

# Allochthonous and autochthonous carbon flows in food webs of tropical forest streams

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## Abstract

1. The River Continuum Concept (RCC) assumes that autochthonous primary production in forest streams is limited by light and is insufficient to sustain secondary production by consumers; they must therefore depend on allochthonous carbon from the surrounding forest. Recent studies have, however, questioned the importance of allochthonous carbon in stream food webs. There is a growing body of evidence using stable-isotope techniques that demonstrate the importance of algae (autochthonous production) in the food webs of tropical streams.
2. The actual contributions of autochthonous and allochthonous resources are rarely evaluated accurately because few studies consider the diet and the trophic efficiencies of the components of the food web or measure primary and secondary production to estimate the energy flow.
3. We estimated the annual net primary productivity of periphytic microalgae (NPP) and the secondary production of macroinvertebrates (SP) from empirical models and we used stable isotopes of carbon and nitrogen to quantify the flow of material in food webs of five forest streams in the Guapi-Macacu catchment, Rio de Janeiro, Brazil.
4. NPP ranged from 46 g to 173 g dry mass (DM) m<sup>-2</sup>, whereas SP ranged from 0.90 g DM m<sup>-2</sup> to 2.58 g DM m<sup>-2</sup>. The contribution of allochthonous carbon to the SP was more important than autochthonous sources and varied from 56% to 74% of all basal energy flow assimilated by primary consumers. The annual ingestion rate of basal sources varied from 8.08 g DM m<sup>-2</sup> to 26.57 g DM m<sup>-2</sup>, with the allochthonous material contributing 76% and 87% of this. The annual ingestion rate of autochthonous material varied from 1.2% to 5.5% of the NPP.
5. The present work suggests that the principal energy source for macroinvertebrates in streams of the Guapi-Macacu catchment came from the riparian forest, as predicted by the RCC. However, this dependence appeared not to be driven by an absolute lack of autochthonous NPP, which seemed more than sufficient to sustain the entirety of macroinvertebrate SP.

## KEYWORDS

benthos, ecosystem, primary production, secondary production, stable isotopes

## 1 | INTRODUCTION

Food webs in running waters are based upon in-stream autochthonous sources, and may also be partially or almost totally sustained by allochthonous material that is derived from the surrounding terrestrial landscape. The River Continuum Concept (RCC, Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), developed in North America, assumes that headwater streams (first to third order) are influenced strongly by riparian vegetation which reduces autotrophic production by shading and contributes large inputs of allochthonous detritus such as leaf litter. Consequently, we expect relatively more assimilation and ingestion of allochthonous rather than autochthonous energy sources by primary consumers in such streams. However, studies in larger rivers have questioned the importance of this terrestrial carbon for in-stream food webs (Forsberg, Araujo-Lima, Martinelli, Victoria, & Bonassi, 1993; Hamilton, Lewis, & Sippel, 1992; Thorp & Delong, 2002). The Riverine Productivity Model (RPM, Thorp & Delong, 2002) emphasises the importance of the microalgae as the main source of carbon that sustains the animal production, as well as the significance of the microbial loop that processes the majority of the – principally allochthonous – transported material. In addition, there is a growing body of evidence using stable-isotope techniques showing that the importance of algae to the food web of tropical streams (e.g. Hong Kong: Salas & Dudgeon, 2001; Mantel, Salas, & Dudgeon, 2004; Li & Dudgeon, 2008; Lau, Leung, & Dudgeon, 2009; Puerto Rico: March & Pringle, 2003; Australia: Douglas, Bunn, & Davies, 2005; Brazil: Brito, Moulton, Souza, & Bunn, 2006; Neres-Lima et al., 2016).

Stable-isotope analysis can be used to elucidate food-web architecture and dynamics in streams (Hershey & Peterson, 1996; Peterson & Fry, 1987), as long as basal sources have distinct signatures (Boon & Bunn, 1994). The carbon signature for terrestrial C3 plants tends to be c.  $-28\text{‰}$  (Peterson & Fry, 1987). On the other hand, algal signatures can be more variable (ranging from  $-16\text{‰}$  to  $-49\text{‰}$ ), depending on habitat, primary productivity, drainage-basin area, seasonality as well as origin and signature of the sources of inorganic carbon assimilated (Boon & Bunn, 1994; Finlay, 2004; Hadwen et al., 2010; Ishikawa, Doi, & Finlay, 2012; MacLeod & Barton, 1998; Peterson & Fry, 1987; Rosenfeld & Roff, 1992). Nitrogen isotopes can indicate trophic position as there is an increase between  $2\text{‰}$  and  $5\text{‰}$  in nitrogen signature of the consumers in relation to their food source (McCutchan, Lewis, Kendall, & McGrath, 2003; Minagawa & Wada, 1984; Post, 2002; Vander Zanden & Rasmussen, 2001; Vanderklift & Ponsard, 2003). Carbon isotopes are indicative of what consumers assimilate over time (Hershey & Peterson, 1996) as there is either no isotopic shift for carbon upon assimilation, or there is a small increase (usually between  $0.3\text{‰}$  and  $1.5\text{‰}$ ) in  $\delta^{13}\text{C}$  from one trophic level to the next (DeNiro & Epstein, 1978; McCutchan et al., 2003; Post, 2002; Vander Zanden & Rasmussen, 2001). Multiple-source mixing models, using data from both elements, can provide estimates of the proportion of different food sources assimilated by consumers (Parnell & Jackson, 2010).

Thus far, few studies have been directed towards verifying whether autochthonous production is sufficient to sustain the secondary production of small streams, or to quantify the flows of allochthonous and autochthonous material through the food webs of forest streams (but see Hall, Wallace, & Eggert, 2000; Lewis, Hamilton, Rodríguez, Saunders, & Lasi, 2001; Whiting, Ehiles, & Stone, 2011). Most of the studies of food webs in streams describe the connective web (qualitative gut content information), or the diet and assimilation web (*sensu* Benke, 2011) that indicates – usually using stable-isotope data – the proportion of each food that is assimilated and hence its contribution to secondary production. Both the connective and assimilation webs are quantitative analyses that reflect dietary or assimilation preferences of each consumer taxon, but do not reflect differences in absolute ingestion or assimilation rates. Neither alone is sufficient to determine the flow of autochthonous or allochthonous material in the food web. Thorp and Delong (2002) consider that a better approach is to (1) measure actual amounts of allochthonous and autochthonous carbon available per unit area and time in the river; (2) calculate assimilation efficiencies for recalcitrant or labile carbon by all major taxa; (3) measure secondary production for the majority secondary consumers and (4) determine trophic pathways for an ecosystem.

We estimated the annual net primary productivity of periphytic microalgae (NPP) and the secondary production of macroinvertebrates (SP) from empirical models (Morin & Bourassa, 1992; Morin, Lamoureux, & Busnarda, 1999) based on observed biomass and water temperature. We used stable isotopes of carbon and nitrogen to quantify the proportions of food sources assimilated by the main macroinvertebrate taxa. We combined these data with trophic efficiencies derived from the literature to quantify the flow of carbon through the food webs of five forested streams in the Guapi-Macacu catchment, Rio de Janeiro, Brazil. Our overall goal was to apply the general food-web modelling framework proposed by Thorp and Delong (2002) to enhance our understanding of the relative importance of allochthonous and autochthonous food sources to food webs in tropical forest streams.

## 2 | METHODS

### 2.1 | Study area

We collected samples of leaves, periphyton, macroinvertebrates, fishes and tadpoles in five forested streams of the Guapi-Macacu catchment, Rio de Janeiro, Brazil ( $22^{\circ}41'$  to  $22^{\circ}14'S$  and  $43^{\circ}01'$  to  $42^{\circ}31'W$ ). One site is in a first-order stream (FRC18), two are second-order (FRC02 and FRC16) and the other two third-order (FRC14 and FRC15). These streams are in a well-preserved dense Atlantic rainforest in the State Park of Três Picos. Closed forest covers more than 90% of the catchment. The catchment area, base flow, pH, conductivity, temperature, canopy cover and wetted width of each site were measured (Table 1). The variables conductivity, pH, dissolved oxygen and temperature were measured *in situ* with a Hydrolab multi-parameter probe (model MS5, Hach Environmental,

**TABLE 1** Characteristics of the sample sites

Characteristics	Sites				
	FRC18	FRC16	FRC02	FRC14	FRC15
Stream order	1st	2nd	2nd	3rd	3rd
Catchment area (km <sup>2</sup> )	0.7	1.5	2.1	6.5	11.0
Forested catchment area upstream (%)	100.0	98.7	96.0	99.6	90.9
Altitude (m a.s.l.)	337	822	325	520	354
Wetted width (m)	8.1	3.9	9.3	9.1	8.5
Depth (cm)	47.4	16.8	27.4	28.3	46.9
Canopy cover (% canopy)	84.0	86.0	77.0	77.0	59.0
Discharge (L per s)	27.9	65.4	95.3	157.5	–
Temperature (°C)	21.6	19.0	20.3	20.8	23.1
Dissolved oxygen (mg/L)	7.1	7.4	7.6	7.4	7.3
pH	7.0	7.1	6.9	7.2	7.2
Conductivity (μS/cm)	20.7	17.2	17.0	19.0	18.8
Total alkalinity (mg/L CaCO <sub>3</sub> )	24.7	37.0	22.6	30.8	32.9
Benthic chlorophyll <i>a</i> (mg Chl <i>a</i> m <sup>-2</sup> )	25.8	5.9	5.6	19.5	23.0

Loveland, Colorado). We measured the canopy cover using a spherical densiometer Model-C (Forest Densimeters, Oklahoma) in ten transects evenly spaced along a 100–120 m reach, at thalweg. We averaged four readings facing north, south, east and west for each measurement. Discharge was measured with inert solute releases, i.e. tracer-dilution technique or slug injection (Kilpatrick & Cobb, 1985).

In our study sites, periphytic algae are the main autochthonous food sources, but filamentous algae and mosses are present in scattered small patches that we assumed to be not important to the food web. Benthic chlorophyll *a* varied from 5.6 mg/m<sup>2</sup> to 25.8 mg/m<sup>2</sup> (Table 1). We did not estimate the input of allochthonous food sources, but it seemed high in all five sites because the litter standing stocks were abundant in the stream and in the riparian corridor. Estimates of annual total input of coarse allochthonous material for similar streams in Atlantic rainforest range between 488 g DM m<sup>-2</sup> year<sup>-1</sup> and 1,135 g DM m<sup>-2</sup> year<sup>-1</sup> [67–713 g DM m<sup>-2</sup> year<sup>-1</sup> for vertical (Afonso & Henry, 2002; Rezende & Mazzoni, 2005; Uieda & Kikuchi, 1995) and 421 g m<sup>-2</sup> year<sup>-1</sup> for lateral input (Afonso & Henry, 2002)].

## 2.2 | Sample collection and analysis

We sampled the sites during the rainy season, February and March 2007. The five sites each consisted of wadeable sampling areas of approximately 100 m of stream length, including at least a pool and a riffle habitat. We collected leaf samples from the stream by hand. We collected periphyton (biofilm) samples from five rock surfaces by

scrubbing them *in situ* using a sampling device. The periphyton sampler device consisted of a kitchen sink plunger with a brush attached to the handle inside the plunger cup and a 60-ml plastic syringe inserted into the side of the plunger (Moulton, Souza, Walter, & Krsulovic, 2009). We collected samples by pressing the plunger to the rocks, scrubbing the rocks with the brush and filling the syringe with the contents from plunger cup.

We employed multi-habitat sampling to collect the macroinvertebrates (Barbour et al., 1996; Gerth & Herlihy, 2006; Hering, Mood, Sandin, & Verdonschot, 2004; Hughes & Peck, 2008; Stoddard et al., 2008), with substrates sampled in proportion to their overall availability in the site. A total of 20 stations (1 m<sup>2</sup> each) were sampled from each site using a 500 μm mesh kick net, and then combined into a single composite sample that was preserved in 80% ethanol. We used one subsample to estimate the density of macroinvertebrates and another subsample to estimate their mean individual body masses using mass–length relationships (Benke, Huryn, Smock, & Wallace, 1999) and to prepare samples for stable-isotope analysis. The subsampling device for macroinvertebrates consisted of a 64 × 36 cm tray divided into 24 quadrats. Analyses indicated that a subsample comprised of six quadrats, randomly designated, including a minimum of 200 individuals, could be used in place of the full sample (Oliveira, Mugnai, Castro, & Baptista, 2011). We collected macroconsumers (tadpoles, fishes, crabs and shrimps) non-quantitatively with nets and trays; these were included in determinations of the assimilation web only.

Leaf samples, periphyton, macroinvertebrates and macroconsumers were prepared for isotopic analysis. Leaf samples were washed to remove the superficial epiphyton (inorganic material, bacteria, algae and fungi). We removed the guts of the aquatic insects by dissection before the whole bodies were processed. We also dissected tadpoles, fish, shrimps and crabs and took lateral muscle tissue for isotope analysis processing, except for crabs, from which we took chela tissue. We oven dried all samples at 60°C and then ground them with pestle and mortar. The isotope samples were analysed at the Center for Nuclear Energy in Agriculture (CENA), São Paulo, Brazil. They were analysed in a continuous-flow isotope-ratio mass spectrometer (ThermoQuest-Finnigan Delta Plus mass spectrometer, interfaced to an elemental analyser Carlo Erba, EA 1110 CHNS) in dual isotope mode to obtain elemental and isotopic values for carbon (C) and nitrogen (N) of the samples. The analytical precisions for carbon and nitrogen were 0.2‰ and 0.3‰, respectively. Isotope ratios are expressed as the relative per thousand (‰) differences between the sample and conventional standards, Pee Dee Belemnite (PDB) for δ<sup>13</sup>C and N<sub>2</sub> in air for δ<sup>15</sup>N as follows:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1,000(\text{‰})$$

where X = <sup>13</sup>C or <sup>15</sup>N and R = <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N.

We did not attempt to separate the microalgae fraction from the rest of the periphyton by density fractionation in colloidal silica (see Hamilton, Sippel, & Bunn, 2005) or by any other method. The non-algal material fraction appeared predominant in periphyton samples

on microscopic inspection and in chlorophyll *a* to dry mass ratios (range: 0.0002–0.0044). Therefore, we derived the algal (“autochthonous”) value for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from known herbivores (cf. Finlay, 2001; Vander Zanden & Rasmussen, 1999). The mean and standard deviation of isotopic values of the baetid mayflies *Baetodes* and *Camelobaetidium*; the helichopsychid caddisfly *Helichopsyche*; the leptocerid caddisfly *Grumichella* and the psephenid beetle *Psephenus* were used for this purpose. These genera are classified as grazers based on the anatomy of their feeding apparatus, habitat preference and/or feeding behaviour (Baptista, Buss, & Dias, 2006; Li & Dudgeon, 2008; Rueda-Delgado, Wantzen, & Tolosa, 2006; Tomanova, Goitia, & Helesic, 2006). Some samples of macroinvertebrates did not have enough mass for isotope analysis; in these cases we used the average isotope values of these taxa in the other sites.

We utilised the package Stable Isotope Analysis in R (R Core Team, 2015), SIAR, version 4.1.1 (Parnell & Jackson, 2011), and spreadsheet IsoError 1.04 (Phillips & Gregg, 2001) to estimate, respectively, the proportional resource contribution to diet of predators and primary consumers in each site. We used isotopic values of allochthonous and autochthonous material as end members for the mixing model of primary consumers (animals that consume allochthonous and/or autochthonous basal dietary resources). We divided the aquatic insects into four trophic guilds for analysis of their contribution to the food sources of higher-order consumers (fishes) and into the three guilds for their contribution to the diet of predatory insects. The guilds were as follows: (1) predominantly detritivorous (assimilation of more than 70% of litter-derived material); (2) predominantly algivorous (more than 70% of algae assimilation); (3) generalist primary consumer (29–69% of algae or litter assimilation) and (4) predator (based on Ramírez & Gutiérrez-Fonseca, 2014). For crabs, *Trichodactylus*, spp. (Trichodactylidae) in addition to these four guilds, autochthonous and allochthonous basal food resources were included as isotope end members in the mixing models.

The use of stable-isotope ratios to trace pathways of organic matter among consumers requires knowledge of the shift (fractionation or trophic enrichment factor) between diet and consumer. The mean values for fractionation and their variability are dependent on the material analysed (McCutchan et al., 2003; Vanderklift & Ponsard, 2003). We used the following trophic enrichment factor based on McCutchan et al. (2003):

Whole organism : + 0.3 (*SD* = 1.28) and 2.1 (*SD* = 1.60),  
respectively for C and N;

Muscle : +1.3 (*SD* = 1.27) and 2.9 (*SD* = 1.24)

For estimates of algal primary production (PP), we measured the fluorescence of the periphyton sample *in vivo* in a hand-held fluorimeter (Aquafluor 8000, Turner Instruments, Sunnyvale) and converted fluorescence into chlorophyll using known calibration relationships (Moulton et al., 2009). We converted chlorophyll mass per volume into mass per area based on the area of the periphyton sampler and we estimated the algal production by using its relationship with chlorophyll *a* and water temperature described by Morin et al. (1999):

$$\text{Log}_{10} \text{PPC} = 0.80 + 0.70 \times \text{Log}_{10} \text{Chl } a + 0.040 \times T$$

where

PPC – Periphyton primary production ( $\text{mg C m}^{-2} \text{ day}^{-1}$ );

Chl *a* – Chlorophyll *a* ( $\text{mg Chl } a \text{ m}^{-2}$ );

*T* – Water temperature ( $^{\circ}\text{C}$ ).

We multiplied the PPC value by 2 to convert from carbon to dry organic mass, assuming algae C content to be 50% of total dry mass (Odum, 1971), and we calculated annual PP expressed in g dry mass (DM)  $\text{m}^{-2} \text{ year}^{-1}$ . Then, we assumed that 50% of PP is respired and the remainder is the net primary productivity (NPP) which is available to primary consumers (Likens, 1975).

We estimated the secondary production (SP) of each macroinvertebrate taxon, expressed in g DM  $\text{m}^{-2} \text{ year}^{-1}$ , using its relationship with its biomass (B) in g DM  $\text{m}^{-2}$ , its mean individual body mass (M) in g DM and water temperature (Morin & Bourassa, 1992):

$$\text{Log}_{10} \text{SP} = -0.750 + 1.010 \times \text{Log}_{10} \text{B} - 0.340 \times \text{Log}_{10} \text{M} + 0.037 \times T$$

where B is the population biomass, i.e. the product between the density of a macroinvertebrate taxon (individuals per  $\text{m}^2$ ) and its mean individual body mass.

We examined the quantitative macroinvertebrate food web by using secondary production and estimates of the proportion of resource contribution to the diet of consumers. We estimated food resource consumption of macroinvertebrate taxa (annual ingestion rate) by dividing secondary production values by literature values of gross production efficiency: i.e. by the product of assimilation efficiency (AE) and net production efficiency (NPE). We assumed a NPE value of 50% for all consumers (this value was used also by Benke & Wallace, 1980), and AE values of 13% for allochthonous consumption (Eggert & Wallace, 2007; Perry, Benfield, Perry, & Webster, 1987), 30% for algae consumption (Benke & Wallace, 1980; Eggert & Wallace, 2007) and 70% for animal consumption (Lawton, 1970). Models and assumptions have been summarised in Table 2.

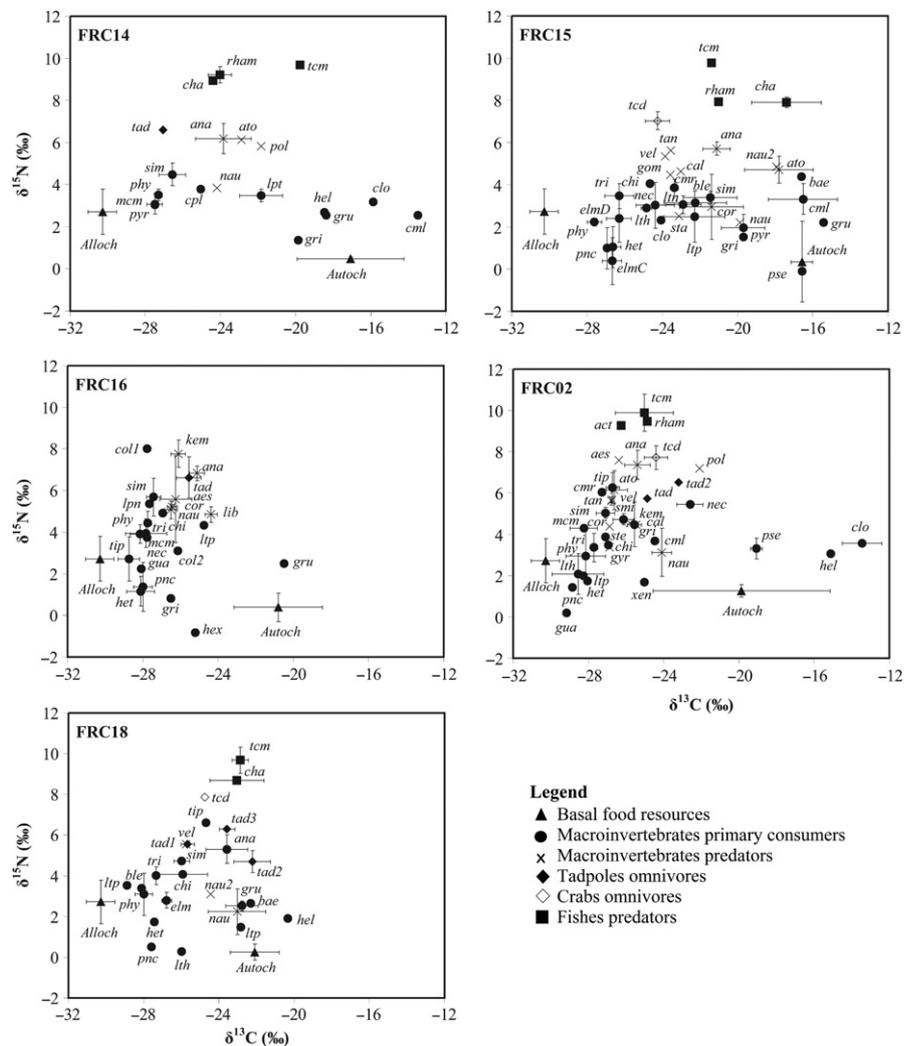
### 3 | RESULTS

We identified 51 insect taxa in the Coleoptera, Diptera, Ephemeroptera, Trichoptera, Hemiptera, Lepidoptera, Megaloptera, Plecoptera and Odonata. The first four orders were most abundant, with Chironomidae, Simuliidae, Leptohiphidae and the genera *Heterelmis* (Elmidae), *Anacroneuria* (Perlidae), *Phylloicus* (Calamoceratidae), *Smicridea* (Hydropsychidae) and *Triplectides* (Leptoceridae) present at highest mean densities in the five study streams (see Table S1 in Supporting Information). In decreasing order, the taxa with highest average individual body mass were as follows: Aeshnidae, *Leptonema*, *Kempnyia* (Perlidae), *Macrogynoplax* (Perlidae), *Corydalus*, (Corydalidae), *Hetaerina* (Calopterygidae), Gomphidae, Tipulidae, *Gyrinus* (Gyrinidae), *Triplectides*, *Anacroneuria* and *Phylloicus* (Table S1).

The annual net primary productivity of periphytic microalgae (NPP) was 164, 46, 50, 125 and 173 g of DM  $\text{m}^{-2}$ , respectively, in FRC18,

**TABLE 2** Summary of models and assumptions

Parameter	Empirical model or factor	Reference
Relationship between <i>in vitro</i> chlorophyll and <i>in vivo</i> fluorescence with the hand-held fluorometer	Chlorophyll ( $\mu\text{g/L}$ ) = 0.204 $\times$ Fluorescence	Moulton et al., 2009
$\delta^{13}\text{C}$ trophic enrichment factor	Whole organism: +3 (SD = 1.28) Muscle: +1.3 (SD = 1.27)	McCutchan et al., 2003
$\delta^{15}\text{N}$ trophic enrichment factor	Whole organism: +2.1 (SD = 1.60) Muscle: +2.9 (SD = 1.24)	McCutchan et al., 2003
Periphyton primary production (PPC; $\text{mg C m}^{-2} \text{ day}^{-1}$ )	$\text{Log}_{10} \text{ PPC} = 0.80 + 0.70 \times \text{Log}_{10} \text{ Chl } a + 0.040 \times T$	Morin et al., 1999
Dry mass (DM) primary production (PP)	Twice carbon PP	Odum, 1971
Net PP	Half gross production	Likens, 1975
Secondary production (SP; $\text{g DM m}^{-2} \text{ year}^{-1}$ )	$\text{Log}_{10} \text{ SP} = -0.750 + 1.010 \times \text{Log}_{10} \text{ B} - 0.340 \times \text{Log}_{10} \text{ M} + 0.037 \times T$	Morin & Bourassa, 1992
Net production efficiency	50%	Benke & Wallace, 1980
Assimilation efficiency	13% for allochthonous consumption; 30% for algae consumption; 70% for animal consumption.	Perry et al., 1987; Eggert & Wallace, 2007; Eggert & Wallace, 2007; Benke & Wallace, 1980; Lawton, 1970
Total input of coarse allochthonous material	488–1,135 $\text{g DM m}^{-2} \text{ year}^{-1}$	Uieda & Kikuchi, 1995; Afonso & Henry, 2002; Rezende & Mazzoni, 2005



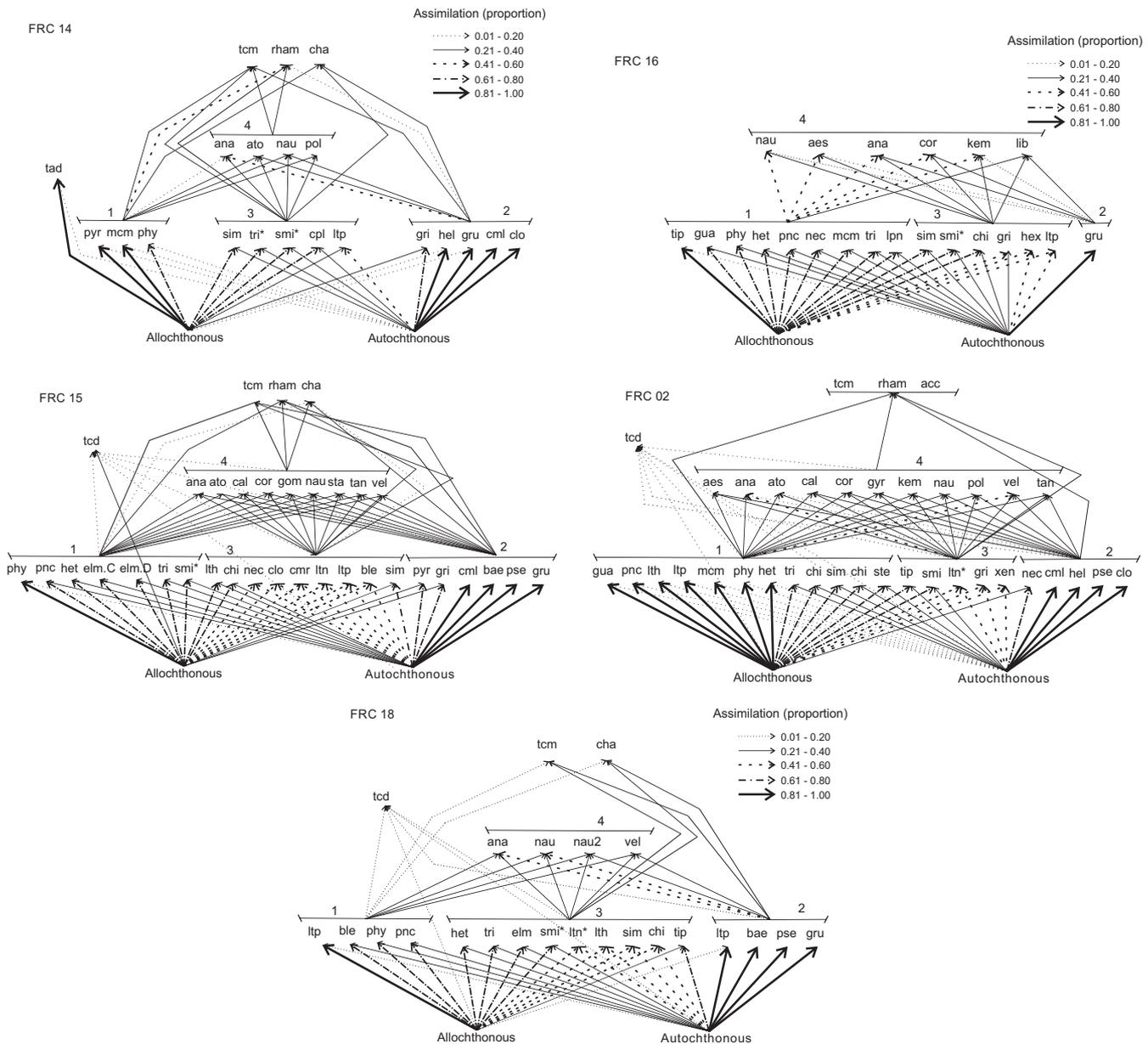
**FIGURE 1** Biplot of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  of sources and consumers in five stream sites of Guapi-Macacu basin, Rio de Janeiro, Brazil. Error bars indicate  $\pm 1$  SD around the mean. Taxa code: *tcd* – *Trichodactylus*; *cha* – *Characidium*, *rham* – *Rhamdioglanis*; *tcm* – *Trichomycterus*; *ace* – *Acentronichthys*. The other codes for the various taxa are in Table S1

FRC16, FRC02, FRC14 and FRC 15. There was no relationship between NPP with canopy/shading, stream order or catchment area.

The  $\delta^{13}\text{C}$  values of the two basal sources were distinctly different from each other at each site; in all the five sites  $\delta^{13}\text{C}$  values of allochthonous material were more depleted than autochthonous. In the smaller streams (FRC02, 16 and 18), the algae signature was lighter and least different to allochthonous plant signatures than in the larger streams (FRC14 and 15). In general, the isotopic values of C and N of the consumers were within the limits of the isotopic values of the food sources considering the isotopic trophic enrichment factors (Figure 1), and the mixing models were able to calculate the proportions of basal sources in the diets. On average, the primary

consumers presented lower  $\delta^{15}\text{N}$  than predator insects, and the  $\delta^{15}\text{N}$  of these was lower than omnivorous *Trichodactylus (tcd)* crabs. Predatory fishes, *Characidium (cha: Crenuchidae)*, *Rhamdioglanis (rham: Heptapteridae)*, *Trichomycterus (tcm: Trichomycteridae)* and *Acentronichthys (ace: Heptapteridae)*, had the highest  $\delta^{15}\text{N}$  (Figure 1).

Both allochthonous and autochthonous sources contributed substantially to the assimilation of the primary consumers in all five study sites (Figure 2). Site FRC16 had the smallest contribution of algae with only three taxa assimilating more than 40% algae. In FRC14, eight taxa assimilated more than 40% of allochthonous material and six more than 40% of algae. In FRC15, fifteen taxa assimilated more than 40% of allochthonous material and thirteen



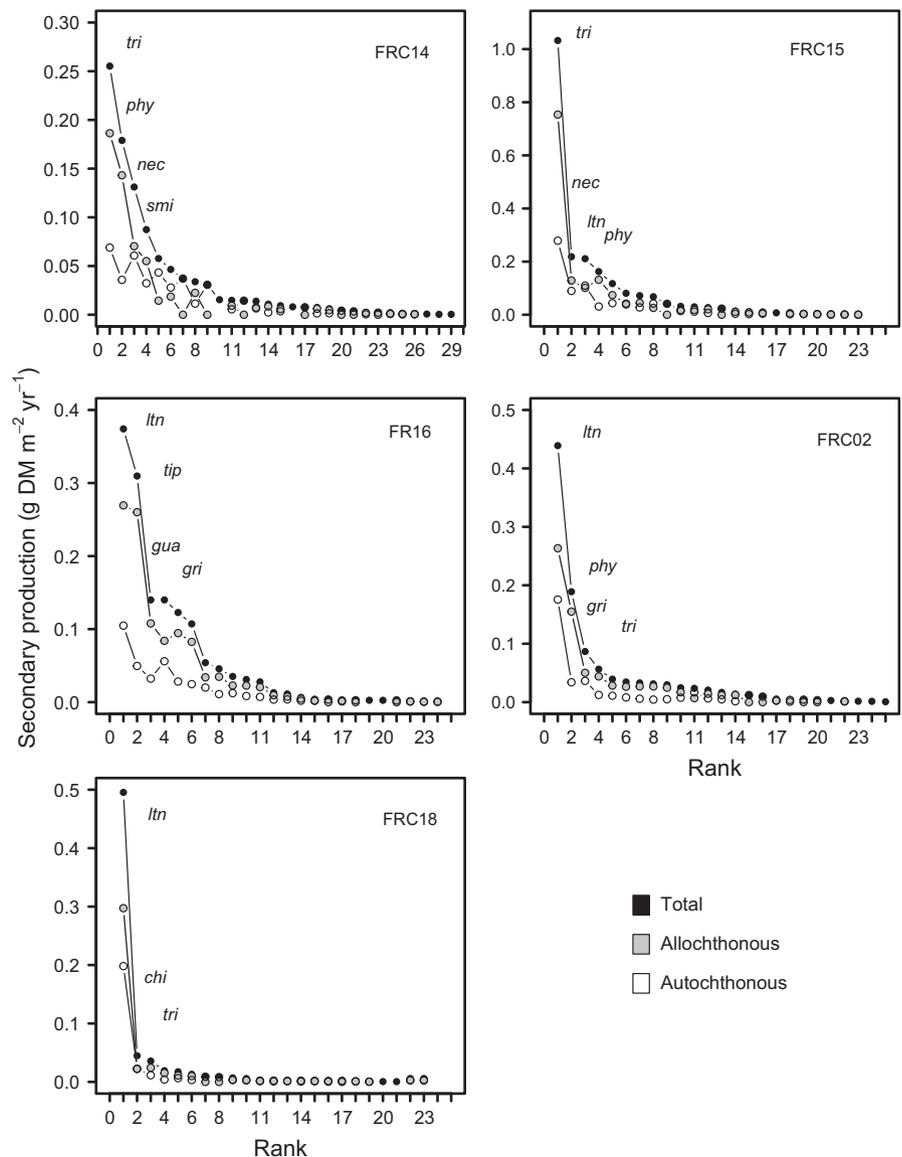
**FIGURE 2** Assimilation web estimated by mixing model of C and N stable isotopes of five stream sites of Guapi-Macacu basin, Rio de Janeiro, Brazil. Lines of different type and thickness connecting an organism with a food source indicate the fraction of each food that contributes to its production. The numbers indicate the four trophic guilds: 1 – assimilated more than 70% of leaf-derived material; 2 – assimilated more than 70% of algae; 3 – 29–69% of algae or leaf assimilation; 4 – predator. The codes for the various taxa are in the legend of Figure 1 and Table S1. \* Indicate taxa that had their isotope values calculated from the average of the other sites

more than 40% of algae. In FRC02, seventeen taxa assimilated more than 40% of allochthonous material and eight more than 40% of algae. In FRC18, twelve taxa assimilated more than 40% of allochthonous material and nine more than 40% of algae (Figure 2). Predatory macroinvertebrates, fishes and crabs generally assimilated similar proportions of the prey guilds except in FRC16 where around half of the energy assimilate by predatory insects (40–60%) were detritivores (Figure 2).

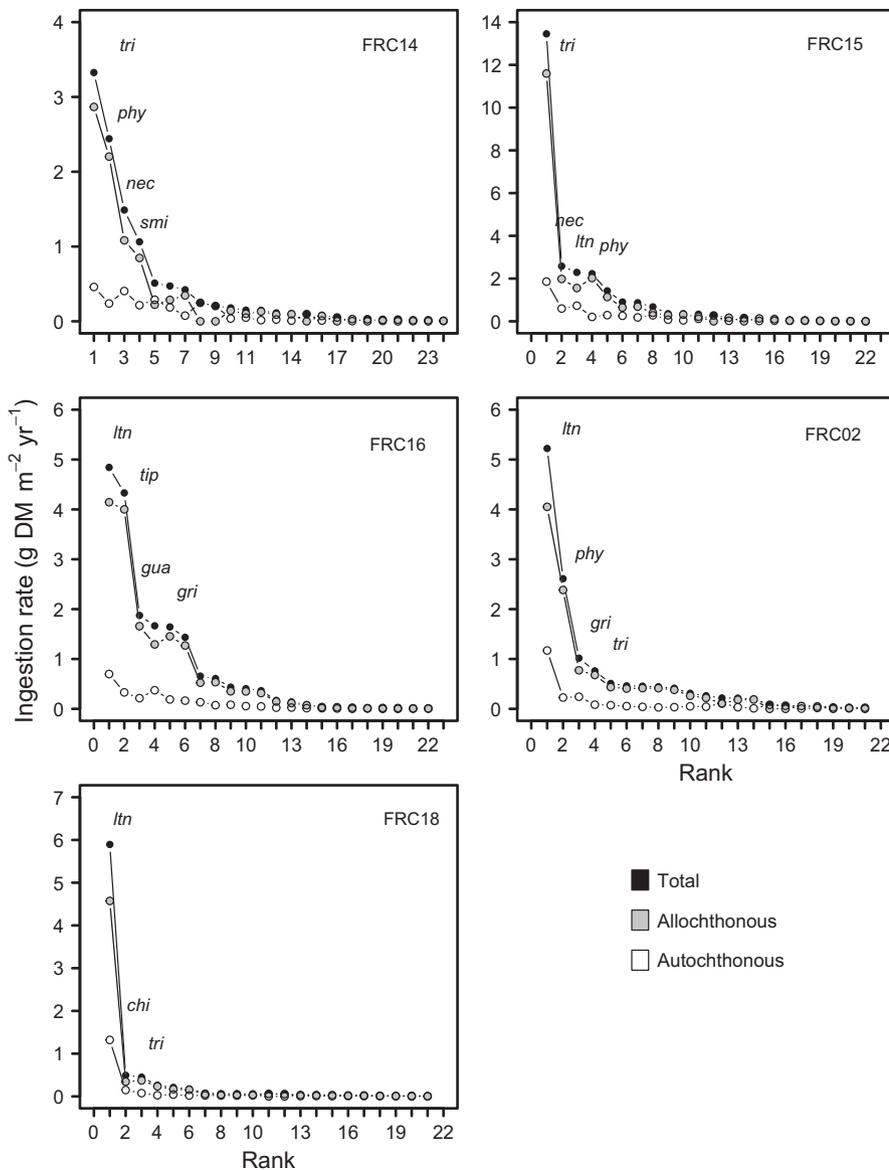
When the biomass and abundance of the different taxa were taken into account, the total secondary production of the sites was 0.90, 2.20, 1.66, 1.47 and 2.58 g DM m<sup>-2</sup>, respectively, in FRC18, FRC16, FRC02, FRC14 and FRC15 (Figure 3). In these sites, the primary consumers represented, respectively, 71%, 77%, 61%, 46% and 83% of the secondary production and, consequently, the predators represented between 10% and 35% of these productions. In general, few taxa contributed disproportionately to the secondary production and to the ingestion rate of primary consumers in all sites (Figures 3 and 4). Among these taxa were the shredder caddisflies *Triplectides* and

*Phylloicus* or the collector-filterers *Smicridea* or *Leptonema* (Hydropsychidae) or shredder craneflies (Tipulidae) which assimilated higher proportions of leaf-derived materials than algae (Figures 3 and 4). The four most productive primary consumer taxa represented between 66% and 96% of total secondary production of the primary consumers. Thus, total flow of allochthonous material to secondary production was more important than autochthonous and varied from 56% to 74% of the basal energy flow assimilated by primary consumers.

Using efficiency of assimilation and of net production from the literature, the annual ingestion rate of basal source varied from 8.08 g DM m<sup>-2</sup> to 26.57 g DM m<sup>-2</sup>. The consumption of allochthonous material represented between 76% and 87% of this annual ingestion rate (Figure 4). The annual ingestion rate of autochthonous material varied from 1.2% to 5.5% of the NPP. The annual ingestion rate of predators varied from 0.39 g DM m<sup>-2</sup> to 1.64 g DM m<sup>-2</sup> and they ingested 51%, 79%, 152%, 90% and 32% of total primary consumer production in FRC18, FRC16, FRC02, FRC14 and FRC15, respectively.



**FIGURE 3** Ranked secondary production of primary consumer macroinvertebrates taxa indicating the absolute flow of basal food type in five stream sites of Guapi-Macacu basin, Rio de Janeiro, Brazil. The codes for the various taxa are in Table S1



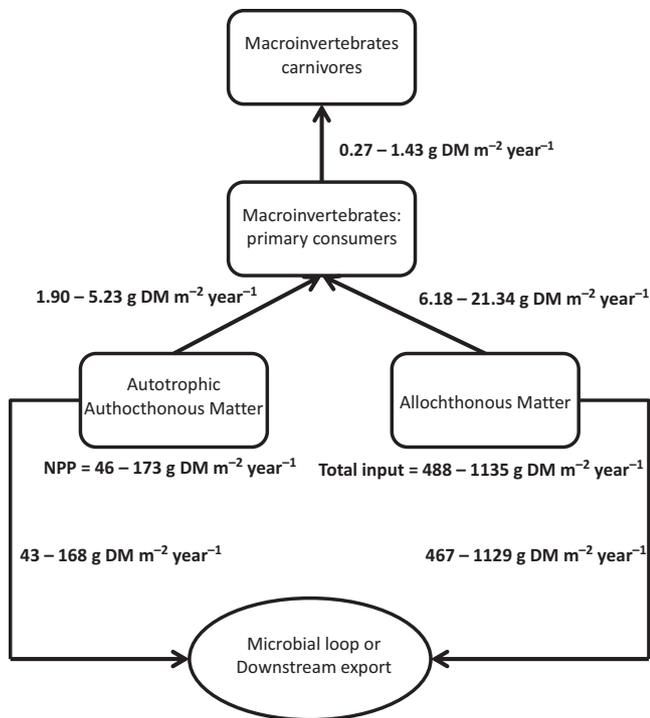
**FIGURE 4** Ranked ingestion rate of primary consumer macroinvertebrate taxa indicating the absolute flow of basal food type in five stream sites of Guapi-Macacu basin, Rio de Janeiro, Brazil. The codes for the various taxa are in Table S1

## 4 | DISCUSSION

The present work suggests that the principal energy source, both assimilated and ingested, for the macroinvertebrates of streams of Guapi-Macacu catchment comes from the riparian forest, in accordance with the predictions of the RCC (Vannote et al., 1980). We presume that allochthonous material was available in excess and unlikely to be limiting for consumers, and probably the proportion of stock consumed was low. Estimates of total input of allochthonous material in Atlantic rainforest streams can extend between  $488 \text{ g DM m}^{-2} \text{ year}^{-1}$  and  $1,135 \text{ g DM m}^{-2} \text{ year}^{-1}$  (Afonso & Henry, 2002; Rezende & Mazzoni, 2005; Uieda & Kikuchi, 1995). However, annual ingestion of all basal food sources in our streams was no more than  $26.57 \text{ g DM m}^{-2}$ . The RCC assumes that the standing stocks of periphytic algae in shaded streams are low and perhaps limiting for herbivores. However, when we compared the PP of algae with the estimated consumption, we found that the autochthonous NPP was more than sufficient to sustain all

secondary production of macroinvertebrates, with less than 10% of NPP consumed by macroinvertebrates. Thus, more than 90% of the NPP could have been processed by microbes or transported downstream (Figure 5). Likewise most of the allochthonous input probably is not eaten by primary consumers leading to the conclusion that processing by the microbial loop, burial of organic matter or downstream transport might be the fate of most of the basal energy sources, whether allochthonous or autochthonous, in our study streams.

The RPM emphasises the importance of microalgae as the main source of carbon that sustains the metazoan production in rivers and streams, and of the microbial loop that processes the majority of the transported material, which is principally allochthonous (Thorp & Delong, 2002). In fact, many studies using stable-isotope techniques show the relative importance of algae in the food web in tropical streams (e.g. Brito et al., 2006; Douglas et al., 2005; Lau et al., 2009; Li & Dudgeon, 2008; Mantel et al., 2004; March & Pringle, 2003; Neres-Lima et al., 2016; Salas & Dudgeon, 2001). On the



**FIGURE 5** Summary model of a simplified annual food web in five forested streams of Guapi-Macacu basin, Rio de Janeiro, Brazil

other hand, reconstruction of food webs based on microscopic observation of gut contents have shown a predominance of allochthonous detritus in the diets of consumers (e.g. in subtropical Brazil: Motta & Uieda, 2005; Uieda & Motta, 2007; tropical Australia: Cheshire, Boyero, & Pearson, 2005; tropical Colombia: Longo-Sánchez, 2012; Kenyan Rift Valley: Masese et al., 2014). This apparent incongruence may be explained by the differential assimilation of generally intractable leaf material and more nutritious and digestible algae (e.g. Benke & Wallace, 1980; Eggert & Wallace, 2007; Perry et al., 1987).

Using procedures that express the extent of allochthony and autochthony in terms of flow (mass area<sup>-1</sup> time<sup>-1</sup>) rather than proportion, which then obey the rules of mass balance (see also Thorp & Delong, 2002), we conclude that algae were not the main energy source flowing through food-webs source in the streams that we studied. Even though many taxa depended on algae as their main sources of energy (see Figure 2 trophic guild 2, taxa with more than 70% of algae assimilation), these taxa had low secondary production (Figure 3) and therefore little matter or energy flowed through them (Figure 4). Instead, allochthonous sources dominated ingestion, assimilation and energy flows in stream food webs. In part, this can be explained by the fact that assimilation of allochthonous material is less efficient than that of algae (see above) so that relatively more of such material needs to be ingested for the same secondary production. However, in general, the most productive primary consumers assimilated higher proportions of allochthonous foods than they assimilated algae, thus contributing to the overall importance of allochthony in our study streams. Using similar procedures to us, Hall et al. (2000) and Whiting et al. (2011) also concluded that

allochthony was more important than autochthony for primary consumers in temperate streams. Nonetheless, algae may be important as sources of nutrients and essential fatty acids to many macroinvertebrates (Guo, Kainz, Sheldon, & Bunn, 2016), as reflected in the dietary contribution of algae to most of the taxa in food webs (Figure 2).

It seems that a few consumer taxa can dominate energy flow and pathways in stream food webs (e.g. Douglas et al., 2005; Hall et al., 2000). In each of our study sties, two or three taxa were particularly important in the main allochthonous pathway (Figures 3 and 4), such as the shredders *Triplectides* and Tipulidae, and the filter-feeder *Leptonema* and *Smicridea*, which all assimilated little algae. Predators consumed large proportions of secondary production, as reported from elsewhere (Hall et al., 2000; Whiting et al., 2011), and possibly exerted a top-down control of primary and even secondary consumers. In FRC02, our estimate of ingestion rate to predators was greater than 100% of the secondary production of primary consumers. This could be because we did not include intraguild predation in the isotopic mixing model.

Stable-isotope signatures can be used to separate allochthonous and autochthonous sources in unshaded or productive sections of streams because the  $\delta^{13}\text{C}$  values of algae are heavier and closer to dissolved inorganic C than those of terrestrial  $\delta^{13}\text{C}$  values. However, when streams are narrower and more shaded, the algae signature tends to become lighter and more similar to C3 plants (Finlay, 2004; Ishikawa et al., 2012). This happens because the source of dissolved inorganic carbon (DIC) is lighter due to inputs of carbon from C3 plants while algae fractionate more due to abundant DIC. In our smaller studied streams (FRC02, 16 and 18), algal signatures are lighter and less different to allochthonous plant signatures than the larger streams (FRC14 and 15). However, they were still sufficiently distinct to allow us to separate the contributions of allochthonous and autochthonous sources to assimilated consumer biomass.

We used empirical models to estimate the primary (Morin et al., 1999) and secondary production (Morin & Bourassa, 1992). Moulton, Lourenço-Amorin, Sasada-Sato, Neres-Lima, and Zandonà (2015) compared empirical models of Morin et al. (1999) with direct measurement of PP in one stream in a well-preserved Atlantic rainforest and the model fitted well to their direct measurements. Such empirical models have sometimes been shown to lack accuracy and precision for secondary production estimation (Ramírez & Pringle, 1998), but they have been helpful, especially in places where the scarcity of information about the natural history of the taxa have precluded the use of direct methods (e.g. Aguiar, Gücker, Brauns, Hille, & Boëchat, 2015). Our estimates of the secondary production of the macroinvertebrate assemblage are among the lowest recorded in the literature, but are within the range reported in other studies (Benke and Huryn, 2006). The estimates for PP lie within the lowest first and second quartiles of the survey of Morin et al. (1999), and thus our estimates of PP and SP are plausible. However, direct measurement of primary and secondary production and estimates of trophic efficiencies combined with consumer diet analysis will certainly improve our understanding of energy flow in streams.

We conclude that the principal energy source for the macroinvertebrates of our study streams came from the riparian forest, although autochthonous energy sources were nonetheless of importance for many primary consumers. We also concluded that most part of allochthonous inputs and the in-stream autochthonous PP did not appear to be eaten by macroinvertebrates or pass through the food web to higher trophic levels. Much of it is probably exported downstream where it may be processed by the microbial loop.

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