



Terrestrial–aquatic trophic linkages support fish production in a tropical oligotrophic river

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Received: 14 November 2017 / Accepted: 10 February 2018 / Published online: 17 February 2018
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Abstract

Despite low in situ primary productivity, tropical oligotrophic rivers support highly diverse fish assemblages and productive fisheries. This raises the question, what energy sources support fish production in these ecosystems? We sampled fish and food resources in the floodplain of a nearly pristine, large, oligotrophic river in western Amazonia. We combined data from stomach contents and stable isotopes to test the hypothesis that floodplain forests sustain fisheries in tropical oligotrophic rivers. Analysis of stomach contents from > 800 specimens of 12 omnivorous fish species demonstrated that during the annual flood, forest plant matter dominated diets. Yet, our isotope mixing models estimated that arthropods from the forest canopy made a greater proportional contribution to fish biomass. Most of these arthropods are entirely terrestrial and, therefore, serve as trophic links between forests and fishes. Our results suggest that forest vegetation, particularly fruits, may provide much of the energy supporting metabolism and arthropods contribute significant amounts of protein for somatic growth. Moreover, the importance of terrestrial arthropods in support of fish biomass in oligotrophic rivers depends on interactions between riparian vegetation, terrestrial arthropods and flood pulse dynamics affecting accessibility of arthropods to fishes. The apparent paradox of high fish diversity in an oligotrophic river with low primary productivity may be explained, at least partially, by dynamic terrestrial–aquatic trophic linkages. This study further emphasizes the importance of seasonally flooded forests for sustaining fisheries in the Amazon.

Keywords Flood pulse · Flooded forest · Food web · Inland fisheries · Trophic subsidy

Introduction

Trophic linkages between consumers and resources in distinct food web compartments can enhance ecosystem productivity and resilience (McCann et al. 2005). The flow of terrestrial invertebrates from riparian forests, for instance,

subsidizes up to 50% of the annual energy budget of fish in temperate headwater streams, whereas emergent aquatic insects account for up to 26% of the annual energy budget of riparian birds (Baxter et al. 2005, and references therein). Although trophic linkages between terrestrial and aquatic food webs are ubiquitous in temperate and tropical streams, we are just now beginning to understand the complexity of these interactions and their influence on ecosystem processes and function (Baxter et al. 2005; Bellmore et al. 2013; Power et al. 2015).

In large river floodplain systems with natural flow regimes, terrestrial and aquatic ecosystems are temporally linked by periodic flow pulses that promote lateral connectivity. However, terrestrial contributions to aquatic food webs are strongly influenced by the duration of these connections as well as sediment and nutrient dynamics (Roach 2013). In Amazonian floodplains, soils and associated biogeochemical processes in watersheds directly influence river sediment loads, nutrient availability and primary and secondary productivity. Amazonian white-water rivers originate

Communicated by Joel Trexler.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-018-4093-7>) contains supplementary material, which is available to authorized users.

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in the Andes and transport large amounts of eroded suspended sediments (e.g., 17.6–213.9 mg l⁻¹ total suspended solids in the Solimões River) that limit light transmission and primary productivity in the river channel (Moreira-Turcq et al. 2003). In white-water systems, phytoplankton productivity is largely restricted to floodplain lakes where lentic conditions facilitate sediment deposition resulting in greater water transparency and light penetration. White-water rivers support extensive beds of diverse floating and emergent aquatic macrophytes, including *Paspalum* spp. and other grasses as well as water hyacinth (*Eichhornia* spp.) and other herbaceous wetland plants. These aquatic macrophytes tend to decompose rapidly and are important contributors to dissolved and particulate organic matter and nutrients that support phytoplankton production in the floodplain (Mortillaro et al. 2016). In the white-water Amazon River, the contribution of aquatic grasses to fish biomass appears to be relatively small, with current evidence from stable isotope analysis indicating assimilation of this production source only by a few specialized herbivorous and detritivorous species, whereas most fishes seem to assimilate material originating from other aquatic herbaceous plants, trees, and algae (phytoplankton and periphyton) (Forsberg et al. 1993; Benedito-Cecilio et al. 2000; Oliveira et al. 2006; Mortillaro et al. 2015). Grasses are more productive than most other aquatic macrophytes but also are less labile and, therefore, not as readily transferred to the upper food web (Mortillaro et al. 2016). In contrast, primary productivity is very limited in Amazonian black-water rivers that drain forested lowland areas with deep sandy soils and carry low amounts of dissolved inorganic nutrients and suspended sediments (e.g., 3.7–11 mg l⁻¹ total suspended solids in the Rio Negro; Moreira-Turcq et al. 2003). Aquatic macrophytes generally are rare or absent in tropical black-water rivers, but decomposing forest litter contributes to high concentrations of dissolved organic carbon. In particular, humic substances that leach from submerged vegetation make the water acidic and stained, which limits light penetration and algal productivity (Moreira-Turcq et al. 2003). Fish biomass in black-water rivers is low compared to that in white-water rivers, but paradoxically, these oligotrophic systems support remarkably high fish diversity (e.g., > 400 species in the Rio Negro, Brazil; Goulding et al. 1988) and sustain important fisheries (Batista and Petrere 2003; Inomata and Freitas 2015). This raises the question, what energy sources support fish production in these ecosystems?

Here, we combined dietary and stable isotope data to analyze the importance of forest subsidies to floodplain fisheries in a nearly pristine, large, oligotrophic river in Western Amazonia. We focused on medium-sized omnivorous species that are abundant and a major component of subsistence and commercial fisheries. In contrast with Amazonian white-water floodplain fisheries that are dominated by migratory

detritivorous prochilodontids and piscivorous pimelodid catfishes (Barthem and Goulding 2007; Lopes et al. 2016), floodplain fisheries in black-water rivers are dominated by omnivorous serrasalmid and cichlid species (Inomata and Freitas 2015). Omnivorous fishes also are major prey of apex predators in Amazonian floodplain systems (Carvalho et al. 2018). Therefore, identifying energy sources for omnivorous fishes is an important first step in efforts to estimate food web subsidies in these oligotrophic ecosystems. Given the low aquatic primary productivity of tropical black-water rivers, we hypothesize that food resources derived from floodplain forests are important to sustain their fisheries.

Methods

Study site

We sampled fishes and their food resources in flooded forests of the lower Apaporis River (Vaupes State, Colombia), a large (1020 km long, 49 236 km² drainage area) black-water river in Northwestern Amazonia (Botero 1999). At an elevation of 100 m.a.s.l., the lower Apaporis drains the southwestern margin of the Guyana Shield, a region characterized by white sands of Miocene origin deposited over a Precambrian basement (Hoorn 2006). The river is acidic [mean (\pm SD) pH: 5.5 \pm 0.04] and oligotrophic (conductivity: 5.5 \pm 0.9 μ S; Secchi transparency: 143 \pm 31 cm; dissolved oxygen: 4.8 \pm 1.3 mg l⁻¹), which is reflected in the absence of floating aquatic macrophytes and low phytoplankton biomass (0.04 mg l⁻¹ chlorophyll-*a*; PAT 1997). A predictable seasonal hydrological cycle driven by precipitation causes a difference of up to 9 m between annual high and low water phases (Correa 2003). We sampled fish and food resources during both flood (late May to middle October, 2009) and dry (November 2009) periods in the floodplain between the villages of Puerto Ñumi (3° 42' 29"S, 70° 34' 49"W) and Bocas de Taraira (3° 41' 78"S, 70° 35' 79"W) and in the Taraira oxbow lake (3° 41' 78"S, 70° 35' 79"W; Fig. 1). The oxbow lake remains connected to the river throughout the year. The floodplain is dominated by old-growth evergreen forest.

Data collection

We sampled adult fishes using hooks and gill nets. We euthanized specimens by applying a lethal dose of 2-phenoxyethanol (MS-222) anesthetic over the gills. Immediately after euthanasia, we collected a ~ 2 cm² sample of muscle tissue from the dorsum below the dorsal fin and removed skin and scales. We then injected each specimen with a solution of 4% formalin to preserve stomach contents and preserved voucher specimens in 10% formalin. We deposited vouchers



Fig. 1 Map of the study site in the lower Apaporis River, Colombia. White dots represent sampling sites. Satellite image was retrieved from ESRI

at the ichthyology collection of the Universidad del Tolima, Colombia. Fish nomenclature follows FishBase (Froese and Pauly 2017).

We removed contents from stomachs, discarded any ingested baits, and identified individual food items to the lowest feasible taxon using a dissecting microscope. We air dried the samples and estimated the volume of each food item by water displacement. Any highly digested and indistinguishable food items and gravel or sand particles were excluded from analyses. We classified food items into six functional categories: (1) algae (i.e., periphyton and filamentous algae), (2) grasses (i.e., emergent C_3 grasses colonizing shallow areas in the littoral zone), (3) aquatic invertebrates (i.e., insects, nematodes and crustaceans), (4) fish, (5) forest

vegetation (i.e., fruits, flowers, leaves, and bark) and (6) terrestrial arthropods (i.e., insects, spiders, centipedes and millipedes).

We collected samples for stable isotope analysis from five food resources: (1) forest plants including fruit, flowers and leaves (flood season: 31 species, $n = 83$; dry season: 7 species, $n = 12$); (2) terrestrial arthropods including insects, spiders and centipedes (sampled by swiping the vegetation with a sweep net, flood season: 7 orders, $n = 28$; dry season: $n = 0$); (3) aquatic insects (sampled from leaf litter collected with a dipnet in shallow areas; flood season: 2 orders, $n = 3$; dry season: 1 order, $n = 1$); (4) periphyton (i.e., phytomicrobenthos, sampled by scraping algae from submerged vegetation; flood season: $n = 3$; dry season: $n = 3$); (5) emergent

aquatic plants including grasses (*Scleria* sp., Cyperaceae) and ferns (*Trichomanes* sp., Hymenophyllaceae) distributed along the littoral zone of the river, and riverweeds (Podostomataceae) anchored to rock outcrops in the river channel (flood season: 1 grass species, $n = 8$; dry season: 4 species, $n = 6$). In addition, we sampled zooplankton by towing a plankton net; however, given that zooplankton abundance was very low and none of the 807 fishes analyzed consumed zooplankton, we excluded this resource from further analyses. We preserved all samples in NaCl for up to seven weeks, which has a negligible effect on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Arrington and Winemiller 2002).

In the laboratory, we rinsed samples with deionized water and soaked them for 24 h. We repeated the process twice. We dried animal and plant tissues in an oven at 60 °C for 24 and 48 h, respectively. We ground dried samples to a fine powder using a mortar and pestle for animal tissues and an electric grinder (Wing-L-Bug by Pike Technologies, 1–5 min) for plant tissues. We weighed samples to the nearest 0.01 mg and packed them into Ultra Pure tin capsules. For each season, we combined three periphyton samples to make a single sample with sufficient material for mass spectrometry analysis. Samples were analyzed for percent composition of C and N and stable isotope ratios for both C and N at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia. C and N isotope ratios are reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which represents the deviation of the sample ratio from that of Pee Dee Belemnite limestone for C, and atmospheric molecular nitrogen for N, based on the equation $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = ((\text{Ratio}_{\text{sample}}/\text{Ratio}_{\text{standard}}) - 1) \times 1000$. Precision of the isotopic analysis was $\leq 0.11\%$ measured as the standard deviation among samples of a reference material.

Data analysis

We first assessed differences in the relative contribution of foods derived from floodplain forests to fish diets using data from stomach contents. We modeled the proportional volume of food in the diet as a function of food type using mixed-effects regression (i.e., volume \sim food type + (1|species) + (1|individual identity), Bates et al. 2015). Because we were interested in assessing the contribution of allochthonous foods to the omnivorous trophic guild and not to individual species, we included species as a random factor. We also included individual identity as a random factor (i.e., individual identity nested in species) to account for the lack of independence in the residuals between food types sampled from the same individual fish. We conducted separate analysis for each season, because availability of many food resources changes according to hydrologic periods in this river (Correa and Winemiller 2014). Because our proportional data contained 0 and 1 values (i.e., interval [0,1]), it cannot be analyzed via logistic regression. Thus,

prior to the analysis we reduced proportional volumes (p) to values > 0 and < 1 via beta transformation (beta transformation = $p \times (n-1) + 0.5/n$, where n = sample size) and then logit transformed the beta-adjusted proportions (p') (logit transformation = $\log [p'/(1-p')]$) (Warton and Hui 2011), using the R package *car* (Fox and Weisberg 2011). We implemented the regression model in the R package *lme4* (Bates et al. 2015) and estimated the significance of the main effect of food type via Type II Wald Chi square test in *car* (Fox and Weisberg 2011). We followed with post hoc pairwise comparisons for food type, adjusting P values for multiple comparisons via Tukey, in the R package *lsmeans* (Lenth 2016).

Next, we estimated the relative contribution of allochthonous foods to fish biomass using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of muscle tissue. We implemented separate mixing models per species and season in the R package *MixSIAR* (3 chains; 300,000 chain length; 200,000 burn-in; 100 thin; Stock and Semmens 2016b). Although *MixSIAR* is capable of accommodating fixed and random factors, small sample sizes prevented the convergence of models that included all species. *MixSIAR* is a Bayesian mixing model that uses Markov Chain Monte Carlo methods to estimate the probability density function of the contribution of each source to consumer biomass, while accounting for variance in the isotopic signatures of consumers and sources, trophic fractionation, and source element concentration (Parnell et al. 2013).

We used different trophic discrimination factors (TDF) for plant and animal foods (Bastos et al. 2017) to account for differences in assimilation induced by variation in the protein content of foods ingested by omnivores (Kelly and Martinez del Rio 2010). For plants and periphyton, we used a TDF of 4.08 ± 0.14 for $\delta^{15}\text{N}$ and 1.75 ± 0.15 for $\delta^{13}\text{C}$ based on TDF estimated for a herbivorous fish (German and Miles 2010); for animals, we used a TDF of 1.77 ± 0.3 for $\delta^{15}\text{N}$ and 0.82 ± 0.47 for $\delta^{13}\text{C}$ based on TDF estimated for carnivorous fishes (Bastos et al. 2017).

We weighted models by source concentration to account for the broad variability in elemental concentrations between algae, plant and animal sources, which can influence estimated contributions (Phillips and Koch 2002). Lastly, our models included a process \times residual error structure to account for differences in the isotopic variance of consumers relative to food sources (Stock and Semmens 2016a). We assessed model convergence via Gelman-Rubin and Geweke tests (Stock and Semmens 2016b). Prior to analyses, we used arithmetic corrections to remove possible bias in the predicted contributions of food sources to consumers due to $\delta^{13}\text{C}$ -depleted signatures of lipids originated by fractionation during the oxidation of pyruvate to acetyl-Co-A (DeNiro and Epstein 1977). We used the equations $\delta^{13}\text{C} = -3.32 + 0.99(\text{C:N})$ and $\delta^{13}\text{C} = -5.83 + 0.14 (\% \text{C})$ to adjust $\delta^{13}\text{C}$ values of samples from consumer and animal

sources with C:N > 3.5 and plants with C > 40%, respectively (Post et al. 2007).

Results

We analyzed stomach contents and stable isotopes of 12 abundant omnivorous fish species in the Apaporis floodplain (i.e., families Bryconidae, Serrasalminidae and Triportheidae; flood season: $n = 651$ stomach samples, $n = 128$ tissue/isotope samples; dry season: $n = 156$ stomach samples, $n = 52$ tissue/isotope samples; Online Resource Table S1). Collectively, omnivorous fishes consumed allochthonous foods from floodplain forests in higher proportions than autochthonous foods, and this was the case during both flood and dry seasons (main effect of food type: Wald $X^2 = 9152$, $df = 5$, $P < 0.0001$ and Wald $X^2 = 1571.3$, $df = 5$, $P < 0.0001$; flood and dry seasons, respectively; Fig. 2, Table 1). Overall, forest vegetation and terrestrial arthropods made significantly higher volumetric contributions to fish diets than all other food types, with forest vegetation contributing a greater volume than terrestrial arthropods (Fig. 2, Online Resource Table S2).

MixSIAR models predicted that terrestrial arthropods made the greatest contribution to collective fish biomass during both the flood and dry seasons (based on mean values calculated across species of the 50% quantiles and the lower level of 95% Bayesian credible intervals; Table 2, Fig. 3). At the species level, terrestrial arthropods were estimated to make the highest contribution to 8 out of 11 species during the flood season, and to 6 out of 8 species during the dry season (Table 2). Forest vegetation and invertebrates contributed equally to the biomass of *Triportheus albus* and *T. angulatus* during the flood season. Forest vegetation was estimated to be the greatest contributor to the biomass of *Brycon amazonicus* during both seasons, and to *B. falcatus* during the dry season (Table 2).

Overall, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values across fish species were similar during the two survey periods (mean \pm SE, $\delta^{13}\text{C} = -26.09 \pm 0.09$ for flood, and -26.61 ± 0.25 for dry; $\delta^{15}\text{N} = 8.16 \pm 0.06$ for flood and 8.05 ± 0.14 for dry; Fig. 4). However, 38% of *Myloplus torquatus* and 29% of *M. schomburgkii* specimens had relatively low $\delta^{13}\text{C}$ values (i.e., -28 to -33.5‰) toward the end of the flood season and during the dry season (Fig. 4).

Discussion

In floodplains of Amazonian white-water rivers, forest coverage is positively associated with fisheries productivity (i.e., fish diversity, abundance and biomass; Lobón-Cerviá et al. 2015; Arantes et al. 2017). Our study adds further

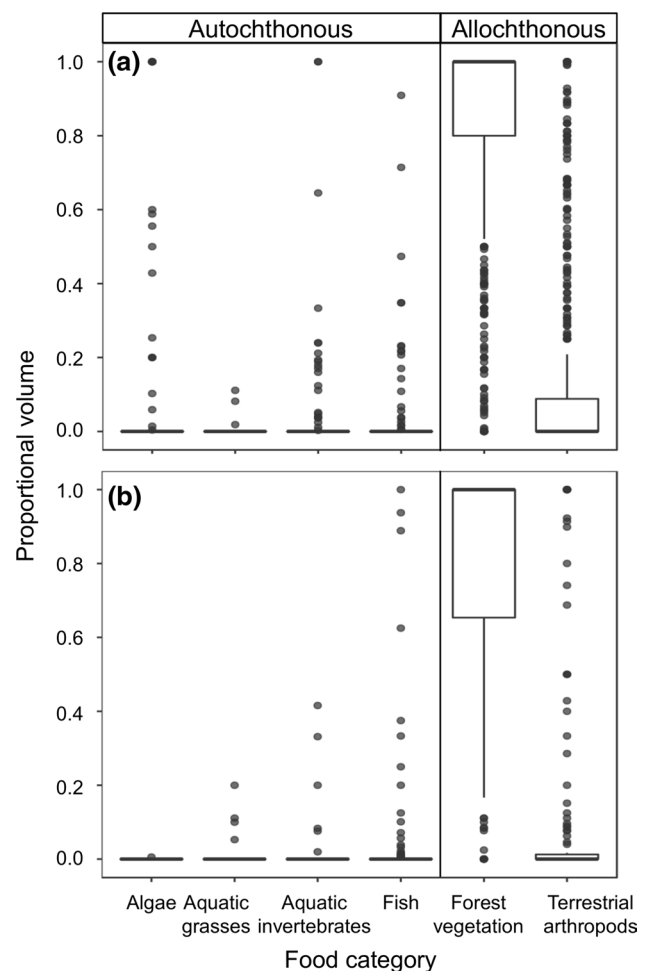


Fig. 2 Comparison of the proportional contribution of autochthonous and allochthonous foods to the diets of 12 omnivorous fish species from the Apaporis River and floodplain during the **a** flood season ($n = 651$ fishes) and **b** dry season ($n = 156$ fishes). Box lower and upper endpoints represent the 25th and 75th quartiles. The horizontal line inside each box represents median proportional volume of the food type in the diet. Whiskers represent the location of the lower and upper 25% of the data, respectively, excluding outliers, which are represented by black dots. See methods for a list of foods included in each category

evidence linking floodplain forests and fisheries productivity in Amazonian rivers by demonstrating extensive consumption and assimilation of terrestrial food resources by omnivorous fishes inhabiting a nearly pristine black-water river. These findings are timely, given that forested floodplains of the Amazon and the fisheries they sustain continue to be impacted by deforestation (Sheikh et al. 2006), proliferation of hydroelectric dams (Winemiller et al. 2016) and climate change (Resende et al. 2014; Flores et al. 2017).

Despite extensive consumption of fruits, flowers and leaves by fishes, estimates from the mixing model indicated that terrestrial arthropods contributed the largest fraction to fish biomass. Mixing model estimates indicated that

Table 1 Comparative contribution of each food category to fish diets during the flood and dry seasons

Season	Food origin	Food type	Parameter estimates	SE	df	t	P
Flood	Allochthonous	Terrestrial arthropods	− 10.57	0.18	3900	− 58.62	< 0.0001
		Autochthonous	Algae	− 13.49	0.18	3900	− 74.78
	Autochthonous	Aquatic grasses	− 13.83	0.18	3900	− 76.67	< 0.0001
		Aquatic invertebrates	− 13.60	0.18	3900	− 75.38	< 0.0001
		Fish	− 13.62	0.18	3900	− 75.53	< 0.0001
Dry	Allochthonous	Terrestrial arthropods	− 8.64	0.34	930	− 25.14	< 0.0001
		Autochthonous	Algae	− 11.02	0.34	930	− 32.07
	Autochthonous	Aquatic grasses	− 10.90	0.34	930	− 31.71	< 0.0001
		Aquatic invertebrates	− 10.82	0.34	930	− 31.48	< 0.0001
		Fish	− 10.27	0.34	930	− 29.87	< 0.0001

Slope values are relative to the food category “Forest vegetation”

Degrees of freedom were approximated with the Satterthwaite method

Table 2 Estimated proportional contribution of five food types to fish biomass during the flood and dry seasons

Season	Species	Forest plants	Terrestrial arthropods	Emergent aquatic plants	Phytoplankton	Aquatic invertebrates
Flood	All species	0.18 ± 0.12 (0.01–0.51)	0.56 ± 0.29 (0.3–0.81)	0.05 ± 0.04 (0.002–0.23)	0.11 ± 0.08 (0.005–0.36)	0.03 ± 0.03 (0.001–0.18)
	BA	0.42 (0.03–0.82)	0.11 (0.003–0.69)	0.08 (0.003–0.45)	0.18 (0.01–0.53)	0.04 (0.001–0.34)
	BF	0.07 (0.002–0.26)	0.81 (0.65–0.93)	0.02 (0.001–0.07)	0.05 (0.002–0.21)	0.01 (0–0.06)
	BM	0.04 (0.001–0.19)	0.87 (0.73–0.96)	0.01 (0–0.06)	0.04 (0.001–0.16)	0.01 (0–0.05)
	MA	0.05 (0.002–0.18)	0.86 (0.73–0.96)	0.01 (0–0.06)	0.04 (0.002–0.16)	0.01 (0–0.05)
	MR	0.11 (0.005–0.37)	0.74 (0.55–0.89)	0.02 (0.001–0.1)	0.07 (0.003–0.25)	0.01 (0.001–0.07)
	MT	0.29 (0.02–0.65)	0.22 (0.04–0.53)	0.08 (0.003–0.32)	0.28 (0.01–0.60)	0.05 (0.002–0.21)
	MSp	0.09 (0.004–0.48)	0.77 (0.27–0.92)	0.02 (0.001–0.1)	0.06 (0.003–0.27)	0.01 (0–0.08)
	PSp	0.15 (0.01–0.63)	0.66 (0.2–0.87)	0.02 (0.001–0.12)	0.09 (0.004–0.33)	0.02 (0.001–0.1)
	TC	0.21 (0.01–0.70)	0.57 (0.06–0.81)	0.03 (0.001–0.15)	0.12 (0.005–0.40)	0.02 (0.001–0.12)
	TA	0.24 (0.01–0.69)	0.28 (0.01–0.70)	0.11 (0.004–0.52)	0.14 (0.01–0.47)	0.08 (0.002–0.47)
TAn	0.26 (0.01–0.67)	0.22 (0.01–0.67)	0.12 (0.004–0.56)	0.17 (0.01–0.53)	0.08 (0.003–0.41)	
Dry	All species	0.20 ± 0.1 (0.01–0.54)	0.20 ± 0.1 (0.1–0.54)	0.13 ± 0.1 (0.005–0.53)	0.20 ± 0.05 (0.01–0.57)	0.12 ± 0.05 (0.01–0.43)
	BA	0.29 (0.01–0.74)	0.13 (0.01–0.7)	0.15 (0.004–0.72)	0.11 (0.004–0.4)	0.09 (0.004–0.33)
	BF	0.28 (0.02–0.67)	0.03 (0.003–0.33)	0.22 (0.01–0.65)	0.23 (0.01–0.6)	0.13 (0.01–0.45)
	BM	0.16 (0.01–0.49)	0.26 (0.1–0.62)	0.09 (0.003–0.44)	0.24 (0.01–0.62)	0.11 (0.005–0.43)
	MA	0.15 (0.01–0.47)	0.31 (0.13–0.67)	0.06 (0.002–0.37)	0.25 (0.01–0.64)	0.10 (0.003–0.4)
	MR	0.34 (0.01–0.73)	0.13 (0.1–0.46)	0.07 (0.002–0.66)	0.22 (0.01–0.61)	0.07 (0.002–0.27)
	MT	0.10 (0.003–0.39)	0.18 (0.1–0.34)	0.22 (0.02–0.53)	0.18 (0.01–0.54)	0.22 (0.01–0.6)
	MS	0.08 (0.003–0.29)	0.42 (0.24–0.69)	0.08 (0.003–0.31)	0.17 (0.01–0.52)	0.15 (0.01–0.47)
	PSp	0.18 (0.01–0.53)	0.16 (0.04–0.49)	0.14 (0.004–0.56)	0.24 (0.01–0.63)	0.14 (0.01–0.49)

Values represent the median and 95% Bayesian credible intervals (2.5–97.5%) per species

Values for all species represent the mean and standard deviation. Species codes follow Fig. 3

assimilation of forest arthropods was disproportionately greater than their amounts ingested based on volumetric proportions from gut contents analysis. These findings suggest that forest vegetation, particularly fruits, may provide much of the energy supporting metabolism while protein derived from arthropods is important for somatic growth (Martinez del Rio and Wolf 2005). It is possible, however,

that our mixing models underestimated the contribution of plant matter to fish biomass due to intra- and inter-specific differences in isotopic routing (Kelly and Martinez del Rio 2010; Wyatt et al. 2010). Experimental work that assesses macronutrient routing and estimates trophic discrimination factors of herbivorous and omnivorous fishes is needed to improve our ability to estimate the contribution of various

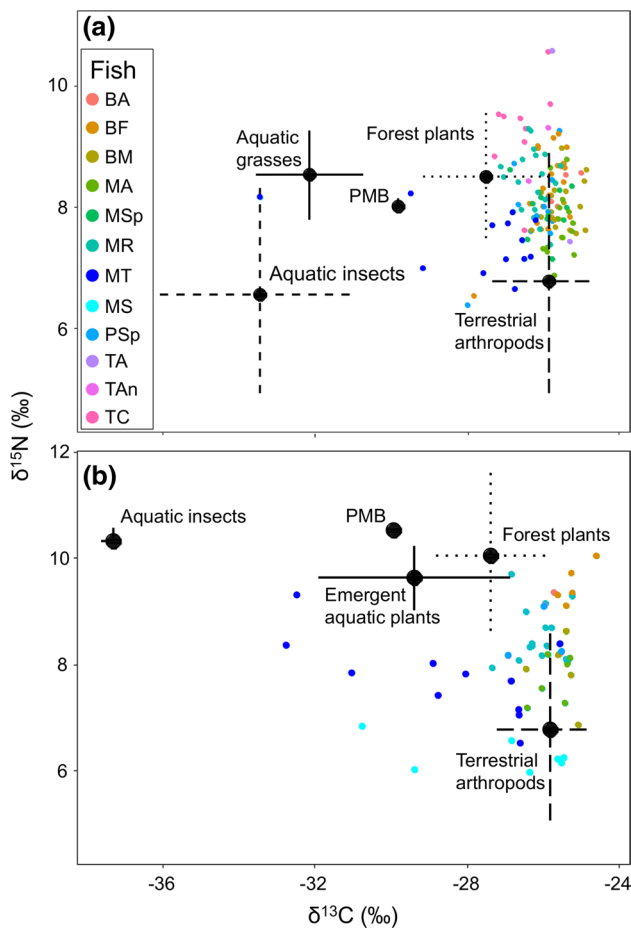


Fig. 3 Plot of C and N stable isotope ratios of 12 omnivorous fish species and five food resources from the Apaporis River and floodplain during the **a** flood season ($n = 128$ tissue samples) and **b** dry season ($n = 52$ tissue samples). Values for fishes were adjusted to account for trophic fractionation. Species abbreviations: BA—*Brycon amazonicus*, BF—*Brycon falcatus*, BM—*Brycon melanopterus*, MA—*Myloplus asterias*, MR—*Myloplus rubripinnis*, MS—*Myloplus schomburgkii*, MT—*Myloplus torquatus*, MSp—*Myloplus* sp.1, PS—*Pristobrycon* sp.1, TA—*Triportheus albus*, TAn—*Triportheus angulatus*, TC—*Triportheus culter*

food sources to consumers with broad diets (Martínez del Rio et al. 2009; Wolf et al. 2015).

The importance of terrestrial arthropods in support of fish biomass in oligotrophic systems likely derives from interactions between riparian vegetation, terrestrial arthropods and flood pulse dynamics affecting accessibility of arthropods to fishes. The floodplain of the Apaporis, like those of most large rivers west of the Rio Negro, is dominated by closed-canopy forests (Melack and Hess 2010). The massive annual flood pulse of the Amazonian lowlands (i.e., > 10 m in depth with a duration of 6–7 months) drives a vertical migration of terrestrial arthropods to the forest canopy. Because flooding limits the dispersal of non-volant species, an enormous terrestrial arthropod biomass, most of

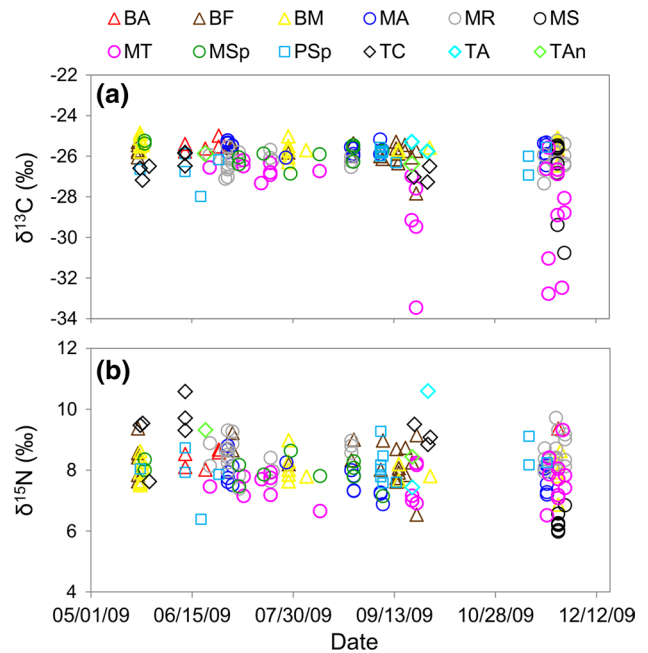


Fig. 4 Small temporal variation in isotopic signatures, **a** $\delta^{13}\text{C}$ and **b** $\delta^{15}\text{N}$, of 12 omnivorous fish species ($n = 180$ tissue samples) from the Apaporis River and floodplain. Isotopic values were not adjusted to account for trophic fractionation. Species abbreviations follow those in Fig. 3

which are herbivorous insects, becomes concentrated within the forest canopy during the flood season (Erwin 1983; Adis et al. 2010). Except for few orders (i.e., Odonata, Coleoptera, Diptera), the terrestrial arthropods that we removed from stomachs of omnivorous fishes are species that complete their lifecycles on land and, therefore, serve as trophic links between forests and fishes.

The production of aquatic arthropods in oligotrophic Amazonian rivers is limited by low aquatic primary production due to the limited availability of dissolved inorganic nutrients, particularly N (Klinge and Furch 1991; Junk and Robertson 1997; Flecker et al. 2002). Likewise, the lack of floating macrophytes, with complex root systems that in white-water systems support abundant and diverse invertebrate communities, together with anoxic conditions near the water–sediment interface in flooded forests, further limits benthic invertebrate production in oligotrophic black-water systems (Junk and Robertson 1997).

Forest vegetation and filamentous algae were identified as the main carbon sources supporting biomass of a small omnivorous fish (cardinal tetra, *Paracheirodon axelrodi*) that drives the ornamental fisheries industry of the Rio Negro, the largest black-water sub-basin in the northern Amazon (Marshall et al. 2008). Spatial variation in the contribution of these sources corresponded to selective algal feeding within interfluvial wetlands (Junk et al. 2011), where forest cover is limited and high light penetration promotes

periphyton growth (Marshall et al. 2008). In our study, low values of $\delta^{13}\text{C}$ for *Myloplus torquatus* and *M. schomburgkii* toward the end of the flood season and during the dry season (Fig. 4) may reflect greater reliance on food resources supported by periphyton or even its direct consumption, although stomach contents analysis revealed little evidence of algal consumption by these fishes.

Although we do not discount a significant contribution of benthic algae to the aquatic food web of the Apaporis River during the peak of the dry season (December–January, Correa 2003), forest resources were estimated to provide greatest support for fish biomass during our 7-month field study. This conclusion is based on the estimates of turnover rates of fish muscle ranging between 1 and 3 months (Jardine et al. 2004; Zuanon et al. 2006; Weidel et al. 2011) and the fact that $\delta^{13}\text{C}$ of fish caught at the beginning of the flood season (May), which likely reflect food consumed during the rising waters season, were similar to those of fish caught throughout the flood period and beginning of the dry season (Fig. 4). The omnivorous fishes that were the focus of the current study appear to have a strong affinity for aquatic habitats with forest cover. In a study of the Taraira oxbow lake in the lower Apaporis River during periods of falling, low and rising water levels (Correa 2008), most omnivorous fishes that had entered flooded forests during the flood period moved into lagoons and connecting channels as the water level receded. While resident in lagoons and channels, these fishes normally were observed or captured from littoral areas near dense canopy cover, lending further evidence that floodplain forests are important for fish production in the Amazon lowlands.

In temperate streams, emerging aquatic insects captured by terrestrial predators and terrestrial invertebrates that fall into the water and are consumed by fishes constitute reciprocal food web subsidies (Baxter et al. 2005). Relatively, little research has been conducted on reciprocal energy and nutrient fluxes between terrestrial and aquatic habitats in Amazonian floodplains. Large quantities of leaves and other plant matter fall into the water and accumulate on the forest floor. Forest litter submerged under acidic black waters may take twice as long to decompose as forest litter submerged in water with more neutral pH (Furch and Junk 1997; Piedade et al. 2001). Thus, consumption of forest vegetation by fishes in black-water systems may be important for nutrient recycling, especially given that shredding aquatic macroinvertebrates tend to have low abundance due to anoxic conditions at the bottom of the water column (Furch and Junk 1997). In addition, by dispersing seeds, some frugivorous fishes have the potential to influence forest dynamics (Anderson et al. 2009; Correa et al. 2015).

The apparent paradox of high fish diversity in oligotrophic systems with low primary productivity may be explained, at least partially, by terrestrial–aquatic trophic

linkages. Our study conducted in the Western Amazon indicated that, in addition to fruits and other plant matter, terrestrial arthropods constitute important trophic links between riparian forests and omnivorous fishes. Seasonal flooding enhances fish access to forest resources. The current study advances our understanding of ecological interactions in a complex and dynamic ecosystem and also reinforces the importance of considering temporal and spatial dimensions in food web research. Our results further emphasize the importance of seasonally flooded forests for sustaining fisheries in the Amazon. Fisheries management in tropical lowland rivers requires an ecosystem-based approach that takes into account the influence of hydrology and land cover on fish foraging success, fitness, and stock dynamics.

Acknowledgements We thank field assistants (J. J. Patarroyo, L. Cruz, I. López, L. Bravo, E. Tanimuka, J. J. Acevedo, B. Mejía, L. Tanimuka, A. Carevilla, and F. Yucuna) and colleagues in Colombia who provided logistic support and access to laboratory facilities (Francis and Edwin Palacios, Conservación Internacional; Santiago Duque, Universidad Nacional de Colombia, Sede Leticia; and Pablo Stevenson, Universidad de los Andes). This research was funded by the Wildlife Conservation Society's Research Fellowship Program (to SBC) and the estate of Carolyn Wierichs Kelso. We thank indigenous leaders of the Resguardo Yaigójé-Apaporis (Puerto Nñumi and Bocas de Taraira) for granting access to their territories. Research permit was granted by the Instituto Colombiano de Agricultura, Colombia. All applicable institutional and/or national guidelines for the care and use of animals were followed.

Author contribution statement SBC and KW designed the study. SBC collected data and conducted analyses. SBC and KW wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Data accessibility The data used in this publication will be archived at the Dryad Digital Repository.

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