






# Variation in basal production sources supporting fish trophic guilds in the channel and floodplain ponds of the Rupununi River, Guyana, during dry season isolation

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Most tropical rivers have a seasonal flood pulse that connects channel and floodplain habitats and facilitates entrance of allochthonous resources into the aquatic food web. Dry season isolation of floodplain habitats should result in greater spatial variation in production sources supporting aquatic food webs and greater input of autochthonous sources. We performed stable isotope analysis on tissue samples from fishes and basal production sources from the channel and three floodplain ponds of the Rupununi River, Guyana, to estimate assimilation of material originating from basal sources by five trophic guilds. Seston was the principal source assimilated by fish trophic guilds at each location, with the only exceptions being invertivores and piscivores inhabiting the river channel. Terrestrial plants were estimated to be the most important basal source supporting piscivores, possibly reflecting a time lag for basal source materials to pass several steps up food chains. Between-pond variation in proportions of basal resources assimilated by guilds was associated with differences in water depth and density of aquatic macrophytes. Findings further support the importance of autochthonous production sources for aquatic food webs of tropical rivers during the dry season and the role of floodplain heterogeneity in creating spatial variation in food web dynamics.

**Keywords:** Food web, Hydrologic connectivity, Neotropics, Stable isotope analysis.

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Muchos ríos tropicales tienen regímenes hidrológicos estacionales, con un pulso que conecta los hábitats del canal y la planicie de inundación, y facilita la entrada de materiales en redes tróficas. Durante el período de sequía, el aislamiento de los hábitats en las planicies inundables debería resultar en mayor variación de las fuentes basales que sustentan las redes tróficas, y más aporte de fuentes de producción autóctonas. Realizamos un análisis de isótopos estables en muestras de tejido de peces dentro de cinco gremios tróficos y fuentes de producción basales en el canal del río y tres lagunas de inundación del Río Rupununi, Guyana. Para los gremios tróficos, se estimó las fuentes basales asimiladas. Seston fue la principal fuente asimilada por los gremios en cada hábitat, las excepciones fueron los invertívoros y piscívoros en el canal del río. Los piscívoros asimilaron material originado de plantas terrestres, posiblemente reflejando un desfase temporal del material transferido a lo largo de las cadenas alimentarias. La variación en las redes tróficas entre las lagunas parece estar asociada con diferencias en la profundidad del agua y abundancia de vegetación acuática. Estos resultados respaldan la importancia de las fuentes de producción autóctonas en las redes tróficas de los ríos tropicales durante la estación seca, y la importancia de la heterogeneidad de planicies de inundación en la dinámica espacial en las redes tróficas.

**Palabras claves:** Análisis de isótopos estables, Connectividad hidrológica, Neotrópicos, Redes tróficas.

## INTRODUCTION

Tropical rivers generally have strongly seasonal flow regimes, with an annual rainy season producing a sustained flood pulse and hydrologic connectivity between the active channel and floodplains (Lowe-McConnell, 1964; Junk *et al.*, 1989; Winemiller, Jepsen, 1998). During the dry season, water levels recede, creating isolated bodies of water in floodplains that vary in physicochemical and biotic features (Rodriguez, Lewis, 1997; Pouilly *et al.*, 2004; Scarabotti *et al.*, 2011). Given the effects of seasonal hydrology on habitat connectivity, primary production, and fish reproduction and dispersal, tropical river food webs are temporally dynamic and spatially variable (Winemiller, 1990, 1996). Decreasing water levels increases fish densities and rates of encounter between predators and their prey. As the dry season progresses, predation mortality reduces prey populations, and predators may switch to consuming sub-optimal prey in accordance with the functional response (Jepsen *et al.*, 1997, Montaña *et al.*, 2011). During high-water periods, herbivores and omnivores have access to and exploit allochthonous food resources in flooded riparian areas (Junk *et al.*, 1989; Correa, Winemiller, 2018; Arantes *et al.*, 2019). Conversely, during low-water periods, herbivores and omnivores rely more on autochthonous basal production (Roach *et al.*, 2009b; Roach, Winemiller, 2015).

The present study compares within-guild and between-guild variation in basal resources assimilation during the dry season among fish inhabiting the channel and floodplain habitats of the Rupununi River, a meandering lowland river draining the Rupununi Savanna in Southwestern Guyana. The Rupununi has a predictable seasonal hydrology, with an annual flood pulse that starts in May and continues through

September. Prior research in this region focused on the seasonal hydrologic connection between the Branco/Amazon and Rupununi/Essequibo basins via seasonally flooded savannas, *i.e.*, the so-called Rupununi Portal (Souza *et al.*, 2012, 2020). Other studies have produced comprehensive species lists of fishes from the Rupununi River and other regions of Guyana (Watkins *et al.*, 2005; Taphorn *et al.*, 2022). Research on fish trophic ecology in the Rupununi region was conducted by the pioneering fish ecologist Rosemary Lowe-McConnell (1964), who analyzed gut contents of fishes from isolated floodplain ponds during the dry season and the flooded savannas during the wet season. She found that fish fed consistently throughout the wet season, but many guts were empty when confined to ponds during the dry season. We aim to further understand food web dynamics in the Rupununi River and its associated floodplain ponds by estimating fish assimilation of material originating from basal production sources by analyzing stable isotope ratios of carbon and nitrogen.

Analysis of stable isotope ratios of carbon and nitrogen ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) in consumer tissues and food resources are commonly used to reveal aspects of trophic structure and food web dynamics (Boecklen *et al.*, 2011; Layman *et al.*, 2012). When basal production sources have sufficiently distinct isotopic ratios,  $\delta^{13}\text{C}$  in particular, mixing models can be used to estimate source contributions to consumer biomass (Hopkins, Ferguson, 2012). The vertical trophic position of consumers can be estimated from their tissue  $\delta^{15}\text{N}$ , and this is because the ratio increases ( $^{15}\text{N}$  enrichment) as food is consumed and assimilated by animals (Post, 2002; Stephan *et al.*, 2023). Several studies have employed stable isotope analysis and mixing models to estimate sources of production supporting fishes in tropical floodplain rivers. For example, fishes in a floodplain lake of the Cuiabá River, Brazil, were found to assimilate high proportions of material originating from terrestrial C3 plants during the flood pulse, with a decline in the vertical trophic positions of omnivorous fishes (Wantzen *et al.*, 2002). During the dry season, there was a decline in assimilation of material from terrestrial sources, and estimated trophic positions of omnivorous fishes shifted to higher values. Roach *et al.* (2008b) analyzed isotopic signatures of fishes in the main channel and a connected floodplain lake of the Cinaruco River, Venezuela, during the dry season. Algae were inferred to be the predominant basal resource assimilated by fishes in all trophic guilds, and the food web structure was consistent between the river and floodplain. Neither of those studies examined basal resource assimilation in relation to floodplain heterogeneity or fish trophic guilds, which is the focus of the present study.

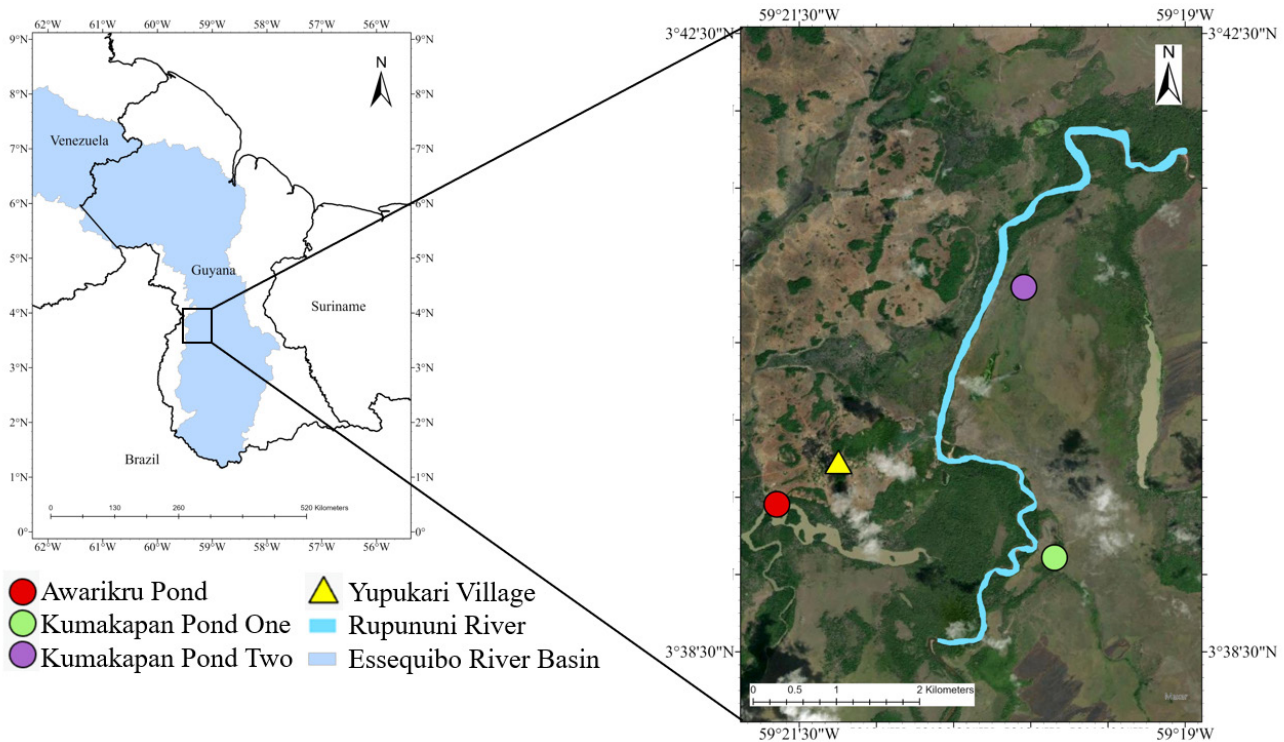
Here, we analyzed isotopic ratios of carbon and nitrogen in fish muscle tissue to estimate the relative importance of the most common basal production sources supporting fish biomass in the channel and floodplain ponds of the Rupununi River. We hypothesized that isotopic ratios of fishes within the same trophic guild would differ between channel and floodplain ponds. This is because the predominate basal production sources are different in lotic and lentic habitats (Roach *et al.*, 2009b). In most tropical floodplain lakes, phytoplankton and aquatic macrophyte production appear to dominate (Roach *et al.*, 2009b), while the main channel is supported almost exclusively by phytoplankton (Cotner *et al.*, 2006). We further hypothesized that basal resources assimilated by fish guilds would differ among floodplain ponds due to variation in geomorphological, physicochemical, and hydrological features. Although autochthonous production is predicted to be the dominant carbon source assimilated in

all habitat types during the dry season, fishes from larger ponds with more persistent hydrologic connections to the active channel should have different isotopic signatures than fishes from the same guild from smaller and more isolated ponds.

## MATERIAL AND METHODS

**Sampling sites.** This study was conducted in the Rupununi River, a lowland river with a meandering channel and a wide floodplain in the Rupununi Savanna region of Guyana (Taphorn *et al.*, 2022) (Fig. 1). Habitats in the main channel consist of sand bars, backwaters, and deeper areas in the mainstem containing submerged woody debris and stronger current velocities. During the dry season, the water of the main channel is clear with pH of 6.4–6.9, whereas water in floodplain ponds varies from clear to slightly turbid due to suspended particles (Lowe-McConnell, 1964). We collected fishes and basal production sources from multiple sites within a 10-km reach of the active river channel (from 03°38'36"N 59°20'20"W to 03°41'43.9"N 59°19'01.5"W) and three floodplain ponds along the same reach. Awarikru Pond and Kumakapan Pond 1 are relatively large oxbow lakes with moderate dissolved oxygen levels and relatively low abundance of submerged aquatic macrophytes. These ponds have substrates of sand and clay overlain with submerged leaf litter, which was especially abundant in the latter. Kumakapan Pond 2 is a shallow depression with a mud substrate rich in organic material and an abundance of emergent and floating aquatic macrophytes. Samples were collected at the end of the dry season, prior to and just as water levels began to rise, when the ponds were disconnected from the main river channel. This sampling time interval afforded the longest possible time for habitat spatial heterogeneity to influence the composition of local fish assemblages as well as fish diets and assimilation of material into muscle tissue.

**Sampling.** Organisms and tissue samples were collected from May 10–25, 2023, from the river channel and floodplain ponds, using a variety of fishing gears that included a seine net (6 x 1.8 m, 6 mm mesh), cast nets (1.8 m diameter, 2 cm mesh), dip nets (40 x 30 cm, 6 mm mesh), and angling with lures and baited hooks. Tissues of common allochthonous and autochthonous production sources were collected from areas within and adjacent to the river channel and ponds. Macrophyte samples included submerged C3 plants, C3 terrestrial plants, and C4 terrestrial grasses. Decaying leaf matter (detritus) was collected from the bottom of the river and ponds. Seston was filtered from the water column using a hand pump and 1.2 µm GF/F filters (Tab. S2). Collected fishes were euthanized with an overdose of clove oil (Fernandes *et al.*, 2016), and specimens were identified using taxonomic keys and descriptions (*e.g.*, van der Sleen, Albert, 2018; Taphorn *et al.*, 2022). Each species was assigned to one of five feeding guilds using published literature in the trophic ecology of Neotropical fishes (*e.g.*, Saul, 1975; Goulding, 1988). Algivores/detritivores (alg/detritivore) consume variable fractions of material from macrophytes, algae, and detritus, which may include associated microbial decomposers (*e.g.*, *Aphanotorulus emarginatus*). Omnivores consume variable fractions of plant and animal matter (especially invertebrates) (*e.g.*, *Amblydoras affinis*). Invertivores consume mostly aquatic and/or terrestrial invertebrates (*e.g.*, *Geophagus surinamensis*). Piscivore/invertivore (pisc/invertivore) consume variable fractions of invertebrates



**FIGURE 1** | Map depicting sampling sites, three floodplain ponds and a location in the mainstem channel of the Rupununi River within the Essequibo River Basin, Guyana.

and fish (e.g., *Saxatilia saxatilis*). Piscivores feed nearly exclusively on fish (e.g., *Cichla ocellaris*). Muscle tissue was obtained from the dorsolateral region of specimens. Tissue samples were placed in individual labeled plastic bags, preserved with salt (NaCl), and transported to the laboratory, where they were stored in a freezer until analysis.

Samples were processed according to methods described in Arrington, Winemiller (2002) and Winemiller *et al.* (2011). Tissue samples were soaked and rinsed with distilled water to ensure the salt was completely removed. Each tissue sample was then placed in a labeled scintillation glass tube and dried in a drying oven at 60 °C for 48 hours. The dried samples were individually ground into a homogenized powder using a mortar and pestle, and then packed into 4 x 6 mm tin capsules (Costech) in portions ranging from 1.5 to 3.0 mg. The subsamples were sent to the Stable Isotope Ecology Laboratory at the University of Georgia, USA, to obtain stable isotope ratios of C and N via mass spectrometry. Results are reported as parts per thousand (‰) change from the standard material (Vienna Pee Dee Belemnite and atmospheric N<sub>2</sub>):

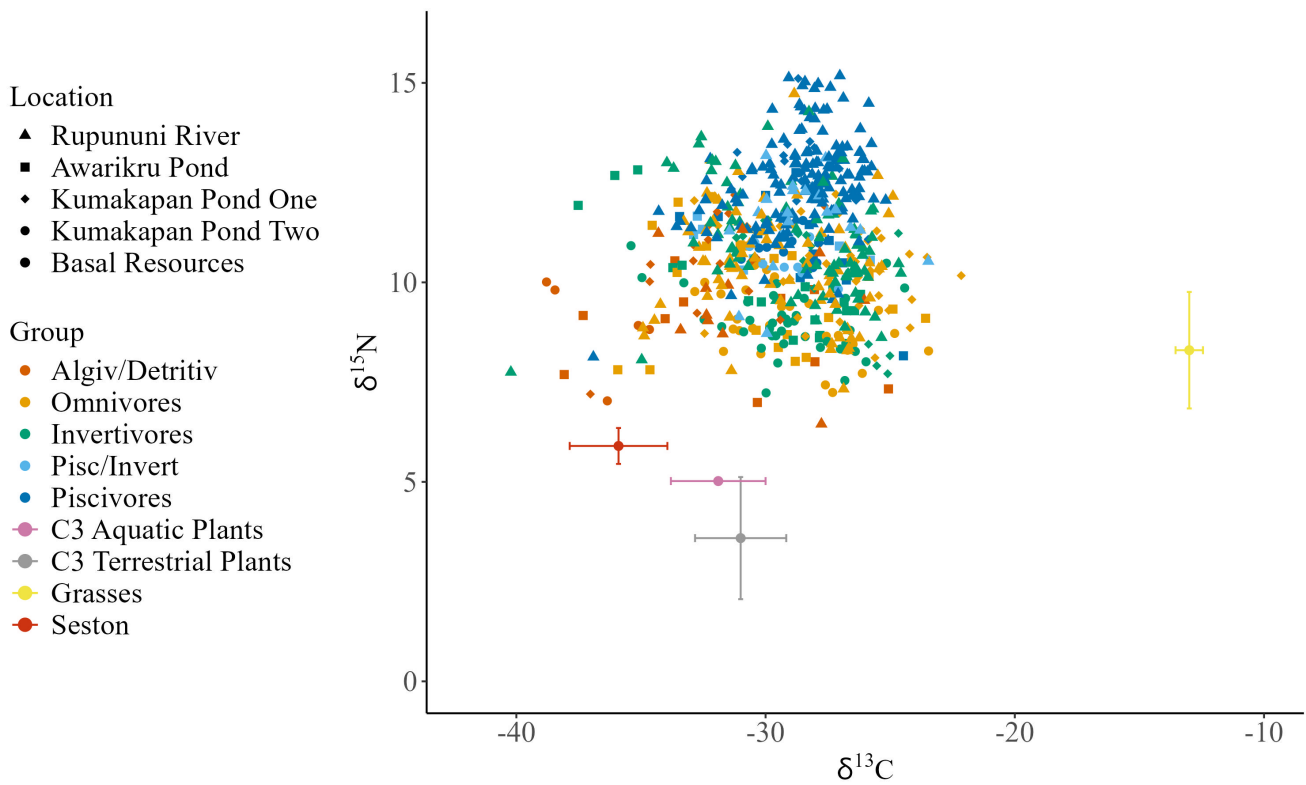
$$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 10^3, \text{ where } R = {}^{13}\text{C}/{}^{12}\text{C} \text{ or } {}^{15}\text{N}/{}^{14}\text{N}.$$

We collected a total of 505 fish tissue samples for stable isotope analysis, representing five feeding guilds: 41 algivore/detritivores, 150 omnivores, 157 invertivores, 31 piscivore/invertivores, and 125 piscivores (Fig. 2). A full list of sampled species and their assigned guilds appears in Tab. 1 (Fricke *et al.*, 2026). The mean and standard deviation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each feeding guild from each of the four water bodies appear in Tab. S1.

**Statistical analyses.** We employed Bayesian mixing models using the MixSIAR package (Stock *et al.*, 2018; v. 3.1.12) in R to estimate the proportional contributions of basal sources to consumer biomass. Model inputs included  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from fish tissue and representative basal sources at each site. Basal sources were assigned to functional groups to reduce the total number of sources and improve model resolution and interpretability (Moore, Semmens, 2008; Arantes *et al.*, 2019) (Tab. S2). A conservative estimate of trophic enrichment for primary consumers is approximately 3.4‰ for  $\delta^{15}\text{N}$  (Post, 2002; Stephans *et al.*, 2023). The highest  $\delta^{15}\text{N}$  value observed for a primary consumer in this study was 12.19‰; therefore, any basal sources with  $\delta^{15}\text{N}$  signatures greater than 8.79‰ were excluded from the mixing model because their  $\delta^{15}\text{N}$  signatures were too high to be assimilated in consumers. Similarly, C4-derived enrichment averages about 1.0‰ for  $\delta^{13}\text{C}$ , and all C4 grasses were excluded because their  $\delta^{13}\text{C}$  values were more than 10‰ heavier than the lightest primary consumer (Fig. 2). Several studies have shown that C4 macrophytes contribute minimally to fish biomass in Neotropical rivers (Benedito-Cecilio, 2000; Jepsen, Winemiller, 2002, 2007; Arantes *et al.*, 2019).

Previous studies have emphasized the importance of periphyton (*e.g.*, microphytobenthos and biofilm) for tropical river food webs during low-water periods (Roach *et al.*, 2014; Roach, Winemiller 2015; Ou, Winemiller, 2016), we were unable to find sufficient periphyton biomass (biofilm) for analysis, possibly because stocks had been grazed down by consumers (Winemiller *et al.*, 2006, 2014). After removing isotopic outliers and aggregating basal sources based on functional similarity, we included three primary basal resources in mixing models for fishes from each of the three ponds. These included C3 aquatic macrophytes (mean  $\delta^{13}\text{C}$ :  $-31.9 \pm 1.9\text{‰}$ ;  $\delta^{15}\text{N}$ :  $5.02 \pm 0.01\text{‰}$ ), C3 terrestrial plants with detritus (coarse particulate organic matter, CPOM) included due to isotopic similarity ( $\delta^{13}\text{C}$ :  $-31.0 \pm 1.83\text{‰}$ ;  $\delta^{15}\text{N}$ :  $3.59 \pm 1.53\text{‰}$ ), and seston, which is assumed to be a mixture of phytoplankton and fine particulate organic matter (FPOM) ( $\delta^{13}\text{C}$ :  $-35.9 \pm 1.96\text{‰}$ ;  $\delta^{15}\text{N}$ :  $5.9 \pm 0.45\text{‰}$ ). For the river channel site, only two basal resources were included in the model: C3 terrestrial plants ( $\delta^{13}\text{C}$ :  $-30.2 \pm 1.49\text{‰}$ ;  $\delta^{15}\text{N}$ :  $3.85 \pm 2.1\text{‰}$ ) and seston ( $\delta^{13}\text{C}$ :  $-30.6 \pm 2.86\text{‰}$ ;  $\delta^{15}\text{N}$ :  $5.8 \pm 0.31\text{‰}$ ). C3 aquatic macrophytes were not included in river models because they were not encountered at any river locations during our field work.

To account for isotopic fractionation between trophic levels, we applied trophic discrimination factors (TDFs) appropriate to each guild. For algivore/detritivores, we used a TDF of 3.4‰ for  $\delta^{15}\text{N}$  and 1.0‰ for  $\delta^{13}\text{C}$  (Post, 2002). For carnivores (invertivores, piscivore/invertivores, and piscivores), we used TDFs of 5.0‰ for  $\delta^{15}\text{N}$  and 2.0‰ for  $\delta^{13}\text{C}$ , reflecting the average  $\delta^{15}\text{N}$  values across two trophic transfers (the TDF for  $\delta^{15}\text{N}$  was 3.4‰ from basal resource to primary consumer, and was 1.6‰ from primary consumer to secondary consumer; the TDF for  $\delta^{13}\text{C}$  was assumed to be constant between resource and consumer at each trophic level) (Madigan *et al.*, 2012; Hussey *et al.*, 2014). Omnivores were assigned intermediate TDF values of  $4.25 \pm 0.33\text{‰}$  for  $\delta^{15}\text{N}$  and  $1.5 \pm 0.33\text{‰}$  for  $\delta^{13}\text{C}$ , with variability included to account for varying basal resource and primary consumer assimilation (Kopf *et al.*, 2025). We used uninformative priors, included only process error, and ran three Markov chains of 100,000 iterations each, with a burn-in of 50,000 and a thinning interval of 50. Model convergence was assessed using Gelman-Rubin and Geweke diagnostics. Final estimates of source contributions to species and each feeding guild were summarized as the mode of the posterior distributions (Kaymak *et al.*, 2023).



**FIGURE 2 |** Biplot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ‰ isotopic ratios for fishes and basal resources collected in May 2023 from Rupununi River and three floodplain ponds near the Yupukari Village, Guyana.

**TABLE 1 |** Species list and trophic guild assignment for the Rupununi River and three floodplain ponds. The taxonomic classification follows Fricke *et al.* (2026).

Waterbody	Order	Family	Genus and species	Trophic guild	N	References
Rupununi River	Characiformes	Acestororhamphidae	<i>Moenkhausia ceros</i>	Omnivore	1	Winemiller (1990)
			<i>Moenkhausia copei</i>	Omnivore	5	Winemiller (1990)
			<i>Moenkhausia lepidura</i>	Omnivore	6	Winemiller (1990)
			<i>Moenkhausia shideleri</i>	Omnivore	5	Winemiller (1990)
			<i>Moenkhausia</i> sp.	Omnivore	4	Winemiller (1990), Baldasso <i>et al.</i> (2019)
		Anostomidae	<i>Leporinus brunneus</i>	Omnivore	2	Lowe-McConnell (1987), Correa (2015)
			<i>Leporinus</i> sp.	Omnivore	2	Lowe-McConnell (1987), Correa (2015)
		Characidae	<i>Aphyocharax erythrurus</i>	Omnivore	4	Winemiller (1990)
			<i>Hemigrammus vorderwinkleri</i>	Omnivore	8	Winemiller (1990), Baldasso <i>et al.</i> (2019)
			<i>Microschemobrycon casiquiare</i>	Invertivore	4	Winemiller (1990), Baldasso <i>et al.</i> (2019)
			<i>Odonstostilbe</i> sp.	Omnivore	1	Winemiller (1990)
			<i>Odonstostilbe gracilis</i>	Omnivore	10	Winemiller (1990)
			<i>Poptella</i> sp.	Omnivore	3	Lowe-McConnell (1987)

TABLE 1 | (Continued)

Waterbody	Order	Family	Genus and species	Trophic guild	N	References	
Rupununi River	Characiformes	Characidae	<i>Roeboides affinis</i>	Pisc/Invert	2	Albrecht <i>et al.</i> (2013)	
			<i>Tetragonopterus argenteus</i>	Omnivore	1	Winemiller (1990)	
			<i>Tetragonopterus chalceus</i>	Omnivore	1	Winemiller (1990)	
		Crenuchidae	<i>Characidium catenatum</i>	Invertivore	1	Casatti (2002)	
			<i>Characidium zebra</i>	Invertivore	1	Casatti (2002)	
		Cynodontidae	<i>Hydrolycus armatus</i>	Piscivore	32	Layman <i>et al.</i> (2005)	
		Erythrinidae	<i>Hoplerythrinus unitaeniatus</i>	Pisc/Invert	1	Belger, Fosberg (2006)	
			<i>Hoplias malabaricus</i>	Piscivore	2	Belger, Fosberg (2006)	
		Serrasalminidae	<i>Pristobrycon striolatus</i>	Piscivore	1	Sá-Oliveira <i>et al.</i> (2017)	
			<i>Pygocentrus nattereri</i>	Piscivore	1	Sá-Oliveira <i>et al.</i> (2017)	
			<i>Serrasalmus altispinis</i>	Piscivore	1	Taphorn <i>et al.</i> (1997)	
			<i>Serrasalmus eigenmanni</i>	Piscivore	1	Taphorn <i>et al.</i> (1997)	
			<i>Serrasalmus rhombeus</i>	Piscivore	13	Taphorn <i>et al.</i> (1997)	
		Cichliformes	Cichlidae	<i>Apistogramma rupununi</i>	Invertivore	4	Winemiller (1990)
				<i>Biotodoma cupido</i>	Invertivore	1	Winemiller (1990)
	<i>Geophagus surinamensis</i>			Invertivore	1	Duque-Correa <i>et al.</i> (2024)	
	<i>Guianacara</i> sp.			Invertivore	1	Lujan <i>et al.</i> (2011)	
	Clupeiformes	Engraulidae	<i>Anchovia</i> sp.	Invertivore	1	Duque, Acero (2003)	
			<i>Anchoviella</i> sp.	Invertivore	3	Silva (2018)	
			<i>Lycengraulis batesii</i>	Invertivore	5	Planquette <i>et al.</i> (1996)	
			<i>Lycengraulis</i> sp.	Invertivore	1	Planquette <i>et al.</i> (1996)	
	Gymnotiformes	Rhamphichthyidae	<i>Gymnorhamphichthys</i> sp.	Invertivore	2	Evans <i>et al.</i> (2019)	
		Sternopygidae	<i>Eigenmannia macrops</i>	Invertivore	1	Evans <i>et al.</i> (2019)	
			<i>Rhabdolichops</i> sp.	Invertivore	1	Evans <i>et al.</i> (2019)	
	Pleuronectiformes	Achiridae	<i>Apionichthys finis</i>	Invertivore	1	Duarte <i>et al.</i> (2003)	
			<i>Hypoclinemus mentalis</i>	Pisc/Invert	4	Duarte <i>et al.</i> (2003)	
	Siluriformes	Auchenipteridae	<i>Ageneiosus</i> cf. <i>ucayalensis</i>	Piscivore	1	Dary <i>et al.</i> (2017)	
			<i>Ageneiosus inermis</i>	Piscivore	16	Dary <i>et al.</i> (2017)	
		Callichthyidae	<i>Corydoras</i> sp.	Invertivore	4	Sazima (1986)	
			<i>Megalechis thoracata</i>	Omnivore	1	Sá-Oliveira <i>et al.</i> (2017)	
		Doradidae	<i>Amblydoras affinis</i>	Omnivore	1	Arce, Birindelli (2025)	
			<i>Doras</i> sp.	Invertivore	4	Arce, Birindelli (2025)	
<i>Oxydoras morei</i> ( <i>Hemiodoras</i> )			Invertivore	4	Arce, Birindelli (2025)		
<i>Oxydoras niger</i>			Omnivore	2	Arce, Birindelli (2025)		
<i>Platydoras costatus</i>			Omnivore	2	Arce, Birindelli (2025)		
<i>Platydoras hancocki</i>	Omnivore	5	Arce, Birindelli (2025)				



TABLE 1 | (Continued)

Waterbody	Order	Family	Genus and species	Trophic guild	N	References	
Rupununi River	Siluriformes	Loricariidae	<i>Platydoras nattereri</i>	Omnivore	1	Arce, Birindelli (2025)	
			<i>Aphanotolurus emarginatus</i>	Detrit/Algiv	7	Dary et al. (2017)	
			<i>Farlowella nattereri</i>	Detrit/Algiv	1	Dary et al. (2017)	
			<i>Limatulichthys griseus</i>	Detrit/Algiv	1	Dary et al. (2017)	
			<i>Rineloricaria</i> sp.	Detrit/Algiv	2	Dary et al. (2017)	
		Pimelodidae	<i>Pimelodella cristata</i>	Invertivore	3	Lowe-McConnell (1987)	
			<i>Pimelodus blochii</i>	Invertivore	10	Lima et al. (2023)	
			<i>Pseudoplatystoma fasciatum</i>	Piscivore	9	Dary et al. (2017)	
			<i>Sorubim</i> sp.	Piscivore	11	Dary et al. (2017)	
			Pseudopimelodidae	<i>Hemisorubim platyrhynchos</i>	Pisc/Invert	7	Erard et al. (2002)
				Awarikru Pond	Acanthuriformes	Sciaenidae	<i>Pachypops</i> sp.
<i>Plagioscion squamosissimus</i>	Pisc/Invert	2	Neves et al. (2015)				
Characiformes	Acestrorhamphidae	<i>Moenkhausia copei</i>	Omnivore		5	Winemiller (1990)	
		<i>Moenkhausia</i> sp.	Omnivore		3	Winemiller (1990), Baldasso et al. (2019)	
		Acestrorhynchidae	<i>Acestrorhynchus falcirostris</i>		Piscivore	1	Dary et al. (2017), Lubich et al. (2022)
	<i>Acestrorhynchus microlepis</i>		Piscivore		1	Dary et al. (2017)	
	Anostomidae	<i>Leporinus ortomaculatus</i>	Omnivore		1	Vari (1992), Correa (2015)	
		<i>Pseudanos</i> sp.	Omnivore		1	Vari (1992), Correa (2015)	
	Characidae	<i>Aphyocharax erythrurus</i>	Omnivore		1	Winemiller (1990)	
	Chilodontidae	<i>Caenotropus maculosus</i>	Detrit/Algiv		2	Vari et al. (1986)	
	Curimatidae	<i>Curimata</i> sp.	Detrit/Algiv		1	Castro, Vari (2004), Correa (2015)	
<i>Psectrogaster</i> sp.		Detrit/Algiv	1	Correa (2015)			
Prochilodontidae	<i>Prochilodus rubrotaeniatus</i>	Detrit/Algiv	1	Duque-Correa et al. (2024), Correa (2015)			
Serrasalminidae	<i>Catoprion mento</i>	Piscivore	3	Kolmann et al. (2018)			
	<i>Serrasalmus eigenmanni</i>	Piscivore	1	Taphorn et al. (1997)			
Cichliformes	Cichlidae	<i>Biotodoma cupido</i>	Invertivore	7	Winemiller (1990)		
		<i>Cichla ocellaris</i>	Piscivore	6	Jepsen et al. (1997)		
		<i>Lugubria acutirostris</i>	Pisc/Invert	1	Winemiller (1990)		
		<i>Lugubria lugubris</i>	Pisc/Invert	3	Winemiller (1990)		
		<i>Mesonauta insignis</i>	Omnivore	1	Winemiller (1990)		
		<i>Satanoperca leucostica</i>	Invertivore	3	Winemiller (1990)		
Clupeiformes	Engraulidae	<i>Amazonsprattus scintilla</i>	Invertivore	1	Silva (2018)		
		<i>Anchoviella</i> sp.	Invertivore	1	Silva (2018)		
Siluriformes	Auchenipteridae	<i>Trachelyopterus galeatus</i>	Invertivore	1	Dary et al. (2017)		
		Doradidae	<i>Platydoras costatus</i>	Omnivore	1	Arce, Birindelli (2025)	
	<i>Platydoras nattereri</i>		Omnivore	1	Arce, Birindelli (2025)		
	<i>Pseudacanthicus</i> sp.		Omnivore	1	Dary et al. (2017)		
	Loricariidae	<i>Rineloricaria</i> sp.	Detrit/Algiv	1	Dary et al. (2017)		
		Pimelodidae	<i>Pimelodus blochii</i>	Pisc/Invert	3	Lima et al. (2023)	
	<i>Pseudoplatystoma fasciatum</i>		Piscivore	2	Dary et al. (2017)		



TABLE 1 | (Continued)

Waterbody	Order	Family	Genus and species	Trophic guild	N	References	
Kumakapan Pond One	Characiformes	Acestrorhamphidae	<i>Moenkhausia</i> sp.	Omnivore	5	Winemiller (1990), Baldasso <i>et al.</i> (2019)	
		Characidae	<i>Aphyocharax erythrurus</i>	Omnivore	5	Winemiller (1990)	
			<i>Ctenobrychon spilurus</i>	Omnivore	4	Winemiller (1990)	
			<i>Hemigrammus</i> sp.	Omnivore	1	Winemiller (1990), Baldasso <i>et al.</i> (2019)	
				<i>Hemigrammus vorderwinkleri</i>	Omnivore	5	Winemiller (1990), Baldasso <i>et al.</i> (2019)
				<i>Moenkhausia</i> sp.	Omnivore	5	Winemiller (1990), Baldasso <i>et al.</i> (2019)
				<i>Tetragonopterus argenteus</i>	Omnivore	1	Winemiller (1990)
			Curimatidae	<i>Curimatella immaculata</i>	Detrit/Algiv	7	Duque-Correa <i>et al.</i> (2024), Correa (2015)
			Erythrinidae	<i>Hoplias malabaricus</i>	Piscivore	2	Belger <i>et al.</i> (2006)
			Serrasalminidae	<i>Pygopristis denticulatus</i>	Piscivore	1	Sá-Oliveira <i>et al.</i> (2017)
			<i>Pygopristis</i> sp.	Piscivore	1	Sá-Oliveira <i>et al.</i> (2017)	
		Cichliformes	Cichlidae	<i>Aequidens tetramerus</i>	Omnivore	1	Winemiller (1990)
		Gymnotiformes	Hypopomidae	<i>Brachyhypopomus</i> sp.	Invertivore	4	Evans <i>et al.</i> (2019)
		Siluriformes	Callichthyidae	<i>Callichthys callichthys</i>	Omnivore	3	Sazima (1986)
				<i>Corydoras</i> sp.	Invertivore	1	Sazima (1986)
				<i>Corydoras</i> sp.	Invertivore	1	Sazima (1986)
			Doradidae	<i>Amblydoras affinis</i>	Omnivore	10	Arce, Birindelli (2025)
				<i>Farlowella</i> sp.	Detrit/Algiv	1	Arce, Birindelli (2025)
			Loricariidae	<i>Hypostomus</i> sp.	Detrit/Algiv	2	Power (1984)
				<i>Loricaria</i> sp.	Detrit/Algiv	7	Power (1984)
			<i>Loricariichthys</i> sp.	Omnivore	1	Power (1984)	
			<i>Rineloricaria</i> sp.	Detrit/Algiv	2	Power (1984)	
			Pimelodidae	<i>Pimelodella</i> sp.	Invertivore	1	Dary <i>et al.</i> (2017)
			<i>Pseudoplatystoma fasciatum</i>	Piscivore	1	Dary <i>et al.</i> (2017)	
Kumakapan Pond Two	Characiformes	Characidae	<i>Aphyocharax erythrurus</i>	Omnivore	5	Winemiller (1990)	
			<i>Ctenobrychon spilurus</i>	Omnivore	5	Winemiller (1990)	
			<i>Hemigrammus</i> sp.	Omnivore	5	Winemiller (1990), Baldasso <i>et al.</i> (2019)	
			<i>Hypessobrycon cf. minor</i>	Omnivore	5	Winemiller (1990)	



**TABLE 1 |** (Continued)

Waterbody	Order	Family	Genus and species	Trophic guild	N	References
Kumakapan Pond Two	Characiformes	Curimatidae	<i>Curimatella immaculata</i>	Detrit/Algiv	1	Duque-Correa <i>et al.</i> (2024), Correa (2015)
		Erythrinidae	<i>Hoplias malabaricus</i>	Piscivore	10	Belger <i>et al.</i> (2006)
		Serrasalminidae	<i>Megalechis thoracata</i>	Omnivore	1	Sá-Oliveira <i>et al.</i> (2017)
			<i>Mesonauta insignis</i>	Omnivore	2	Sá-Oliveira <i>et al.</i> (2017),
	Cichliformes	Cichlidae	<i>Acaronia nassa</i>	Pisc/Invert	5	Lujan <i>et al.</i> (2011)
			<i>Apistogramma</i> sp.	Invertivore	5	Winemiller (1990)
			<i>Cichlasoma bimaculatum</i>	Omnivore	5	Winemiller (1990)
			<i>Saxatilia saxatilis</i>	Pisc/Invert	1	Winemiller (1990)
	Gymnotiformes	Hypopomidae	<i>Brachyhypopomus</i> sp.	Invertivore	26	Evans <i>et al.</i> (2019)
			<i>Hypopygus</i> sp.	Invertivore	2	Evans <i>et al.</i> (2019)
Osteoglossiformes	Osteoglossidae	<i>Osteoglossum bicirrhosum</i>	Pisc/Invert	4	Lowe-McConnel (1987)	
Siluriformes	Loricariidae	<i>Hypoptopoma guianense</i>	Detrit/Algiv	3	Arce, Birindelli (2025)	
		<i>Hypoptopoma</i> sp.	Detrit/Algiv	1	Arce, Birindelli (2025)	
	Pseudopimelodidae	<i>Microglanis poecilus</i>	Invertivore	1	Winemiller (1990)	
Synbranchiformes	Synbranchidae	<i>Synbranchus marmoratus</i>	Invertivore	3	Galvis <i>et al.</i> (1997)	

**TABLE 2 |** Mixing model estimates for proportions of basal production sources assimilated (mean ±1 SD) by fish trophic guilds in the Rupununi River and three floodplain ponds.

Water body	Feeding guild	C3 Aquatic plants	C3 Terrestrial plants	Seston
Rupununi River	Algil/ Detritivore		0.04 ± 0.11	0.96 ± 0.11
	Omnivores		0.00 ± 0.01	1.00 ± 0.01
	Invertivores		0.44 ± 0.06	0.56 ± 0.06
	Pisc/Invert		0.78 ± 0.11	0.22 ± 0.11
	Piscivores		0.98 ± 0.05	0.02 ± 0.05
Awarikru Pond	Algil/ Detritivore	0.01 ± 0.05	0.01 ± 0.02	0.98 ± 0.05
	Omnivores	0.64 ± 0.20	0.01 ± 0.03	0.35 ± 0.18
	Invertivores	0.13 ± 0.12	0.64 ± 0.14	0.23 ± 0.15
	Pisc/Invert	0.01 ± 0.01	0.04 ± 0.05	0.86 ± 0.10
	Piscivores	0.09 ± 0.08	0.03 ± 0.04	0.89 ± 0.08
Kumakapan 1	Algil/ Detritivore	0.01 ± 0.04	0.01 ± 0.05	0.98 ± 0.07
	Omnivores	0.90 ± 0.10	0.00 ± 0.01	0.10 ± 0.10
	Invertivores	0.11 ± 0.12	0.50 ± 0.14	0.34 ± 0.17
	Pisc/Invert			
	Piscivores	0.04 ± 0.06	0.01 ± 0.02	0.94 ± 0.07
Kumakapan 2	Algil/ Detritivore	0.01 ± 0.04	0.01 ± 0.03	0.98 ± 0.05
	Omnivores	0.80 ± 0.12	0.01 ± 0.03	0.19 ± 0.11
	Invertivores	0.37 ± 0.16	0.52 ± 0.12	0.10 ± 0.08
	Pisc/Invert	0.42 ± 0.14	0.05 ± 0.06	0.53 ± 0.12
	Piscivores	0.41 ± 0.15	0.03 ± 0.04	0.56 ± 0.14

## RESULTS

**Assimilation of basal production sources.** Assimilation of material originating from alternative basal production sources varied among trophic guilds, but there were differences between the river channel and ponds in the floodplain (Tab. 2). In the river channel, seston was the most important basal source supporting algivore/detritivores and omnivores (mean estimate from mixing model probability distribution >95%). Terrestrial plants were increasingly important for fishes at higher trophic levels. Invertivores assimilated approximately 56% material originating from seston and 44% from C3 terrestrial plants. Piscivore/invertivores predominantly assimilated material originating from C3 terrestrial plants (~78%), and most piscivores appeared to exploit food chains with C3 terrestrial plants at the base (>97%).

Estimated proportions of material from basal production sources assimilated by trophic guilds differed not only between ponds and the river channel, but in some cases varied among ponds (Tab. 2). In all three ponds and similar to the river channel, algivore/detritivores assimilated material from seston almost exclusively (mean estimate 98%). Omnivores primarily assimilated material from C3 aquatic macrophytes, though estimated proportions varied among ponds. In Kumakapan Pond 1, omnivores assimilated material from C3 aquatic plants almost exclusively (~90%). In Awarikru and Kumakapan Pond 2, material from seston made larger contributions to omnivore biomass (~35% and ~19%, respectively) compared to omnivores in Kumakapan Pond 1. C3 terrestrial plants contributed between 50% and 67% of the material assimilated by invertivores in ponds. The estimated importance of other basal production sources for invertivores varied by pond; seston was relatively important in Awarikru and Kumakapan Pond 1, and C3 aquatic plants were relatively more important in Kumakapan Pond 2. Piscivores/invertivores and invertivores showed similar proportional assimilation estimates within each pond, but these estimates varied among ponds. In Awarikru and Kumakapan Pond 1, these two guilds were estimated to assimilate material originating from seston almost exclusively (>85%). In contrast, in Kumakapan Pond 2, piscivore/invertivores and piscivores assimilated nearly equal proportions of material from C3 aquatic plants and seston (~41% and ~55%, respectively).

## DISCUSSION

Seston was estimated to be the primary carbon assimilated by about half of the trophic guilds across the habitats surveyed, consistent with previous research in tropical floodplain rivers (Araujo-Lima *et al.*, 1986; Benedito-Cecilio *et al.*, 2000; Lewis *et al.*, 2001), especially during the dry season (Roach *et al.*, 2009b; Ou, Winemiller, 2016). Our study was conducted at the end of the dry season at the start of annual rains, the period associated with lowest water levels. At these low water levels, water body shorelines have receded away from riparian vegetation, which presumably reduces inputs of allochthonous food resources (plant material and invertebrates) to aquatic food webs. The quality of available allochthonous resources also may be reduced during the dry season, if many plants are not producing flowers, fruits or seeds. In the Cinaruco River, Venezuela, aquatic ecosystem primary production was highest during the annual

low-water period in both the river channel and floodplain lakes (Cotner *et al.*, 2006; Montoya *et al.*, 2006). Other studies in Neotropical rivers have also documented the importance of phytoplankton biomass within floodplain lakes during low-water periods (Rai, Hill, 1984; Putz, Junk, 1997). However, isotopic signatures of seston do not necessarily reflect those of phytoplankton in rivers and floodplains (Arantes *et al.*, 2019), and seston (suspended fine particulate organic matter) in these systems likely contains variable fractions of detritus, microbial decomposers, and phytoplankton). In the river channel and the three floodplain ponds, algivore/detritivores assimilated material almost entirely from seston, as did omnivores captured from the active channel. Much of this material likely was ingested directly by benthivorous fishes that graze FPOM (seston) that settles from the water column and accumulates on substrates (Montoya *et al.*, 2006; Winemiller *et al.*, 2006). Seston was estimated to be of relatively low importance for omnivorous fishes in Kumakapan ponds 1 and 2, where material originating from aquatic macrophytes had greater importance in supporting their biomass during the dry season. Seston was estimated to have relatively low importance supporting biomass of invertivores in all three ponds. Terrestrial plants were the most important basal production source supporting invertivore biomass in ponds. This was likely due to consumption of terrestrial invertebrates by certain invertivorous fishes, such as anchovies (Engraulidae) as well as benthivorous invertivores (*e.g.*, *Apistogramma*, *Characidium*, *Geophagus*, *Satanoperca*, *Pimelodella*) consuming aquatic insects that assimilated detritus of allochthonous origin. Invertivorous fishes in the river channel assimilated material from terrestrial plants and seston in similar proportions.

Piscivore/invertivores tended to reflect basal source assimilation proportions of piscivores more closely than invertivores. In the river channel, both of these trophic guilds were estimated to have assimilated much larger fractions of terrestrial sources compared to guilds at lower trophic levels. This disparity could result from a time lag for assimilation of material originating from basal production sources to pass through several steps along food chains (Tieszen *et al.*, 1983; O'Reilly *et al.*, 2004; Thomas, Crowther, 2015). At the time of our study, the floodplain ponds had been isolated for several months, presumably sufficient time for fishes to assimilate *in situ* basal production sources. During the wet season, many Neotropical fishes enter flooded riparian areas to feed directly on allochthonous food resources, such as seeds, fruits, flowers, leaves, and terrestrial invertebrates (Goulding, 1980; Correa, Winemiller, 2018). If one assumes an elemental turnover rate of approximately 1–2 months for fish muscle tissue (C half-life ~ 26 days, N half-life ~ 35 days; Mont'Alverne *et al.*, 2016), then it might take 3–6 months for a significant amount of material from basal production sources to pass through 2–3 trophic levels to become assimilated within piscivore biomass. In contrast, herbivores and omnivores at low trophic positions should reflect a history of feeding and growth over the previous few weeks, which in our study would fall entirely within the dry season. Although tissue elemental turnover rate is affected by several factors, including body mass and temperature (Thomas, Crowther, 2015), our findings for the river channel are consistent with this time-lag hypothesis; estimates for assimilated material derived from terrestrial plants were greater for fishes at higher trophic levels. Interestingly, the same pattern was not found for piscivores in ponds, where seston was estimated to be most important, along with aquatic macrophytes in Kumakapan Pond 2, a shallow pond with high density of aquatic macrophytes.

Our study design carries three assumptions: 1) fish samples reliably represented local assemblages, 2) fishes were resident in the habitat long enough for their isotopic signatures to reflect assimilation of material from local resources, and 3) samples were obtained for all important basal sources with sufficient isotopic discrimination for estimating proportional assimilation. With regards to the first two assumptions, our study included several species known to be migratory, such as *Hydrolycus scomberoides*, that could have recently moved into the channel location from an upstream or downstream reach. This seems plausible with respect to the river channel, but seems unlikely for ponds that had been isolated from the channel for several months before we sampled them.

Our third assumption has greater uncertainty. A limitation of isotopic mixing models is that the inclusion of multiple sources reduces the ability to discriminate their contributions to consumer biomass with precision. This problem is compounded when sources overlap in their isotopic ratios (Moore, Semmons, 2008). To limit the number of sources used as inputs for the models, we excluded C4 grasses because their  $\delta^{13}\text{C}$  was much higher than any of the fishes, and previous research has shown that few Neotropical fishes appear to assimilate appreciable amounts of material derived from these grasses (Benedito-Cecilio, 2000; Jepsen, Winemiller, 2002, 2007; Arantes *et al.*, 2019). We attempted to obtain samples of common basal production sources at each survey site, and our assessments were based on visual inspection of submerged substrates, vegetation, leaf litter and other forms of detritus in littoral and riparian zones. Nonetheless, some important sources could have been missed. Other studies have revealed evidence for the importance of microphytobenthos (biofilms), periphyton, and particulate organic matter (POM) in tropical river food webs (Winemiller, 1990; Wantzen *et al.*, 2002; Roach, Winemiller, 2015; Ou, Winemiller, 2016; Arantes *et al.*, 2019). Visible stands of microphytobenthos or periphyton were not present in the habitats we sampled, and POM in our seston samples could have included variable fractions of phytoplankton and detritus of either aquatic or terrestrial origin. Interestingly, a few of the fish specimens we collected had extremely low  $\delta^{13}\text{C}$  values ( $<-40\text{‰}$ ), values commonly associated with methanogenesis in microbial communities (Qin *et al.*, 2020). Six of these fishes were algivore/detritivores in the families Curimatidae and Loricariidae, and three others were planktivorous anchovies (*Amazonsprattus*, *Anchoviella*) with high trophic positions (high  $\delta^{15}\text{N}$ ) that likely fed from food chains that include methanogenic bacteria at their base. We also cannot rule out fractions of phytoplankton with low  $\delta^{13}\text{C}$  in our seston samples, and the relative influence of phytoplankton vs detritus on isotopic signatures of bulk seston samples is vexing problem (Marty, Planas, 2008; Karlsson *et al.*, 2014).

In conclusion, stable isotope analysis revealed variation in estimates of assimilated material from basal production sources both between-guilds within a habitat and within-guilds among habitats of the Rupununi River during the dry season. Our findings support previous research that autochthonous primary production broadly supports tropical river food webs during the low-water phase of the seasonal flood cycle. For some guilds within certain habitats, terrestrial or aquatic vegetation was estimated to more important basal sources supporting fish biomass, however, the influence of time lags for element assimilation in muscle tissue cannot be discounted for fishes at high trophic levels. Isotopic differences of individual trophic guilds between floodplain ponds were associated with differences in floodplain pond water depth and the density of aquatic vegetation. Future research on food webs of tropical rivers should further examine the relationship between floodplain heterogeneity and community trophic and food web structures.

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**AUTHORS' CONTRIBUTION** 

**Benton L. Fry:** Conceptualization, Formal analysis, Investigation, Methodology, Visualization, Writing–original draft, Writing–review and editing.

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**DATA AVAILABILITY**

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

**AI STATEMENT**

The authors did not use any AI-assisted technologies in the creation of this manuscript or its figures.

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The authors declare no competing interests.

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Supplementary material S1

Supplementary material S2

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