1 **Large herbivorous wildlife and livestock differentially influence the**

2 **relative importance of different sources of carbon for riverine food webs**

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19   **Abstract**

20   In many regions around the world, large populations of native wildlife have declined or been

21   replaced by livestock grazing areas and farmlands, with consequences on terrestrial-aquatic

22   ecosystems connectivity and trophic resources supporting food webs in aquatic ecosystems.

23   The river continuum concept (RCC) and the riverine productivity model (RPM) predict a shift

24   of carbon supplying aquatic food webs along the river: from terrestrial inputs in low-order

25   streams to autochthonous production in mid-sized rivers. Here, we studied the influence of

26   replacing large wildlife (mainly hippos) with livestock on the relative importance of C3

27   vegetation, C4 grasses and periphyton on macroinvertebrates in the Mara River, which is an

28   African montane-savanna river known to receive large subsidy fluxes of terrestrial carbon

29   and nutrients mediated by LMH, both wildlife and livestock. Using stable carbon (δ^{13}C) and

30   nitrogen (δ^{15}N) isotopes, we identified spatial patterns of the relative importance of

31   allochthonous carbon from C3 and C4 plants (woody vegetation and grasses, respectively)

32   and autochthonous carbon from periphyton for macroinvertebrates at various sites of the

33   Mara River and its tributaries. Potential organic carbon sources and invertebrates were

34   sampled at 80 sites spanning stream orders 1 to 7, various catchment land uses (forest,

35   agriculture and grasslands) and different loading rates of organic matter and nutrients by

36   LMH (livestock and wildlife, i.e., hippopotamus). The importance of different sources of

37   carbon along the river did not follow predictions of RCC and RPM. First, the importance of C3

38   and C4 carbon was not related to river order or location along the fluvial continuum but to

39   the loading of organic matter (dung) by both wildlife and livestock. Notably, C4 carbon was

40   important for macroinvertebrates even in large river sections inhabited by hippos. Second,

41   even in small 1st -3rd order forested streams, autochthonous carbon was a major source of

42   energy for macroinvertebrates, and this was fostered by livestock inputs fuelling aquatic

43   primary production throughout the river network. Importantly, our results show that

44   replacing wildlife (hippos) with livestock shifts river systems towards greater reliance on

45   autochthonous carbon through an algae-grazer pathway as opposed to reliance on

46   allochthonous inputs of C4 carbon through a detrital pathway.

47   **Keywords:** aquatic-terrestrial connectivity, C4 carbon, organic matter, nutrient loading,

48   MixSIAR models, resource subsidies

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51 1. Introduction

52 While resource transfers from terrestrial to riverine aquatic ecosystems can occur passively

53 through wind and atmospheric deposition, overland and riverine flow (Abrantes and

54 Sheaves, 2010; Lamberti et al., 2010; Wipfli et al., 2007), animals are major active resource

55 vectors through defecation (egestion), urination (excretion) and in the form of carcasses

56 (Naiman and Rogers, 1997; Subalusky et al., 2015; Subalusky et al., 2017). Resource subsidies

57 by large mammalian herbivores (LMH) are particularly interesting because of their capacity

58 to transfer large amounts of high-quality, nutrient-rich resources that strongly influence

59 abiotic conditions, productivity, community structure and trophic interactions in recipient

60 aquatic ecosystems (Vanni, 2002; Masese et al., 2018; Stears et al., 2018).

61 Along their longitudinal gradient, rivers are postulated to exhibit a prominent shift in trophic

62 resources supporting aquatic communities, influencing their structure and functional

63 organization besides physical and chemical factors (Vannote et al., 1980; Atkinson et al.,

64 2017). In temperate headwater streams, allochthonous carbon from C3-plants (woody

65 vegetation) dominates the base of food webs. As streams widen, however, in-stream

66 primary production grows, while allochthonous inputs decrease to subsidies leaking from

67 upstream (Vannote et al., 1980; Thorp and Delong, 1994). In contrast, in Afrotropical

68 savanna rivers, mega-herbivores including hippos (*Hippopotamus amphibius*), elephants,

69 buffalo, other ungulates, such as wildebeest, transfer substantial amounts of terrigenous

70 carbon and nutrients to entire river networks (Naiman and Rogers, 1997; Mosepele et al.,

71 2009, Hulot et al., 2019), challenging existing models of riverine ecosystem functioning.

72 Notably, this allochthonous carbon is mainly derived from C4 plants in surrounding

73 grasslands and seems to critically need grazing LMH as subsidy vectors (Marwick et al.,

74   2014). Indeed, hippo egestion can account for up to 88% of total carbon inputs into lowland

75   rivers (Subalusky et al., 2015), which may play a similar role as leaf litter in headwater

76   streams in stimulating microbial processes and supporting food webs (Webster, Benfield et

77   al. 1999). Large quantities of hippo dung have also been found to be detrimental to aquatic

78   biodiversity, with fish kills occurring during phases of reduced flow and high hippo density

79   (Dutton et al., 2018a; Stears et al., 2018).

80   Populations of native LMH have declined in their natural range and have been replaced by

81   human settlements, farmlands and livestock (Doughty et al., 2013; Ogutu et al., 2016;

82   Veldhuis et al., 2019). Large herds of livestock (mainly cattle, goats and sheep) may

83   compensate losses of resource subsidies to aquatic ecosystems arising from wildlife declines

84   (Iteba et al., 2021; Masese et al., 2020), but the quality, quantity (rate), timing and location

85   of inputs can substantially differ (Subalusky and Post, 2019), with ensuing implications for

86   aquatic ecosystem functioning. For instance, nutrient-rich cattle dung was found to increase

87   primary production relative to hippo dung (Masese et al., 2020). And, since high-quality algal

88   carbon contributes higher proportions of carbon to metazoan biomass relative to woody

89   vegetation and grasses (Thorp and Delong, 2002; Douglas et al., 2005; Lau et al., 2009),

90   livestock may shift aquatic food webs to be more reliant on autochthonous sources of

91   carbon. This may be facilitated by the increased transportability of cattle dung due to

92   smaller particle sizes and faster leaching and remineralization (Masese et al., 2020), while

93   hippo faeces contain large particles that settle on the river bottom and decompose slowly

94   (Dawson et al., 2016; Dutton et al., 2020).

95   The Mara River (Kenya, Tanzania) traverses a landscape gradient, that makes it well suited to

96   study the influence of land use change and altered LMH populations on the terrestrial-

97   aquatic linkages achieved through resource subsidies. The forest in the upper reaches

98   contrasts mixed small-scale and large-scale agriculture and human settlements in mid-

99   reaches (Mati et al., 2008). The region hosts livestock (mainly cattle, goats and sheep) at

100   varying densities, grazing in an overlapping distribution with wildlife (Lamprey and Reid

101   2004; Veldhuis et al., 2019). In the lower reaches, protected savanna grasslands in the

102   Kenyan Maasai Mara National Reserve (MMNR) harbour over a million migratory herbivores

103   (Ogutu et al., 2016), including >4000 hippos (Kanga et al., 2011). Per-capita input of organic

104   matter and nutrients into streams and rivers by individual livestock is small compared to

105   hippos (Sualusky et al., 2015; Masese et al., 2020) due to smaller body sizes and shorter time

106   of presence in or near water, but livestock can appear in large numbers (Iteba et al., 2021).

107   Also, resource subsidies of livestock and wildlife differ in quality, with likely impacts on

108   aquatic ecosystem functioning. A good assessment of subsidies transferred to the Mara

109   River critically needs comparative data for livestock and wildlife and how their inputs

110   interact with river size.

111   Here, we investigate carbon sources fuelling aquatic food webs at various sites along the

112   Mara River, specifically the interaction between river size and subsidy fluxes driven by

113   livestock and large wildlife (hippos) at various densities. In the greater Mara River network,

114   we sampled 80 sites in streams differing in catchment land use and LMH abundance. We

115   used natural abundance stable isotope analysis (SIA) of carbon (δ^{13}C) and nitrogen (δ^{15}N) to

116   distinguish three main sources of carbon (C3 vegetation, C4 grasses and periphyton) for

117   macroinvertebrates. Contrary to predictions of the river continuum concept (RCC) and the

118   riverine productivity model (RPM), we hypothesise that LMH have an overriding influence

119   over stream size in determining sources of carbon for food webs in savanna rivers.

120   Specifically, in lower sections of the river, autochthonous production and C3 carbon should

121   decrease in importance while C4 carbon subsidies by livestock and large wildlife should

122   become more prominent in the diets of invertebrates.

2. Materials and Methods

2.1 Study area

125   This study was conducted in the Kenyan part of the Mara River catchment. Two perennial

126   tributaries, the Nyangores and Amala rivers drain the Mau Forest, which is the most

127   extensive tropical moist broadleaf forest in East Africa, before joining to form the Mara

128   mainstem in the lowlands (Fig. 1). In the middle reaches, several seasonal tributaries,

129   including the Talek, Olare Orok, Ntiakntiak, Molibany and the Sand, drain the semi-arid

130   livestock grazing lands and wildlife conservancies outside the Maasai Mara National Reserve

131   (MMNR). Annual rainfall varies from about 2000 mm in the highlands to around 1000 mm in

132   the lowland savanna (Jackson and McCarter, 1994). January to March is typically a dry

133   period, while March-July and October-November are wet periods known as long and short

134   rains, respectively.

135   The Kalenjin ethnic group live on the highlands while the Maasai pastoralists occupy the

136   middle and lower portions of the basin. The basin hosts substantial numbers of livestock but

137   densities differ across the catchment as the Kalenjin have diversified to crop farming and

138   husbandry of small herds of improved breeds of cattle, while the Maasai´s large herds of

139   cattle are the mainstay of their livelihoods (Lamprey and Reid, 2004). Agricultural expansion

140   is ongoing across the basin (Mati et al., 2008).

141   The middle reaches of the Mara River and its tributaries within the MMNR host >4,000

142   hippos (Kanga et al., 2011), which graze in savanna grasslands at night and rest in or near the

143   river during the day, transferring ~36,000 kg of organic matter in the form of dung per day

144   from the terrestrial to the aquatic domain (Kanga et al., 2011; Subalusky et al., 2015). In the

145   same region, Maasai pastoralists graze nearly 200,000 cattle and large numbers of goats and

146   sheep in communal lands adjoining the MMNR and utilize rivers as watering points (Lamprey

147   and Reid, 2004; Ogutu et al., 2016; Veldhuis et al., 2019). In communal conservancies

148   outside the MMNR, people graze their livestock in a manner that allows livestock to co-exist

149   with wildlife (Kanga et al., 2013). This distribution results in a displacement pattern with

150   hippo areas inside the reserve, mixed hippo and livestock (mainly cattle) areas in the

151   conservancies and only livestock grazing areas outside the conservancies (Kanga et al.,

152   2013).

153   **2.2 Study design**

154   A total of 80 sites were selected for sampling during the beginning of the dry season in

155   January 2018. All sites were sampled only once unless specified otherwise. In most cases, we

156   sampled at confluences, i.e., working in both tributaries and a third downstream mainstem

157   site after effective mixing of water from the two tributaries. Sites were selected depending

158   on both catchment-scale (mainly land use) and reach-scale influences by human activities,

159   cattle and wildlife. Sites were then grouped into 5 broad regions: forested (19), agricultural

160   (26), low-density livestock (15), high-density livestock (12), and wildlife (i.e., hippo) (10) sites.

161   Forest sites had C3 vegetation dominating the catchment and riparian areas, and were used

162   as a reference for the human and LMH influences. Agricultural sites were in farming areas

163   (crop cultivation), although most farmers in the area also own low numbers (<20 per km^2) of

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164   livestock (mainly cattle). The low-density livestock sites were also in agricultural areas but

165   had a higher density of livestock (20-50 per km^2). The high-density livestock sites were

166   located in conservancies outside the MMNR where the only land use activity is the grazing of

167   large herds of cattle (> 100 heads per km^2), goats and sheep; although some wildlife such as

168   zebra, wildebeest and other herbivores (but rarely hippos) also occur in these areas. Finally,

169   hippo sites were located on the Mara River mainstem and tributaries in the MMNR

170   downstream of river sections inhabited by large populations of hippos (Kanga et al., 2011).

171   **2.3 Sample collection**

172   At each site, samples of the dominant riparian plants were collected by hand into aluminium

173   envelopes. Macrophytes were rare and not considered to be an important resource. We

174   collected triplicate samples of cattle and hippo dung when encountered at a site. Triplicate

175   periphyton samples were scrubbed from submerged surfaces after gentle washing to remove

176   invertebrates and debris. At each site macroinvertebrates were collected from riffles, runs,

177   pools and marginal vegetation using a dip net (500 μm mesh-size) and sorted alive into

178   Eppendorf vials. Plant, dung, periphyton slurry (in HDPE bottles) and invertebrates were

179   frozen for transport to the laboratory pending further processing.

180   **2.3.1 Physical and chemical variables**

181   To explore relationships between catchment land use and the importance of various sources

182   of carbon for invertebrates in the Mara River, sub-catchments for all sites were delineated

183   based on a digital elevation model of Kenya (90 m resolution, Shuttle Radar Topography

184   Mission) and their land cover analyzed according to the major types; forest (both natural and

185   plantation), agriculture (cropland) and settlements, grasslands (grazing lands) and

186   shrublands.

187   At each site, we measured average stream width at 20-30 randomly located transects and

188   average depth and velocity at a minimum of 100 randomly located points. Discharge was

189   estimated using the velocity-area method at one transect. Dissolved oxygen concentration

190   (DO), pH, temperature and electrical conductivity were measured *in situ* using a WTW

191   Multiprobe 3320 (pH320, OxiCal-SL, Cond340i; Weilheim, Germany).

2.3 Sample preparation and stable isotope analysis

193   On return to the laboratory, samples were immediately prepared for isotope analysis or

194   preserved at -20˚C. To clean periphyton, the slurry was decanted onto a petri dish and excess

195   water evaporated in an oven at 60 °C for 48 h. The dry sample was ground using a mortar and

196   pestle, an aliquot was weighed into a tin cup. Macroinvertebrate specimens were thawed

197   and examined under a dissecting microscope to confirm identity and remove stomach

198   contents before drying at 60 °C for 48 h. These samples were ground with an IKA A 11 Basic

199   mill (IKA-Werke GmbH & Co. KG, 79219, Staufen, Germany) and weighed into tin cups.

200   Macroinvertebrates were identified mostly to the genus level. Several individuals of a given

201   taxon from each site were pooled to produce sufficient dry tissue mass except for species

202   with larger body sizes such as crabs (*Potamonautes* spp.), dragonflies and damselflies

203   (Odonata), some beetles (Coleoptera) and bugs (Hemiptera). To avoid contamination by

204   carbonates, which can be enriched in ^{13}C compared to living tissue, we only used soft tissues

205   from crabs and Mollusca.

206   Stable isotope analysis was done on a Thermo Finnigan DeltaPlus Advantage isotope ratio

207   mass spectrometer (IRMS, Thermo Scientific) coupled to an ECS 4010 EA elemental analyzer

208   (Costech Analytical Technologies). Stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) are expressed

209   in parts per mil (‰) deviations to the international standard, as defined by the equation:

210      $\delta^{13}C$, $\delta^{15}N = [(R_{sample}/R_{reference}) - 1] \times 10^3$, where R = $^{13}C/^{12}C$ for carbon and $^{15}N/^{14}N$ for

211   nitrogen. $\delta^{13}C$ values were normalized to the international scale Vienna Pee Dee Belemnite

212   (VPDB) and $\delta^{15}N$ values to atmospheric nitrogen, by analyzes of the international standards

213   USGS40 and USGS41 (L-glutamic acid) within the sequence (Qi et al. 2003). In addition, a

214   laboratory standard ($\delta^{13}C$ = -27.11 ‰, C% = 48.12; $\delta^{15}N$ = 0.48 ‰, N% = 2.17), which was

215   calibrated directly against USGS40 and USGS41, was measured at different positions within

216   the run. Precision, defined as the standard deviation (±1σ) of the laboratory control standard

217   along the run was better than ±0.79‰ for C and ± 0.55‰ for N.

218   **2.4 Functional feeding groups and trophic groups**

219   Macroinvertebrate taxa were assigned to functional feeding groups (FFGs) and trophic

220   groups based on (Masese et al., 2014) and references therein. FFGs considered included

221   shredders feeding on coarse particulate organic matter (CPOM), scrapers feeding on

222   autochthonous production (periphyton), collector-filterers feeding on suspended fine

223   particulate organic matter (FPOM), collector-gatherers feeding on deposited FPOM and

224   predators feeding on live animal tissue (Merritt et al., 2017). Shredders, scrapers and

225   collectors were also subsumed as herbivores.

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2.5 Data analysis

All physical and chemical data were transformed using natural-log transformations before analysis. We used one-way analysis of variance (ANOVA) to test for differences in water quality, stream size and land use variables among the five regions, followed by post hoc Tukey's Honestly Significant Difference (HSD) multiple comparisons of means.

We used MixSIAR Bayesian mixing model to estimate the contributions of different basal sources to consumer diets (Parnell et al., 2010; Stock and Semmens, 2013). Models were run for each site separately for each FFG and common family. Only C3 and C4 plants and periphyton were included in the models as possible sources of carbon and nitrogen (Masese et al.; 2015, 2018). For periphyton, we calculated standard deviations of source values for input into MixSIAR from triplicate samples collected from the same site. Because the isotopic values of vegetation are influenced by elevation, for C3 and C4 sources we grouped sites into three groups defined by elevation: headwaters (> 2800 m a.s.l.), middle reaches (2000-2800 m a.s.l.) and lower reaches in the MMNR and surrounding areas (<2000 m a.s.l.). Trophic enrichment factors (TEFs) were set to zero after manually correcting for trophic fractionation in the stable isotope composition of consumers. For $\delta^{15}N$, we used a trophic fractionation of 0.6 ± 1.7 ‰ and 1.8 ± 1.7 ‰ for herbivorous and predatory macroinvertebrates, respectively (Bunn et al., 2013). For $\delta^{13}C$, we used a trophic fractionation of 0.5 ± 1.3 ‰ (McCutchan Jr et al., 2003). Concentration dependencies were set to zero.

For each site, river distance from the source (RDS) was calculated as the square root of the drainage area (Rasmussen et al., 2009) as a general measure reflecting the linear dimension of a watershed. This is based on the finding that the average length of stream paths leading to a point in the drainage can be expressed as a power function of the drainage area

250   (Gregory and Walling, 1973) with the exponent 0.5 (Smart, 1972). We used RDS and LMH

251   (livestock and hippos) density per sampling site as independent variables against which

252   longitudinal changes in fractional contributions of periphyton, C3 and C4 carbon to

253   invertebrates in the river were explored using simple linear regression (SLR). Relationships

254   were tested separately for the different FFGs.

255   Data on livestock (cattle, sheep, goats, and donkeys) and wildlife (ungulates and hippos)

256   numbers were obtained from Development Plans for Bomet and Narok Districts (Plan, 2007,

257   2008), Ministry of Agriculture and Livestock Production, and Kenya National Bureau of

258   Statistics reports (KNBS-IHBS, 2007; KNBS-LS, 2009; KNBS, 2016, 2018), and other

259   unpublished and published reports (Ottichilo et al., 2000; Lamprey and Reid, 2004; Kanga et

260   al., 2011; Kiambi et al., 2012; Ogutu et al., 2016). For livestock and other LMH, density was

261   expressed as the number of individuals per km^2 in the catchment area of the river sampling

262   site, while for hippos, count data were expressed as the number of individuals per river km.

263   We used generalized additive models (GAMs) (Wood, 2017) to assess how the relative

264   importance of C3 carbon, C4 carbon and periphyton for individual FFGs and all FFGs

265   combined varied with stream size (RDS) and density of LMH. GAMs incorporate smooth

266   functions that are more flexible in modelling nonlinear relationships (Hastie and Tibshirani,

267   1990). Typically, the importance of different sources of carbon varies non-linearly with

268   stream order or distance from the source (Vannote et al., 1980). GAMs were built using

269   penalized cubic regression splines with degrees of freedom automatically identified based on

270   the generalized cross-validation score (GCV) using the mgcv-package (Wood and Wood,

271   2015) in the R platform (R-Development-Core-Team, 2017). GAMs were used further to

272   investigate the influence of region, stream size (RDS) and LMH density, including potential

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273   interactions, on the relative importance of the three sources of carbon for FFGs in the river.

274   GAMs included region, RDS and LMH density as fixed effects, and individual sampling sites as

275   a random effect. All analyses were performed using R 3.4.4 (Team, 2017).

3.   Results

3.1 Physico-chemical variables

278   There was spatial variation in many physical and chemical variables (Table 1). LMH density

279   increased with the proportion of forest cover and decreased with the proportion of

280   grassland. Electrical conductivity and water temperature increased with LMH density but

281   were low at the forested, low livestock density and agricultural regions/ sites (Table 1). Apart

282   from the hippo sites, there were no differences in river distance from the source (RDS), river

283   width, depth, or discharge among the five regions.

3.2 Basal resources

285   The C3 and C4 plants collected at the various sites did not differ significantly in δ^{13}C and δ^{15}N

286   (Table 1), nevertheless mean isotopic signatures were calculated for each of three elevation

287   levels for use in the MixSIAR models. The δ^{15}N values of C4 plants were generally higher than

288   those of C3 plants. δ^{13}C, but not δ^{15}N, of cattle dung, varied considerably among sites and

289   regions (Table 2). In contrast, δ^{13}C and δ^{15}N of hippo dung showed little variation among

290   regions with hippos. δ^{13}C and δ^{15}N of periphyton were highly variable among sites and

291   regions (Figure 2, Table 1); specifically, agricultural and livestock sites had elevated δ^{15}N

292   values compared to forested areas and the MMNR, where hippos had a strong influence

293 (Figure 2). In MixSIAR models, site-specific isotopic signatures were used for all resources

294 with detectable variation among regions.

3.3 Longitudinal trends in basal resources

296 Longitudinal patterns in δ^{13}C of periphyton in the Mara River were wedge-shaped (Figure 2).

297 Periphyton δ^{13}C responded to both measures of stream size RDS (r = 0.23, p < 0.01) and

298 stream order (r = 0.35, p < 0.01). At shorter RDS, agricultural and low density (LD) livestock

299 sites had the widest range of periphyton δ^{13}C, while values at forested sites were invariably

300 low (-25.9±2.6‰, Table 2). The narrowest ranges of δ^{13}C were recorded for high density (HD)

301 livestock and hippo sites, which appeared at longer RDS. At these sites, δ^{13}C (HD livestock: -

302 23.2±1.2‰, hippo sites: -22.7±1.8‰) was on average higher than at forested sites. δ^{13}C of

303 periphyton was positively related to agricultural land use (r = 0.24, p < 0.05) and negatively

304 to forest cover (r = -0.44, p < 0.01). Overall, periphyton δ^{13}C responded positively to LMH

305 density (r = 0.52, p < 0.01), which itself was highly positively correlated with % grassland

306 cover in the catchment (r = 0.89, p < 0.01).

307 Longitudinal patterns of periphyton δ^{15}N were similar to δ^{13}C, yet we could not detect a

308 significant change of the mean value with any measure of stream size. Periphyton δ^{15}N was

309 higher at agricultural and LD livestock sites (Figure 2) with shorter RDS, but lower at both the

310 forested sites with short RDS and hippo sites at longer RDS. Unexpectedly, δ^{15}N at LD

311 livestock sites also surpassed HD livestock sites. δ^{15}N of periphyton was positively related to

312 agricultural land use (r = 0.29, p < 0.01) and negatively to forest cover (r = -0.31, p < 0.01).

313 Interestingly, there was no significant relationship between δ^{15}N of periphyton and LMH

314 density.

3.4 Importance of different carbon sources for invertebrates

A total of 47 taxa in the five macroinvertebrate FFGs were collected in the study area (Table S1). The importance of C3 vegetation, C4 grasses and periphyton for invertebrates differed among the five regions, but patterns were similar for scrapers and collectors (Figure 3). Overall, periphyton was either the major or second-most important source of carbon for all FFGs at forested, agricultural and livestock sites, and predators were more reliant on this energy pathway than the rest of the FFGs (Figure 3). Except for shredders in forested streams, the importance of C3 vegetation was reduced for the rest of FFGs in the other regions and was lowest at the hippo sites. On the contrary, the importance of C4 carbon responded strongly to LMH density and was the most important source of carbon (>50%) for all FFGs at hippo sites, except shredders (Figure 3).

Source contributions followed similar patterns for all FFGs except predators and shredders (Figure 3). Predators seemed to draw most of their nutrition from the periphyton pathway at all sites except those with hippos. Shredders, on the other hand, displayed an overreliance on C3 vegetation as their main source of carbon at all sites, which is consistent with their feeding habits on coarse particulate organic matter, i.e., mostly leaves of C3 vegetation of terrestrial origin. Thus, shredders were least influenced by inputs of C4 carbon into the river via LMH.

3.5 Longitudinal trends in the importance of different carbon sources

We explored relationships between stream size (i.e., river distance from the source, RDS) and LMH density as predictors of the importance of the three differentiated sources of carbon (C3 vegetation, C4 grasses and periphyton) for macroinvertebrates in the Mara River

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337   (Figure 4). The relative importance (fractional contribution) of the three sources of carbon

338   changed with stream size (RDS) and LMH density (Figure 4a, b). Periphyton was the most

339   important source of energy in headwater and mid-sized streams, contributing on average

340   more than 40% to invertebrate biomass, but decreased to the second most important source

341   of carbon further downstream. C3 vegetation (woody vegetation) was almost as important

342   as periphyton in headwater streams, contributing nearly 40%, but its importance declined

343   from mid-sized streams onwards, becoming the least important source of carbon with

344   contributions <20% in large river sections (Figure 4a). C4 plants (grasses) were not relevant

345   in small streams contributing less than 20% to invertebrates' energy requirements, but their

346   importance markedly increased in mid-sized and large river sections, where they became the

347   dominant source of energy with a contribution of nearly 60% to the total energy

348   requirements for macroinvertebrates. The influence of LMH on the longitudinal importance

349   of carbon sources for macroinvertebrates in the river (Figure 4b) mirrored that of RDS,

350   although patterns for C4 carbon were stronger. Patterns with stream order as a proxy for

351   stream size were identical to those with RDS (data not shown).

352   We also explored longitudinal relationships between stream size (i.e., river distance from the

353   source, RDS) and LMH density as predictors of the importance of the three sources of carbon

354   (C3 vegetation, C4 grasses and periphyton) for individual FFGs (Figure 5). There were

355   significant positive relationships (linear regressions, $p < 0.05$) between RDS and the

356   importance of C4 to all FFGs except shredders (Figure 5g, h). In parallel, C3 carbon from

357   terrestrial vegetation became less important with RDS for collector-filters (Figure 5a, b) and

358   collector-gatherers (Figure 5c, d). Also, LMH density had strong influences on the importance

359   of carbon sources for all FFGs except shredders, by reducing the contribution of C3 while

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360   increasing that of C4 carbon. As expected, shredders were mainly reliant on C3 vegetation

361   and were neither influenced by stream size nor LMH density (Figure 5g, h).

362   We found a significant influence of stream size and region on the relative importance of C3

363   and C4 carbon for combined and individual FFGs, except shredders, in the river (Table 2). The

364   independent effects of LMH density on the relative importance of C4 carbon was limited to

365   scrapers and predators only, implying increasing LMH density did not necessarily increase

366   the importance of C4 carbon for invertebrates. This is in agreement with observations that

367   livestock increased the importance of periphyton while hippos increased the importance of

368   C4 carbon for most FFGs, but increasing densities of both livestock and hippos decreased the

369   importance of C3 carbon for invertebrates (Figure 3). There were significant interactions

370   between LMH density and region in the importance of C4 carbon for all FFGs, except

371   shredders. Overall, patterns in the importance of the three sources of carbon for predators

372   were similar to those of all FFGs combined.

373   To eliminate potential confounding by organic matter and nutrient inputs by other

374   agricultural activities not associated with LMH, the influence of stream size and LMH density

375   on the relative importance of carbon sources for invertebrate FFGs were evaluated in

376   forested sites only where LMH (both livestock and wildlife) were limited (Supplementary

377   Information, Figures S1). Remarkably, no major effect of stream size was noted for most

378   FFGs, further reinforcing the important role of LMH as drivers of food resources for

379   macroinvertebrates in the river.

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18

382   **4. Discussion**

383   This study shows that the importance of different sources of carbon for consumers in

384   savanna rivers is spatially variable in response to changes in abundance and distribution of

385   large mammalian herbivores, both livestock and wildlife, and stream size or river distance

386   from the source. Overall, (i) periphyton was the most important source of energy for

387   macroinvertebrates in low order and mid-sized rivers, (ii) periphyton and C4 vegetation

388   became more important carbon sources at the cost of C3 plants at high-density livestock and

389   hippo sites, respectively, and (iii) lower sections of the river hosting large populations of

390   LMH relied largely on C4 vegetation with very little contributions of C3 plants. Our findings

391   thus confirm our hypothesis of an overriding influence of LMH over stream size or location

392   along the fluvial continuum in determining sources of carbon for food webs in savanna

393   rivers.

394   Although previous studies in African savanna rivers have shown that LMH foster the

395   importance of C4 carbon as a major source of carbon for aquatic consumers (Masese et al.

396   2015, McCauley et al., 2015, Dawson et al., 2020), no study has evaluated the importance of

397   these resource subsidies on entire gradients of rivers and at the scale that we have done in

398   this study. The many stream sites sampled that differed in size and LMH density enabled us

399   to evaluate the interaction of stream size with subsidy quantity as determinants for the base

400   of riverine food webs. Our results depart from predictions on the importance of resources

401   along the river continuum. While a reduction in the contribution of C3 carbon is

402   hypothesized in mid-sized rivers as periphyton becomes dominant (Vannote et al., 1980;

403   Thorp and Delong, 1994), an increase in the importance of fresh C4 vegetation inputs to mid-

404   sized and large rivers is less intuitive and not hypothesized in existing models of riverine

405   ecosystem functioning. Instead, mid-sized and large rivers are thought to be

406   disproportionately reliant on autochthonous production, and leakage of unutilized materials

407   from upstream supply food webs of large rivers (Vannote et al., 1980, Thorp and Delong,

408   2002; Thorp et al., 2006).

409   Although LMH density and the proportion of C4 grasses in the catchments were strongly

410   correlated ($r = 0.89$), the increased importance of C4 carbon in the diet of most

411   macroinvertebrates in this study was assumed to be mediated via the vectoring role of LMH

412   when they defecate in the river. Indeed, in the absence of LMH, the contribution of C4

413   carbon to riverine food webs is less than expected based on areal landcover (Abrantes and

414   Sheaves, 2010; Marwick et al., 2014), and given lower C4 vegetation height direct riparian

415   inputs were minimal. Without LMH-mediation, C4 carbon would hardly reach aquatic food

416   webs and dominance of C3 carbon could be expected in larger rivers, either supplied via

417   leakage from upstream or through direct deposition from riparian vegetation. Headwater

418   streams and riparian areas of most savanna rivers contain more C3 than C4 vegetation

419   (Table 1), implying that LMH are the critical vectors for C4 carbon, especially during the dry

420   season.

421   Although both livestock and hippos largely facilitated the disproportionate contribution of

422   C4 carbon from grasses to invertebrates in the river, there were interesting differences in

423   the contribution of other sources (C3 vegetation and periphyton) between sites receiving

424   inputs by livestock and hippos, which can be linked to differences in the quality, amount and

425   characteristics of the inputs these two types of LMH transfer into rivers (Iteba et al., 2021;

426   Masese et al., 2020). While increasing livestock density increased both the importance of

427   periphyton and C4 carbon for macroinvertebrates in the river, hippo populations only

428   increased the importance of C4 carbon further and reduced that of periphyton further

429   (Figure 3). Although hippo dung has been reported to fertilize aquatic ecosystems increasing

430   primary and secondary production (Grey and Harper, 2002; Mosepele et al., 2009), other

431   studies have shown that large particles in hippo dung can have detrimental effects on

432   benthic production, especially during the dry season when they settle at the bottom of hippo

433   pools and downstream sections of rivers (Dawson et al., 2016; Dutton et al., 2018a, b).

434   Hippos also spend long periods in the water for thermoregulation, approximately 12 h of

435   daytime (Subalusky et al., 2015), and their wallowing activity is known to increase turbidity

436   that can further limit primary production (Dutton et al., 2018). Comparative studies with

437   cattle dung have also shown that the weakly digested hippo dung with high C: nutrients (N

438   and P) ratios support heterotrophic microbial activity, while cattle dung with lower

439   stoichiometric ratios can increase primary production faster (Subalusky et al., 2018; Masese

440   et al., 2020). Thus, replacing wildlife (hippopotamus) with livestock (cattle) in savanna

441   landscapes will most likely weaken detrital food web links based on allochthonous C3 and C4

442   material (Dawson et al., 2020) and foster an algal-grazer food chain by increasing the

443   abundance of autochthonous material.

444   The proportional acquisition of energy from terrestrial C3 and C4 plants and periphyton

445   showed specific patterns for different FFGs (Zeug and Winemiller, 2008; Pingram et al.,

446   2014). Further, the importance of different sources was influenced by land use and the

447   density of LMH. For instance, in forested streams, there was no effect of stream size on the

448   relative importance of the three sources (C3 and C4 producers and periphyton) for most of

449   the FFGs (Figure S1). There was significant partitioning among FFGs on the utilization of

450   various resources, with scrapers and predators relying more on periphyton while collector-

451   gatherers and, as expected, shredders relying more on C3 vegetation (Figure 1). However,

452   facultative shredders, such as Potamonautidae (freshwater crabs) that dominated

453   invertebrates most forested and agricultural streams, can obtain a significant amount of

454   energy from periphyton during their omnivorous feeding (Masese et al., 2014). The

455   importance of trophic sources was also related to the trophic position of the

456   macroinvertebrates, with autochthonous production becoming more important with an

457   increase in trophic level (Figures S1).

4.1 Longitudinal trends of the relative importance of trophic resources

459   Even in the absence of LMH (both livestock and wildlife) longitudinal patterns of organic

460   matter and nutrient loading into the Mara River and its tributaries (Figures 4 and 5) departed

461   significantly from existing predictions for river continuum (Vannote et al., 1980; Thorp and

462   Delong, 2002; Thorp et al., 2006). Periphyton, and not leaf litter from C3 vegetation, was the

463   most important source of energy for invertebrates in low-order forested streams by

464   contributing nearly 50%, on average, of the energy requirements of all invertebrates while

465   C3 vegetation contributed no more than 40%. These results have been supported by

466   previous studies in tropical and temperate regions whereby carbon from autochthonous

467   production contributes significantly to aquatic animal biomass in mid-sized and large rivers

468   despite forming a small proportion of available food resources (Douglas et al., 2005; Hayden

469   et al., 2016).

470   The importance of C3 vegetation for invertebrates declined predictably in mid-sized rivers,

471   but an expected rebound in lower reaches of the river where turbidity limits primary

472   production and the river becomes heterotrophic with an overreliance on fine particulate

473   organic matter, mainly from C3 vegetation, escaping from upstream (Vannote et al., 1980),

474   did not occur. Instead, the importance of C3 carbon further plummeted, while that of C4

475   carbon, mediated by large populations of livestock and large wildlife (mainly hippos), gained

476   more importance. Moreover, the expected increase in the importance of autochthonously

477   produced carbon in large rivers (Thorp and Delong, 1994, 2002) did not occur, further

478   highlighting the predominant role played by LMH as drivers of ecosystem productivity and

479   functioning in savanna rivers (Stears et al., 2018; Subalusky et al., 2018; Dawson et al., 2020;

480   Masese et al., 2020).

481   Recognizing that carbon flow in riverine food webs is context-dependent, both temporally in

482   terms of flow variability and spatially in terms of the strength of lateral and longitudinal

483   connectivity, it is conceivable that the patterns we report here are transient. However,

484   studies during both the dry and wet seasons, have indicated the overriding influence of LMH

485   inputs on river water quality and biogeochemistry (Stears et al., 2018; Dutton et al., 2018b,

486   2020), ecosystem productivity (Subalusky et al., 2017, 2018), community composition and

487   diversity of invertebrates and fishes (Masese et al., 2018; Stears et al., 2018). The

488   discrepancies between the results of this study, on the relative importance of different

489   sources of carbon for supporting riverine food webs on the fluvial continuum of savanna

490   rivers, and existing models of riverine ecosystem functioning suggests that a new model is

491   needed that recognizes the intimate linkage between terrestrial and aquatic ecosystems in

492   savanna landscapes mediated by the active transfer of organic matter by LMH.

493

494   **5. Conclusions**

495   An understanding of terrestrial-aquatic ecosystems connectivity and the main sources of

496   energy supporting riverine food webs is critical for the conservation and management of

497   African savanna rivers. The novel findings of this study show the distinct functioning of these

498   rivers in terms of the major energy sources fuelling food webs along their riverine continuum

499   and highlight the important role played by LMH as vectors enhancing aquatic productivity

500   through strengthened terrestrial-aquatic subsidy fluxes. We show that terrestrial and

501   autochthonous sources of energy are relatively important along the longitudinal gradient of

502   savanna rivers, and identify LMH as critically enhancing the contribution of C4 carbon far

503   above potential contributions in their absence. The findings of this study also show that

504   different resources are partitioned among macroinvertebrates depending on their feeding

505   modes and location on the fluvial continuum. At a local scale, this study presents further

506   evidence on the species-specific influences of different species of LMH on the functioning of

507   aquatic ecosystems in African savannas. It also suggests that replacing native populations of

508   large herbivores (such as hippos) with livestock (such as cattle) may alter the major sources

509   of energy supporting aquatic communities in savanna rivers, with consequences on

510   ecosystem structure and functioning.

519

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685   **Figure captions**

686   **Figure 1**. Map of the Mara River catchment showing the position of the sampling sites.

687   **Figure 2**. Longitudinal trends in the mean (±SD) of (a) δ^{13}C and (b) δ^{15}N values (‰) of

688   periphyton with increasing stream size in the Mara River and its tributaries. FOR = forested

689   sites, AGR = agriculture sites, LD_Livestock = low density livestock sites, HD_Livestock = high

690   density livestock sites, and Hippos = hippopotamus sites.

691   **Figure 3**. Box-and-whisker plots of fractional contributions of C3 vegetation (grey), C4

692   grasses (light grey) and periphyton (dark grey) to all macroinvertebrates FFGs in the Mara

693   River. (a) all taxa, (b) collector-gatherers, (c) predators, (d) collector-filterers (e) shredders,

694   and (f) scrapers. C3 = C3 plants; C4 = C4 plants.

695   **Figure 4**. Longitudinal trends in source contributions to macroinvertebrates along the Mara

696   River. Longitudinal variability in the relative importance (fractional contribution) of C3

697   vegetation (sky blue), C4 grasses (orange) and periphyton (dark green) as sources of carbon

698   for macroinvertebrates in the Mara River in response to changes in (a) river distance from

699   the source (RDS in km) and (b) density of large mammalian herbivores (LMH Density). To test

700   the significance of the relationships, we fitted a GAM model with a smoothing function. The

701   black line with shaded area represents smoother mean and s.e.; smoother significance, R^2

702   and GCV are supplied in the figures.

703   **Figure 5**. Source contributions to FFGs along the Mara River. Longitudinal trends in fractional

704   contributions of trophic source (C3= C3 vegetation, C4 = C4 grasses and periphyton) to

705   macroinvertebrate functional feeding groups (FFGs) in the Mara River. Source contributions

706   are assessed in response to changes in river distance from source (RDS) as a measure of

707   stream size (a, c, e, g, i) and density of large mammalian herbivores (LMH), b, d, f, h, j). a, b =

708   collector-filterers, c, d = collector-gatherers, e, f = scrapers, g, h = shredders, and I, j =

709   predators. To test the significance of the relationships, we fitted a GAM model with a

710   smoothing function. The black line with shaded area represents smoother mean and s.e.;

711   smoother significance, R^2 and GCV are supplied in the figures. Note changes on the x-axis

712   and y-axis.

713

714 **Table 1.** River size, the density of large mammalian herbivores, catchment land use characteristics and $\delta^{13}C$ and $\delta^{15}N$ values of the main carbon
715 sources (periphyton, C3 and C4 carbon, dung) across 80 sites of the Mara River, Kenya, grouped into five regions: Forested, Agricultural, with
716 low density (LD) livestock, with high density (HD) livestock, and with a dominance of hippos. All values are means (± SD) and $\delta^{13}C$ and $\delta^{15}N$
717 values are in ‰ units.

Characteristics	Regions					Statistics	
	Forested	Agricultural	LD livestock	HD livestock	Hippos	F - value	p - value
Stream and sub-catchment characteristics							
Stream order	4.0±1.5 [a]	3.7±1.6 [a]	4.8±2.1 [ab]	4.0±1.9 [a]	6.4±1.6 [b]	5.26	0.001
River distance from source (RDS)	12.5±6.4 [a]	12.2±9.2 [a]	26.0±17.4 [b]	17.2±15.8 [ab]	52.6±23.2 [b]	7.37	0.001
LMH density (individuals / km^2)	9.3±4.1 [a]	28.0±16.8 [b]	44.8±12.5 [b]	102.9±17.7 [c]	111.9±10.8 [c]	11.21	0.001
% Agriculture	27.1±24.9 [a]	61.1±22.2 [b]	63.5±23.9 [b]	1.9±0.5 [c]	22.4±17.3 [ab]	18.91	0.001
% Grasslands	5.6±5.2 [a]	7.2±5.1 [a]	16.5±13.9 [b]	59.9±10.8 [c]	49.2±16.0 [c]	93.21	0.001
% Forest	64.7±28.5 [a]	39.3±22.9 [b]	25.4±15.4 [b]	37.2±11.5 [b]	27.97±8.9 [b]	9.47	0.001
River width (m)	7.9±5.0 [a]	7.1±6.1 [a]	8.7±5.8 [a]	6.6±3.5 [a]	15.84±9.9 [b]	4.35	0.003
Water depth (m)	0.20±0.1 [a]	0.2±0.1 [a]	0.2±0.2 [a]	0.2±0.1 [a]	1.0±0.4 [b]	5.45	0.001
River discharge (m^3/s)	0.23±0.2 [a]	0.4±0.2 [a]	0.5±0.4 [a]	0.3±0.2 [a]	17.4±6.9 [b]	7.57	0.001
pH (units)	7.6±0.3 [a]	7.6±0.3 [a]	7.7±0.2 [a]	7.6±0.1 [a]	7.8±0.0 [a]	0.40	0.804
Temperature (°C)	15.8±1.8 [a]	18.5±3.2 [b]	20.3±2.5 [b]	23.7±2.1 [c]	23.9±2.2 [c]	27.9	0.001
Dissolved oxygen (mgL^{-1})	7.8±0.4 [a]	7.0±1.1 [bc]	6.3±0.9 [c]	7.3±1.0 [ab]	8.0±1.1 [a]	7.36	0.001
Electrical conductivity (µScm^{-1})	74.1±29.4 [a]	103.2±50.0 [a]	260.3±128.9 [b]	309.0±172.8 [b]	325.0±178.7 [b]	18.12	0.001
Stable isotopes of basal resources							
$\delta^{13}C$ of C3 vegetation	-26.56±2.08 [a]	-27.14±3.37 [a]	-27.62±1.37 [a]	-25.36±1.98 [a]	-26.13±1.97 [a]	1.05	0.407
$\delta^{13}C$ of C4 vegetation	-13.22±6.27 [a]	-12.08±1.56 [a]	-16.44±7.95 [a]	-11.04±2.13 [a]	-15.64±11.01 [a]	1.32	0.294
$\delta^{13}C$ of periphyton	-25.93±2.58 [a]	-24.34±2.64 [ab]	-23.7±2.15 [ab]	-23.21±1.23 [b]	-22.66±1.80 [b]	4.24	0.004
$\delta^{13}C$ of cattle dung	-20.96±7.31 [a]	-15.78±2.36 [ab]	-13.49±1.73 [b]	-14.27±5.01 [b]	-13.58±2.85 [b]	5.08	0.002
$\delta^{13}C$ of hippo dung	-	-	-	-11.89±2.14 [a]	-14.13±2.72 [a]	2.11	0.169
$\delta^{15}N$ of C3 vegetation	4.06±1.69 [a]	5.47±4.96 [a]	5.24±2.65 [a]	4.61±2.36 [a]	3.37±2.91 [a]	1.83	0.119
$\delta^{15}N$ of C4 vegetation	6.09±2.59 [a]	5.98±3.07 [a]	4.76±4.79 [a]	5.57±3.25 [a]	4.81±2.74 [a]	0.15	0.988
$\delta^{15}N$ of periphyton	7.13±0.84 [a]	7.56±1.49 [ab]	8.53±1.44 [b]	8.11±0.79 [b]	7.29±0.71 [ab]	3.16	0.019
$\delta^{15}N$ of cattle dung	6.79±1.79 [a]	5.37±1.29 [a]	7.29±0.94 [a]	5.89±1.29 [a]	4.55±0.20 [a]	1.34	0.257
$\delta^{15}N$ of hippo dung	-	-	-	6.56±1.96 [a]	4.93±0.63 [a]	2.19	0.158

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718

719 **Table 2**. Summary of generalized additive mixed models (GAMs) of the effects of stream size (river distance from source {RDS}), region and
720 density of large mammalian herbivores (LMH density) (stream size) on the relative importance (fractional contribution) of C3 vegetation (C3
721 carbon), C4 grasses (C4 carbon) and periphyton as sources of carbon/energy for macroinvertebrate FFGs (collector-filterers, collector-
722 gatherers, scrapers, predators and shredders) and all combined taxa (FFGs) in the Mara River, Kenya. RDS, region and LMH density were
723 treated as fixed factors while each study site was used a random factor. In all cases, d.f. = 1.

Source Contributions	Macroinvertebrate FFGs					
Sources	Collector-filterers	Collector-gatherers	Scrapers	Predators	Shredders	All taxa
C3 carbon						
RDS F, *p*-value	21.21, <0.001***	17.01, <0.001***	21.14, <0.001***	12.48, <0.001***	0.26, 0.612	60.1, <0.001***
Region F, *p*-value	10.47, 0.002**	23.95, <0.001***	24.32, <0.001***	5.02, 0.028*	0.053, 0.819	39.7, <0.001***
LMH density F, *p*-value	1.30, 0.260	3.32, 0.073	3.62, 0.062	0.02, 0.878	1.65, 0.208	6.12, 0.014*
RDS x region F, *p*-value	2.15, 0.150	1.80, 0.185	3.45, 0.068	3.87, 0.053	1.51, 0.228	9.11, 0.003**
RDS x LMH density F, *p*-value	0.09, 0.761	0.04, 0.846	0.001, 0.972	1.52, 0.222	1.72, 0.199	0.16, 0.691
Region x LMH density F, *p*-value	0.03, 0.857	0.003, 0.957	0.04, 0.848	5.54, 0.022*	0.83, 0.371	0.24, 0.624
RDS x region x LMH density F, *p*-value	0.07, 0.796	0.06, 0.805	0.001, 0.972	0.01, 0.905	0.058, 0.812	0.02, 0.887
Adj. R2	0.692	0.365	0.401	0.227	-0.024	0.271
Scale est.	0.001	0.0004	0.0005	0.001	0.019	0.014
Residual deviance	0.68	0.949	0.903	0.817	0.774	5.44
C4 carbon						
RDS F, *p*-value	67.10, <0.001***	95.89, <0.001***	120.7, <0.001***	129.6, <0.001***	0.001, 0.969	481.1, <0.001***
Region F, *p*-value	45.18, <0.001***	60.52, <0.001***	74.21, <0.001***	111.7, <0.001***	0.60, 0.445	272.3, <0.001***
LMH density F, *p*-value	1.13, 0.293	1.28, 0.262	3.45, 0.068	11.24, 0.001**	4.43, 0.043*	13.7, <0.001***
RDS x region F, *p*-value	1.58, 0.215	1.63, 0.207	0.55, 0.463	7.24, 0.009**	3.00, 0.093	9.82, 0.002**
RDS x LMH density F, *p*-value	0.56, 0.460	0.80, 0.376	1.78, 0.187	18.06, <0.001***	0.09, 0.766	13.5, <0.001***
Region x LMH density F, *p*-value	7.22, 0.010*	5.21, 0.026*	6.25, 0.015*	3.36, 0.072	0.36, 0.550	30.3 <0.001***
RDS x region x LMH density F, *p*-value	0.96, 0.333	0.03, 0.874	1.74, 0.192	8.85, 0.004**	3.92, 0.056	12.1 <0.001***
Adj. R2	0.13	0.699	0.747	0.795	0.121	0.739
Scale est.	0.031	0.002	0.002	0.001	<0.001	0.004
Residual deviance	0.51	0.351	0.300	0.315	0.066	1.43

Periphyton

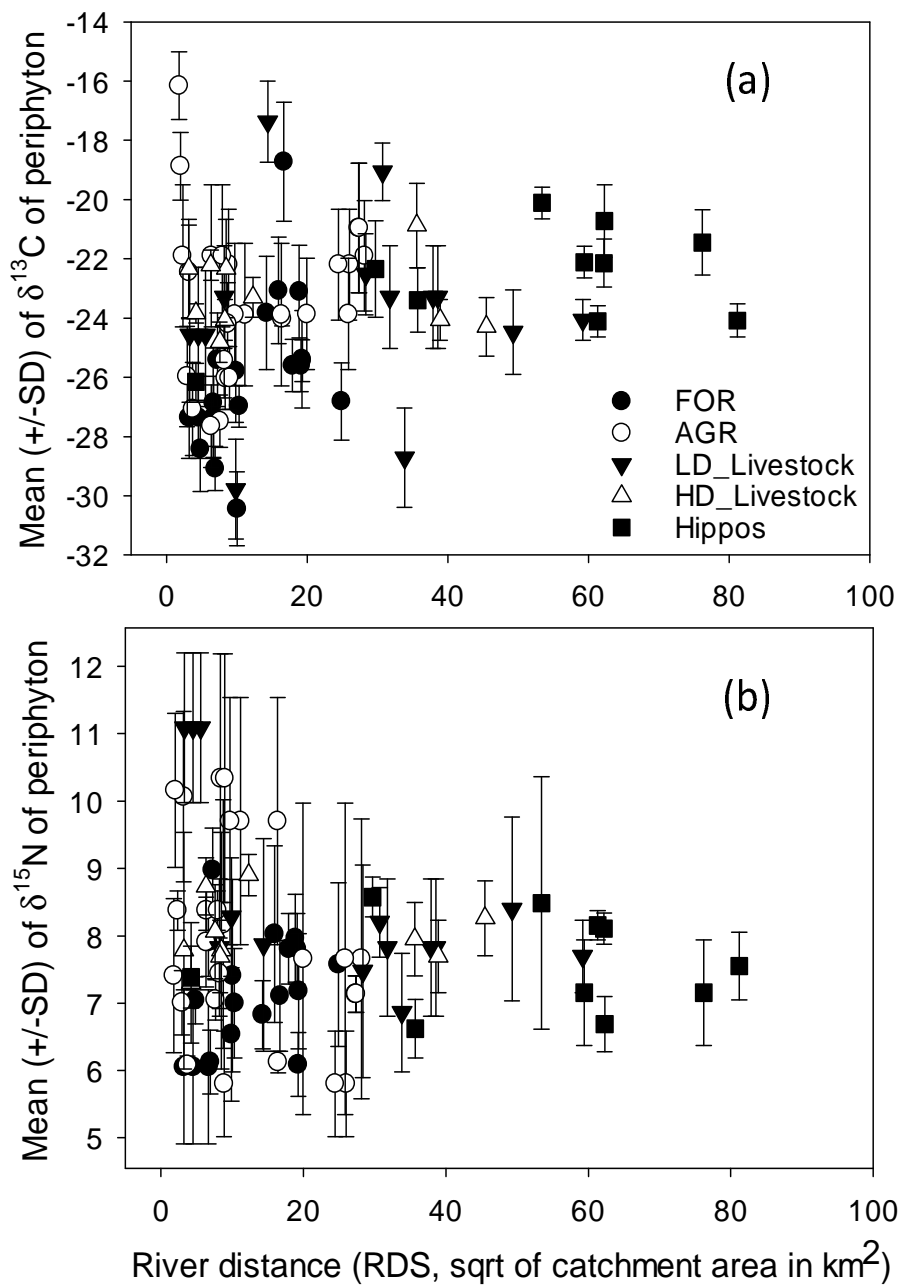|						
RDS F, *p*-value	0.05, 0.829	2.87, 0.095	2.24, 0.140	10.57, 0.002**	0.28, 0.599	10.9, 0.001**
Region F, *p*-value	0.10, 0.754	0.0004, 0.984	0.06, 0.805	15.05, <0.001***	0.0003, 0.976	4.5, 0.034*
LMH density F, *p*-value	1.74, 0.194	1.48, 0.229	0.58, 0.449	3.08, 0.084	0.56, 0.458	0.20, 0.653
RDS x region F, *p*-value	4.29, 0.043*	2.96, 0.090	3.41, 0.069	11.39, 0.001**	0.66, 0.424	18.4, <0.001***
RDS x LMH density F, *p*-value	0.05, 0.816	0.89, 0.348	0.49, 0.483	1.49, 0.227	2.68, 0.111	3.03, 0.085
Region x LMH density F, *p*-value	1.42, 0.247	1.32, 0.256	2.43, 0.125	1.22, 0.273	0.75, 0.392	5.14, 0.024*
RDS x region x LMH density F, *p*-value	0.04, 0.841	0.08, 0.771	0.30, 0.584	3.32, 0.073	0.208, 0.651	1.91 ,0.172
Adj. R2	0.013	0.037	0.035	0.992	-0.050	0.113
Scale est.	0.002	0.002	0.002	0.001	0.014	0.015
Residual deviance	1.01	1.14	1.15	0.349	0.571	5.95

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726

Figure 1

Figure 2

Figure 4

Figure 5