ORIGINAL ARTICLE

Trophic structure of an African savanna river and organic matter inputs by large terrestrial herbivores: A stable isotope approach

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Abstract

1. Knowledge of trophic structure is important to understand sources and pathways of energy resources in community ecology and to identify determinants of ecosystem changes. Yet, little is known from rivers of African savanna receiving large inputs of terrestrial organic matter and nutrients by large mammalian herbivores.

2. We used Stable Isotope (δ^{13}C and δ^{15}N) Bayesian Ellipses in R (SIBER) and Layman's community-wide metrics to describe seasonal variation in trophic niches and trophic structures in midorder river reaches in the Mara River (Kenya) that differed in environmental conditions (agricultural vs. forested) and amounts of organic matter and nutrients (low vs. high inputs by livestock and hippopotami, *Hippopotamus amphibius*). These analyses were supplemented with data on the trophic diversity of macroinvertebrate functional feeding groups (FFGs) and fish trophic guilds.

3. The δ^{13}C and δ^{15}N of basal resources and consumers differed between sites and changed with seasons. Sites in agricultural areas that were utilised by livestock and a site with hippopotami had higher δ^{13}C than the forested site due to the presence of C4 carbon from egestion and excretion by the grazers.

4. The forested site recorded the most taxon-rich and trophic-diverse invertebrate community, suggesting both autochthonous and allochthonous sources of energy were available. Agricultural sites and the site with hippopotami recorded high abundances of collector taxa in response to large inputs of organic matter. Fish trophic guilds were less diverse and were dominated by insectivores.

5. The food web at the forested site had the widest trophic niche size and highest isotopic trophic diversity compared to sites in areas with large mammalian herbivores. Invertebrate and fish trophic niche sizes changed according to food resources varying with space and time. Invertebrates had higher δ^{13}C values during the dry season. In contrast, fish showed higher δ^{13}C values during the wet season, and trophic niche sizes were constricted and considerably overlapping, suggesting feeding on a narrow range of food sources with high trophic redundancy.

6. This study showed that increased terrestrial organic matter by large mammalian herbivores affected trophic diversity and niche sizes for aquatic consumers in rivers draining the African savanna. Linking the density of terrestrial large mammalian herbivores to aquatic ecosystem structure and function could help manage their populations sustainably.

1 | INTRODUCTION

Large inputs of organic matter are typically associated with low-order (1st–3rd order) streams which are often heterotrophic with an allochthonous food base (Vannote, Minshall, Cummins, Sedell & Cushing, 1980). As streams widen, increased autochthonous production is predicted as a result of opening up of the canopy cover which broadens the food base and niche sizes of aquatic consumers (Thorp & Delong, 1994; Vannote et al., 1980). However, animal and human activities can cause localised differences in energy sources, functional organisation of aquatic communities and trophic structure among comparable and similar sized river reaches (Cross et al., 2013; Mosepele, Moyle, Merron, Purkey, & Mosepele, 2009; Raymond, Oh, Turner, & Broussard, 2008; Zeug, Peretti, & Winemiller, 2009).

In their mid- and lower reaches, African savanna rivers in conservation areas are inhabited by mega-herbivores such as hippopotami (hippos, *Hippopotamus amphibius*, Field, 1970; Kanga, Ogutu, Olff, & Santema, 2011; Naiman et al., 2003; Wilbroad & Milanzi, 2011). African hippos transfer large amounts of organic matter and nutrients from savanna grasslands into aquatic ecosystems through egestion and excretion (Subalusky, Dutton, Rosi-Marshall, & Post, 2015). Other large herbivores such as wildebeest, zebra, elephant and buffalo also occur in these landscapes and can contribute substantial amounts of organic matter and nutrients into rivers through direct defecation and urination during their migrations and watering (du Toit, 2003; Wolf, Doughty, & Malhi, 2013; Pringle, 2018). Although the numbers of large herbivorous wildlife have declined in many areas (e.g., Ogutu, Owen-Smith, Piepho, & Said, 2011), they have often been replaced by livestock (Prins, 2000), which can also contribute substantial amounts of organic matter (in the form of faeces) and nutrients into streams and rivers (Bond, Sear, & Sykes, 2014; Mesa, Mayora, Saigo, & Giri, 2015).

A number of studies associated animal-mediated inputs of organic matter and nutrients with microbial contamination and primary production in aquatic systems (Grey & Harper, 2002; Mosepele et al., 2009; Strauch, 2013). Other studies noted changes in community structure of benthic and fish communities (Dawson, Pillay, Roberts, & Perissinotto, 2016; O'Brien, 2016). Compared with autochthonous energy sources and C3 carbon from riparian vegetation, the excreta of large mammalian herbivores consist mainly of C4 grasses with lower quality (i.e., low C/N ratio; Clapcott & Bunn, 2003; Roach, 2013). Thus, most studies have focused on the importance of C4 carbon as a food resource (Bunn, Davies, & Kellaway, 1997; Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993; McCauley et al., 2015). However, how specific properties of food webs respond to changes in allochthonous carbon quality and amount is unclear and are not conceptualised in existing models of river ecosystem functioning.

Depending on the amount of animal-mediated inputs of organic matter and nutrients relative to the size of the recipient ecosystem, negative or beneficial trophic dynamics may result (Dawson et al., 2016; Gereta & Wolanski, 1998). When organic matter and nutrient loading rates do not exceed ecosystem requirements, primary production increase with a shift in algal abundance and species composition, which may in turn be beneficial to higher trophic levels (Del Rosario, Betts, & Resh, 2002; Polis, Anderson, & Holt, 1997). Animal dung can also be directly consumed by both invertebrates and fish (McCauley et al., 2015; Mesa et al., 2016). These changes in consumer resource dynamics have been found to increase the abundance and alter the composition of invertebrate and fish communities (Rader & Richardson, 1994; Townsend, Arbuckle, Crowl, & Scarsbrook, 1997; Weigel, Lyons, Paine, Dodson, & Undersander, 2000). However, if rates and magnitudes of inputs exceed rates of utilisation, especially as happens during low-flow conditions (Dawson et al., 2016; Dutton et al., 2018), then accumulation occurs leading to deterioration of water quality and physiological stresses on communities (Pennisi, 2014). River reaches receiving high amounts of animal inputs of organic matter have been reported to have a different community of invertebrates, mostly consisting of soft-bodied collector-gatherers (Masese & Raburu, 2017; Masese et al., 2014a; Mesa, 2016; Shivoga, 2001). These changes in the trophic diversity and quality of food resources (C4 vs. C3 carbon) would reduce the sizes of trophic niches of consumers.

Recent studies have shown that hydrological regimes can significantly influence autochthonous production and contributions to food webs (Roach & Winemiller, 2015; Roach, Winemiller, & Davis, 2014). During the wet season, increased turbidity is a limiting factor to riverine primary production, and thus, the assimilation of autochthonous energy sources by aquatic consumers varies with the flow (Douglas, Bunn, & Davies, 2005; Junk, Bayley, & Sparks, 1989). In general, algae contribution to macroinvertebrates and fish communities tends to be higher during the low-flow dry season, whereas terrestrial organic matter is more important during the wet season (Masese et al., 2015; Roach & Winemiller, 2015; Zeug & Winemiller,

2008). During the wet season, terrestrial organic matter is transported into the riverine environment by surface run-off, leading to an increased input of allochthonous material. Thus, the wet season is often associated with an increased range of available food sources, leading to a higher consumer trophic diversity and expanded niche sizes (Junk et al., 1989). In addition, high flows enhance longitudinal connectivity and homogenise food webs, as compared with the dry season when longitudinal connectivity may be reduced (Reid, Delong, & Thoms, 2012). Increased longitudinal connectivity would increase overlaps in niche sizes through consuming similar basal food resources. Thus, the spatial and seasonal shifts in flow levels can interact with animal and human activities to influence availability of food sources and pathways for consumers and ultimately trophic diversity and food-web structure (Paetzold, Sabo, Sadler, Findlay, & Tockner, 2008; Roach et al., 2014; Zheng et al., 2018).

Community-wide metrics based on stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have been used to quantify trophic structure at the food web level of entire communities or populations using a number of quantitative metrics (Layman, Arrington, Montaña, & Post, 2007). This approach has been used to determine catchment-scale influences on the functioning of aquatic systems (Abrantes, Barnett, & Bouillon, 2014; Kaartinen & Roslin, 2012; Layman et al., 2007) and the effects of land use change on trophic structure of streams and rivers (de Carvalho, de Castro, Callisto, Moreira, & Pompeu, 2017; de Castro et al., 2016).

Some of the data set used in this study has previously been used to examine the sources of nutrition to consumers in relation to differences in land use and inputs of organic matter by large mammalian herbivores (Masese et al., 2015). That study showed that terrestrial carbon transported into the river by the action of large herbivores (both livestock and wildlife) is an important energy source for macroinvertebrates and fish during the wet season, whereas autochthonous production was the dominant source of energy during the dry season (Masese et al., 2015). However, that study did not consider how subsidies influence the trophic diversity and overall food-web structure. Here, we used a more extensive data set, stable isotope-based community-wide metrics and standard ellipse areas (SEAs) to describe and compare trophic diversity and food-web structure among sites and between seasons (wet vs. dry) along the Mara River, Kenya. We took into account differences in environmental conditions such as catchment land use (agricultural vs. protected areas) and inputs of organic matter by large mammalian herbivores (livestock and hippopotami). In addition, we measured trophic diversity by analysing the relative abundance and taxon richness of macroinvertebrate functional feeding groups and fish trophic groups.

We hypothesised that changes in the quantity (low vs. high) and quality (C3 vs. C4 carbon) of organic matter from human activities and different densities of large mammalian herbivores will affect the trophic diversity and niche sizes of consumers and that the effects of these inputs would depend on flow conditions (dry season low flows vs. wet season high flows) in the rivers. Specifically, we hypothesised that relative to food webs in agricultural or wildlife (hippo)-influenced areas, food web at the forested site (with minimal human and animal inputs of organic matter and nutrients) would have high trophic diversity and broad niche sizes because of availability of both allochthonous and autochthonous food sources. In contrast, trophic diversity and niche sizes at sites receiving animal inputs (livestock and hippos) will respond depending on the amount of inputs, with high inputs of organic matter likely to reduce trophic diversity and trophic niche sizes because of increased turbidity (which limit primary production). In addition, we expected less overlap in trophic niches among sites during the dry season due to localised reach-scale influences and more overlap during the wet season due to the uniformity of basal resources as a result of increased flow-mediated terrestrial–aquatic connectivity.

2 | METHODS

2.1 | Study sites

This study was conducted in the Kenyan part of the Mara River Basin (Figure 1). The Mara River drains into Lake Victoria through Tanzania. Six sites representing natural forest, agricultural areas and hippo-influenced sites were selected for sampling. Study sites included a forested site (4th order); four agricultural sites: Nyangores (5th order), Amala 1 (4th order), Amala 2 (5th order) and Mara 1 (6th order); and one hippo-influenced site: Mara 2 (6th order; Figure 1). The study sites represented a gradient of C3- to C4-dominated vegetation. The forested site is located in the Mau Forest where C3 vegetation dominates both the riparian and terrestrial areas of the catchment, while the most downstream site (Mara 2) is located in a savanna ecosystem dominated by C4 grasses and strongly influenced by hippo inputs of terrestrial organic matter through defecation. The agricultural sites receive mixed inputs of both C3 and C4 carbon and increased amounts of nutrients under the influence of agricultural lands, human settlements and varying densities of livestock (goats, sheep, cattle and donkeys) that water in the river (Table 1).

While the forested site was located in a natural forest, some human activities (livestock grazing, hunting and firewood collection) took place in adjacent areas. Livestock numbers were reduced adjacent to the forest site (5 livestock/river kilometre; Table 1), and their effects on water quality were expected to be minimal. The agricultural sites (Nyangores, Amala 1, Amala 2 and Mara 1) were located in areas where people living in the catchments and adjoining areas are involved in small-holder mixed agriculture (livestock rearing, cash and subsistence crops such as tea, maize and potatoes), which is not mechanised but involves substantial fertiliser application. A number of small towns are spread throughout these areas, which are not supplied with sewerage systems. Human and livestock populations in the adjacent land are potential sources of both organic matter and nutrients into these sites (Table 1). Livestock (cattle, donkeys, goats and sheep) deposit substantial amounts of organic matter and nutrients (through faeces and urine) when watering in the river. Preliminary data showed that on a daily basis, a minimum of 20 and 30 cattle visited watering sites on the Nyangores and Amala rivers and tributaries, respectively, with more than 25% defecating and/or
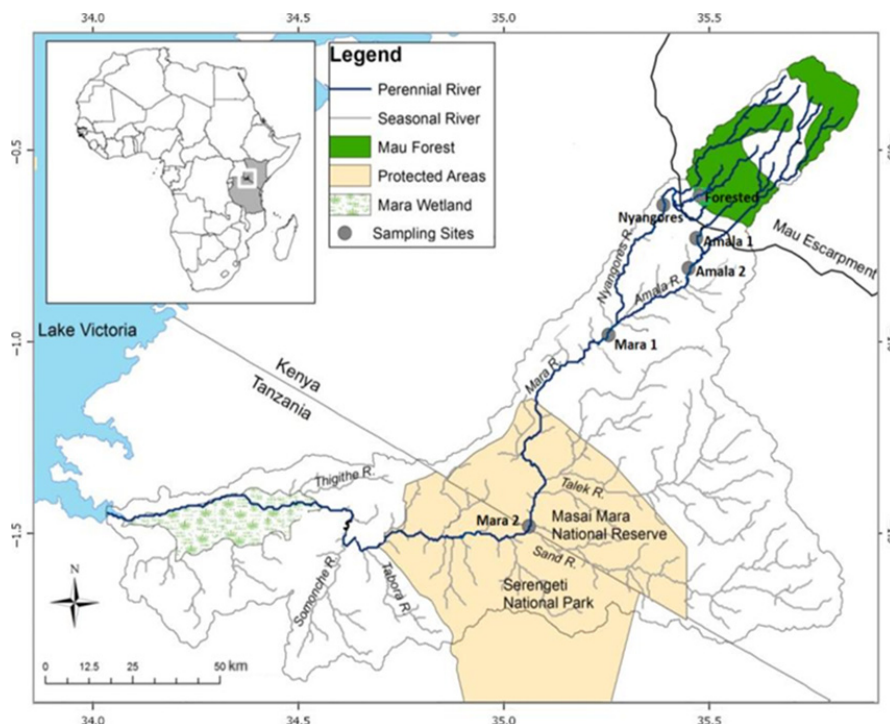
FIGURE 1 Map of the Mara River Basin and the location of sampling sites (in bold) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Characteristics of the sampling sites along the Mara River. Herbivores = large mammalian herbivores that include cattle, donkeys, goats, sheep and wildlife, including hippopotami

Site	Reach-scale influences	Elevation (m)	RDIS	% AGR	% Grasslands (mainly C3 VEG)	% FOR (mainly C4 VEG)	Herbivore density (individuals/km^2)	Human density (individuals/km^2)[b]
Forested	Forest	2,063	12.3	21.7	0.9	76.9	5	0[c]
Nyangores	Agriculture and livestock grazing	1,937	25.7	34.4	3.1	62.5	24	465
Amala 1	Agriculture and livestock grazing	1,980	8.0	37.5	3.9	58.6	35	412
Amala 2	Agriculture and livestock grazing	1,935	31.5	58.0	18.0	36.0	67	366
Mara 1	Agriculture and livestock grazing	1,692	49.5	64.0	15.0	21.0	73	320
Mara 2	Savanna grasslands and hippos	1,475	80.7	23.2	53.4	23.4	104[a]	20[d]

AGR: agricultural land; FOR: forested land; RDIS: river distance from source, calculated as the square root of the entire catchment area upstream of the sampling site; VEG: vegetation.

Modified from Masese et al. (2015).

[a]Corresponds to the number of hippos per river kilometre upstream of the sampling site.

[b]Data obtained from the Kenya Election Database http://kenyaelectiondatabase.co.ke.

[c]Despite absence of people residing in the forest, human activities in the forest include hunting and grazing.

[d]This number includes people resident in tourism facilities in the Maasai Mara National Reserve and conservancies around the reserve.

urinating in the river (Iteba J., personal communication). Over 75 and 350 cattle, accompanied with an appreciable number of sheep and donkeys, have been recorded to visit a watering point per day on the Nyangores and Amala rivers, respectively. There are also a number of watering points along both rivers and their tributaries accessed by individual livestock owners with less than 10 cattle. Although livestock is present in this region, there are no extensive

C4 pastures. Rather, C3 vegetation dominates the riparian zone along the agricultural river reaches.

Both the Mara 1 and the Mara 2 sites are located on the Mara River mainstem, downstream of the confluence of the Nyangores and Amala tributaries (Figure 1). The hippo-influenced Mara 2 site is located in the Maasai Mara National Reserve just downstream of river sections inhabited by large hippo populations (>4,000

individuals; Kanga et al., 2011). Hippos graze on savanna C4 grasses and deposit C4-derived faeces into the river. According to recent estimates, an average hippo delivers nearly 9 kg (wet weight) of terrestrial organic matter into the Mara River daily (Subalusky et al., 2015).

2.2 | Sample collection, processing and analysis

To determine the spatial and temporal variation in the trophic structure in the Mara River, primary producers, macroinvertebrates and fish were collected for trophic structure and stable isotope analysis (SIA) both during the wet (May–July 2011) and dry (January–April 2012) seasons. Because flow in the Mara River is highly variable, seasonal differences in basal and consumer stable isotope composition were expected. Basal sources and macroinvertebrates were collected within eight weeks in the dry and wet seasons prior to fish sampling. Samples of basal sources included C3 and C4 vegetation, coarse particulate organic matter (CPOM), fine benthic organic matter (FBOM), seston, periphyton and filamentous algae. Samples were collected and processed as described by Masese et al. (2015). Results of SIA are expressed as parts per thousand (‰) deviations from the standard, as defined by the equation: $\delta^{13}C$, $\delta^{15}N = [(R_{sample}/R_{reference}) - 1] \times 10^3$, where $R = {}^{13}C/{}^{12}C$ for carbon and ${}^{15}N/{}^{14}N$ for nitrogen.

2.3 | Data analysis

A two-way ANOVA was used to compare $\delta^{13}C$ and $\delta^{15}N$ values of basal sources among sites and seasons. The trophic diversity of macroinvertebrates and fish for each site for the dry and wet seasons was determined using taxon richness and relative abundance of functional feeding groups (macroinvertebrates) and trophic guilds (fish). Classifications of fish trophic guilds/groups were based on available literature regarding consumer diets of riverine fishes in the Lake Victoria Basin (Corbet, 1961; Raburu & Masese, 2012) and analysis of stomach contents from fish we collected. Fish species representing the insectivorous guild included *Labeobarbus altianalis*, *Enteromius cercops*, *E. paludinosus*, *E. kerstenii*, *E. neumayeri*, *Chiloglanis* sp. and *Clarias liocephalus*. The omnivorous guild was represented by *Labeo victorianus* and *Clarias gariepinus*, while *Bagrus dokmac* was the only representative of the predator trophic group. Macroinvertebrate functional feeding groups (FFGs) were based on Masese et al. (2014b) and references therein and included collector-gatherers (henceforth collectors), collector-filterers (henceforth filterers), predators, scrapers and shredders (Merritt, Cummins, & Berg, 2008).

To investigate differences in community trophic niche size among sites and seasons, stable isotope niches were quantified and compared with standard ellipse areas (SEAs; expressed in ‰^{2}) using the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson, Inger, Parnell, & Bearhop, 2011) of SIAR (Stable Isotope Analysis in R; Parnell, Inger, Bearhop, & Jackson, 2008, 2010). Bayesian SEA in bivariate data is similar to *SD* is univariate data (Batschelet, 1981).

The reported SEAs for comparison of sizes across sites and seasons are based on SEA$_B$, which is a Bayesian small sample size-corrected SEA (Jackson et al., 2011). SEAs typically contain about 40% of the data and can be used as a measure of isotopic trophic niche width of populations or communities (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004). SEA analyses were carried out for invertebrates and fish separately. For invertebrates, all species were included in these analyses, as a similar representation of all functional feeding groups was present at all sites and seasons (Table 2). For fish, only insectivorous species were used because the other trophic guilds did not occur at all sites and seasons.

For each season, the percentage overlap of the 95% ellipses between pairs of sites was also calculated. Similarly, for each site, the 95% ellipse overlap between the wet and dry seasons was calculated. Overlap values are presented as a proportion of the total area that overlaps in the two 95% ellipses and range from 0% when the ellipses are separated to 100% when the two ellipses fully overlap. An overlap is a measure of the extent to which consumers are dependent on the same food sources, with higher percentages of overlap depicting high reliance on the same food sources (i.e., more similar trophic niches) and vice versa.

The trophic structure of the macroinvertebrate and fish assemblages was described for each site for the dry and wet seasons separately using Layman's Bayesian stable isotope-based community-wide metrics (Layman et al., 2012; R Development Core Team, 2007). Because not all species occurred at all sites, macroinvertebrate FFGs and fish trophic guilds were used to run the analyses (de Castro et al., 2016; Sepúlveda-Lozada, Saint-Paul, Mendoza-Carranza, Wolff, & Yáñez-Arancibia, 2017). The five Layman's community metrics considered were as follows: (a) $\delta^{13}C$ range (CR), which depicts basal source diversity; (b) $\delta^{15}N$ range (NR), which describes trophic length; (c) the mean distance to centroid (CD), which is the mean Euclidean distance of each assemblage component to the centroid and a measure of community niche width (related to trophic diversity) and species spacing; (d) the mean nearest neighbour distance (MNND), which is the mean Euclidean distance from each group to its nearest neighbour in the $\delta^{13}C$-$\delta^{15}N$ biplot space, an estimate of density and clustering of species within the community; and (e) the standard deviation of the nearest neighbour distance (SDNND), which measures the uniformity (evenness) of the groups' spacing in the biplot space (Jackson et al., 2011, 2012; Layman et al., 2007). Both MNND and SDNND provide information about trophic redundancy, whereby a small MNND means increased trophic redundancy, that is, that there are many groups with similar trophic ecologies, and a lower SDNND means more even distribution of species, suggesting a increased trophic redundancy as different groups have more similar trophic ecologies (Abrantes et al., 2014; Layman et al., 2007). Results were graphically compared between sites and seasons based on the visual analysis of the credibility intervals, where the degree of overlap between the Bayesian distributions was used as an indication of similarities or dissimilarities between sites and seasons (Abrantes et al., 2014).

TABLE 2 Diversity and relative abundance (percentage) of invertebrate functional feeding groups and fish trophic groups across sites in the Mara River. Invertebrates were identified to the lowest taxon level possible, mostly genus, while fish were identified to species. Dashes (–) indicate that the fishes were not captured at the sites

Trophic metrics	Dry season						Wet season					
	Forested	Nyangores	Amala 1	Amala 2	Mara 1	Mara 2	Forested	Nyangores	Amala 1	Amala 2	Mara 1	Mara 2
Invertebrates												
Total number of invertebrate taxa	60	57	49	52	42	38	56	51	43	52	41	33
Number collector taxa	13	12	8	9	10	9	13	11	9	13	9	6
Number filterer taxa	6	5	5	5	4	4	5	5	4	3	5	5
Number scraper taxa	10	12	8	10	5	7	10	9	7	8	4	5
Number shredder taxa	11	10	5	6	4	2	11	9	4	4	5	2
Number predator taxa	20	18	23	22	19	16	17	17	19	24	18	15
Percentage collector individuals	35.1	51.9	29.0	63.5	50.4	60.9	32.0	56.4	46.0	45.6	50.4	60.1
Percentage filterer individuals	34.3	22.1	56.4	17.5	33.1	20.8	31.6	23.8	38.7	37.3	27.7	26.6
Percentage scraper individuals	15.7	12.1	4.1	10.9	5.4	8.3	14.0	9.3	5.6	7.5	7.1	2.1
Percentage shredder individuals	7.5	3.9	0.9	1.8	1.1	0.1	13.1	5.7	1.7	1.3	2.4	0.2
Percentage predator individuals	7.4	10.1	9.6	6.3	10.0	9.8	9.3	4.8	7.9	8.3	12.4	10.9
Fishes												
Number insectivore species	1	4	4	4	7	2	1	4	4	4	8	3
Number omnivore species	–	–	–	1	2	2	–	–	–	1	1	2
Number predator species	–	–	–	–	1	1	–	–	–	–	–	–
Percentage insectivore individuals	100	100	100	77.8	92.6	39.2	100	100	100	78.5	96.2	70.2
Percentage omnivore individuals	–	–	–	22.2	5.3	59.4	–	–	–	21.5	3.8	29.8
Percentage predator individuals	–	–	–	–	2.1	1.4	–	–	–	–	–	–

3 | RESULTS

3.1 | δ¹³C and δ¹⁵N values of sources and consumers

Primary producers showed a wide variability in $\delta^{13}C$ and $\delta^{15}N$ values in the dry and wet seasons (Figure 2). C3 terrestrial producers typically had the lowest $\delta^{13}C$ values (−28.7 ± 1.7‰), and C4 terrestrial producers the highest (−12.9 ± 0.7‰; Figure 2). The range in potential source $\delta^{13}C$ (CR) was also similar for all sites (Figure 2), meaning that the community-wide metrics are comparable among sites and seasons (Layman et al., 2007). At the forested site, aquatic producers had relatively low $\delta^{13}C$ values (−27.1 ± 1.4‰), close to the dominant C3 vegetation, while at the most downstream, Mara 2 site these producers had the highest $\delta^{13}C$ values (−19.1 ± 1.1‰;

Figure 2). In the remaining sites, aquatic sources had intermediate $\delta^{13}C$ values.

Overall, consumer $\delta^{13}C$ values were lowest at the forested site and highest at the Mara 2 site (Figure 2), which coincided with the increase in livestock and wildlife density in the areas adjoining the sampling sites (Table 1). Macroinvertebrates generally had higher mean $\delta^{15}N$ (9.5 ± 1.1‰) than primary producers (6.3 ± 2.3‰) and lower $\delta^{15}N$ than fishes (12.7 ± 1.0‰) at all sites during both the dry and wet seasons (Figure 2). $\delta^{13}C$ and $\delta^{15}N$ values of collectors, filter-feeders and scrapers were not strongly differentiated, but $\delta^{15}N$ values of predators were slightly higher (Figure 2). Where present, shredders had the lowest $\delta^{13}C$ (−24.0 ± 1.4‰) and $\delta^{15}N$ (9.3 ± 1.1‰), and predators the highest values (−22.7 ± 1.8‰; 10.5 ± 0.9‰) among invertebrates. Predatory fishes had the highest $\delta^{15}N$ where present; 14.7 ± 0.2‰ for Mara 1 site during the dry
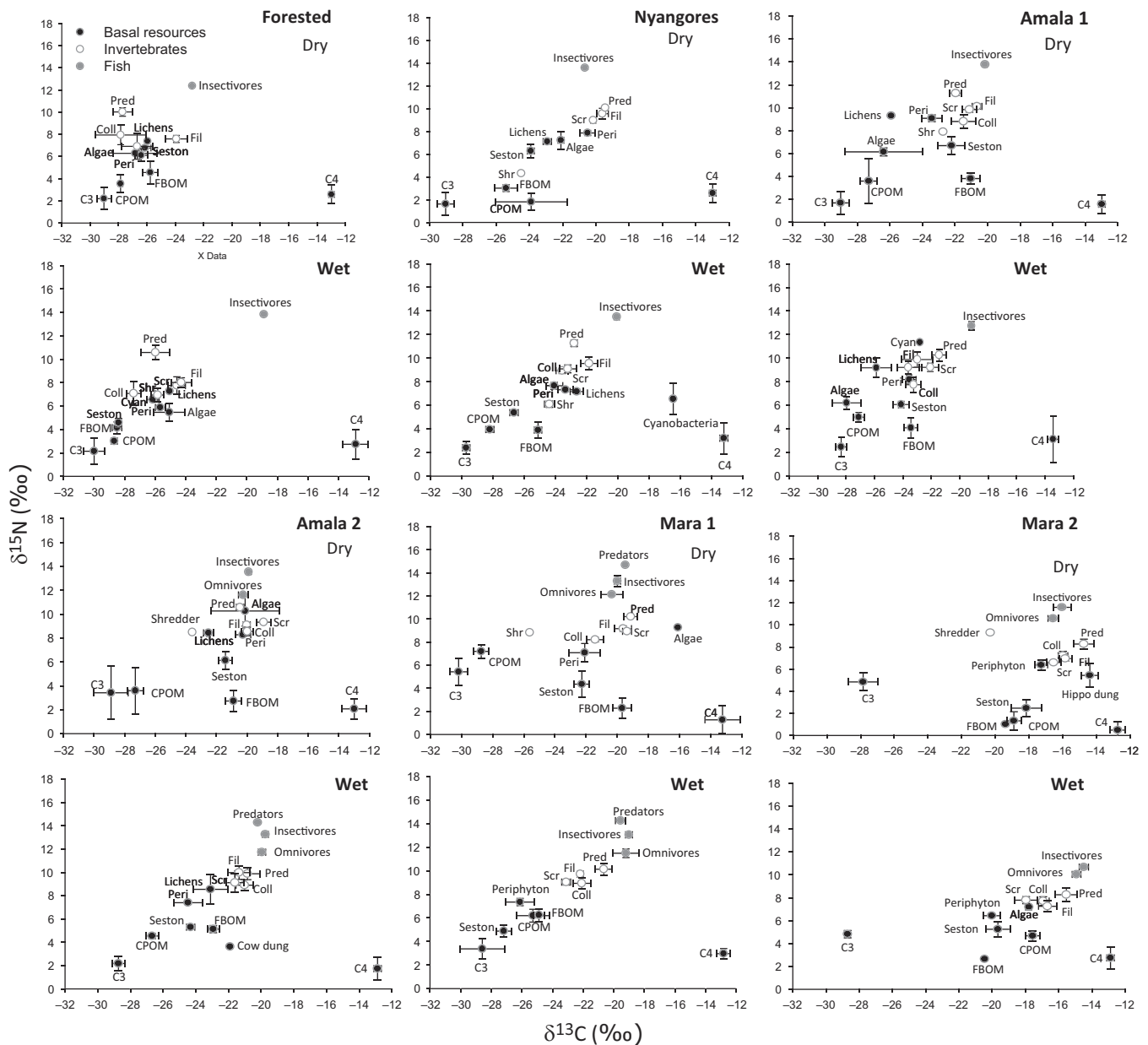
FIGURE 2 Mean (±*SD*) $\delta^{13}C$ and $\delta^{15}N$ of basal sources, invertebrates and fish in the Mara River during the dry and wet seasons. C3 = C3 plants, C4 = C4 plants, CPOM: coarse and particulate organic matter; FBOM: fine benthic organic matter, Peri: periphyton; invertebrates functional feeding groups, Scr: scrapers, Fil: filter-feeders, Coll: collectors, Pred: predators, Shr: shredders; omnivores: omnivorous fishes, Insectivores: insectivorous fishes, and Predators: predatory fishes

season and 14.3 ± 0.1‰ for both Amala 2 and Mara 1 sites during the wet season (Figure 2).

3.2 | Spatiotemporal differences in trophic diversity and structure

The forested site recorded the highest taxon richness of macroinvertebrates during the dry (60) and wet (56) seasons, while the hippo-influenced Mara 2 site recorded the lowest (Table 2); 38 and 33 during the dry and wet seasons, respectively. Similarly, the forested site had the highest relative abundance of scrapers (15.7% and 14.0%) and shredders (7.5% and 13.1%) during the dry and wet seasons,

respectively. This reflects the abundance and availability of both autochthonous and allochthonous energy sources at the site. Agricultural and the hippo-influenced Mara 2 sites recorded low taxon richness but high relative abundances of collectors, signifying the high amount of organic matter input by livestock and hippopotami. The fish community was dominated by insectivores, while predators were generally less diverse and abundant in the study area (Table 2). The Mara River mainstem sites (Mara 1 and Mara 2) recorded the most trophic-diverse fish assemblage, with all the three trophic guilds collected in the study area: insectivores, omnivores and predators. However, the Mara 2 site recorded the highest relative abundance of omnivores during the dry (59.4%) season.

SEAs of macroinvertebrates and insectivorous fishes differed in size, shape and position in the $\delta^{13}C$ vs. $\delta^{15}N$ plots (Figure 3), and these reflected shifts in main sources of carbon for consumers across the three site categories (forested, agricultural and hippo-influenced). For both invertebrates and fish, the hippo-influenced Mara 2 site showed SEAs in the region of highest and lowest $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Figure 3). This resulted in the lowest overlap between the Mara 2 site SEAs with those from other sites (Table 3), indicating that consumers at these sites depended on different sources. For invertebrates, SEAs of the C3-dominated forested site also showed minimal overlap with the agricultural sites during both seasons, as SEAs showed low $\delta^{13}C$ and $\delta^{15}N$ values (Figure 3). Fish data from this forested site were not included, as only one species (*Clarias liocephalus*) was collected here and in low abundance (Table 2). For the remaining sites, SEAs for insectivorous fishes showed intermediate $\delta^{13}C$ and $\delta^{15}N$ values and relatively high overlaps (Figure 3, Table 4), suggesting that consumers in these sites relied on similar food sources.

Within sites, there were also differences in $\delta^{13}C$ and $\delta^{15}N$ values of SEAs between seasons (Figure 3; Supporting Information Figures S1 and S2). Invertebrates from all sites, except for the forested site, showed SEAs with higher $\delta^{13}C$ values in the dry season, as opposed to the wet season when $\delta^{13}C$ values were lower (Supporting Information Figure S1). This difference was particularly strong for the agricultural sites Nyangores and Mara 1, where the 95% ellipse overlaps between seasons were relatively low (mode: 18% and 35% respectively; Table 3). For fish, there were also seasonal changes in SEA position with higher $\delta^{13}C$ values in the dry season and lower $\delta^{13}C$ values in the wet season for most sites (Figure 3; Supporting Information Figure S2). These shifts were more evident at sites strongly influenced by inputs of organic matter (C4 carbon) by livestock and hippos (Amala 1, Mara 1 and Mara 2), where 95% ellipse overlap between seasons was <50% (Table 3). These findings suggest that, during the dry season, trophic niche sizes widened because of an increase in C4 carbon deposited by large mammalian
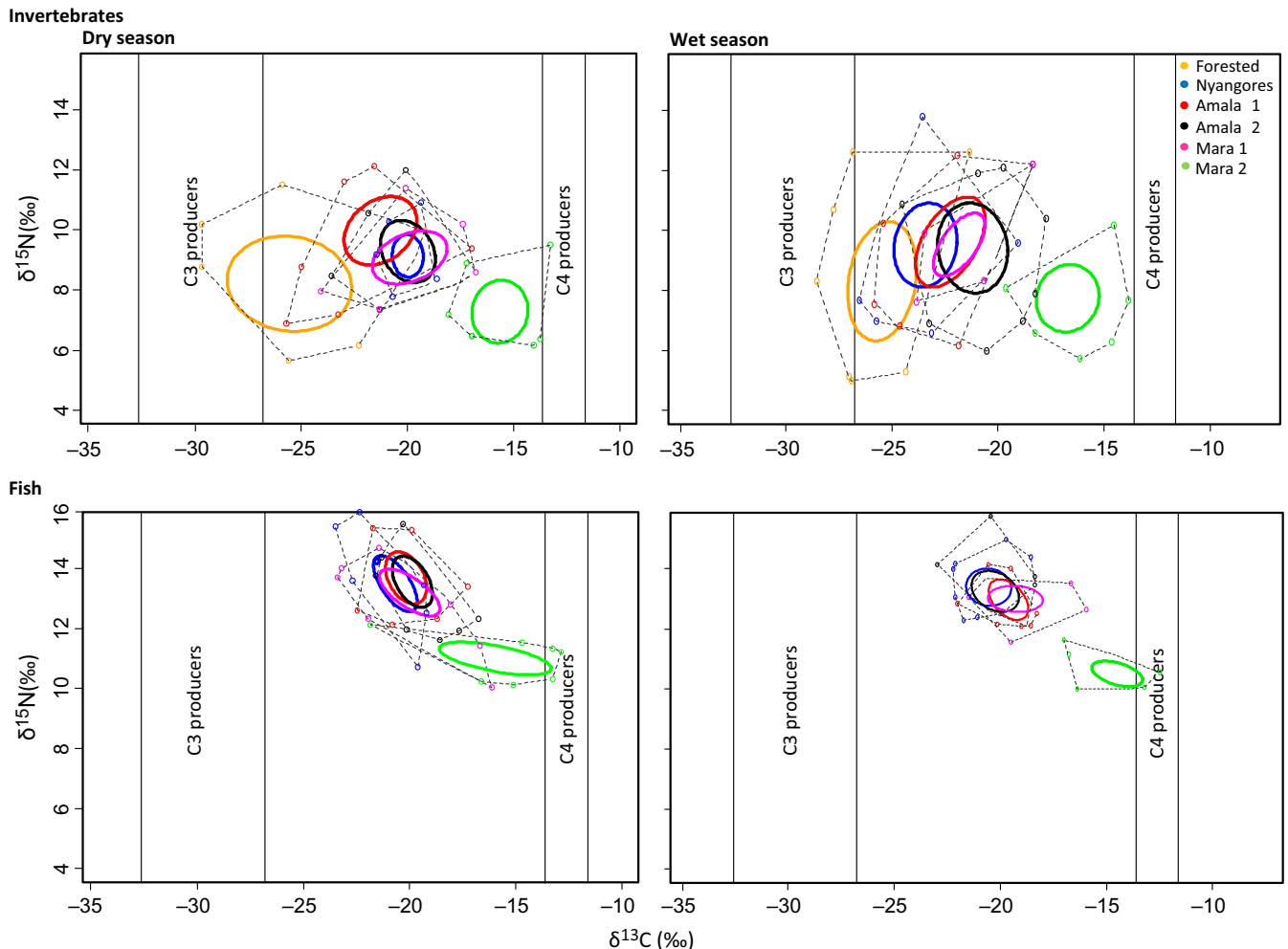

FIGURE 3 Standard ellipse areas (SEAs; solid lines), representing the isotopic niche of the invertebrate (upper panel) and insectivorous fish (lower panel) communities during the dry (left) and wet (right) and seasons. Dotted lines are the convex hull areas of the communities, corresponding to the area encompassing all groups in the $\delta^{13}C$–$\delta^{15}N$ plot. Vertical dashed lines indicate the range in $\delta^{13}C$ of C3 and C4 terrestrial producers collected from all study areas combined [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Bayesian standard ellipse areas (SEA$_B$) of macroinvertebrates, along with the probability that the SEA in the dry season is larger than the SEA in the wet season, 95% ellipse overlap between seasons for the same site and 95% ellipse overlap between pairs of sites for the dry and wet seasons. Overlaps (%) represent the proportion of the sum of the nonoverlapping areas of the two ellipses (ranges from 0% when the ellipses are completely separated to 100% when ellipses fully overlap). Values are modes followed by 95% credibility intervals (in brackets)

| | | | | 95% ellipse overlap between pairs of sites (%) | | | | |
Sites	SEA$_B$ (‰^{2})	p Value SEA dry > SEA wet	95% ellipse overlap between seasons (%^{2})	Nyangores	Amala 1	Amala 2	Mara 1	Mara 2
Dry season								
Forested	14.4 (8.7–21.3)	0.911	52 (27–75)	7 (2–16)	22 (12–37)	14 (6–28)	15 (5–24)	0 (0–12)
Nyangores	1.6 (1.0–2.4)	0.000	14 (9–22)		24 (13–42)	41 (22–64)	37 (16–61)	0 (0–10)
Amala 1	5.8 (4.0–8.1)	0.289	63 (38–80)			45 (29–66)	44 (32–57)	0 (0–0)
Amala 2	4.0 (2.9–5.3)	0.003	47 (30–66)				57 (45–76)	7 (0–19)
Mara 1	4.5 (3.2–5.9)	0.923	35 (27–51)					7 (0–18)
Mara 2	4.3 (2.7–6.1)	0.259	56 (35–73)					
Wet season								
Forested	9.9 (6.6–13.8)			42 (31–52)	28 (20–41)	19 (9–35)	15 (6–23)	0 (0–2)
Nyangores	6.4 (4.9–8.1)				62 (41–74)	44 (28–58)	37 (26–53)	0 (0–8)
Amala 1	6.7 (4.6–9.1)					55 (41–79)	47 (25–73)	2 (0–12)
Amala 2	7.7 (5.1–10.1)						39 (21–61)	14 (0–27)
Mara 1	3.2 (2.1–4.4)							0 (0–9)
Mara 2	5.2 (3.2–7.6)							

TABLE 4 Bayesian standard ellipse areas of insectivorous fish (SEA$_B$), along with probability that the SEA in the dry season is larger than the SEA in the wet season, 95% ellipse between seasons for the same site, and 95% ellipse overlap between pairs of sites based on insectivorous fishes for the dry and wet seasons. Overlaps (%) represent the proportion of the sum of the nonoverlapping areas of the two ellipses (ranges from 0% when the ellipses are completely separated to 100% when ellipses fully overlap). Values are modes followed by 95% credibility intervals (in brackets)

| | | | | SEA$_B$ overlap between pairs of sites (%) | | | |
	SEA$_B$ (‰^{2})	p Value SEA dry > SEA wet	95% ellipse overlap between seasons (%^{2})	Amala 1	Amala 2	Mara 1	Mara 2
Dry season							
Nyangores	2.2 (1.6–2.9)	0.704	55 (35–66)	60 (45–86)	53 (40–59)	56 (41–78)	7 (0–15)
Amala 1	2.3 (1.8–3.0)	0.912	47 (28–67)		73 (53–91)	54 (43–74)	4 (0–18)
Amala 2	2.1 (1.5–2.8)	0.154	63 (39–87)			54 (36–75)	5 (0–19)
Mara 1	2.5 (1.9–3.4)	0.737	51 (36–75)				10 (2–24)
Mara 2	3.4 (2.3–5.3)	0.999	32 (10–55)				
Wet season							
Nyangores	1.9 (1.4–2.7)			48 (25–70)	66 (45–91)	45 (30–63)	0 (0–0)
Amala 1	1.6 (1.1–2.4)				58 (40–85)	51 (38–67)	0 (0–6)
Amala 2	2.1 (1.4–3.0)					50 (33–69)	0 (0–1)
Mara 1	1.6 (1.2–2.2)						0 (0–0)
Mara 2	1.3 (0.8–1.9)						

herbivores in the river, coupled with increased primary production due to low levels of suspended sediments.

Regarding SEA sizes, for macroinvertebrates, the C3-dominated forested site had the largest SEA$_B$ both during the dry (14.4‰^{2}) and wet (9.9‰^{2}) seasons (Figure 4, Table 3). For the dry season, SIBER indicated that the SEA$_B$ at this forested site had >99% probability of being larger than the SEAs at all other sites, while for the wet season, it had >95% probability of being larger than the SEA$_B$ at most of the agricultural sites. The smallest SEA was detected for an agricultural site. Interestingly, for insectivorous fish, in the dry season, SEA was largest at the hippo-influenced Mara 2 site than at the remaining sites (Figure 4, Table 4; note, however, that fish SEA was not measured at the forested site). In the wet season, however, SEA sizes did not differ among sites (Figure 4).
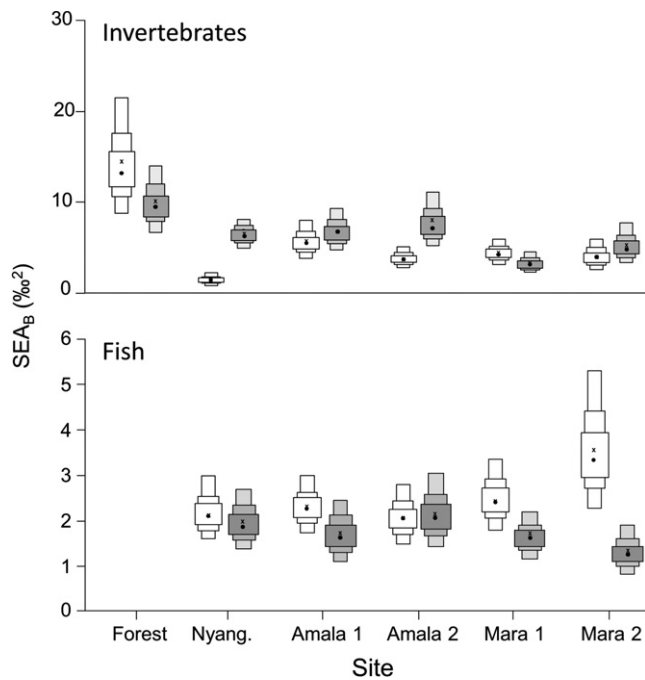
FIGURE 4 Density plots showing the credibility intervals of the standard ellipse areas (SEAs), representing the core isotopic niche space of the invertebrate (upper panel) and insectivorous fish (lower panel) communities at each site. Black circles are the mode SEA, and boxes indicate the 50%, 75% and 95% credible intervals for the dry season (white boxes) and wet season (grey boxes), from wider to thinner. Black crosses are the sample size-corrected SEA (SEA$_C$)

Layman's community metrics also varied among sites and seasons (Figures 5 and 6). For the wet season, all metrics showed the widest range of values in the forested site compared with all other sites. For the dry season, the Nyangores site showed the widest range of values for all metrics, compared to all other sites. The $\delta^{13}C$ range (CR), a measure of trophic breadth and diversity, was typically narrower in the dry season than in the wet season, and this was more evident at the Mara 2 site, suggesting that accumulation of animal faeces during low flow reduces isotopic trophic diversity. There was no evidence of seasonal differences in $\delta^{15}N$ range (NR) or niche width (CD) with the exception of the forested site where values were higher in the wet season (Figure 5). In general, species clustering and trophic redundancy (MNND) and evenness of spatial density and packing (SDNND) did not differ among sites for the dry season but differed in the wet season (Figure 6). Only the forested site and Mara 2 site showed seasonal differences in trophic redundancy with higher levels during the dry season than in the wet season (Figure 6).

4 | DISCUSSION

There were notable shifts in stable isotope values of basal sources and consumers across sites and between seasons. The forested and hippo-influenced Mara 2 sites were at the extreme ends of the C3-

C4 carbon gradient in the landscape and were the least influenced by either human or livestock inputs; but note that the Mara 2 site received the highest amount of animal dung (mainly C4 carbon) in the study area. On the other hand, sites in agricultural areas, where human and livestock numbers were higher than at the forested site, had higher $\delta^{13}C$ and $\delta^{15}N$ than the forested site. High $\delta^{15}N$ in basal sources and consumers in aquatic ecosystems has been associated with nitrate inputs from agriculture and animal excreta (Anderson & Cabana, 2005; Bateman & Kelly, 2007; Kendall, 1998). The Mara River Basin does not have a major city, but the river runs through a number of small towns and settlements that do not have sewerage facilities, which could contribute to the higher $\delta^{15}N$ values in these agricultural sites.

Given that the study sites are all in midorder river reaches, the changes in consumer $\delta^{13}C$ values are as a result of the variation in the importance of terrestrial C3 versus C4 producers supporting aquatic food webs and not an instream natural gradient in stable isotope composition of the same (aquatic) sources (e.g., Finlay, 2004). Note also that without herbivore-mediated inputs, in this case livestock, we would expect to see lower consumer $\delta^{13}C$ values of sources at the agricultural sites because the riparian vegetation at those sites is dominated by C3 vegetation.

4.1 | Spatial differences in trophic diversity and food-web structure

The forested site recorded the highest taxon richness and trophic-diverse community of macroinvertebrates, while the hippo-influenced Mara 2 site recorded the lowest (Table 2). Because of the gradient in organic matter and nutrients loadings by large mammalian herbivores (here livestock and hippopotami), from low in the Forested site, intermediate in Agricultural sites and highest at the Mara 2 site, it is likely that the inputs exceeded ecosystem requirements, especially during the dry season when flushing cannot occur due to low flows (Dutton et al., 2018), leading to reduction in water quality at the Mara 2 site (Dawson et al., 2016). During the dry season, mobilisation of accumulated dung in the benthos and pools can cause further physiological stress to communities, and this likely explains the taxon low richness and trophic diversity of invertebrates at the Mara 2 site during both the dry and wet seasons. Previous studies have noted a low diversity of both macroinvertebrates and fish at sites receiving high inputs of hippo faeces (Masese & Raburu, 2017; O'Brien, 2016).

Similarly, food-web structure differed the most between the C3-dominated forested site and the C4-dominated Mara 2 site, while the remaining sites in agricultural areas differed little. For macroinvertebrates, the forested site had the largest SEA$_B$ during both the dry and wet seasons, while smaller SEAs were reported at the agricultural areas during the dry season and at the Mara 2 site during the wet season. Large SEA$_B$ at the forested site suggests a more diversified food web, also supported by high CR and CD values. This could be related to the high water clarity, which allows for increased aquatic primary production, and to the presence of substantial
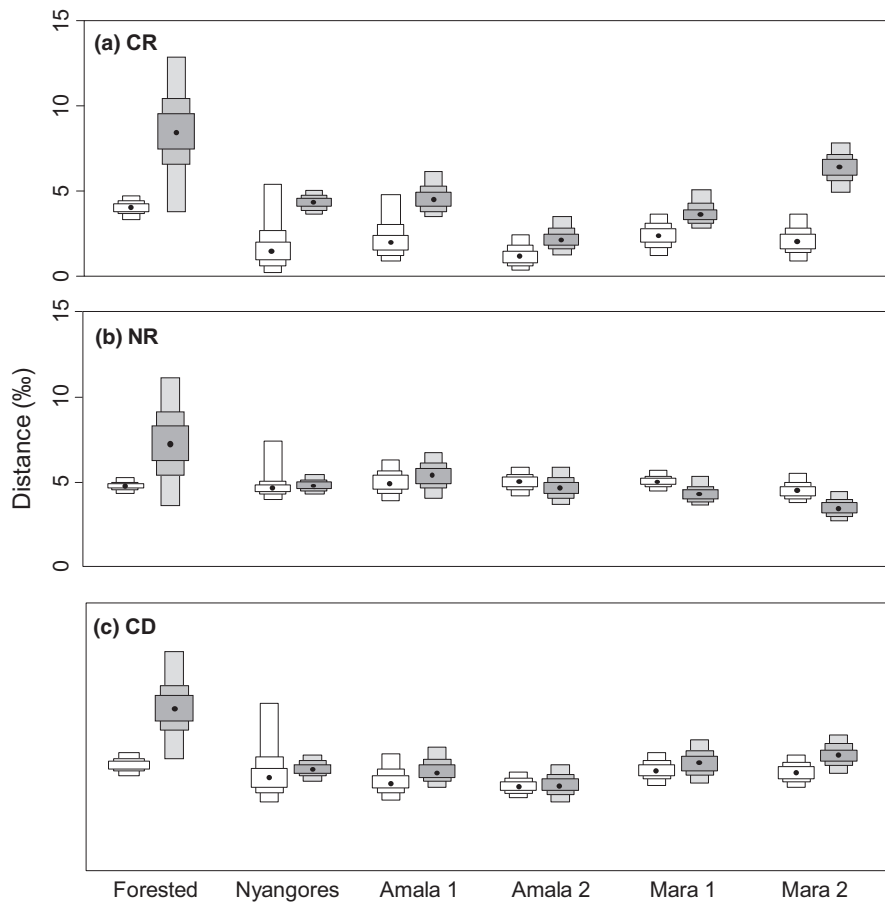
FIGURE 5 Layman stable isotope-based community-wide metrics (mode and 95% credible intervals) for the invertebrate and fish community at the different sites: Stable isotope of carbon ($\delta^{13}C$) range (CR) is a measure of trophic diversity; stable nitrogen isotope ($\delta^{15}N$) range (N) is a measure of trophic length; mean distance to centroid (CD) is a measure of trophic width or breadth. White = dry season, grey = wet season
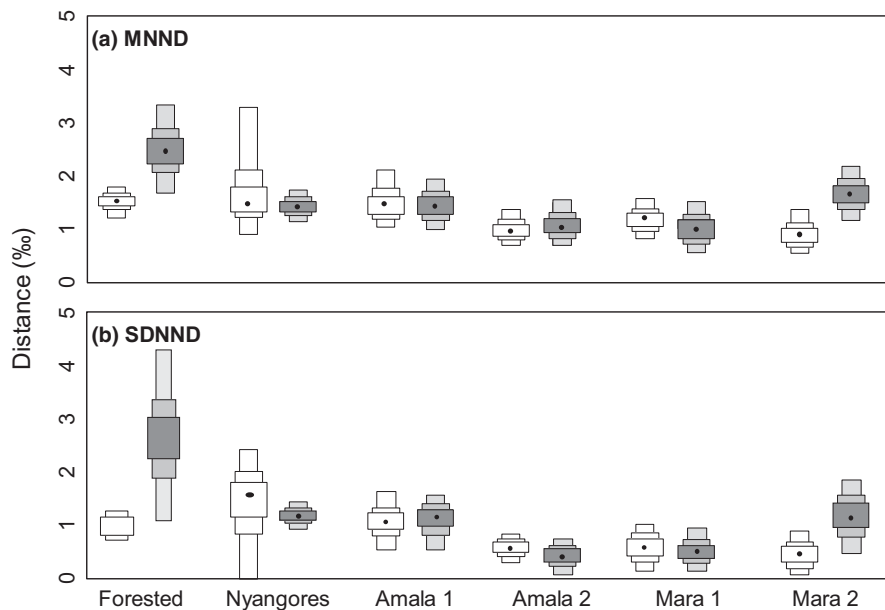

FIGURE 6 Layman stable isotope-based community-wide metrics (mode and 95% credible intervals) for the invertebrate and fish community at the different sites: mean nearest neighbour distance (MNND) and standard deviation of mean distance to centroid (SDNND) are both measures of trophic redundancy. White = dry season, grey = wet season

amounts of leaf litter of terrestrial origin which support a diverse detritivorous assemblage (Masese et al., 2014a, 2014b). On the other hand, high levels of suspended materials at the agricultural and hippo-influenced sites limit instream primary production (Dutton, Anisfeld, & Ernstberger, 2013; Kilonzo et al., 2014; Masese, Salcedo-Borda, Gettel, Irvine, & McClain, 2017; Subalusky, 2016), with the food webs becoming more dependent on external (allochthonous) sources (Masese et al., 2015), a result similar to that found for other east African systems (Abrantes, Barnett, Marwick, & Bouillon, 2013). In addition to increased sedimentation in agricultural sites which reduces instream primary production (Kilonzo et al., 2014), habitat degradation that has been reported in these sites likely reduced trophic diversity of macroinvertebrates (Masese et al., 2014b; Minaya, McClain, Moog, Omengo, & Singer, 2013), especially during the dry season when instream influences are increased due to high numbers of livestock visiting watering sites. These findings showed that an increase in large mammalian herbivores reduced trophic diversity, and potentially niche sizes, directly through inputs of high amounts of organic matter which cause physiological stress to biological communities, with sensitive taxa disappearing (Masese & Raburu, 2017), and indirectly through negative influences on primary production through increased sedimentation.

For both invertebrates and fish, the hippo-influenced Mara 2 site showed SEAs with the highest $\delta^{13}C$ values. This suggests a strong influence of C4 sources supporting aquatic consumers. Contrary to the C3-dominated Forested site, the C4-dominated Mara 2 site had a compact and less diverse food web, with a short trophic length (NR). This can be partly explained by high levels of suspended sediments that limit both primary production and the diversity of sources available to consumers (Masese et al., 2015). Moreover, the dominance of the C4 pathway and lower isotopic trophic diversity at the Mara 2 site are also likely a result of the annual mass drownings of wildebeest (*Connochaetes taurinus*) whose carcasses have the same $\delta^{13}C$ value as the C4 grasses they feed on (Subalusky, Dutton, Rosi, & Post, 2017). Wildebeest carcasses have recently been shown to have both short- and long-term ecosystem effects directly through mineralisation of soft tissue by fish or indirectly through biofilm growth on bones that are later fed on by insects and fish after soft tissue decomposition (Subalusky et al., 2017).

There were also significant differences in trophic structure among sites as a result of differences in the quality of organic matter entering the streams. The forested site had the lowest trophic redundancy and the widest resource diversity. Both low trophic redundancy (high MNND value) and a nonuniform trophic niche distribution (high SDNND value) were recorded at the forested site. This is most likely a result of the greater availability of a range of aquatic sources ranging from the C3 riparian vegetation and autochthonous production in the relatively clear waters. A significant input of leaf litter from C3 vegetation at this site, which is of higher quality than C4 grasses, supported a greater diversity of shredders compared to other sites (Table 2). Similar findings have been reported from other sites in the Mara River Basin whereby forested streams are reported to have a greater diversity of shredders

compared to agricultural streams where resource availability and quality are much lower (Masese et al., 2014a, 2014b). The diverse invertebrate assemblage at the forested site (Table 2) can therefore consume a wide range of both terrestrial and aquatic sources in various combinations, resulting in greater distance among consumers in the isotopic space (Layman et al., 2007).

The findings of this study show that the presence of herbivore-mediated subsidies can affect trophic diversity and food-web structure. Were it not for the influence of large mammalian herbivores and the predominance of laterally vectored organic matter of C4 origin, sources would be expected to be more diverse at the hippo-influenced Mara 2 site compared to the most upstream forested site (Thorp & Delong, 2002; Vannote et al., 1980). This would likely have resulted in a trophic structure characterised by high trophic diversity, increased niche sizes and reduced trophic redundancy. However, the opposite was observed, as the Mara 2 site presented lower isotopic trophic diversity and trophic length, despite the increased input of C4 organic matter. Similarly, reduced trophic niche sizes and trophic redundancy were reported at the agricultural sites receiving both human and animal nutrient and organic matter inputs. Therefore, inputs of C4 carbon by large mammalian herbivores do not necessarily lead to an increase in trophic diversity in savanna river systems.

4.2 | Seasonal differences in food-web structure

There were seasonal differences in both invertebrates and fish SEAs that could be related to temporal changes in sources of nutrition among sites. However, for insectivorous fish, there were large SEA overlaps between seasons and fish isotopic niches were much smaller than invertebrate SEAs. The constricted and considerably overlapping SEAs suggest that insectivorous fishes exploit a relatively narrow range of food sources, resulting in increased trophic redundancy. This could also suggest that insectivorous fish feed on a select group of invertebrates that responded to seasonality in a different way to the overall invertebrate assemblage. Analysis of fish stomach contents indicated that insectivorous fish feed mainly on scrapers and filter-feeders (Masese FO, unpublished data). Scrapers are very sensitive to sedimentation which smothers their food and reduces algae and periphyton upon which they feed. It has also been noted that the quality of suspended organic matter is substantially reduced in agricultural areas (Masese et al., 2017). It is therefore likely that the increase in suspended sediments during the wet season led to a decrease in abundance of these invertebrate groups and to a reduced range of available sources for insectivorous fishes, leading to reduced niche sizes in the wet season when compared to the dry season.

There was also a lack of congruence in the shape and seasonal responses of invertebrates and fish SEAs. Invertebrate SEAs changed more in shape and size than fish. With the exception of the forested site, dry season invertebrate SEAs showed higher $\delta^{13}C$ values when compared to wet season SEAs (Supporting Information Figure S1). On the other hand, fish SEAs showed lower $\delta^{13}C$ values during the

dry season (Supporting Information Figure S2). This suggests a shifting basal energy source during the dry season, but with contrasting responses for invertebrates and fishes.

We expected food webs to be more homogenous among sites during the wet season because of increased longitudinal connectivity and hydrological transfer of ^{13}C-depleted carbon from upstream C3-dominated vegetation, but this is not supported by our data. Moreover, the influence of seasonality on trophic niche size was not uniform across sites (Figure 4). For the Mara 1 and hippo-influenced Mara 2 sites, larger SEAs during the dry season reflect an interesting phenomenon of increased niches during the dry season likely due to herbivore-mediated inputs of organic matter. Besides the semiaquatic resident hippos, other herbivores such as wildebeest and zebra usually congregate along river networks during the dry season (Ogutu et al., 2014) and by so doing deposit organic matter and nutrients into the rivers (du Toit, 2003; Naiman et al., 2003). Because of the low flows, most of this material accumulates in pools and backwaters where it increases aquatic production. During the wet season, the resuspension of this material limits aquatic primary production due to increased turbidity, therefore decreasing the range of available sources for consumers. This is supported by the significantly high contribution of periphyton and algae to consumers downstream of hippo aggregation points during the dry season, but a reversal during the wet season where C4 carbon dominates contributions to food webs at the same sites (Masese et al., 2015).

5 | CONCLUSIONS

The role played by large mammalian herbivores as vectors of transfer of terrestrial organic matter and nutrients into streams and rivers is increasingly being recognised, making it important that we understand effects of either losses or increasing populations of large mammalian herbivores on ecosystem structure and function. The results of this study indicate that increased inputs of terrestrial organic matter by large mammalian herbivores in African savanna streams and rivers reduce trophic diversity and niche sizes for aquatic consumers, but these effects also depended on the seasonally driven flow variations in the rivers. The findings also show that organic matter and nutrient inputs under certain conditions, especially the dry season low flows, may induce stimulatory bottom-up effects with contrasting responses in macroinvertebrates and fish trophic diversity and trophic niche sizes. Illustrating the relationships between organic matter and nutrients loading by large mammalian herbivores and aquatic ecosystem structure and function is a prerequisite for understanding fully how linked ecosystems respond to changes in the populations of large mammalian herbivores.

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