46 taxa ate VPM and algae, respectively. We classified 23 taxa (14 predators, 1 shredder, 8 collectors, and 2 scraper) based on literature because their guts were empty or food items were indistinguishable (Appendix S2).

Dietary groups differed in gut contents for every food item (Fig. 3A–F). Group I mostly contained predators, and an average of 85.5% of their gut contents consisted of animal material. This group had the highest number of taxa (24) and included 7 Diptera, 8 Odonata, 2 Hemiptera, 4 Trichoptera, and 1 Coleoptera, Ephemeroptera, and Plecoptera each. Group II had 14 taxa that were specialist shredders. An average of 74% and 21% of their gut contents were VPM and CPOM, respectively. This group included 7 Trichoptera, 3 Diptera, and 2 Coleoptera and Ephemeroptera. Group III, with 16 taxa, consisted mainly of collectors. An average of 69% of their gut contents was FPOM, 7% was VPM, and 12% was algae. This group included 6 Ephemeroptera, 4 Oligochaeta, 4 Diptera, and 2 Trichoptera. Group IV had 17 taxa and consisted mainly of scrapers. Guts of these taxa contained an average of 36% algae, 34% FPOM, and 21 and 14% inorganic material and CPOM, respectively. This group included 6 Ephemeroptera, 5 Trichoptera, 3 Coleoptera, and 1 Diptera, Gastropoda, and Lepidoptera each. Group V had 9 taxa that were mainly predators and generalist shredders. Their gut

contents consisted of 42% animal material, 26% VPM, and 20% CPOM. This group included 5 Diptera, 2 Decapoda (crabs), 1 Coleoptera, and 1 Lepidoptera. Group VI had 6 taxa and consisted of generalist collectors. The group contained 1 Decapoda (shrimp, Atyidae) and 5 Trichoptera (Hydropsychidae). Their guts contained 49% CPOM, 18% FPOM, and 15% VPM.

The allocation of taxa to FFGs was as follows. Predators were all taxa in group I and those in group V whose guts contained >50% animal material. Shredders were all taxa from group II and some taxa of group V (those whose gut contained >50% VPM and CPOM combined). Collectors were species from groups III and VI. Scrapers were all taxa in group IV. Some taxa in group III were classified as collector/scrapers because their guts contained >20% algae. Including invertebrates whose guts were not analyzed, a total of 44 predators, 27 collectors, 18 scrapers, and 19 shredders were collected in the study area (Appendix S2). Shredder taxa included 7 Trichoptera (3 Leptoceridae, 2 Pisuliidae, 1 Calamoceratidae, and 1 Lepidostomatidae), 5 Diptera (4 Tipulidae and 1 Limoniidae:Limoniinae), 2 Ephemeroptera (Baetidae), 2 Coleoptera (1 Elmidae:Larainae and 1 Curculionidae), 2 Decapoda (2 crabs, Potamonautidae) and 1 Lepidoptera (Crambidae).

Community structure and functional organization

We collected a total of 20,757 individuals from 109 taxa during the study (81 and 93 taxa during the dry and wet seasons, respectively). Total abundance was higher during the wet than dry season (2-way ANOVA, $F_{1,1}$ = 11.01, p < 0.01) but did not differ between canopy types. Collectors were numerically dominant during both seasons regardless of canopy cover (Fig. 4A). Shredder abundance was lower at open- than in closed-canopy sites, whereas scraper abundance was higher at open- than closed-canopy sites during the dry season. *Lepidostoma* sp. was the most widespread and abundant shredder. In closed-canopy sites, its abundance was 10.3 ± 2.4. Crabs were the next most abundant (9.3 ± 5.0), followed by tipulids (3.3 ± 3.4). In open-canopy sites, tipulids were most abundant (13.67 ± 8.67), followed by *Lepidostoma* sp. (6.2 ± 1.6).

Total macroinvertebrate biomass was higher at closed- than open-canopy sites ($F_{1,1}$ = 4.16, p < 0.05), but did not differ between seasons. Appendix S3 presents combined dry and wet seasons biomass data of macroinvertebrate taxa per sampling site. Collectors dominated standing biomass at open-canopy sites during the dry and wet seasons (Fig. 4B). Shredder biomass was lower at open- than closed-canopy sites, except during the dry season when there was an increase in biomass at open-canopy sites. Scraper biomass was higher at open-canopy sites during the dry than the wet season. Crabs and tipulids contributed >80% of the total biomass at most closed-canopy sites. At open-canopy sites, crabs were rarely encountered,

Table 1. Geographical location and mean (± SE) values for physicochemical characteristics of the study sites. Means are given for variables measured more than once during the dry and wet seasons. % litter = % of substrate covered by leaf litter, # indicates closed-canopy streams.

| Sites	Altitude (m asl)	Depth (m)	Width (m)	Discharge (m³/s)	Stream order	% canopy cover	% leaf litter	% riffle	% pool	pH	DO (mg/L)	Conductivity (µS/cm)	Turbidity (NTU)	Temperature (°C)
Chepkosiom I[#]	2191	0.11 ± 0.05	1.8 ± 0.6	0.01 ± 0.02	1st	85	85	70	30	7.6 ± 0.1	5.7 ± 1.0	97.4 ± 2.3	8.5 ± 1.5	14.6 ± 0.3
Issey I[#]	2146	0.28 ± 0.15	3.1 ± 0.5	0.08 ± 0.03	2nd	70	60	70	30	7.2 ± 0.1	8.3 ± 0.3	60.5 ± 3.6	55.3 ± 8.9	14.4 ± 0.3
Issey II[#]	2087	0.16 ± 0.09	4.1 ± 0.7	0.12 ± 0.04	2nd	65	68	60	40	7.2 ± 0.1	8.2 ± 0.6	74.2 ± 14.2	56.9 ± 21.3	17.3 ± 3.0
Ngatuny[#]	2063	0.25 ± 0.7	4.3 ± 0.5	1.25 ± 0.90	3rd	60	50	65	35	6.5 ± 0.8	7.9 ± 0.3	50.0 ± 2	40.4 ± 15.6	13.6 ± 0.6
Philemon[#]	2286	0.08 ± 0.03	2.2 ± 0.2	0.01 ± 0.004	1st	90	80	80	20	7.3 ± 0.5	6.6 ± 0.5	44.0 ± 3.9	23.4 ± 8.4	12.4 ± 0.3
Sambambwet[#]	2096	0.07 ± 0.02	2.1 ± 0.2	0.01 ± 0.005	1st	90	90	55	45	7.1 ± 0.8	7.7 ± 0.3	91.0 ± 4.2	5.8 ± 1.6	12.2 ± 0.4
Chepkosiom II[#]	2060	0.12 ± 0.02	2.5 ± 0.4	0.08 ± 0.01	2nd	80	75	40	60	7.0 ± 0.6	6.8 ± 0.9	75.3 ± 0.3	10.2 ± 2.4	13.4 ± 0.6
Saramek[#]	2091	0.19 ± 0.11	1.9 ± 0.4	0.04 ± 0.12	2nd	80	85	60	40	6.9 ± 0.5	7.3 ± 0.4	63.9 ± 0.9	35.6 ± 13.9	13.8 ± 0.8
Katasiaga[#]	2020	0.19 ± 0.11	1.4 ± 0.4	0.16 ± 0.03	2nd	70	70	65	35	7.3 ± 0.2	6.9 ± 1.1	72.7 ± 3.2	41.5 ± 13.5	14.1 ± 0.6
Mosoriot[#]	2058	0.15 ± 0.05	1.5 ± 0.3	0.12 ± 0.10	2nd	80	80	55	45	7.1 ± 0.2	6.6 ± 1.4	66.3 ± 2.3	9.8 ± 4.8	13.1 ± 0.4
Chepkosiom III	2056	0.12 ± 0.05	3.3 ± 0.3	0.11 ± 0.09	2nd	40	50	50	50	6.9 ± 0.3	4.6 ± 2.1	56.7 ± 2.1	159.5 ± 117.5	21.6 ± 0.8
Issey III	2030	0.21 ± 0.13	2.3 ± 0.7	0.08 ± 0.06	3rd	50	48	40	60	8.1 ± 0.6	7.0 ± 0.1	123.5 ± 6.5	180.0 ± 56.8	19.2 ± 0.4
Issey IV	1982	0.18 ± 0.08	3.7 ± 0.5	0.12 ± 0.10	3rd	50	59	40	60	7.6 ± 0.8	6.4 ± 0.4	148.0 ± 2.0	277.6 ± 56.2	20.6 ± 0.9
Keno	2041	0.07 ± 0.04	3.2 ± 0.4	0.10 ± 0.01	2nd	35	40	55	45	7.0 ± 0.6	5.6 ± 0.9	90.2 ± 8.3	124.1 ± 15.9	16.2 ± 1.8
Mugango	1965	0.23 ± 0.18	5.8 ± 4.2	0.46 ± 0.22	3rd	40	40	55	45	7.3 ± 0.4	8.3 ± 0.5	89.0 ± 2.3	94.6 ± 27.8	15.6 ± 0.7
Nyangores	2043	0.22 ± 0.02	4.6 ± 0.8	0.72 ± 0.30	3rd	45	45	65	35	7.3 ± 0.7	7.5 ± 0.9	58.4 ± 4.4	49.3 ± 29.3	17.5 ± 3.5
Kenjirbei	1979	0.11 ± 0.03	5.5 ± 0.5	0.15 ± 0.12	3rd	45	50	55	45	7.4 ± 0.3	7.2 ± 1.3	78 ± 2.3	132.6 ± 23.4	17.2 ± 0.4
Borowet	2050	0.09 ± 0.03	2.1 ± 0.8	0.02 ± 0.13	1st	40	30	55	45	7.1 ± 0.4	5.6 ± 1.2	130.3 ± 5.2	194 ± 56.7	17.6 ± 0.5
Tenwek	1953	0.15 ± 0.3	1.3 ± 0.2	0.04 ± 0.02	2nd	50	65	40	60	6.9 ± 0.5	7.2 ± 0.4	75.3 ± 5.9	124.0 ± 30.7	19.3 ± 1.4
Bomet	1911	0.30 ± 0.15	4.6 ± 0.9	0.10 ± 0.10	1st	40	20	55	45	7.1 ± 0.4	6.8 ± 1.5	87.3 ± 9.7	160.2 ± 44.9	19.9 ± 0.2
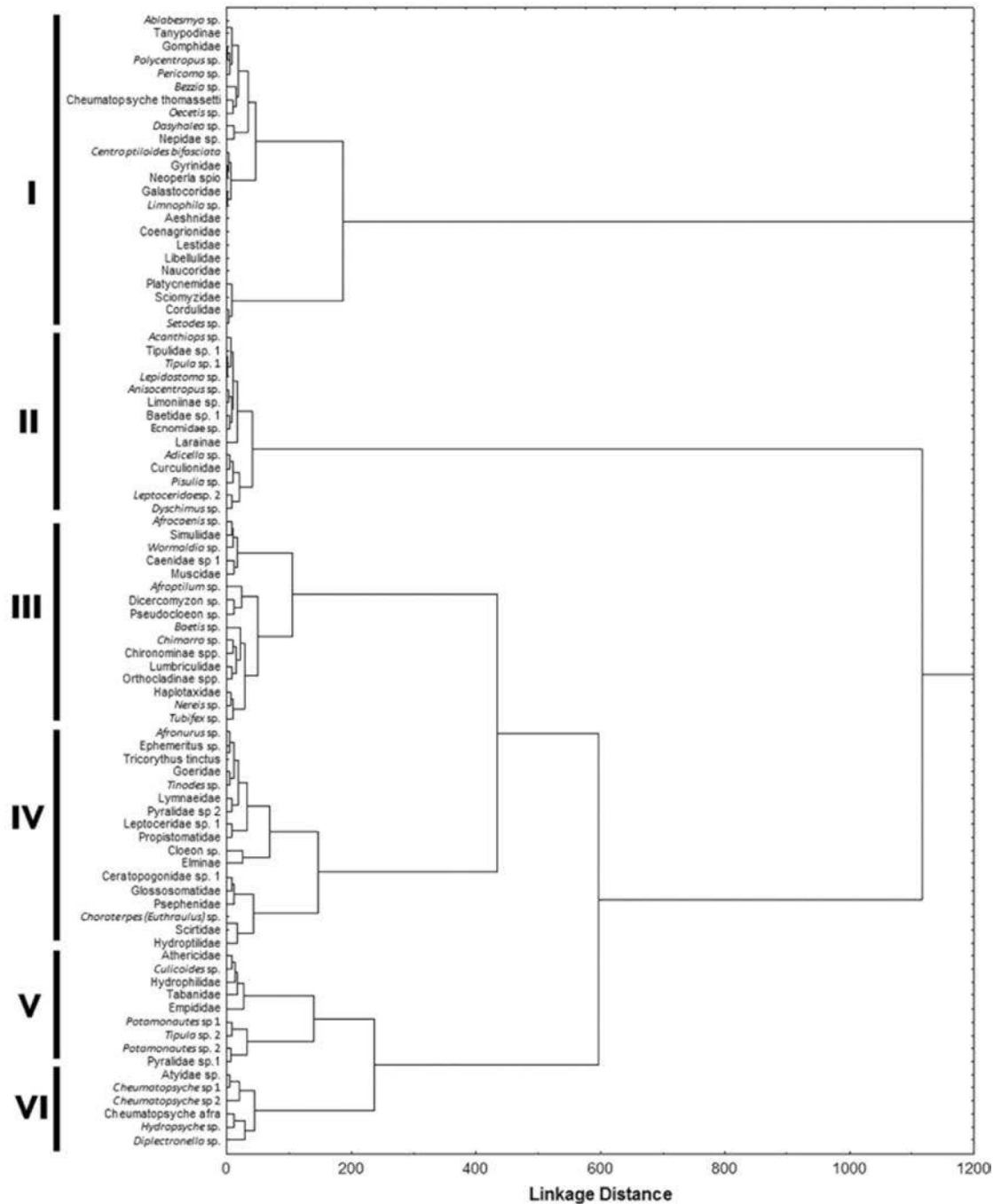
Figure 2. Cluster diagram (Ward's method) for macroinvertebrate species based on the proportion of different food types in their guts. Group I consists of predators, group II of specialist shredders, group III of mostly collectors, group IV of mostly scrapers, group V of predators and generalist shredders, and group VI of generalist collectors.

but tipulids occurred at all sites and contributed up to 60% of shredder biomass in the absence of crabs. Large crabs (3536.4 ± 157.2 mg wet mass, up to 56 mm carapace width) and tipulids (59.1 ± 28.9 mg wet mass, up to 54 mm long) were collected in the study area.

Taxon richness was higher at closed- than open-canopy sites ($F_{1,1} = 3.02$, $p < 0.05$) but did not differ between seasons. At open- and closed-canopy sites, richness was dominated by predators during the wet season and by collectors during the dry season (Fig. 4C). The number of collector ($F_{1,1} = 6.39$, $p < 0.05$) and scraper taxa ($F_{1,1} = 9.63$, $p < 0.01$) differed between seasons, and the number of shredder taxa ($F_{1,1} = 8.39$, $p < 0.001$) differed between canopy types. A season × canopy-type interaction affected
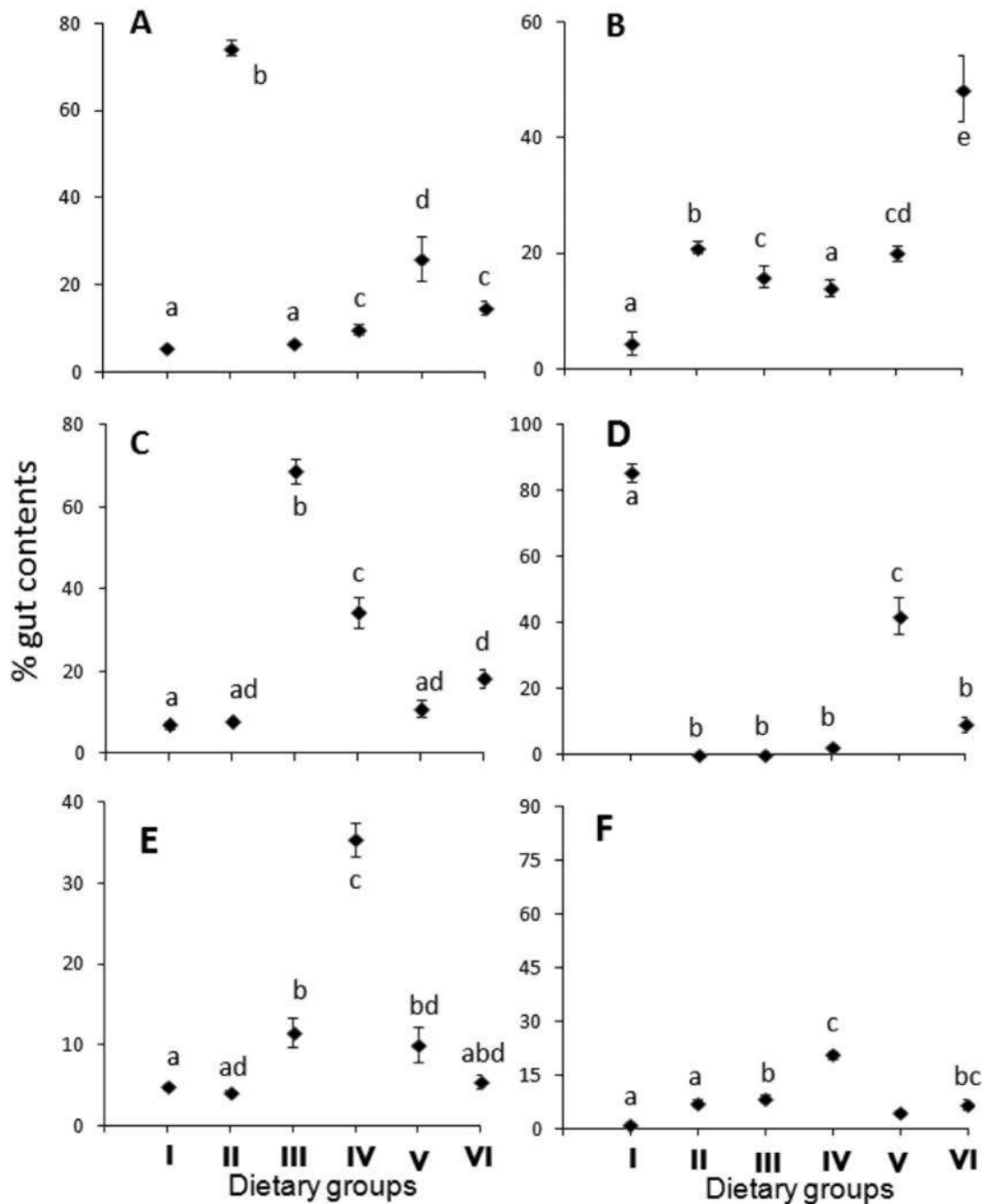
Figure 3. Mean (±1 SE) percentages of vascular plant material (VPM; >1 mm) (A), coarse particulate organic matter (CPOM; 50 μm–1 mm) (B), fine particulate organic matter (FPOM; <50 μm) (C), animal material (AM) (D), algae (ALG) (E), and inorganic matter (IM) (F) in the gut contents of individuals belonging to dietary groups I–VI. Points with the same lowercase letter are not significantly different among dietary groups ($p < 0.05$). See Fig. 2 for a description of dietary groups.

the number of shredder ($F_{1,1} = 3.94$, $p < 0.05$) and scraper ($F_{1,1} = 2.96$, $p < 0.05$) taxa. During the rainy season, more shredder taxa were found at closed- than open-canopy sites, whereas fewer scraper taxa were found at open- than at closed-canopy sites.

Macroinvertebrate structural and functional attributes were related to organic matter characteristics (% canopy cover, % leaf litter, and litter biomass), water-quality variables (turbidity and conductivity), and measures of stream size (discharge and width) (Table 2). Total abundance (num-

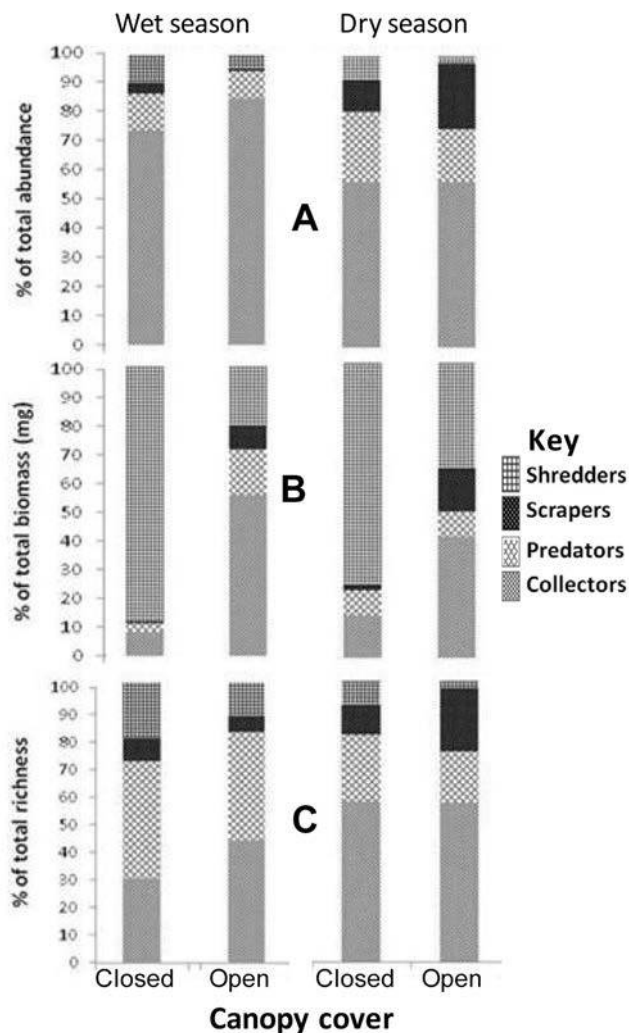Figure 4. Percentage composition of functional feeding groups in terms of relative abundance (A), biomass (B), and species richness (C) for closed- and open-canopy streams during the wet and dry seasons.

ber of individuals/sample) and collectors were favored by high turbidity and conductivity in open-canopy agricultural streams. In contrast, abundances of predators and shredders were negatively related to the same variables but were positively related to % leaf litter, canopy cover, and litter biomass. Scraper abundance was negatively associated with canopy cover, turbidity, and % leaf litter and positively associated with discharge and width. Shredder abundance, biomass, and richness differed among streams and between canopy types. Litter biomass was significantly associated with shredder richness and marginally related to shredder biomass (p = 0.08) (Table 3). Season affected shredder biomass and richness, whereas the influence of % leaf litter on shredder biomass and richness was marginally significant (p = 0.06 and p = 0.06, respectively). Stream size had a minimal effect on shredder distribution and abundance, and discharge only influenced species richness.

Ecosystem attributes

P/R ratios based on abundance and biomass data indicated that 9 of 10 closed-canopy and 7 of 10 open-canopy streams were heterotrophic (P/R < 0.75; Table 4). Use of biomass data yielded stronger indications of heterotrophy than use of abundance data in closed-canopy streams. The effect was reversed in most open-canopy streams. The CPOM/FPOM ratio addressed the integrity of the riparian zone. Abundance data indicated that 6 closed- and 8 open-canopy streams did not have a functioning riparian zone, but biomass data indicated that all streams except 1 open-canopy stream had a functioning riparian zone (CPOM/FPOM > 0.75). Abundance data indicated that 4 closed- and 5 open-canopy streams had an overabundance of predators (predator/prey > 0.2; Table 4). Biomass data indicated that 3 closed- and 5 open-canopy streams had an overabundance of predators.

DISCUSSION
Gut analyses

Our study is one of the few studies in the Afrotropics in which the analysis of gut contents of a large number of stream macroinvertebrates was used to assign taxa to FFGs (Palmer et al. 1993, Dobson et al. 2002). Use of diet rather than morphological and behavioral adaptations for acquiring food to classify macroinvertebrates into FFGs has been questioned because of ontogenic shifts and opportunistic feeding (Palmer et al. 1993 and references therein). Nevertheless, analysis of gut contents enabled us to classify taxa into collector, scraper, shredder, and predator FFGs and has improved our knowledge of the functional composition and trophic relationships among macroinvertebrates in tropical streams. Our work is valuable because growing evidence indicates that taxonomically related species may have different diets in tropical and temperate areas, and discrepancies have been reported when temperate keys have been used to assign tropical-stream invertebrates to FFGs (Yule 1996, Dobson et al. 2002, Cheshire et al. 2005).

Taxonomic fidelity to particular diets was not evident for most taxonomic groups in our study, and omnivory was prevalent in many taxa. Odonata was the only order that contained specialist predators, although Gomphidae fed on substantial amounts of detritus. The Leptoceridae, represented by specialist shredders elsewhere (Cheshire et al. 2005), included scrapers and predators. The Ephemeroptera and Hydropsychidae (Trichoptera), which usually are collector–gatherers/scrapers and collector–filterers, respectively (Merritt et al. 2008), included predators. *Afroptilum* sp., *Baetis* sp., *Dicercomyzon* sp., and *Pseudocloeon* sp. (Ephemeroptera) showed no preference for a particular food type(s) and were difficult to place into a single FFG. They fed on fine amorphous detritus that could not be easily differentiated, so we had to classify them as either

Table 2. Spearman's correlation analysis among macroinvertebrate community attributes and stream characteristics that represent organic matter and riparian conditions (% canopy cover, % leaf litter, and litter biomass), water quality (turbidity and conductivity), and stream size (discharge, depth, and width). Values in bold are significant at $p < 0.05$.

Community attributes	Physical habitat characteristics							
	% canopy cover	% leaf litter	Litter biomass (g/m^2)	Turbidity (NTU)	Conductivity $(\mu S/cm)$	Discharge (m^3/s)	Depth (m)	Width (m)
Total abundance	−0.20	−0.14	0.10	**0.33**	**0.33**	−0.02	0.19	0.01
Shredder abundance	**0.37**	**0.33**	−0.05	−0.21	0.18	0.06	0.02	−0.11
Nonshredder abundance	0.21	0.28	−0.12	0.14	**0.45**	0.00	0.04	−0.15
No. total taxa	0.26	0.22	0.12	−0.22	−0.20	0.17	−0.08	−0.17
No. collectors	**−0.35**	**−0.35**	−0.15	**0.46**	0.12	0.00	0.11	−0.11
No. predators	**0.35**	**0.34**	0.10	**−0.33**	−0.22	−0.08	−0.24	−0.16
No. scrapers	0.02	−0.06	−0.04	**−0.38**	−0.22	**0.36**	−0.18	0.23
No. shredders	**0.40**	**0.37**	**0.32**	**−0.31**	**−0.41**	**−0.33**	0.16	−0.01
% collector individuals	**−0.31**	**−0.41**	−0.14	0.23	**0.43**	0.04	−0.01	0.11
% predator individuals	0.18	0.11	−0.02	**−0.34**	**−0.31**	0.04	−0.18	0.27
% scraper individuals	**−0.39**	−0.28	**−0.31**	0.11	−0.19	**0.37**	−0.01	**0.33**
% shredder individuals	**0.31**	0.24	0.25	**−0.34**	−0.07	0.07	−0.07	−0.10
Collector biomass	−0.30	−0.12	−0.13	0.21	0.16	−0.02	0.01	−0.02
Predator biomass	−0.21	−0.08	−0.01	0.13	0.00	0.15	0.01	0.18
Scraper biomass	−0.30	−0.15	−0.05	**−0.45**	0.05	−0.02	−0.06	0.09
Shredder biomass	**0.34**	0.17	0.13	0.13	−0.13	0.07	−0.01	0.09

collectors or scrapers. In Madagascar, *Afroptilum* sp. rely more on algal C sources in agricultural streams (where they also have much higher biomass) and amorphous detritus in forested streams (Benstead and Pringle 2004). Omnivory in Crambidae sp. 2, *Potamonautes* sp. 1, *Potamonautes* sp. 2, and *Tipula* sp. 2 indicates that they are facultative detrital shredders. For example, *Potamonautes* spp. consumed high proportions of leaf litter, but they also forage in the riparian zone and adjoining forests to hunt for prey to supplement their diet of leaf litter (Abdallah et al. 2004, Lancaster et al. 2008). During our study, we observed several crabs hiding under rocks and in crevices in the riparian zone, and during the rainy season, we captured a gravid female in the riparian zone, 10 m from the stream.

Shredder diversity and abundance

Diverse shredder guilds have been reported from tropical areas where few taxa were expected (Cheshire et al. 2005, Yule et al. 2009, Chará-Serna et al. 2012, Salmah et al. 2013). We also found that shredders were diverse (19 taxa) and abundant in closed-canopy forested streams and made up ~17 and 20% of all taxa, and 75 and 84% of total macroinvertebrate biomass during the dry and wet seasons, respectively. This result differs strongly from results of previous studies in eastern Africa in which, ac-

cording to Tumwesigye et al. (2000), Dobson et al. (2002), Abdallah et al. (2004), and Masese et al. (2009b), 6% of all individuals, 17% (5 of 36 taxa), 7% (3 of 41 taxa), and 11% of taxa (6 of 56 taxa), respectively, were shredders. We see 4 possible explanations for the large number of shredder taxa recorded in our study. First, earlier investigators placed taxa into FFGs based solely on literature for temperate streams, except that Dobson et al. (2002) also examined mouthparts of 44% and gut contents of 11% of taxa collected. Dobson et al. (2002) noted that they may have allocated taxa to FFGs incorrectly when they found that a tropical African baetid, *Acanthiops* sp., was a shredder (baetids in northern temperate streams are usually scrapers or collector–gatherers; e.g., Merritt et al. 2008). This kind of discrepancy suggests that tropical shredders may be overlooked (misclassified) when temperate-stream keys are used (Camacho et al. 2009). Second, the coarse taxonomic resolution (mostly to family) used by Dobson et al. (2002) also contributed to the low number of shredder taxa identified. Examples in Dobson et al. (2002) include a shredder, Larainae sp., that was classified with scrapers as part of Elmidae, 3 leptocerids and 4 tipulids that were each grouped under 1 family as Leptoceridae and Tipulidae, respectively. Third, the abundance and distribution of shredders in tropical streams can be temporally and spatially variable (Pearson et al. 1989, Cheshire et al. 2005, Camacho et al. 2009), and the study by Dobson

Table 3. Results of analysis of covariance showing variation of shredder abundance, biomass, and species richness with season and stream and the covariates canopy cover, litter biomass, % leaf litter, discharge, and stream depth and width. * = $p < 0.05$.

Source or variation	df	MS	F	p
Shredder abundance				
Stream	23	38019.8	7.33	**<0.01***
Season	1	34342.6	3.08	0.10
Canopy	1	28582.3	18.62	**<0.01***
Litter biomass	1	20421.4	1.33	0.27
% leaf litter	1	8384.6	0.48	0.49
Discharge	1	10852.9	0.63	0.43
Depth	1	2099.1	0.12	0.73
Width	1	4027.1	0.23	0.63
Error	26	1759.3		
Shredder biomass				
Stream	23	65.5	4.17	**0.03***
Season	1	71.6	5.45	**0.03***
Canopy	1	75.8	15.69	**0.02***
Litter biomass	1	40.1	3.05	0.08
% leaf litter	1	45.6	3.67	0.06
Discharge	1	37.8	2.87	0.10
Depth	1	24.5	1.86	0.18
Width	1	6.3	0.48	0.49
Error	26	13.14		
Shredder species richness				
Stream	23	7.3	6.43	**0.02***
Season	1	9.5	8.41	**0.01***
Canopy	1	27.1	23.94	**<0.01***
Litter biomass	1	11.3	9.49	**<0.01***
% leaf litter	1	4.4	3.99	0.06
Discharge	1	32.2	28.43	**<0.01***
Depth	1	0.4	0.38	0.54
Width	1	0.2	0.14	0.71
Error	26	7.51		

et al. (2002) did not consider seasonal changes. The potential for higher diversity and abundance of macroinvertebrate taxa during the rainy than the dry season cannot be ignored. For instance, as part of their life-history strategies, some tropical insects mature and emerge during the rainy season (Mathooko 2001, Jacobsen et al. 2008). Moreover, water quality in some streams deteriorates during the dry season (Masese et al. 2009a). Most shredder taxa in our study occurred in low abundance, so a seasonal sampling scheme is needed to avoid missing important taxa. For example, we collected 4 of the 19 shredders identified only during the rainy season. Last, we adjusted our sampling method to ensure that we would capture large invertebrates that could avoid capture by standard sampling methods. Our rapid sampling method enabled capture of many crabs in closed-canopy streams where they were

most prevalent. Crabs (*Potamonautes* spp.) occurred in some streams sampled by Dobson et al. (2002), but many were not captured by the method they used. Later studies have revealed high density and biomass of crabs in Kenyan highland streams (Dobson et al. 2007, Magana et al. 2012).

Most of the shredder taxa identified in our study are represented in temperate streams. Baetids (Ephemeroptera), crabs (Potamonautidae), and Pisuliidae (Trichoptera) are the exceptions. The 2 baetid shredders so far identified in Kenyan streams (Dobson et al. 2002, this study), the genera *Barba* (Leptophlebiidae) from Papua New Guinea (Yule 1996), and *Atalophlebia* (Leptophlebiidae) from the Australian tropics (Cheshire et al. 2005) are shredders, whereas members of these groups are mostly collector–gatherers or scrapers in temperate streams (e.g., Merritt et al. 2008). Crabs are widespread in African streams where

Table 4. Mean values of stream ecosystem attributes derived from ratios of macroinvertebrate functional feeding groups in the upper Mara River basin, Kenya. Ratios are based on numerical abundance and biomass of functional feeding groups (FFGs). The autotrophy to heterotrophy (production [P]/respiration [R]) index was calculated as the ratio of scrapers to (shredders + total collectors). Coarse particulate organic matter (CPOM)/fine particulate organic matter (FPOM) is the ratio of shredders to total collectors. Top-down predator control is the ratio of predators to all other FFGs. [#] indicates closed-canopy streams. Boldface indicates autotrophy, functioning riparian zone, or an over-abundance of predators with a strong top-down control.

| | Ecosystem attributes | | | | | |
| | Abundance | | | Biomass | | |
Sites	P/R	CPOM/FPOM	Top-down predator control	P/R	CPOM/FPOM	Top-down predator control
Chepkosiom I[#]	0.13	0.14	**0.22**	0.59	**1.05**	**0.39**
Issey I[#]	0.52	**0.29**	0.12	0.01	**36.69**	0.08
Issey II[#]	0.27	0.05	0.05	0.03	**20.59**	0.01
Ngatuny[#]	**1.61**	**0.37**	0.18	0.07	**13.65**	0.03
Philemon[#]	0.49	**0.29**	**0.31**	0.25	**0.26**	0.10
Sambambwet[#]	0.25	**0.33**	**0.23**	0.03	**11.65**	**0.25**
Chepkosiom II[#]	0.52	0.14	**0.29**	0.31	**3.65**	**0.26**
Saramek[#]	0.28	0.21	0.19	0.01	**20.02**	0.03
Katasiaga[#]	0.51	0.12	0.18	0.05	**19.82**	0.04
Mosoriot[#]	0.37	0.17	0.08	0.06	**4.55**	0.15
Chepkosiom III	0.62	0.03	0.13	**1.35**	**0.87**	0.09
Issey III	0.38	0.01	0.11	0.56	0.03	**0.35**
Issey IV	0.15	0.01	0.03	0.23	**0.47**	0.15
Keno	**0.97**	**0.40**	**0.31**	0.04	**32.89**	0.02
Mugango	**1.28**	**0.43**	0.05	0.58	**6.91**	0.02
Nyangores	**1.53**	0.09	**0.25**	**0.85**	**5.02**	**1.00**
Kenjirbei	0.43	0.05	**0.23**	0.19	**0.57**	**1.06**
Borowet	0.48	0.09	**0.40**	**0.85**	**1.76**	**0.29**
Tenwek	0.20	0.01	0.01	0.29	**0.37**	0.14
Bomet	0.68	0.10	**0.37**	**0.79**	**0.29**	**3.00**

they display high endemism (Dobson 2004) and are responsible for rapid breakdown of leaf litter (Hill and O'Keeffe 1992, Moss 2007). On the other hand, key shredder taxonomic groups in temperate streams were either poorly represented or absent in our streams. Plecoptera, which is diverse with many shredder species in temperate streams, was depauperate in our streams and was represented by only 1 species (*Neoperla spio*, Perlidae), which is a predator. Decapod shrimps are major shredders in temperate and some tropical streams, but the single Atyidae species in our streams is a collector. Common shredder taxa in temperate streams that have been found in other tropical streams, but not in our study, include Limnephilidae, Sericostomatidae, Peltoperlidae, Leuctridae, and Nemouridae (Cheshire et al. 2005, Yule et al. 2009, Salmah et al. 2013).

Most remarkable were the large sizes, high densities, and high biomasses of *Potamonautes* spp. and *Tipula* spp. in closed- and open-canopy streams, respectively. Large size seems to be common feature of *Potamonautes* spp. in east African highland streams (Abdallah et al. 2004, Dobson 2004, Dobson et al. 2007, Moss 2007) and is important for the breakdown of recalcitrant leaves in tropical streams (Wantzen and Wagner 2006, Moss 2007, Yule et al. 2009). No detailed analysis has been done of nutritional quality of riparian vegetation in highland streams in Kenya, but most tree species have waxy leaves that are not favorable to shredders (Dobson et al. 2002).

Physical-habitat effects

Season influenced structural and functional organization of macroinvertebrates by accentuating differences in water quality and habitat characteristics. The abundance of most taxa was considerably lower in the dry than in the wet season (see also Harrison and Hynes 1988, Mathooko and Mavuti 1992, Masese et al. 2009a). However, in other studies of tropical streams, abundance increased during

the dry season (Tumwesigye et al. 2000, Arimoro et al. 2012). Flow reduction during the dry season contributes to seasonal variability in physicochemical conditions that could influence macroinvertebrate communities. For instance, we recorded the lowest DO and highest conductivity during the dry season in open-canopy streams. These streams were in areas frequented by people and livestock and were subject to sedimentation and input of nutrients and organic wastes during spates. Thus, algal food sources for scrapers probably were smothered during the wet season. An increase in the number of scrapers in these streams during the dry season probably was related to increased algal availability as a result of reduced turbidity.

Canopy cover strongly influenced the distribution and abundance of scrapers and shredders. Nine of the 19 shredder taxa found during our study occurred only in closed-canopy streams. Crabs do occur in open-canopy streams in agricultural areas, but their abundance is very low (occasionally 1 or 2 mature individuals were captured). The importance of canopy cover is supported by observations that reproduction in crabs is more successful in forest streams which serve as nurseries from which adults migrate downstream (Dobson et al. 2007). Changes in water temperature, conductivity, and litter input probably contributed to the skewed occurrence of shredder taxa in closed-canopy streams. Open-canopy streams were warmer and leaf-litter input was lower and dominated by the exotic *Eucalyptus* spp. than closed-canopy streams where riparian vegetation was speciose. Water temperature and leaf-litter characteristics are globally important factors affecting shredder abundance and diversity (Boyero et al. 2011a, b).

Difference in stream size as determined by discharge, width, and depth were a reflection of human activities both at the reach and catchment scales. Open-canopy streams were flashy resulting in higher discharge levels during spates. In-stream human and livestock activities also widened channels in open-canopy streams. These human- and livestock-induced changes in stream size are different from the natural increases in stream order whose effects on FFGs were not evident in the 1st-3rd order streams considered in this study.

Ecosystem attributes

We used the ratio of scrapers to (shredders + total collectors) as a surrogate for P/R, and applied thresholds proposed by Cummins et al. (2005) for tropical Brazilian streams to the P/R ratios in our streams. Most streams were heterotrophic, but open-canopy streams in agricultural areas tended to be autotrophic. Some open-canopy streams, such as Issey III, Issey IV, and Tenwek, receive organic pollution from livestock. These streams had high abundances of collectors (oligochaetes and Chironominae), which shifted abundance-based P/R ratios in these potentially autotrophic streams toward heterotrophy. Most

shredders in the study area, such as crabs, tipulids, and trichopterans (*Pisulia* sp. and *Lepidostoma* sp.), were large. The presence of large shredders, especially crabs (*Potamonautes* spp.), in closed-canopy and in some open-canopy agricultural streams shifted biomass-based P/R ratios toward greater heterotrophy.

The influence of shredder body size also was evident in the CPOM/FPOM ratio that addresses the integrity of the riparian zone. When biomass data were used, all closed-canopy streams and 9 of 10 open-canopy streams passed the criteria for a functioning riparian zone. However, when abundance data were used, only 4 of the closed- and 2 of the open-canopy streams passed this criterion. These results raise the issue of potential bias in biomass-based surrogates for measures of ecosystem functioning when large-bodied shredders are dominant. Assessments based on abundance-based surrogate ratios reflected assessments based on visual evidence of impacted riparian zones and removal of indigenous vegetation along open-canopy streams in agricultural areas. Closed-canopy streams are not spared from human influences, and it is common to find domestic animals grazing and selective cutting of trees for timber and firewood (Minaya et al. 2013). Thus, the uniformly positive biomass-based assessments of riparian-zone integrity in closed-canopy streams are suspect.

Overabundance of predators was evidence of strong top-down control in some open canopy streams, such as Bomet and Borowet, where flow decreased considerably during the dry season and pools were dominated by predacious families, such as Notonectidae (backswimmers) and Lestidae. Fewer closed-canopy streams had an overabundance of predators, but this assessment probably would change if omnivorous crabs were included in the predator category. Crabs exert top-down controls on other macroinvertebrates and take part in rapid breakdown of leaf litter in other streams in the region (Moss 2007, Lancaster et al. 2008).

Overall, the FFG ratios provided evidence of widespread human influences in the study area. Examination of mouth parts to separate collectors into filterers and gatherers will provide more rigorous and complete criteria for assessing the effects of riparian disturbances, sedimentation, and the quality of FPOM transported by these streams (Merritt and Cummins 2006). The threshold values for heterotrophy vs autotrophy should be re-examined in these streams, given that very few studies are available in the tropics for comparison, and the role of livestock should be investigated further.

Conclusions

The task of assigning stream macroinvertebrates to FFGs is not straightforward, and is, at times, controversial, especially when assignments are not supported by details on feeding modes and the structure of mouthparts. Some

taxa have too variable a diet to be assigned to a FFG, and some taxa undergo ontogenic shifts in diet. Nevertheless, gut-content analysis enabled us to classify macroinvertebrates collected in this study into FFGs and to contribute information to the growing data on the functional organization of tropical streams, including dietary requirements and trophic relationships. The FFG ratios used in our study offered a glimpse into the overall functioning of these streams and reflected a shift from heterotrophy to autotrophy arising from changing land use and clearing of riparian vegetation. Our study highlights the importance of shredders in these streams and the effects of riparian alterations on invertebrate community composition and ecosystem functioning. The wider consequence of these effects on ecosystem services merits further research and serious consideration when planning future landuse changes in eastern Africa.

ACKNOWLEDGMENTS

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