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Seasonal Forest Resources Support Fish Biomass in Floodplain Lakes of an Amazonian Tributary

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ABSTRACT

1. The Flood Pulse Concept is a foundational ecological theory that emphasizes the critical role of lateral connectivity between a river channel and its floodplain. Many tropical rivers inundate the surrounding floodplain in the flood stage, thereby receiving large amounts of terrestrial organic matter that can be decomposed by microbes and directly consumed by animals. This dynamic could simultaneously drive down oxygen concentrations while also supporting fish production.
2. We used two lines of evidence to investigate the fate of terrestrial organic matter during the low- and high-water seasons in the Juruá River, Amazonas, Brazil: spot measurements of dissolved oxygen and isotopic measurements (δ^{13}C, δ^{15}N) of fishes and food source pathways originating from C3 and C4 plants, phytoplankton, and periphyton.
3. Dissolved oxygen concentrations were low (mean $\leq$3.0 mg/L) throughout the floodplain during high water, while higher values (mean = 6.5 mg/L) were evident during low water, suggesting variable rates of ecosystem respiration, production and atmospheric exchange across seasons.
4. Most fish species, including the commercially and culturally important pirarucu (*Arapaima* sp.), had a strong dependence on terrestrial C3 plants during the falling-water season (median source proportions 34%–77%), while fishes shifted to rely on the phytoplankton pathway (median proportions 11%–82%) during low water. Our results demonstrate that terrestrial C3 plant resources are channeled into the food web through detritivorous fishes, such as bodó (*Liposarcus pardalis*), and frugivorous fishes, such as pacu (*Mylossoma aureum*).
5. During high water, a dispersed food web takes shape as fish move into the flooded forest, driven by terrestrial resources and accompanied by low oxygen conditions. During low water, a concentrated food web emerges in the remaining oxbow lakes, consistent with fast-growing algal resources.

1 | Introduction

Exchanges of organic matter across ecosystem boundaries provide resources for the growth of consumers (Polis et al. 1997). The quality, quantity, timing, and duration of these exchanges vary seasonally and have concomitant effects on individual consumers and overall food-web structure (Marcarelli et al. 2011; McMeans et al. 2015; Subalusky and Post 2019; Simon and Vasseur 2021). Flows of terrestrial plant matter to aquatic ecosystems are among the highest rates of carbon flux in the world (Gounand et al. 2018), especially in periodically flooded rainforests where rates can reach as high as 10 t/ha/year (Chave et al. 2010). There are two potential fates for this carbon—respiration by microbes via decomposition (Tiegs et al. 2024) and/or direct entry into the metazoan food web (Marcarelli et al. 2011).

Leaf litter is rarely an important primary resource for aquatic metazoan food webs (Roach 2013), even when it is abundant, because it is much poorer quality than algae and phytoplankton (Elser et al. 2000; Hixson et al. 2015; Brett et al. 2017). For example, in floodplain food webs of open savannas, there is sufficient attached algal production to make these algae the dominant source of organic matter for fishes and benthic macroinvertebrates (Jardine et al. 2012, 2013). Even in some floodplain ecosystems with greater forest coverage, the fate of most terrestrial organic matter subsidies is respiration by microbes rather than incorporation into metazoan food webs (Lewis et al. 2000; Thorp and Delong 2002; Brett et al. 2017). However, evidence suggests that terrestrial organic matter can subsidize metazoans in large tropical riverscapes when it is modified by fungi and bacteria through trophic upgrading (Moore et al. 2004; Hiltunen et al. 2017) or when it is delivered as nutritious fruits, seeds or insects (Correa and Winemiller 2014). In these forested ecosystems, terrestrial organic matter is believed to come to the trophic rescue of aquatic consumers whose nutritional needs cannot be met by aquatic productivity alone (Goulding 1980; Junk and Wantzen 2004). Unlike the aforementioned savanna floodplains, many large tropical riverscapes have reduced algal productivity due to shading and low nutrient concentrations (Bayley 1989). The original flood-pulse concept envisages an aquatic–terrestrial transition zone where growth of aquatic plants occurs in newly flooded areas coincident with leaf-litter breakdown (Junk and Wantzen 2004). Therefore, unlike in other global riverscapes, we hypothesize that terrestrial organic matter resources substantially subsidize both the microbial and metazoan food webs in forested tropical floodplains, especially in the high-water season compared to the low-water season (Wantzen et al. 2002; Venarsky et al. 2020). To test this hypothesis, we combine measurements of the oxygen environment (indicators of the relative balance of primary production and ecosystem respiration) with isotopic analyses of fishes to reveal the likely role of terrestrial organic matter in both metazoan and microbial food webs (Marcarelli et al. 2011).

Most rivers are net heterotrophic (Battin et al. 2023), driven by organic matter inputs that are respired by microbes (Duarte and Prairie 2005). In tropical systems, rates of primary production and respiration mirror those of temperate systems, with larger rivers having higher production and respiration rates (Marzolf and Ardón 2021). Warm temperatures in the tropics likely lead to persistently high respiration rates because respiration increases linearly with temperature across biomes (Yvon-Durocher et al. 2012). In larger tropical rivers and their floodplains, oxygen measurements are rare, likely owing to logistical challenges in accessing often remote, dynamic systems. Prolonged bouts of hypoxia in large tropical river floodplains suggest intense respiration of decaying leaves and soil organic matter (Hamilton et al. 1997; Lewis et al. 2000; Holtgrieve et al. 2013), but the uptake of this organic matter into the metazoan food web has not been demonstrated (Lewis Jr et al. 2001).

The source pathways supporting the biomass of fishes and other aquatic consumers can be revealed with ecological tracers because the chemical fingerprints of sources are often distinct and preserved from the bottom of the food chain to top predators. Stable isotopes of C and N show how different sources (e.g., algae, aquatic plants, leaf litter) contribute to animal nutrition (Jardine et al. 2017). Early work in Amazonian systems identified that many fishes rely on phytoplankton rather than higher plants, while C4 aquatic plants were not being consumed in the food web despite their numerical abundance (Hamilton et al. 1992; Forsberg et al. 1993). Knowing the origins of organic matter in the animal food chain can reveal much about ecosystem stability (Rooney et al. 2006) and the need to maintain or enhance certain source pathways for conservation (Vadeboncoeur et al. 2003), but it also has implications for exposure to contaminants, such as mercury, that are derived from the diet (Nyholt et al. 2022).

Our goal was to determine the importance of terrestrial organic matter to food webs in oxbow lakes of a large Amazonian tributary, the Juruá River, Brazil. Previous work in this system suggests top-down control by arapaima (*Arapaima* sp., also known as pirarucu) that would imply feeding on a phytoplankton pathway during low water (Campos-Silva et al. 2021). However, observations of forest feeding by fishes in the region, the high prevalence of detritivory in the fish community, and the prolonged flood pulse would suggest a potential role for terrestrial organic matter in aquatic food webs. We therefore hypothesized that food webs would shift from those supported by algal organic matter in the low-water season to a dominance of terrestrial organic matter in the high-water season, and that these shifts would be accompanied by changes in oxygen concentrations as indicators of whole-ecosystem metabolism (primary production and respiration). We used C and N stable isotopes to estimate dietary source proportions for fishes in the low-water and falling-water seasons, the latter representing growth during the high-water season. We complemented these estimates with spot measurements of dissolved oxygen (DO) in high- and low-water seasons to infer the role of forest litter in metazoan and microbial food webs.

2 | Methods

2.1 | Study Area

We sampled oxbow lakes and the main channel of the Juruá River in Amazonas, Brazil (Figure 1), one of the largest tributaries (~3280 km long) of the Amazon River. Human population density in the basin is low, and there are two large protected areas (the Médio Juruá Extractive Reserve and the

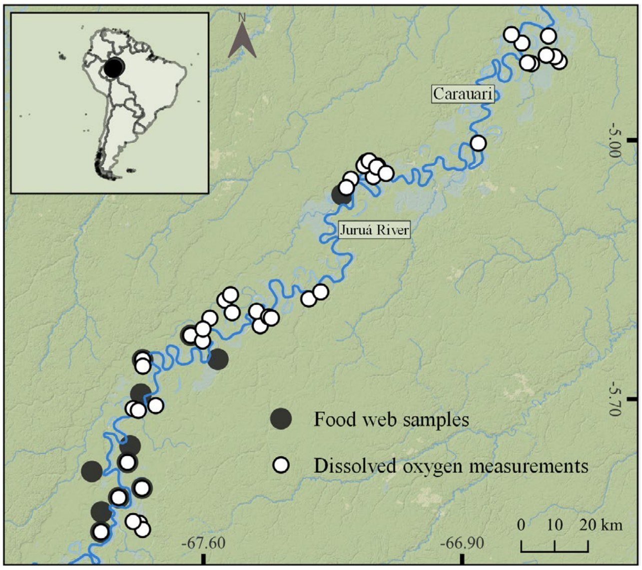

FIGURE 1 | Sampling locations for food-web samples (fishes and baseline organisms) and dissolved oxygen measurements along the Juruá River, Brazil.

Uacari Sustainable Development Reserve) in the study region. Though some of the study lakes are outside of the protected areas, all are surrounded by intact forest with limited agricultural development, urbanization or mineral extraction. The Juruá River was declared a Ramsar site in 2018 and has a highly rhythmic flood pulse (Jardine et al. 2015) with consistent timing and magnitude of floods each year. Discharge typically peaks between 8000 and 9000 m^3/s in April and drops to ~1000 m^3/s in September (Jackson et al. 2022). Oxbow lakes remain connected to the river for approximately 6 months before receding and disconnecting, leaving high densities of fishes (Silvano et al. 2000) that are captured by local communities for subsistence and some commercial fishing (Newton et al. 2012; Endo et al. 2016; Ferreira et al. 2021). Lakes are designated with different levels of local protection from fishing to rebuild populations of the iconic arapaima, a valuable resource (Campos-Silva and Peres 2016). Fish and food-web sampling took place in the same lakes during the low- and falling-water seasons 8 months apart in a paired design (Table S1), whereas DO measurements were made opportunistically at different locations and times but in the same reach of the river (Figure 1). While we did not link the DO measurements directly to the food web measurements, we used the two as parallel lines of evidence to infer the role of terrestrial inputs in food web structure and ecosystem metabolism.

2.2 | Dissolved Oxygen Measurements

We measured DO concentrations during high water in 2 years (Table S2). First, we took depth-specific measurements from 31 oxbow lakes during late March and April 2017, all of which were connected to the main river channel by floodwaters. We used a DO probe and sampled at 30 cm increments for the 1st meter and every 1 m thereafter until we reached bottom, using these measurements to assess stratification. Later, in April 2023, we used a simple titration kit (Hach Model OX-2P) to estimate surface-water DO concentrations in 13 locations across the floodplain, again at locations that were connected to the main channel. Though this kit likely produced less sensitive and precise DO readings, we assumed similar accuracy as the probes that we used elsewhere and applied this method to examine general patterns in these remote areas. We followed the manufacturer's protocol by adding supplied reagents to a measured volume of water, mixing and adding a solution drop by drop until the sample became clear. Measurements were taken as early in the day as possible to capture DO minima and again as late in the day as possible to capture DO maxima. We tested at a range of sites, from the main river channel to deep (> 1 km) into the floodplain forest as well as in oxbow lakes. At each site we qualitatively described the canopy cover as open, partially open, or closed and took readings of temperature, pH and conductivity with a handheld device (Hanna) as well as a Secchi depth reading (Table S2).

During the low-water season, we used Hobo oxygen loggers suspended just below the surface to measure DO in eight oxbow lakes in September 2022. All of these sites were either completely disconnected from the main channel or had small channels draining water away from the lake at the time of sampling. We were unable to obtain depth-specific data during this season with this method and assume that lakes may have been thermally stratified at this time, with correspondingly variant DO concentrations in the epilimnion and hypolimnion (Tundisi et al. 1984). Though we obtained continuous data for 24–48 h at each lake, we report here the mean, minimum and maximum for sites between the hours of 06:00 and 18:00 to allow direct comparison with our spot measurements during the high-water season, and group the data as two times of day—early (06:00 to 12:00) and late (12:00 to 18:00) – to reduce confounding diel variation. All of these sites had open canopies and we also took readings of pH, temperature, conductivity and Secchi depth.

2.3 | Food-Web Sample Collection

We collected muscle tissue samples from the dominant fish species during the low-water season in September 2018 and again during the falling-water season in June 2019. Fishes were captured with gill nets by local community members in disconnected oxbow lakes and therefore represent the most numerically abundant large-bodied species but not the overall diversity of the community. We removed muscle samples from above the lateral line of each fish and stored these samples frozen until they were transported to the laboratory at the Instituto Nacional de Pesquisas da Amazônia in Manaus, Brazil for processing.

To represent the basal source pathways available to fishes, we used a mix of primary producers and primary consumers (Jardine et al. 2017). We used primary consumers when possible because they have less temporal isotopic variation relative to primary producers (Cabana and Rasmussen 1996) and therefore represent longer-term average isotope values for the source of interest (Finlay 2001; Post 2002). For the phytoplankton baseline, we collected zooplankton using multiple vertical hauls of a plankton net in the center of each oxbow. For the periphyton baseline, we collected snails (Ampullariidae) by hand in shallow areas. Although Ampullariidae eat a

TABLE 1 | $\delta^{13}C$ and $\delta^{15}N$ values of sources used in the isotope mixing models.

	Low-water season					Falling-water season				
	N	Mean $\delta^{13}C$	±SD	Mean $\delta^{15}N$	±SD	*N*	Mean $\delta^{13}C$	±SD	Mean $\delta^{15}N$	±SD
Benthic algae (estimated from snails)	7	−27.8	5.3	4.5	1.6	7	−25.9	6.2	6.2	1.5
C3 plants	22	−30.8	1.2	3.1	2.0	24	−31.0	1.6	3.4	1.5
C4 plants	2	−13.0	0.2	5.9	2.2	2	−13.0	0.2	5.9	2.2
Phytoplankton (estimated from zooplankton)	33	−35.6	5.1	5.6	1.6	29	−40.9	2.6	6.8	0.7

mixed diet that includes attached algae (López-van Oosterom et al. 2016), these snails were the best representative of the benthic pathway because obligate scraping insects (e.g., mayflies) are rare in these systems. For the terrestrial baseline, we collected leaves that had fallen into the water and rinsed them of attached algae, as well as fruits and seeds gathered from the forest floor. Though aquatic plants were relatively rare, especially during the low water phase, we collected any that were seen and stored them separately, using the isotope data to determine whether they used the C3 or C4 photosynthetic pathway (Ehleringer and Cerling 2002). All samples were stored frozen on board a research boat and transported to Manaus for processing.

In Manaus, samples were freeze-dried and ground to a powder. Samples were weighed to 1 mg (animal tissue) or 4 mg (plant tissue) and shipped to the University of California Davis Stable Isotope Facility for analysis. Samples were combusted in a PDZ Europa ANCA-GSL elemental analyzer and resultant gases delivered to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Standards that were analyzed alongside samples had standard deviations of ~0.2‰ for $\delta^{13}C$ and ~0.3‰ for $\delta^{15}N$.

2.4 | Data Analysis

For the isotope data, we first lipid-corrected all fish $\delta^{13}C$ values using C/N ratios as a proxy for lipid content and the formula for all fish tissues ($\delta^{13}C_{corr} = \delta^{13}C + 3.093 \times \ln(C/N) - 2.976$) from Logan et al. (2008). We then ran mixing models using MixSIAR (Stock et al. 2018) in R v. 4.3.1 with four basal sources (Table 1) after correction for trophic enrichment. To do so, all basal sources needed to be standardized to the same trophic level (primary producers) (Jardine et al. 2017). To estimate the phytoplankton baseline value, we subtracted mean trophic discrimination values of 0.4‰ (Post 2002) and 0.6‰ (Bunn et al. 2013) from the mean zooplankton $\delta^{13}C$ and $\delta^{15}N$ values, respectively. For the periphyton baseline, we subtracted these same amounts from the mean snail values. For C3 and C4 plants, we used the isotope values of the plants themselves, grouping leaves, fruits/seeds and C3 macrophytes together into a C3 plants category because their isotope ratios were similar. Even though C4 plants were isotopically distant from all consumers, suggesting a limited role in the food web, we retained this source in the model because eliminating sources that contribute minimally can distort the mixing polygon and give erroneous source proportion estimates (Phillips et al. 2014). There were no significant differences in source values between seasons (Friedman test; $\delta^{13}C$ $p = 0.56$, $\delta^{15}N$ $p = 0.08$), but the probability value was low indicating a possible type II error. Therefore, we used season-specific source values in the mixing models to attempt to temporally match values with fish consumers.

We grouped the fish community into three trophic categories. Herbivore-detritivores included bodó (*Liposarcus pardalis*), curimatã (*Prochilodus nigricans*), pacu (*Mylossoma aureum*), tapioca (*Potamorhina pristigaster*) and tambaqui (*Colossoma macropomum*). Omnivores included cichlids, characids, pimelodids, tripotheids, and anostomids. Predators included arapaima, aruanã (*Osteoglossum bicirrhosum*), piranha (Serrasalmidae), tucunaré (*Cichla* spp.), and traira (*Hoplias malabaricus*). For each of the categories, we applied $\delta^{15}N$ trophic discrimination factors from basal source to consumer estimated from Bunn et al. (2013). These values were 3.9‰ ± 1.4‰, 4.3‰ ± 1.5‰, and 5.7‰ ± 1.6‰, respectively for herbivorous-detritivorous species, omnivorous species, and predatory species. For $\delta^{13}C$ trophic discrimination, we used the value of 0.4‰ ± 1.3‰ from Post (2002) and applied it increasingly from 0.4‰ ± 1.3‰ for herbivorous-detritivorous species, to 0.6‰ ± 1.3‰ for omnivorous species, and 0.8‰ ± 1.3‰ for predators as we assumed herbivore-detritivores would be one trophic level above basal sources, omnivores would be 1.5 trophic levels above basal sources, and predators would be two trophic levels above basal sources. In MixSIAR, we ran one model for each season with uninformative priors (25% contribution from each of the four sources), separated by trophic group with lake as a random factor. We used the "normal" run time function for all model runs, which includes 3 chains, a chain length of 100,000 and burn-in of 50,000. Models have failed to converge when Gelman-Rubin values are > 1.05 (a value of 1 indicates convergence) and more than 5% of Geweke z-scores fall outside the 95% confidence interval comparing the first and second parts of the chain (±1.96 standard deviations). When this occurred, we re-ran the model in "long" or "very long" mode and used outputs from the latter models (Table S3). We then used the lake- and species-specific median values produced by MixSIAR to test for seasonal effects in source proportions, with season as a fixed factor and species nested in lake as random factors in a linear mixed effects model with the R package lme4 (Bates et al. 2015). Model assumptions were evaluated by examining residuals versus

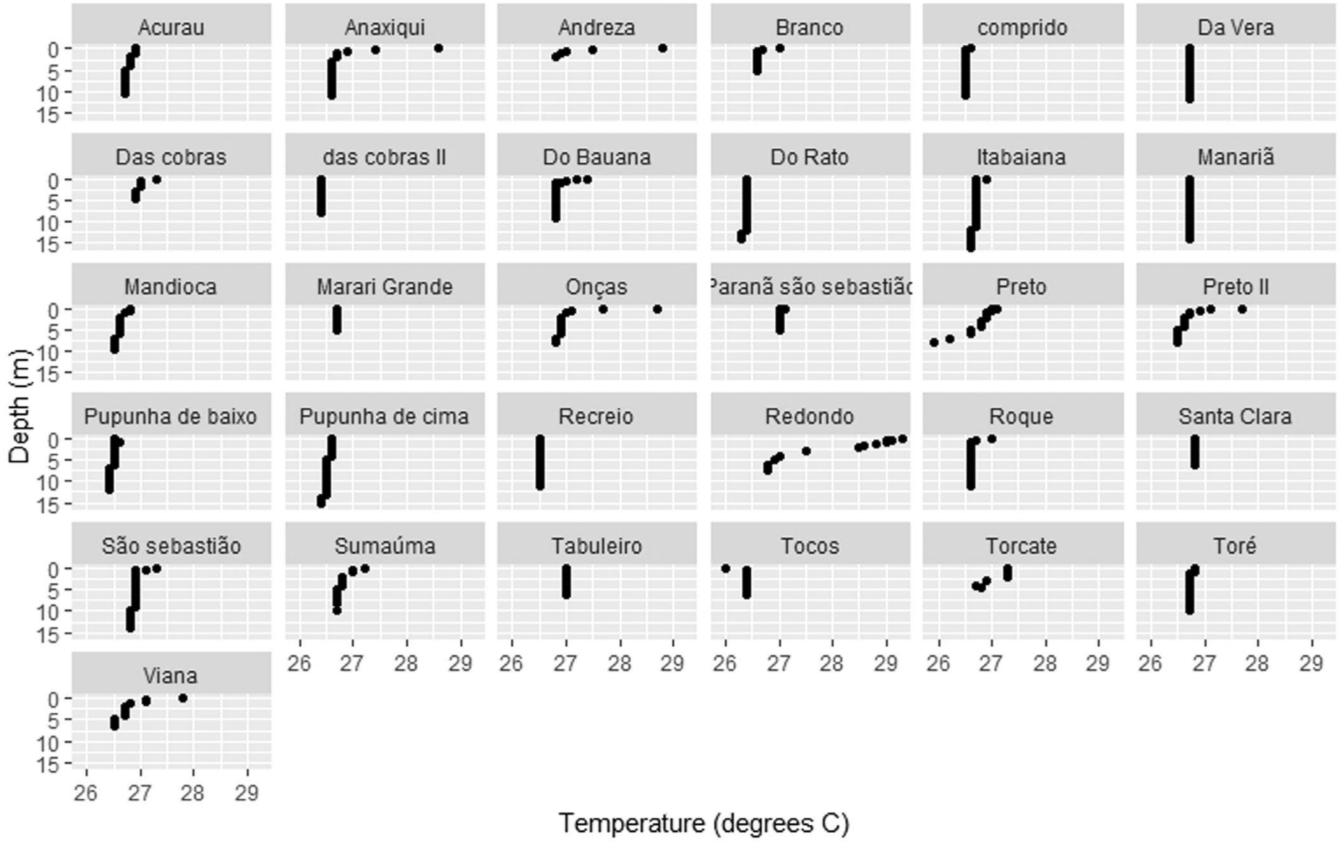

FIGURE 2 | Temperature (°C) versus depth in oxbow lakes of the Juruá River during the high-water season illustrating limited thermal stratification.

fitted values and Q-Q plots. We used the model estimates and associated error (standard error and 95% confidence intervals), rather than *p*-values, to compare among seasons and sources.

3 | Results

3.1 | Dissolved Oxygen Concentrations

Oxbow lakes were well mixed during the high-water season with limited evidence of thermal stratification except for a few of the lakes (Figure 2). Dissolved oxygen concentrations were always below 5 mg/L (66% saturation) and declined with depth in some lakes (Figure 3). The mean concentration was 2.9 mg/L (36% saturation, $n = 417$ observations). Likewise, DO concentrations measured throughout the flooded forest during the high-water season were also low, indicative of hypoxic conditions in some cases (Figure 4a). Despite sampling at the end of sunny days in open waters (the main river channel and oxbows), concentrations were always below 5.5 mg/L and averaged 3.0 mg/L, corresponding to 38% saturation ($n = 25$ observations). Concentrations were generally lowest early in the day and under closed canopies, with our lowest reading of 0.2 mg/L occurring at 08:15 under a partial canopy. The pH values were always below 7.0, ranging from 5.5–6.8, and temperatures were high, ranging from 26.1°C to 33.0°C (Table S2). Variability among sites was much smaller in the floodplain during high water (Figure 4a) than in the lakes during low water (Figure 4b), when mean daytime DO concentrations ranged from 3.1–9.2 mg/L (mean = 6.5 mg/L). During low water, pH averaged 6.5 (range = 5.5–7.5), conductivity ranged from 0 to 125 μS/cm, and Secchi depths ranged from 12 to 65 cm (Table S2).

3.2 | Stable-Isotope Ratios

Mean isotope values for basal sources were well differentiated in dual isotope space ($\delta^{15}N$ vs. $\delta^{13}C$ biplots, Figure 5), but there was considerable variation within sources (Table 1). As expected, phytoplankton (estimated from zooplankton) were ^{13}C-depleted relative to the other sources, averaging −37.7‰ across all sites and times. C3 plants also had relatively low $\delta^{13}C$ values (mean = −30.9‰), but their $\delta^{15}N$ values were lower than those of plankton. Periphyton (estimated from grazing snails) had higher $\delta^{13}C$ values (mean = −26.4‰) than both plankton and C3 plants, but this source was the most variable (range −34.7‰ to −18.0‰). C4 plants were enriched in ^{13}C (mean $\delta^{13}C$ = −13.0‰) relative to all sources and had elevated $\delta^{15}N$ values (mean = 5.9‰), but the sample size for this group was small ($n = 2$).

Fishes had a broad range of $\delta^{13}C$ values but a relatively narrow range of $\delta^{15}N$ values (Figure 5). During the low-water season, among the herbivore-detritivores, bodó and curimatã had low (mean = −31.5‰ and −32.2‰) but variable (−37.2‰ to −25.8‰ and −36.0‰ to −27.1‰) $\delta^{13}C$ values, while pacu had more constrained $\delta^{13}C$ values (mean = −26.9‰, range −27.8‰ to −25.8‰) (Figure 5a). The mean $\delta^{13}C$ value during the low-water season for all herbivore-detritivores was −31.5‰ ± 3.3‰.

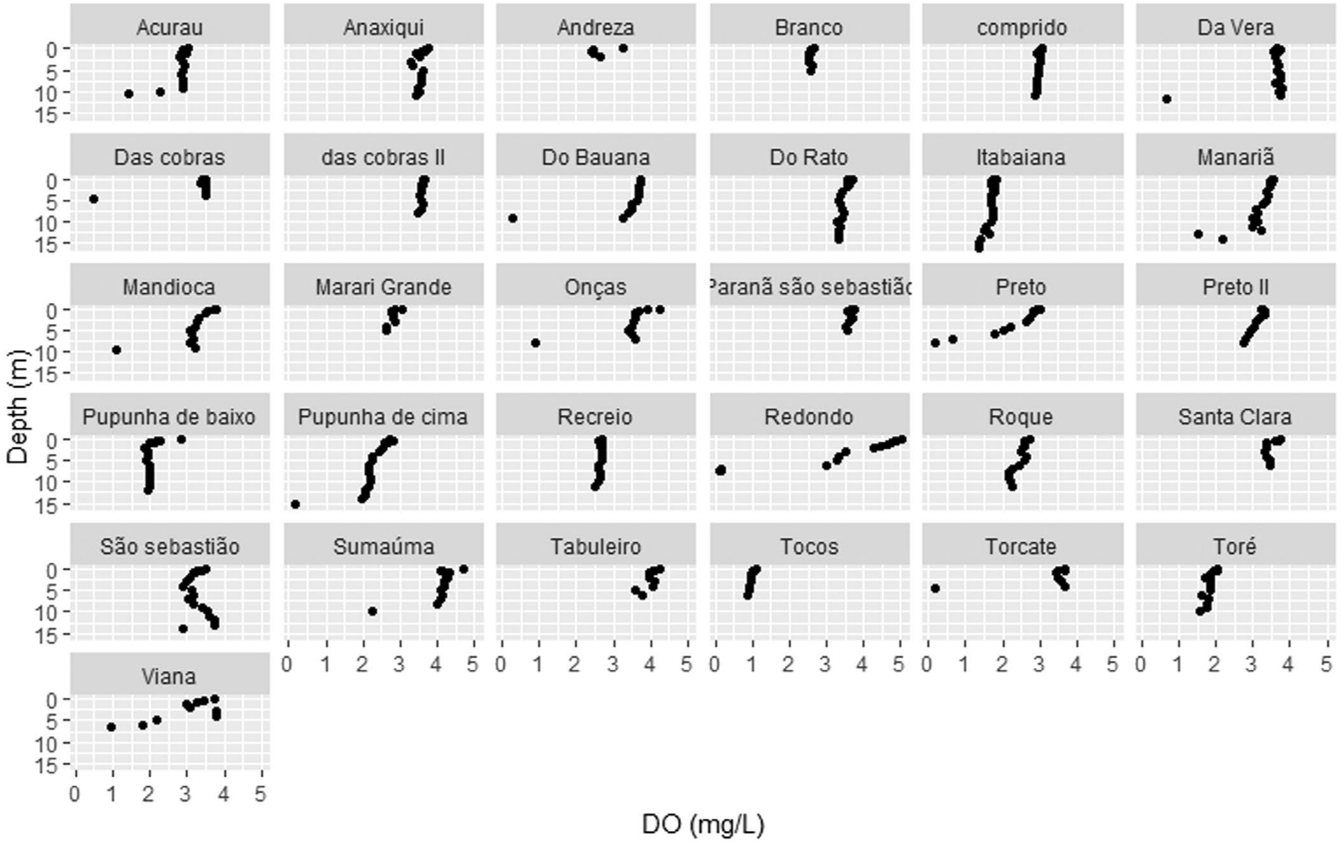

FIGURE 3 | Dissolved oxygen concentrations (mg/L) versus depth in oxbow lakes of the Juruá River during the high-water season, highlighting low and stable DO concentrations throughout the water column in most lakes.

During the falling-water season, these isotope patterns largely held (Figure 5b), and pacu and tambaqui became more dominant in the sample, making up 51% of the individuals as opposed to only 16% in the low-water season. This led to a slightly higher mean $\delta^{13}C$ value for all herbivore-detritivores during the falling-water season (−30.6‰ ± 4.1‰) (Figure 5b). Omnivores had a wide range of $\delta^{13}C$ values (−35.6‰ to −26.9‰) during the low-water season and a mean value of −30.5‰ ± 2.7‰, but comparisons to the falling-water season were made difficult by relatively small sample sizes for omnivores in the latter season. As expected, omnivores had $\delta^{15}N$ values between those of herbivore-detritivores and predators in both seasons. Predators had the highest $\delta^{13}C$ values (low water = −30.1‰ ± 1.9‰, falling water = −29.7‰ ± 1.8‰) and $\delta^{15}N$ values (low water = 10.4‰ ± 0.9‰, falling water = 10.7‰ ± 0.6‰), but variation among individuals was lower than that in herbivore-detritivores and omnivores.

3.3 | Mixing-Model Outputs

Mixing models suggested seasonal shifts in sources used by fishes (Figure 6, Table S4). During the falling-water season, the C3 plant pathway made the greatest contribution, accounting for more than 50% of the diet in herbivore/detritivores (estimate = 0.52 ± 0.05 SE, t = 10.74), omnivores (estimate = 0.63 ± 0.04 SE, t = 16.16) and predators (estimate = 0.51 ± 0.02 SE, t = 23.08). Species that had the highest contribution from this pathway in this season included bodó, pacu, and arapaima (Table S4). As evidenced by non-overlapping 95% confidence intervals, the contribution of the C3 plant source significantly declined in all three trophic groups between the falling-water and low-water seasons, with low-water season estimates of 0.24 ± 0.04 SE, 0.12 ± 0.00 SE, and 0.15 ± 0.02 SE for herbivore/detritivores, omnivores, and predators, respectively (Figure 6). During the falling-water season, phytoplankton made only a minor contribution to diets, but this increased significantly during the low-water season. In herbivore/detritivores, phytoplankton contributions increased from 0.32 ± 0.06 SE (t = 5.34) to 0.49 ± 0.05 SE (t = 3.30); in omnivores it increased from 0.12 ± 0.07 SE (t = 1.7) to 0.46 ± 0.07 SE (t = 4.74); and in predators it increased from 0.19 ± 0.03 (t = 6.75) to 0.51 ± 0.02 SE (t = 14.06). Like the corresponding decrease in C3 plant importance, the increase in phytoplankton proportions was significant between seasons for all three trophic groups. Species with the largest contributions from plankton in the low-water season were the herbivores curimatã and tapioca and the predators piranha and tucunaré (Table S4). Periphyton made only modest contributions to diet with slight increases between the falling-water and low-water seasons. The highest proportions were for omnivores in the low-water season, with an estimate of 0.26 ± 0.04 (t = 4.58). C4 plants played the smallest role in fish diets, with model estimates below 0.10 for all seasons and trophic groups except herbivore/detritivores in the falling-water season, when the estimate for this source was 0.14 ± 0.01 (t = 9.66). This slightly higher value was driven by pacu and tambaqui that had median contributions of 0.24 and 0.27, respectively (Table S4).

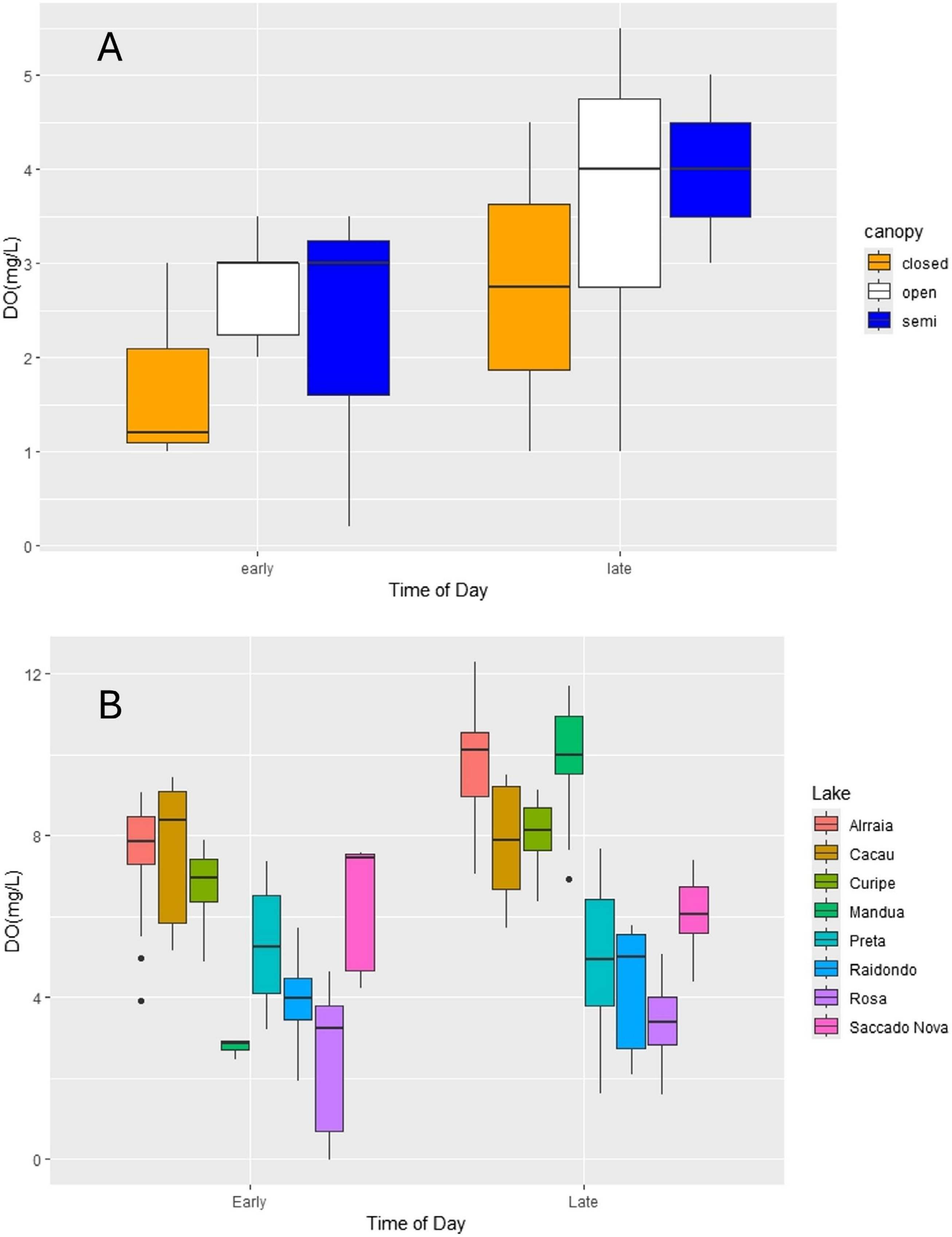

FIGURE 4 | Dissolved oxygen (DO) concentrations measured (A) on the Juruá River floodplain during high water in the morning (early) and afternoon/evening (late) under full, open, or partial canopy and (B) in oxbow lakes of the Juruá River during the low-water season in the morning (early) and afternoon/evening (late). All lakes measured during low water had open canopies.

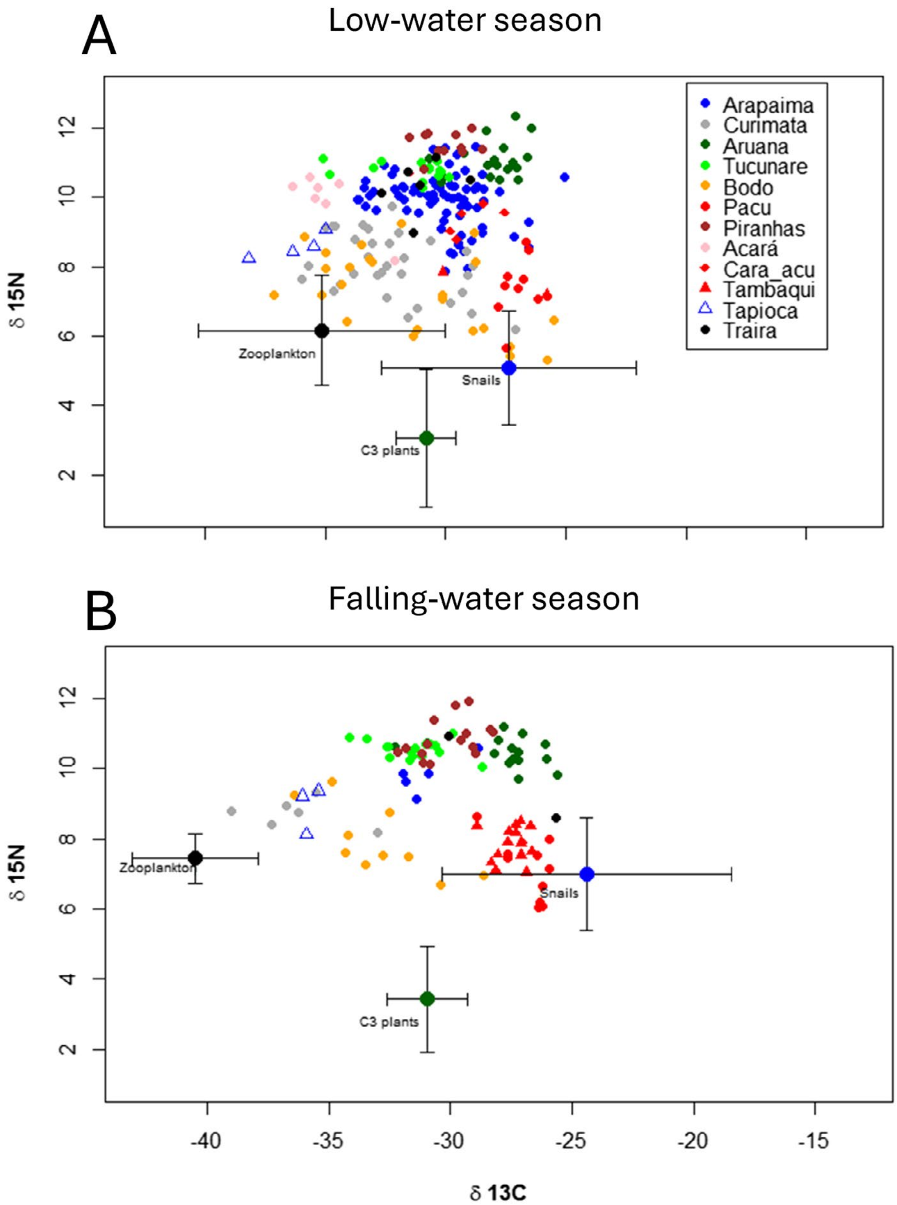

FIGURE 5 | Dual-isotope biplot of fishes and baseline organisms in the Juruá River during (A) low-water and (B) falling-water. Note that C4 macrophytes are not shown on the plot for clarity but were included as a potential source in mixing models. Sample sizes for baseline organisms are in Table 1.

4 | Discussion

We found evidence for seasonally alternating energy channels (Rooney et al. 2006) that supported the fish community in the Juruá River. During the falling water period, fish diets depended more on C3 plants originating from the surrounding forest, indicating enhanced consumption of these resources during flood conditions, consistent with our hypothesis and earlier studies of seasonal effects in other tropical freshwaters (Wantzen et al. 2002; Neves et al. 2021). These food-web results, coupled with the low DO concentrations measured in floodwaters, indicative of low primary production and/or high respiration (Tundisi et al. 1984), suggest a role for forest resources in driving both microbial and metazoan food webs (Marcarelli et al. 2011; Brett et al. 2017) in this densely forested region.

Few other studies have tracked metazoan food web source proportions over multiple seasons in the tropics. The shifts that we hypothesized and observed from algal dominance in the low-water season toward more terrestrial resources in diets during the high-water flood season align with similar observations in an Australian tropical floodplain river (Venarsky et al. 2020), where the fish community dominated by invertivore/piscivores had the highest terrestrial-carbon proportions in tissues during the early dry season. Likewise, Wantzen et al. (2002) observed lower $\delta^{13}C$ and $\delta^{15}N$ values in various species during the wet season that suggested increased consumption of terrestrial resources. In contrast, Pease et al. (2020) found limited evidence for large seasonal shifts in diet in the fish community in the La Venta River, Mexico. Terrestrial plants supported some species in some locations, and this support occurred during the dry season

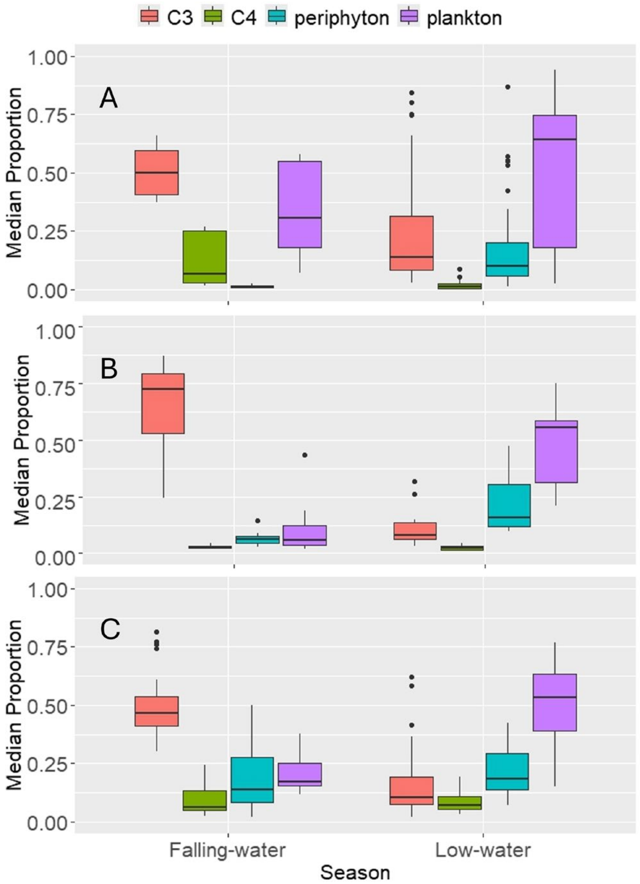

FIGURE 6 | Dietary-source proportions for (A) herbivore/detritivores, (B) omnivores, and (C) predators during the low- and falling-water seasons. Each point represents a median value for a given species in a given lake, estimated using MixSIAR.

in some cases (Pease et al. 2020). Cazzanelli et al. (2023) found limited input to floodplain-lake food webs by riparian carbon sources (< 20% contribution) in the Usumacinta River, Mexico, though they did find slightly higher contributions during the dry season, opposite to our observations. Identifying the timing of resource shifts is complicated by rates of isotopic turnover in response to these shifts. While young and rapidly growing fishes are expected to equilibrate quickly with the isotope ratios of the new diet (Vander Zanden et al. 2015), larger adult fish, such as those we sampled here, could exhibit long lag times that mask seasonal variation in diet.

Dissolved oxygen concentrations in large waterbodies are driven by three main factors: respiration, primary production, and atmospheric exchange, and the balance of these dictates measured values. Our low DO values in the Juruá floodplain during high water (~0 to 6 mg/L) are comparable to those reported by Holtgrieve et al. (2013) for a flooded-forest section of the Tonle Sap in the lower Mekong River, Cambodia. In our study system, even areas with open canopies (oxbow lakes) had low O_2 concentrations during high water. Since rainwater is expected to be well-oxygenated (Valappil et al. 2020), the low values suggest that river waters that dominated water balance in flooded conditions had inadequate turbulence/entrainment to replenish low O_2 levels found in the hypolimnion of these lakes. Additionally, plankton or submerged vegetation O_2 production rates were low and probably could not counteract the respiration of organic matter throughout the forested environment (Gagne-Maynard et al. 2017). Conversely, the higher values we observed during low water (Tundisi et al. 1984) suggest intense phytoplankton production in the epilimnion of oxbow lakes during this phase, with maximum daily O_2 concentrations as high as 12.3 mg/L, corresponding to 179% saturation, following rapid increases during daylight. These results align with those measured in the lower Amazon Basin, where the low-water season was characterized by high O_2 concentrations and low CO_2 concentrations, while the high-water season had low O_2 concentrations and high CO_2 concentrations (Gagne-Maynard et al. 2017). High CO_2 concentrations also occur in flooded forests of the central Amazon (Abril et al. 2014), indicative of respiration exceeding photosynthetic oxygen production, and can be attributed to the combined effects of aerobic respiration and root respiration (Amaral et al. 2020). Together, this supports our second hypothesis that shifts in food webs are accompanied by changes in DO concentrations and lends further support to the idea that these systems alternate between aquatic and terrestrial production and consumption phases. Further work examining rates of gross primary production and respiration as well as algal biomass in different seasons would help further characterize these patterns.

Multiple terrestrial organic matter sources likely contribute to fish diets during the high-water season, including fruits/seeds, tree leaves, and terrestrial insects (Correa and Winemiller 2014; Bokhutlo et al. 2021). We could not isotopically differentiate feeding on these different forms of terrestrial organic matter from each other or from C3 aquatic plants. However, in the densely forested floodplain of the Juruá River, these latter aquatic plants are relatively uncommon, unlike expansive mats formed in tropical floodplains elsewhere (e.g., Orinoco River, Venezuela, Hamilton et al. 1992; Magela Creek, Australia, Pettit et al. 2011; Ouémé River, Benin, Jackson et al. 2013). As for differentiating among terrestrial sources, the feeding ecology of individual species can help identify the most likely pathway. Known frugivores pacu and tambaqui represented a larger proportion of the catch in the falling water season. These species have fuller stomachs and higher fruit consumption during the high-water season (Da Silva et al. 2000; Mateus et al. 2022) which would explain why the C3 plant contribution was highest during this season. They had $\delta^{13}C$ values (~−26‰) that were very similar to frugivores in another Amazonian flooded forest (Correa and Winemiller 2014). Detritivores had far more variable isotope ratios indicating a range of source contributions from plankton, periphyton, and leaves, but direct consumption of conditioned terrestrial leaves was likely responsible for the high proportion of C3 plants in benthic-feeding bodó. Finally, terrestrial organic matter could enter these food webs via dissolved organic carbon originating from decaying leaves (Baldwin et al. 2016; Saintilan et al. 2021), which would occur with a time lag since the leaves were deposited. However, we were unable to test for the importance of this microbial pathway in these systems.

Use of additional tracers such as compound-specific amino acids or fatty acids (Nielsen et al. 2018) could help further resolve if and how detrital carbon enters the metazoan food web via fungi or other microorganisms, as well as reveal the nutritional quality of different resources. Many of the fish muscle samples had surprisingly high lipid content, evidenced by an oily appearance and texture and by high elemental C/N ratios (e.g., 43 of 85 arapaima samples had $C/N > 5$ corresponding to % lipid as high as 15%; Post et al. 2007, Logan et al. 2008). Since aquatic microalgae are a major source of long-chain omega-3 fatty acids (Harwood 2019) and they are concentrated by zooplankton (Brett et al. 2009), determining the concentrations and origin of these compounds in fish muscle would reveal much about whether the forest-litter subsidy is providing lipid resources or whether low-water season consumption of zooplankton (or zooplanktivorous fishes) instead is responsible for lipid provision. Elsewhere, zooplankton blooms occur in slow-moving water on floodplains (Furst et al. 2014; Yanygina et al. 2024) and can provide high-quality food for fishes resulting in faster growth rates (Holmes et al. 2021).

Variation in diet among species will also affect exposure to mercury (Nyholt et al. 2022), which is presumed to be naturally high in the region and could be enhanced by the annual flood conditions (Kasper et al. 2017). For example, bodó had higher mercury concentrations during the falling-water season after flooding (Nyholt et al. 2022), while pacu had consistently low mercury concentrations during both seasons (T. Jardine, unpublished data). As a result, predators feeding on these herbivorous species, including humans (Passos and Mergler 2008), will similarly experience differential mercury exposure, and additional shifts in trophic positions of predators (McMeans et al. 2019) will influence their mercury concentrations across seasons (Nyholt et al. 2022).

Predators are connected to the terrestrial organic matter pathway by consuming prey that have directly ingested various forest resources. For example, arapaima move up an elevation gradient into flooded forests during high water (Castello 2008; Campos-Silva et al. 2019) where they encounter prey species that are feeding on forest resources, including pacu (Jacobi et al. 2020). Other predators that consume an array of herbivorous-detritivorous and omnivorous fishes and those that consume terrestrial insects (Neves et al. 2021) will also obtain forest-derived nutrition (and mercury) via those species. As such, the Juruá River expresses strong seasonal variation in food-web composition. During the low-water season, food webs are largely driven by fast-growing plankton and are constrained to oxbow lake habitats when arapaima exert top-down control on resources (Campos-Silva et al. 2021). During the high-water season, the food web drastically shifts toward a dispersed food web during floods when forest resources are channeled from the bottom up to top predators (Wantzen et al. 2002; McMeans et al. 2015; Neves et al. 2021), potentially weakening density-dependent interactions and releasing prey species from predation pressure and competitive exclusion. As such, maintaining intact forests (de Resende et al. 2019) and hydrological connectivity between the main river channel, the floodplain and the forest (Hurd et al. 2016) will ensure the long-term sustainability of vital fisheries resources in the region. Diversity (Correa et al. 2025) and productivity (Castello et al. 2019) of Amazon fisheries are intimately linked to flood pulses, and such pulses are being increasingly threatened by upstream water resource development (Forsberg et al. 2017).

We demonstrated evidence for forest resources in the diets of fishes in a tropical-rainforest floodplain, but the sources of production underpinning floodplain–forest food webs differ from those in floodplain–savanna food webs, and patterns of primary production and respiration may also differ. In savanna floodplains, high nutrients and high light availability during the flood stage trigger strong growth responses in phytoplankton (Høberg et al. 2002) and periphyton (Jackson et al. 2013; Adame et al. 2017), which can lead to their greater importance in the food web (Jardine et al. 2012, 2013; Jackson et al. 2013). Lower rates of organic-matter inputs in savanna systems likely lead to reduced respiration as well. For example, Holtgrieve et al. (2013) reported higher DO in open water versus flooded forest in the Tonle Sap floodplain. In the savanna-dominated Zambezi/Chobe floodplain, DO values were higher during high water (5.7 mg/L) versus low water (4.3 mg/L). Likewise, DO concentrations in the savanna Mitchell River floodplain averaged 5.6 mg/L (T. Jardine, unpublished data) and always exceeded 5.0 mg/L, unlike the multiple instances of hypoxia we report here. Given that rates of aquatic primary productivity in shaded headwater streams tend to be much lower than those of open-canopied mid reaches of rivers (Marzolf and Ardón 2021) and that the light environment and organic matter load both affect ecosystem metabolism, we should expect higher ratios of primary production to respiration in open-canopied floodplain systems with fewer organic-matter inputs from the surrounding catchment. This hypothesis warrants testing with a broad scale comparison among tropical biomes that takes into consideration the relative proportions of flooded forest and open canopy (Abril et al. 2014). Such an analysis would build on the results presented here and allow greater understanding of the relative importance of forest resources for both ecosystem metabolism and fisheries production.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available from the authors upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Locations of sampling sites for stable isotope analysis of food webs in the Juruá River, Amazonas, Brazil. **Table S2:** Locations, depth, turbidity, pH, conductivity, Secchi depth and dissolved oxygen concentrations for sampling sites in the Juruá River, Amazonas, Brazil. **Table S3:** Geweke and Gelman-Rubin statistics for Bayesian stable isotope mixing models of fish food webs in the Juruá River, Amazonas, Brazil. **Table S4:** Median (±95% credible intervals) source proportions for fish trophic categories in the Juruá River, Amazonas, Brazil.