

# **Spatial factors overcome seasonality in increasing the consumption of allochthonous food resources by fishes from tropical lotic ecosystems**

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## **Abstract**

1. In lotic ecosystems, it is expected higher availability of allochthonous food resources during floods and rainfall events, which may yield a higher consumption of these resources by consumers. However, both the allochthonous input in aquatic ecosystems and seasonality in environmental conditions are locally dependent, thus dietary responses of freshwater consumers to seasonality should also be local-dependent. Herein, we apply a meta-analytical approach to unraveling which environmental variables drive the seasonal relative consumption of allochthonous food resources by fishes from tropical lotic ecosystems.
2. We gathered 656 observations of the diet of fish populations (*i.e.*, restricted to the same sampling event) from 83 localities across the tropics during flood and drought periods (hereafter, high-water and low-water periods, respectively). For each locality, we retrieved latitude, channel width, terrestrial biomass, and elevation. Then, we applied meta-regression models using the environmental variables as fixed effects and the proportion of allochthonous food resources in the diet of each observation (%Allo) as the response variable.
3. Our models revealed that the diet of fish from tropical lotic ecosystems is mostly autochthonous independently of the hydrological period (high-water or low-water), with the predominance of aquatic invertebrates consumed. Terrestrial

biomass and elevation were revealed as the main predictors of increasing allochthony also for both high-water and low-water periods. However, we did not find any relationship between latitude and channel width with allochthony.

4. Our results highlight the importance of considering scale dependence for understanding the seasonal relative consumption of allochthonous and autochthonous food resources by fish. The little importance of seasonality when compared to spatial factors (terrestrial biomass and elevation) in increasing allochthony, is probably due to the different effects of seasonality across tropical lotic ecosystems and unseasonal rain in the tropics. Lastly, the non-relationship between channel width and allochthony may be one piece of evidence that the River Continuum Concept is better suited to temperate lotic ecosystems.
5. This study is an initial endeavor to gather fragmented information in a meta-analysis on this subject. Our results give novel insights and may serve as a new big-picture source of knowledge for future local empirical studies, improving the forecasting of the relationship between the factors underpinning the availability of allochthonous and autochthonous food resources and the diet of freshwater consumers.

### **Keywords**

Allochthony, allochthonous resource, feeding ecology, freshwater fish, seasonality, tropical lotic ecosystems

## 1 | INTRODUCTION

Food resource availability is a major determinant in the structure and dynamics of freshwater food webs by affecting consumption and assimilation patterns of organisms. For example, the increasing availability of food resources in larger lowland rivers compared to small headwater streams or during rainfall seasons (Junk et al., 1989; Vannote et al., 1980) promotes major changes in freshwater food webs. Primary changes are related to the relative importance of allochthonous food resources coming from terrestrial environments and autochthonous food resources based on the instream primary productivity. Studies in tropical freshwaters may report high amounts of allochthonous food resources in the diet of consumers under specific environmental conditions (Cardoso et al., 2017; Neves et al., 2018; Benone et al., 2020), but, still, the larger importance of autochthonous resources to the assimilation by most consumers have been pointed out (Thorp & DeLong, 2002; Neres-Lima et al., 2016; Reis et al., 2020). This contrasting evidence makes it difficult to reach to a general theory on how these systems work.

In lotic ecosystems, the seasonal variation in precipitation and river discharge promotes the increase of the water level in certain periods, called floods (Lake et al., 2006). Flood periods intersperses with periods of drought, in which the water level decreases. Rivers and streams from the tropical region are commonly affected by periodic floods (e.g. Correa & Winemiller, 2014; Peterson et al., 2017; Davis et al., 2018; Duarte et al., 2019; Liu et al., 2019a). Overall, during floods, the availability of food changes by the higher input of allochthonous resources into the water. Seeds, fruits, and terrestrial insects, turn into an abundant food resource for consumers (Goulding, 1980; Correa & Winemiller, 2014). As the aquatic habitat shrinks, allochthonous food resources become less available. Thus, during periods of drought, autochthonous food resources (aquatic invertebrates and plants) may turn into the easiest source of food to be foraged by consumers. Additionally, floods can increase turbidity, which limit in-water productivity and decreases autochthonous food availability by reducing algal biomass (Roach et al., 2014; Roach & Winemiller, 2015). Due to these changes on the relative availability of allochthonous and autochthonous food resources, we must also expect a shift in the diet of consumers between seasons. Overall, we expect that freshwater consumers display an allochthonous-based diet during floods and an autochthonous-based diet during periods of drought. However, the main mechanisms modulating the availability of food resources vary between lowland and upland lotic ecosystems (Sedell et al., 1989; Lake et al., 2006).

Lowland rivers may present marginal floodplain areas that are inundated during floods. These areas are called “River-Floodplain System” (Junk et al., 1989), characteristic of some large tropical rivers (e.g. Correa & Winemiller, 2014; Duarte et al., 2019). Inundated floodplain areas are extensive new aquatic habitats linked to the terrestrial surroundings in which consumers explore new resources for spawning, refuge, and feeding on allochthonous food that entered the water (Junk et al., 1989; Winemiller & Jepsen, 1998). On the contrary, in headwater streams, the increased input of allochthonous food resources during floods and rainfall events is mainly driven by runoff, as they lack floodplain areas (Lake et al., 2006). In these small ecosystems, the water velocity is increased carrying resources downstream (Lake et al., 2006). The increased water velocity and carrying of resources may be also enhanced by stochastic flashfloods that occur in some streams (Borga et al., 2014). In addition, the dense surrounding vegetation of narrow upland waters increases the input of allochthonous resources and decreases autochthonous primary productivity by canopy shading, conditions that tend to change along the longitudinal gradient as the channel becomes wider and terrestrial biomass less influential (Vannote et al., 1980).

Nonetheless, these features might display geographical variation. For example, some upland waters located at high latitudes and arid regions lack riparian vegetation, a feature that yields high autochthony productivity even at high altitudes (Vannote et al., 1980). The role of latitude on the relative availability of allochthonous and autochthonous food resources is by constraining the effects of climatic variables, such as temperature, radiation, and precipitation (Dodds et al., 2019). There is a trend of increasing values for these variables towards lower latitudes, so ecosystems at lower latitudes are warmer, moister, and present higher primary productivity than those located at mid or high latitudes (Gillman et al., 2015). In these ecosystems, temperature, radiation, and precipitation, by increasing terrestrial primary productivity (Yuan et al., 2021), and solely precipitation by runoff facilitation (Lisboa et al., 2015), turn into the most important local drivers of allochthonous food resources availability for consumers. During warm periods, these variables act as an enhancing factor to fruiting and vegetal development by increasing photosynthesis rates (Vitousek, 1984). Additionally, temperature and radiation may enhance the in-water primary productivity of shadeless lotic ecosystems through light incidence by both algae acceleration growth and periphyton biomass increase (Singh & Singh, 2015; Graça et al., 2018). The higher availability of autochthonous resources can enhance their importance to the diet of aquatic consumers.

Due to their intrinsic environmental spatial and temporal heterogeneity, tropical lotic ecosystems are great models to test how seasonal and spatial variations shift the availability of allochthonous and autochthonous food resources, and how it affects the diet of consumers. Studies have shown the importance of such spatial and temporal variations for tropical aquatic consumers (e.g. Baptista et al., 1998; Tomanova et al., 2007; Correa & Winemiller, 2014; Davis et al., 2018; Benone et al., 2020), but since seasonality in environmental conditions are locally dependent, so might be the response of consumers to these variations. To our knowledge, no effort has yet been made to synthesize local environmental determinants of the seasonal relative consumption of these food resources by consumers from tropical lotic ecosystems in a large-scale approach. Within this topic, freshwater fishes are a great group to test such ecological forecasts as they tend to shift their diet to cope with seasonal and spatial variations due to their high trophic plasticity (Abelha et al., 2001; Mortillaro et al., 2015). Additionally, the use of gut contents of fish in feeding ecology and food web studies is especially advantageous for some reasons. First, fishes can exert many trophic positions in a food web, from the bottom as prey to top predators. Second, they can easily be sampled in high numbers. Third, the methodological approaches for their gut content analyses are accessible and of simple identification, as most swallow their prey whole and have a well-defined stomach (Amundsen & Sánchez-Hernández, 2019). Lastly, gut content analyses are great to picture the moment as they highlight recent, not past, trophic relationships.

We herein conducted a meta-analysis to identify local spatial environmental determinants of the seasonal relative consumption of allochthonous and autochthonous food resources by fishes from tropical lotic ecosystems. The increased input of allochthonous food resources during periods of rainfall and flood events may yield a higher consumption of these resources by fishes. However, the allochthony increase in the diet of fish may be also local-dependent. Thus, we expect that: (i) overall, there is a higher consumption of allochthonous food resources during periods of flood than during periods of drought; (ii) allochthony increases towards lower latitudes due to the climatic conditions near the Equator that enhance terrestrial primary productivity, such as high temperature, radiation, and precipitation; and (iii) allochthony is higher in lotic ecosystems located at high elevation, with narrow channel width, and high terrestrial biomass. In the latter, these relationships will be more pronounced during periods of flood.

## 2 | MATERIAL & METHODS

### 2.1 | Studies selection and diet data extraction

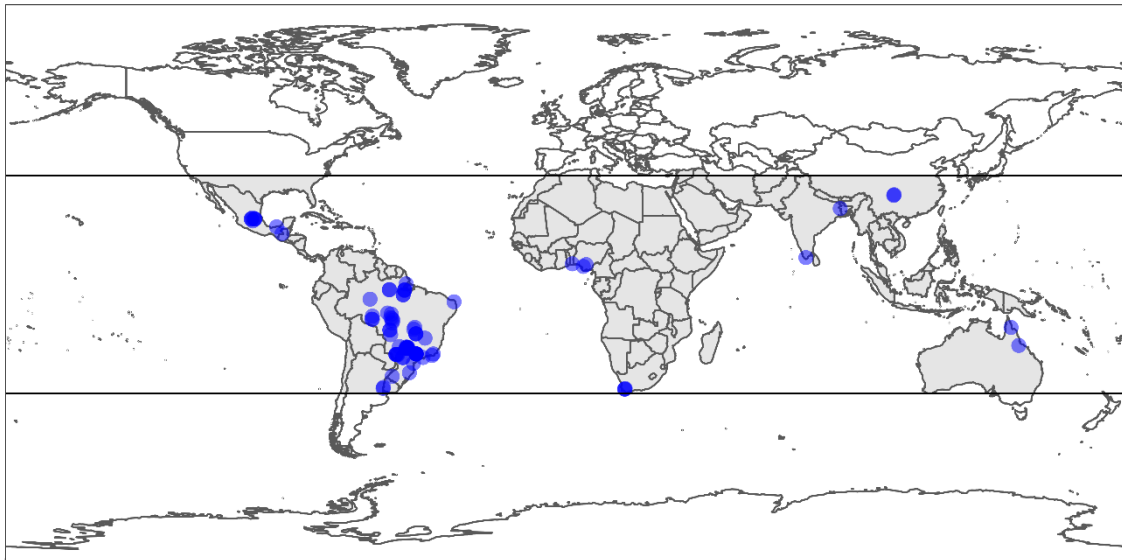
We conducted an extensive search in the literature for articles published until 2022 using the Scopus database (Figure S1). We used the following keywords in the literature search: (Fish\*) AND (River\* or Stream\*) AND (Diet or Feeding). Our search returned a total of 11,444 articles. In this search, we included only articles written in English, Spanish, and Portuguese. The two latter were included because of the high number of studies locally published in the Neotropical region. Our first step was to select only articles with stomach content analysis of fish in natural environments, which resulted in 1,651 studies. During this phase, we also added 36 articles from other sources (e.g., references and Scielo database).

Then, we selected relevant studies by the following eligibility criteria: (i) studies conducted only in lotic ecosystems of the tropical or subtropical regions; (ii) studies conducted either at only one or several months, well-defined seasons of the year (e.g. winter, summer), and/or hydrological periods (e.g. wet, dry). When conducted throughout several periods, we included only those reporting diet data separately for each period; (iii) studies that reported the number of stomachs analyzed; and (iv) preferably studies with well-defined origin and types of resources. In this latter step, some studies did not report the origin of the resources, so we used our own criteria. After checking the eligibility of the studies, we extracted data from 49 articles (Table S1).

We extracted the data about fishes' diet from tables, images, and text presented in the articles. Data presented in images were extracted through the software GetData Graph Digitizer (version 2.26.0.20). We extracted many different diet descriptors, such as proportional measurements (volume, dominance, relative abundance and weight) and indices. The most common index was the Alimentary Index ( $IA_i$ ; Kawakami and Vazzoler, 1980). Both proportional measurements and indices were utilized, but we prioritized indices because they provide a more accurate description of diet. Therefore, when studies did not report indices but reported any proportional measurements and the frequency of occurrence of the items, we calculated the  $IA_i$ :  $IA_i = FO \times V / \sum (FO \times V) \times 100$ ; whereas  $FO$  = frequency of occurrence (%) of each item and  $V$  = volume (%) of each item.

We had observations as sample units. We considered each observation as one population, i.e., individuals of a single species sampled during a given period, such as month(s), season(s), or hydrological period(s) of one or several years (studies with

replicates). Individuals from different size classes or ontogenetic stages (juveniles and adults) were considered as different observations because most fish species consume different types of food in different stages of its lifetime. In the end, we gathered a total of 656 observations within 323 fish species from 83 localities across the tropics, with the Neotropical region comprising most records (Figure 1).



**FIGURE 1** Map of the 83 localities considered in this study. Lines are tropical region limits, crossed in 35°N and 35°S. We use point opacity ( $\alpha = 0.5$ ) to highlight the overlap among localities.

The selected studies used their own criteria to identify the food items. We standardized the identification of food items in broad categories (e.g., algae, aquatic insect, terrestrial invertebrate). From this information, we classified trophic guilds and categorized the origin of the food items (allochthonous or autochthonous) for the studies that did not report it. Strictly detritivorous and piscivorous were removed for further analyses ( $n = 30$ ) because they consume exclusively autochthonous items.

For comparison purposes, we standardized the seasonality of each study to two hydrological periods: high-water and low-water (hereafter HW and LW, respectively). For this, we used the hydrological period (e.g. dry, rainy, wet) stated in the article for each locality. For example: dry and drought was assigned as low-water periods, and rainy and wet as high-water periods. We also used local climatic variables retrieved from worldwide databases as a guidance to standardize the hydrological periods (Figure S2). These variables were utilized especially for those studies that did not mention any

hydrological period, and the only information we had were seasons (e.g. summer, winter) or months. Of the total 656 observations, HW periods comprised 246 observations, whereas LW periods comprised 410.

## **2.2 | Geographical and environmental variables**

We extracted the latitude and channel width for each sampling site from the studies. Latitude was utilized as a constraint factor of climatic variables. When the channel width of the sampling site was not reported in the study, we manually estimated it on Google Earth. Additionally, we retrieved terrestrial biomass and elevation from worldwide databases to use as moderators in our models aside from latitude and channel width. To avoid many zeros for terrestrial biomass, we used a buffer size equal to 25% of the channel width of each sampling site. The retrieved values were the mean within the buffer area. Terrestrial biomass was utilized as a proxy for terrestrial vegetation cover and litter input (Goetz & Dubaya, 2014, Spadoni et al., 2020), and it represents the remotely sensed land-cover biomass (woody, grassland, and cropland) measured in 2010 at a 300-m spatial resolution (Spawn & Gibbs, 2020). Elevation was retrieved from WorldClim 2.1 at a 30-s grain size (Fick & Hijmans, 2017).

## **2.3 | Effect size and data analysis**

We used as an effect size the proportion of allochthonous resources in the diet of each observation (hereafter, %Allo). This is a proportion metric; so %Allo plus %Auto is the full diet of each observation. We opted to use %Allo as the main effect size for the sake of simplicity, as our hypotheses were based on premises of increasing availability of allochthonous food resources for consumers. Meta-regression models with weighted mixed effects were utilized to test our predictions. The %Allo was our response variable, while the localities were our random factor. Here, we assumed that the variance associated with each observation was inversely related to the number of stomachs analyzed ( $1/n$ ), once we could not calculate the variance of the %Allo. Fixed effects were latitude, channel width, terrestrial biomass, and elevation. We tested the degree of correlation between pairs of variables to avoid possible redundancy among variables, and no high correlation ( $r \geq 0.8$ ) was found. The selection of the best-fit set of explanatory variables of each model was made by running different sets of combinations for each hydrological period separately (HW and LW) and comparing their Akaike's Information Criterion (AIC). The selected models of each hydrological period comprised those with the

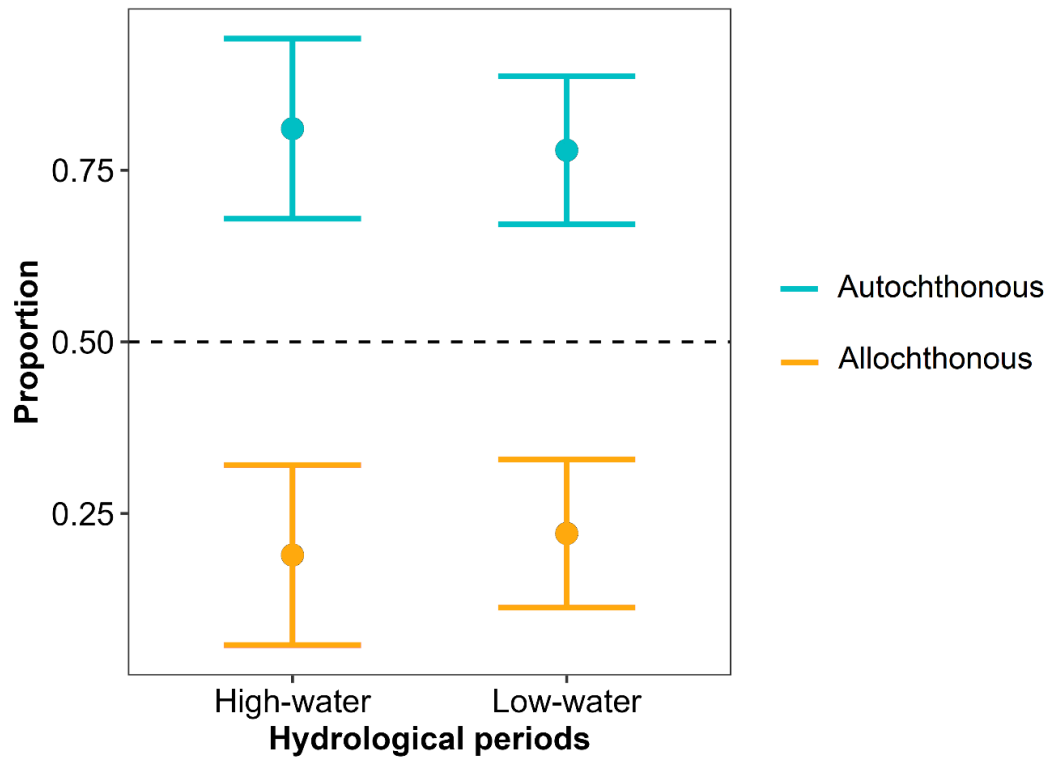


minimum AIC plus two AIC units. The effects of each model were evaluated by the heterogeneity from the model ( $Q_M$ ) and the unexplained heterogeneity ( $Q_E$ ). An adequate model has a significant  $Q_M$ , and a significant  $Q_E$  indicates high residual heterogeneity within the model. Weighted mixed-effects models were performed using the `rma.mv` function of the *metafor* package (Viechtbauer, 2010) in the R environment (version 4.0.5). Our analyses followed the same procedure as Leal et al. (2023).

### 3 | RESULTS

Allochthonous food resources were minor components in the diet of fishes from tropical lotic ecosystems (Figure 2). For both hydrological periods (HW and LW), the diet of fishes was composed mostly of autochthonous food resources (Figure 2), dominated by aquatic invertebrates (Figure S3). We did not verify any significant difference in the proportion of allochthonous resources between HW and LW hydrological periods. But, on average, the proportion of allochthonous resources in the diet of fishes was higher in LW than in the HW period (Figure 2).

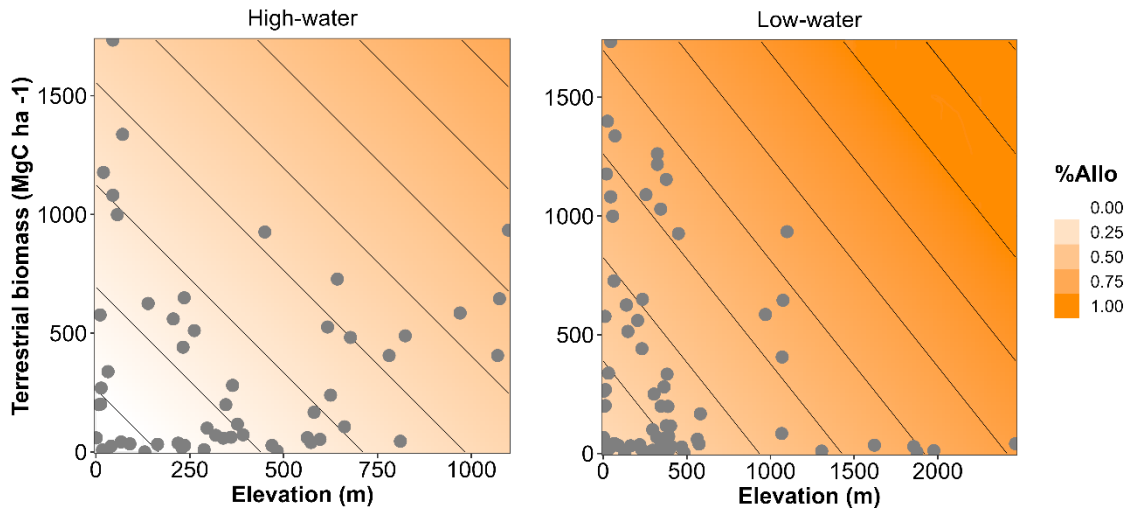
Our models revealed that terrestrial biomass and elevation were the main drivers of allochthony in the diet of fishes, independently of the hydrological period. Terrestrial biomass and elevation were the only significant variables in the best-fit models (Table 1; Figure 3). In HW periods, the %Allo increased as the elevation and terrestrial biomass increased (estimate<sub>elevation</sub> = 0.0004, CI 95% [0.0001, 0.0006], p-value = 0.0082; estimate<sub>terrestrial biomass</sub> = 0.0002, CI 95% [0.0000, 0.0004], p-value 0.0281). We also observed the same pattern for LW periods (estimate<sub>terrestrial biomass</sub> = 0.0002, CI 95% [0.0001, 0.0004], p-value = 0.0059; estimate<sub>elevation</sub> = 0.0002, CI 95% [0.0001, 0.0003], p-value = 0.0065).



**FIGURE 2** Proportion and the confidence intervals (95%) of autochthonous and allochthonous food resources consumed by fish from tropical lotic ecosystems during high-water and low-water periods. The dashed horizontal line indicates no responses (50% autochthonous and 50% allochthonous).

**TABLE 1** Best-fit meta-regression models of the % Allo in the diet of fishes during high-water (246 observations) and low-water (410 observations) ordered by the Akaike's information criteria (AIC). We also show the between study variance (BSV), the residual heterogeneity ( $Q_E$ ) and model heterogeneity ( $Q_M$ ). Asterisk (\*) means significance ( $p < 0.05$ ) of the variable within the model.

<b>Models</b>	<b>BSV</b>	<b><math>Q_E</math> (p-value)</b>	<b><math>Q_M</math> (p-value)</b>	<b>AIC</b>
<b>%Allo during High-water ~</b>				
Elevation* + Terrestrial biomass*	0.062	652.719 (< 0.0001)	11.805 (0.0027)	137.743
Elevation* + Terrestrial biomass* + Channel width	0.060	650.578 (< 0.0001)	13.430 (0.0038)	138.447
Elevation* + Terrestrial biomass + Latitude	0.061	622.873 (< 0.0001)	12.110 (0.0070)	139.557
<b>%Allo during Low-water ~</b>				
Terrestrial biomass* + Elevation*	0.066	1475.280 (< 0.0001)	12.316 (0.0021)	378.065
Terrestrial biomass* + Elevation* + Latitude	0.066	1474.269 (< 0.0001)	12.661 (0.0054)	379.756
Terrestrial biomass* + Elevation* + Channel width	0.066	1448.745 (< 0.0001)	12.318 (0.0064)	380.064



**FIGURE 3** The interplay between terrestrial biomass and elevation in increasing the %Allo in the diet of fish during each hydrological period. Grey circles are localities.

#### 4 | DISCUSSION

Here we unraveled the seasonal variation in the relative importance of allochthonous and autochthonous food resources in the diet of fishes from tropical lotic ecosystems. Our results are two-fold. First, we found that, overall, autochthonous-based diet prevails among fishes independently of the hydrological period: high-waters (HW) and low-waters (LW) periods, mostly because of the high consumption of aquatic invertebrates across the tropics. Second, the allochthony in the diet of fishes is mainly determined by terrestrial biomass and elevation for both hydrological periods. We found that as terrestrial biomass and elevation increase, the consumption of allochthonous food resources increases. Thus, in this study, we give novel insights into common predictions concerning the seasonal consumption of these two types of food resources by fishes of rivers and streams across the tropics. Contrary to what is historically predicted, we did not find higher consumption of allochthonous food resources during HW periods than during LW periods. And, although we did not find any relationship between channel width and allochthony, we also discuss how spatial local factors (terrestrial biomass and elevation) overcome seasonality in increasing the consumption of allochthonous food resources by fish.

The higher consumption of allochthonous food resources during HW periods is a common expectation. For instance, the Flood Pulse Concept (Junk et al., 1989) postulates that the periodic lateral exchange of nutrients in the high-water period is the major force controlling biota in large rivers. We did not confirm this prediction as we found that,

overall, fishes from tropical lotic ecosystems have an autochthonous-based diet independently of seasons. In fact, we argue that the support for this prediction depends heavily on the local characteristics of the sampling sites, the taxonomic resolution, and the trophic guild composition included in studies. If we consider the population level of an omnivorous-insectivorous stream fish species, individuals indeed may consume higher amounts of allochthonous food resources during HW periods, but still presenting autochthonous-based diet in some streams (Benone et al., 2020). When dealing with herbivorous inhabiting flood-plain systems, then individuals will consume more allochthonous food resources during floods (Correa & Winemiller, 2014). Conversely, studies comprising large fish assemblages, regardless of trophic guild composition, found that allochthonous food resources contributed relatively little to the assemblages' diet, with the predominance of aquatic invertebrates being consumed across every season (Bonato et al., 2012; Dary et al., 2017; Peterson et al., 2017). This particular result enlightens us about the scale-dependence on this matter (Hewitt et al., 2017; Evangelista et al., 2019): the importance of autochthonous resources to the diet of fish increases with large-scale studies. Although we found the higher consumption of autochthonous food in this large-scale approach, small-scale studies often support the higher consumption of allochthonous food during HW periods depending on the environment, species, and trophic guild composition studied.

We found that terrestrial biomass and elevation were the main drivers of allochthony for both hydrological periods. According to the River Continuum Concept (RCC; Vannote et al., 1980), upland streams tend to present dense riparian vegetation, which facilitates the input of terrestrial resources. However, the processes behind the interplay between these two factors in increasing allochthony shall be different among hydrological periods, as each period feature different environmental conditions. During HW periods, our finding is probably mainly due to the interplay between floods and rainfall on the lateral and vertical input pathways (Lisboa et al., 2015). The high rate of the lateral input pathway of allochthonous resources is mainly related to high bank slope and steepness, and the vertical input pathway depends on the density of the canopy cover (Kochi et al., 2010; Hart et al., 2013; Lisboa et al., 2015). Steep banks and dense canopy cover are common features in upland waters (Dodds et al., 2019), converging with our finding. Thus, allochthonous food resources input is facilitated by rain-induced runoff and floods through these pathways, increasing their availability to be consumed by fishes.

As for LW periods, the lateral pathway is still important for at least litter input in tropical streams. The lateral input pathway for litter is higher in localities with more pronounced and frequent drought, as dry litter seem to be more easily transported to the aquatic ecosystem (Tonin et al., 2017). Also, higher litter input through the vertical pathway during the driest months of tropical forests worldwide has been reported, which might be related to the water stress release of leaves during these periods (Zhang et al., 2014; Tonin et al., 2017). We also may point out the importance of benthic stocks of organic matter to fishes (i.e. allochthonous organic matter retained by the riverbed) on the relationship between elevation and terrestrial biomass for LW periods. Floods, rainfall, and increased water discharge generate high stress in upland waters (Lake et al., 2006). Thus, during HW periods, we argue that the input occurs at a high rate, but the food resources are promptly consumed by the fishes because the benthic stocks of organic matter of upland waters are carried downstream, reducing their availability for upstream consumers. On the other hand, during LW periods, due to the lack of intensity of floods or water discharges, the input of allochthonous food resources occurs at a low rate, but it accumulates on the bottom and turns into a standing benthic stock available for consumers locally (Graça et al., 2015; Tonin et al., 2017).

Although we found terrestrial biomass and elevation as the main drivers of allochthony, we did not find any relationship between channel width and allochthony. This could be one piece of evidence that the RCC assumptions are not fully applicable to the tropical region. Many other ecosystem features of tropical rivers and streams compared to their temperate counterparts are different. Aside from climate and hydrology, tropical and temperate lotic ecosystems differ in their geological history and geomorphology features, which lead to differences in organic matter dynamics (Boulton et al., 2008). In fact, within our selected studies, channel width and elevation were barely correlated, thus many sampling sites considered here do not follow the predicted longitudinal model stated in the RCC. Another variable that was not revealed as a predictor in our models was latitude. The selected region for our study (tropical and subtropical regions, ranging from  $-35^{\circ}$  to  $35^{\circ}$ ) may be not sufficient to find any pattern. A global approach of this matter may reveal strong patterns between tropical and temperate lotic ecosystems.

Our models revealed that spatial variables overcome seasonality in increasing the consumption of allochthonous food resources by fish. Two main factors might underpin the little importance of seasonality in determining prey source for these fishes. The first

would be the variety of lotic ecosystems with differences in seasonality across the tropics. For instance, mid-latitude large rivers considered are characterized by quick and intense floods that wash out resources (Davis et al., 2018; Liu et al., 2019a, 2019b), which differs from those at lower latitudes, such as lowland rivers of the Amazon basin (Correa & Winemiller, Duarte et al., 2019), in which species trophic dynamics rely on large, gradual, and long-lasting floods (Winemiller et al., 2014). The second would be that the tropics are constantly exposed to unseasonal rain, even more nowadays with climate change increasing the frequency and intensity of precipitation and floods (Eccles et al., 2019). Thus, this might be hiding any potential seasonal effect in our models. We argue that the nutrients exchange in the aquatic-terrestrial transition zone is idiosyncratic, depending on the intrinsic characteristics of each lotic ecosystem. But, overall, here we show that seasonality is little important to the input of allochthonous resources and their consumption by fish across the tropics.

We consider that there are three caveats in our meta-analysis. First, we did not measure channel width during different hydrological periods because this data was not available. Thus, width values were treated as equal in both HW and LW periods. Instead, for comparison between localities, we assumed that the seasonal variability in width due to the formation of floodplain systems or general inundations of marginal areas would be proportional to the ecosystems' channel width. We are aware of this drawback, as the extent to which floodplain system remain available for freshwater consumers, as well as its magnitude, dictate the contribution of allochthonous nutrients to freshwater food webs (Jardine et al., 2012). So, we encourage future studies to relate the duration and magnitude of floods in floodplain systems with the increase in the allochthony in the diet of fishes. Second, we must highlight again the differences in taxonomic and/or trophic guild resolution of fish assemblages among studies that certainly have an important role in the patterns herein observed. But here we sought to understand the big picture concerning the role of the main features of lotic ecosystems that might determine the allochthony in the diet of tropical fishes. That said, future studies may consider finer resolutions. Third, the residual heterogeneity in our models was high. High heterogeneity in ecological syntheses is common due to the intrinsic nature of each biological system or species (Senior et al., 2016). In our case, we deal with the diet of fish populations from different locations across the tropics, and it's very likely that the effect size of each population comes with variations.

Despite these limitations we can draw important conclusions from our results. Overall, contrary to what we expected, the diet of fishes from tropical lotic ecosystems are predominantly autochthonous, and we addressed this particular result to the large-scale approach of our synthesis. We also found that increasing terrestrial biomass and elevation increased the allochthony in the diet of fish. This observed pattern was expected as our hypotheses were based on the RCC assumptions. Conversely, no relationship between channel width and allochthony was found. The lack of this relationship is a new piece of evidence that the RCC predictions are better suited to temperate rivers and streams. Lastly, we found that seasonality is less important than spatial factors in increasing allochthony in the diet of fish. We argue that the unseasonal rain enhanced by climate change on lotic ecosystems across the tropics might be one factor that hide potential seasonal effects. Our study is an initial endeavor to understand how lotic ecosystem features determine the allochthony in the diet of fish through an integrative and meta-analytical approach. Overall, our findings may serve as a basis for further studies by giving novel and important insights into widespread predictions about the seasonal relative consumption of allochthonous and autochthonous food resources by fish from tropical lotic ecosystems.

#### **AUTHOR CONTRIBUTIONS**

Conceptualization: VMBF, BES, JSL, MPA. Developing methods: VMBF, BES, JSL, MPA. Conducting the research: VMBF. Data analysis: VMBF, BES. Data interpretation: VMBF, BES, JSL. Preparation of figures & tables: VMBF. Writing: VMBF, BES, JSL, MPA.

#### **ACKNOWLEDGEMENTS**

We are grateful to the Programa de Pós-Graduação em Ecologia of the Universidade Federal do Rio de Janeiro (PPGE – UFRJ), and to J. L. Nessimian, A. P. F. Pires, and L. Casatti for participating on VMBF appraisal committee.

#### **FUNDING INFORMATION**

VMBF is grateful to Conselho de Aperfeiçoamento de Pessoal de Nível Superior (CAPES; finance code: 001).



## DATA AVAILABILITY STATEMENT

The dataset will be available in an open repository upon acceptance.

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