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ORIGINAL ARTICLE

Variation of stream metabolism along a tropical environmental gradient

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ABSTRACT

Stream metabolism is affected by both natural and human-induced processes. While metabolism has multiple implications for ecological processes, relatively little is known about how metabolic rates are influenced by land use in tropical streams. In this study, we assessed the metabolic characteristics and related environmental factors of six streams located in a transition area from Cerrado to Atlantic Forest (São Carlos/Brazil). Three streams were relatively preserved, while three were flowing through more agriculturally and/or urban impacted watersheds. Surface water samples were analyzed for biological and physico-chemical parameters as well as discharge and percentage of canopy cover. Metabolism was determined through the single-station method to estimate gross primary production (GPP), ecosystem respiration (ER) and net ecosystem production (NEP) with BAyesian Single-station Estimation (BASE). Nutrient concentrations tended to be higher in impacted *versus* preserved streams (*e.g.*, average total phosphorus between 0.028-0.042 mg L^{-1} and 0.009-0.038 mg L^{-1}, respectively). Average canopy cover varied between 58 and 77%, with no significant spatial or seasonal variation. All streams were net heterotrophic (ER exceeded GPP) in all sampling periods. GPP rates were always lower than 0.7 gO_2 m^{-2} d^{-1} in all streams and ER varied from 0.6 to 42.1 gO_2 m^{-2} d^{-1}. Linear Mixed-Effect models showed that depth, discharge, velocity and total phosphorus are the most important predictors for GPP. For ER, depth, velocity and canopy cover are significant potential predictors. Canopy cover was the main light limiting factor and influenced stream metabolism. Our findings reinforced the concepts that shifts in the shading effect provided by vegetation (*e.g.*, through deforestation) or changes in discharge (*e.g.*, through land use conversion or water abstractions) can impact freshwater metabolism. Our study suggests that human activities in low latitude areas can alter tropical streams' water quality, ecosystem function, and the degree of riparian influence. Our data showed that tropical streams can be especially responsive to increases of organic matter inputs leading to high respiration rates and net heterotrophy, and this should be considered to support management and restoration efforts.

Key words: Ecosystem function; first-order streams; primary production; trophic state; functional indicators.

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INTRODUCTION

Stream metabolism, defined by the balance between organic matter produced via photosynthesis and consumed through aerobic respiration, is an important property of ecosystems, with significant influences on energy fluxes and ecosystem functioning (Fellows *et al.*, 2006; Correa-González *et al.*, 2014). The relative importance of Gross Primary Production (GPP) and Ecosystem Respiration (ER) defines the prevalence of either autotrophy or heterotrophy, affecting the role of the aquatic systems in carbon dynamics, nutrient cycling and dissolved oxygen production (Dodds and Cole, 2007). The metabolic activity in streams is regulated by factors such as light, flow regime, and seasonal variation of nutrient availability. It can be further affected by land use conversion and anthropogenic impacts, causing overall environmental degradation (*e.g.*, eutrophication and biodiversity loss) (Dodds *et al.*, 2013; Capps *et al.*, 2016). Metabolism has multiple implications for ecological processes. It affects the nutritional quality of resources available for consumers in the food chains, and therefore secondary productivity (Boëchat *et al.*, 2011). Metabolism also plays an important role in providing ecosystem services related to drinking water quality, pollution abatement and nutrient retention (Hall and Tank, 2003; Sobota *et al.*, 2012). Nitrogen and phosphorus retention depends on the environmental concentrations, contribution of internal loads, and relative importance of different biogeochemical processes. Such retention can be altered by the anthropogenic influences on GPP and ER (Gücker and Pusch, 2006; Merseburger *et al.*, 2011). Organic matter processing, which is directly linked with the self-depuration capacity of the water bodies, can covary with metabolism and depends on biotic (*e.g.*, uptake) and abiotic (*e.g.*, adsorption) processes (Tank *et al.*, 2010).

Low-order streams are more numerous and greater in length, in comparison to higher order streams and rivers (Loiselle *et al.*, 2016). Headwaters can be especially important for biodiversity (Meyer *et al.*, 2007; Finn *et al.*, 2011) and hotspots for biological processes such as degradation of leaf litter and other organic matter (Gessner *et al.*, 2010; Casas *et al.*, 2013; Longhi *et al.*, 2016). However, most monitoring programs, especially in low-latitude areas, focus on larger waterbodies, and smaller-size streams remain often unmonitored (Loiselle *et al.*, 2016). Low-order streams with significant canopy cover frequently have a prevalence of heterotrophic processes, due to inputs of allochthonous organic material (*e.g.*, leaf decomposition) and less solar radiation available for photosynthesis (Marzolf *et al.*, 1994).

Multiple and cumulative anthropogenic stressors (*e.g.*, acidification, temperature and flow regime shifts, contamination, droughts and invasive species) (see Jackson *et al.*, 2016) influence headwater streams (Bunn *et al.,* 1999; Fellows *et al.,* 2006; Young *et al.,* 2008), including impacts to biological communities (Rasmussen *et al.*, 2013), changes in flow dynamics and water temperature associated with global change (Taniwaki *et al.*, 2017), and water quality, due to urban and agricultural land uses, in both riparian and whole watershed scales (Foley, 2005; Meyer *et al.*, 2005; Tromboni and Dodds, 2017). Stream metabolism in altered sites can be influenced by shifts in water chemistry and characteristics of substrate and canopy cover, changes in land use and other anthropogenic disturbances (Mulholland *et al.*, 2005). Lower GPP is frequently associated with increasing water turbidity (Hall *et al.*, 2015) and population density in the catchments (Izagirre *et al.*, 2008). Canopy deforestation can increase autochthonous primary production (Bleich *et al.*, 2015). Autotrophic conditions can also be found under nutrient-enrichment conditions that stimulate benthic algae during day, and normally associated with high respiration rates during the night. This is commonly observed for urban catchments receiving effluent discharges (Halliday *et al.*, 2015), eutrophic river segments with altered hydrology (Pinardi *et al.*, 2011; Pinardi *et al.*, 2014), or under other conditions of high organic matter supply (*e.g.*, leaf inputs, organic content of the substrate) (Young and Huryn, 1999).

Metabolism is thus influenced by both natural and human-induced processes. Landscape (*e.g.*, riparian vegetation) and stream restoration techniques can also affect metabolic rates (Roley *et al.*, 2014; Burrell *et al.*, 2014). To develop a biome-specific view of the main factors controlling lotic systems worldwide (Dodds *et al.*, 2015), inter-biome, inter-regional comparisons of factors controlling stream metabolism are warranted (Mulholland *et al.*, 2001; Bernot *et al.*, 2010). Tropical areas have lower natural climate variability (Mora *et al.*, 2013) when compared to their temperate counterparts, as well as higher absolute water temperatures and rainfall (Dai and Trenberth, 2002; Boulton *et al.*, 2008). Faster chemical weathering (White *et al.*, 1998), significant leaching of the surrounding areas, as well as greater inputs of solar radiation (depending on the canopy cover), are expected in tropical streams and might influence oxygen saturation and metabolism. However, there is still missing information about spatial and temporal factors related to stream metabolism in tropical and subtropical zones, especially in biomes like the Atlantic Rainforest and Cerrado biomes in Brazil (except see Tromboni *et al.*, 2017).

The objective of this study was to estimate metabolic rates in tropical streams located in a transition area between Cerrado and Atlantic Forest biomes under pristine or impacted conditions. We investigated the correlations between environmental variables and stream metabolism to assess the role of land use and seasonality on GPP and ER. We hypothesized that the studied streams would be net heterotrophic, with the allochthonous contribution being predominant compared to the autochthonous production (Neres-Lima *et al.,* 2017). We also hypothesized that GPP and ER would be greater in these tropical streams compared to temperate streams, because they receive higher solar irradiance (influencing GPP) and higher temperature (influencing ER). Finally, we expected GPP and ER to increase with anthropogenic modification in the watershed, as a consequence of both greater light availability and higher temperatures from the decreased shading effect due to riparian deforestation, and increased nutrient inputs.

METHODS

Study area

Six tropical first-order streams were selected for this study (Tab. 1 and Supplementary Material with a map), located in São Carlos and Brotas (São Paulo State, Southeastern Brazil) and with discharges always below 100 L s^{-1}. These stream catchments had various degrees of disturbance (*e.g.*, in relation to canopy cover, substrate and soil degradation) ranging from more preserved conditions (streams Espraiado, Fazzari, Broa) to altered sites impacted by urbanization and soil erosion due to rainwater discharge (stream Mineirinho), agriculture (stream Canchim) and sugarcane crops and fragmented riparian forest (stream Santa Maria). We assessed reach lengths between 33 and 110 m (Tab. 1), chosen to have a minimum travel time of around 20 minutes. There were negligible lateral inflows (*i.e.*, increases in discharge from the upper to lower stations were mostly below 5%).

Total annual precipitation in the region is around 1500 mm, with rainy summers (average generally >150 mm/month) and dry winters (averages <70 mm/month). Air temperatures typically range from 17 to 23°C. The riparian vegetation is mostly characterized by second growth vegetation typical of Cerrado (Brazilian Savannah) and its transition to Atlantic Rainforest. Streams are therefore shaded most time of the year, with a slightly increase in light availability in the dry season, due to the presence of some deciduous plant species.

Field measurements

Sampling campaigns were carried out in October (14th to 29th) and December (1st to 16th) 2015 and February/March (23rd to 9th), May (3rd to 12th), June/July (28th to 7th) and August (9th to 19th) 2016, to encompass natural variations of the climate conditions in the region (*i.e.*, air temperatures and rainfall patterns). During those months, total monthly precipitation was 45, 157, 191, 10, 118 and 51 mm with average air temperatures of 24.0, 23.6, 23.9, 22.9, 16.5 and 19.3°C, respectively. The percentage of canopy cover was assessed during each sampling date with a spherical densiometer (concave model from Forestry Suppliers®, by Lemmon, 1956), as a proxy for the temporal variation in vegetation shading.

Metabolism measurements

The reaeration coefficients (k_{O2}) of each stream were directly estimated at base flow and at least once across the sampling periods. Mean velocity and discharge were estimated through the conservative tracer method, with a NaCl pulse and a conductivity meter (Hanna® 9828, Hanna Instruments, Limena, Italy) measuring downstream from the release point (Webster and Valett, 2006). To estimate the k_{O2} values, the same solute tracer was associated with a gas tracer (SF_6) in a continuous release (constant rates with a FMI Lab Pump - model QBG). After we established *plateau* conditions for conductivity throughout the reaches, samples for SF_6 were collected in six transects, with glass vials previously rinsed and stream water was collected to avoid air bubbles. SF_6 concentrations were estimated with a gas chromatography (Thermo Scientific®) at a laboratory at the Brazilian Agricultural Research Corporation (Embrapa Pecuária Sudeste, Fazenda Canchim, São Carlos). We measured the gas loss along the reach length stations and use one-dimensional advection-dispersion equation for the estimation of the SF6 reaeration coefficient (Benson *et al*., 2014):

$$C_x = C_0 \, e^{-(k/U)x} \qquad \text{(eq. 1)}$$

where: U is the mean stream velocity; x is the distance downstream of release; C_x is the concentration of gas tracer at the point x; C_0 is the initial concentration of gas tracer at the injection point (x=0).The k_{O2} was determined through a conversion factor ($k_{O2} = 1.38 \times k_{SF6}$) provided by Canale *et al.* (1995), and the k_{O2} was normalized for 20°C. The k_{SF6} values were determined at least once across the sampling periods and we recognize discharge variations can cause variation in k_{O2} values and therefore uncertainty in metabolic rates estimates. Average width values were measured in each sampling date in six transects in all the reaches (the total length from each reach, Tab. 1, was divided into six parts). The average depth was calculated from velocity and width.

Sensors with data loggers were deployed to monitor changes in PAR (Onset-HOBO® UA-002-64, Onset Computer Corporation, Bourne, MA, USA), barometric pressure (Onset-HOBO® U20L-04), dissolved oxygen (DO) and temperature (Onset-HOBO® U26-001) every ten minutes for two days. Probes were calibrated prior to deployment, and post deployment calibrations were used to correct drift in the data provided by the sensors. Metabolism was measured at relatively low flows (not

Tab. 1. Information about the studied first-order streams, including their names, codes, drainage areas, reach lengths used for metabolism estimations and geographic coordinates (latitude/longitude). The acronyms for the streams bring information about their condition, where (P) stands for preserved and (I) stands for impacted sites.

Stream	Acronym	Drainage area (km²) of the reach	Reach length (m)	Geographic coordinates
Espraiado	ESP (P)	2.49	110	S21° 58.831’ W47° 52.418’
Fazzari	FAZ (P)	0.69	33	S21° 58.134’ W47° 53.138’
Broa	BRO (P)	2.68	68	S22° 11.682’ W47° 53.930’
Canchim	CAN (I)	1.17	70	S21° 58.012’ W47° 50.562’
Mineirinho	MIN (I)	0.82	98	S22° 0.213’ W47° 55.680’
Santa Maria	SMA (I)	6.24	75	S22° 2.672’ W47° 58.083’

during or soon after storms) so aeration estimates, also measured at base flow, would be comparable at times when we were not able to directly measure aeration.

Metabolism modeling

Metabolism was determined through the single-station method (Odum, 1956; Bott, 2006), and the rates of GPP were estimated from the rates of ER and NEP:

$$GPP = ER + NEP \qquad \text{(eq. 2)}$$

The rates of ER and NEP were determined through the BAyesian Single-station Estimation (BASE v2.0, updated in July 2016), model proposed by Grace *et al.*, (2015) with measured data of Photosynthetically Active Radiation (PAR), barometric pressure, dissolved oxygen, temperature and reaeration coefficient (k_{O2}). A two-parameter model was used (because k_{O2} was measured and fixed) and, following the default of BASE, 20,000 iterations were performed with 10,000 burn-in and theta (constant for temperature dependence, by Van't Hoff-Arrhenius equation) fixed (1.07177). BASE used the model of diurnal regression, developed by Odum (1956), with the diel variations in stream O_2 concentrations to calculate GPP and ER. The model considered the reaeration rate measured and water temperature.

$$\frac{dC}{dt} = GPP - ER + k_{O2}(Cs - C) \qquad \text{(eq. 3)}$$

where C is O_2 concentrations (mg L^{-1}), Cs is saturating O_2 concentration (mg L^{-1}), k_{O2} is reaeration coefficient (d^{-1}). The detection limit of the GPP and ER rates were assumed as 0.1 mgO_2 L^{-1} d^{-1}. Such metabolic rates estimated by the model in mgO_2 L^{-1} d^{-1} were converted to gO_2 m^{-2} d^{-1} using the mean depth (m) of each site as calculated from average velocity and average width.

Water and substrate variables

Surface water samples were analyzed for the following parameters according to APHA (2012) methods: conductivity, pH, turbidity, total suspended solids (and their organic and inorganic fractions), total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate (NO_3^-), nitrite (NO_2^-), total Kjeldahl nitrogen (TKN), dissolved organic (DOC) and inorganic carbon (DIC). Substrate characterization (*e.g.*, sand, silt, rock, roots or leaves composition) was performed across the study reaches with 20 transects with 5 points each, or 10 transects with 10 points each, if average widths were lower or higher than 1 m, respectively. We sampled six replicates per stream of the most dominant substrata (making up 80% or more of the total). Chlorophyll-a was determined following hot ethanol extraction (Sartory and Grobbelaar, 1984), followed by the calculation of weighted chlorophyll averages (mg m^{-2}), according to the relative contribution of each substratum.

Statistical analyses

To assess statistically significant differences in all studied variables regarding season (*i.e.*, the temporal effect) and site condition (*i.e.*, merging all data for pristine *versus* all data for impacted sites), as well as their interaction (temporal and site factors), was used a Mixed Effects Model (MEM) with streams as a random variable and impact and campaign (six campaigns) as fixed factors. Was used the lme4 packages (Bates *et al.* 2014) in R software (R Core Team, 2015). All residuals were analyzed. The p values with Satterthwaite approximation for denominator degrees of freedom were obtained using the lmerTest R package (Kuznetsova *et al.* 2016). All data were previously normalized (as ln+1) before the statistical analyses.

Linear Mixed-Effects models were then applied to explain variations in GPP and ER, with stream as a random variable, time as an independent factor and the physico-chemical variables as fixed effects. Models' selection was based on the Akaike's Information Criterion (AIC). The P-values, with Satterthwaite approximation for denominator degrees of freedom, were obtained using the lmerTest R package (Kuznetsova *et al.* 2016), for the independent variables of the models. All analyses were conducted using the R software (R Core Team, 2015).

RESULTS

The study streams presented a range of water quality conditions in relation to the examined physical and chemical variables. Average water temperature, turbidity and TSS in the streams ranged between 18.0-21.7°C, 1-49 NTU and 1-7 mg L^{-1} respectively (Tab. 2), with no significant impact difference for the former variables ($P>0.05$, Tab. 3). Average pH (6.4-6.7) and electric conductivity (29-39 µS cm^{-1}) were greater in the impacted sites ($P<0.05$, Tab. 3). ESP(P), FAZ(P), BRO(P) and CAN(I) showed predominance of organic fraction of TSS: 53, 54, 81 and 60%, respectively, while MIN(I) and SMA(I) presented predominance of inorganic fraction, with 69 and 52% respectively.

Average DIC concentrations varied between 0.6 to 2.2 mg L^{-1} in preserved sites and 2.2-3.0 mg L^{-1} in impacted (Tab. 2), with significant temporal difference ($P<0.05$, Tab. 3). The DOC concentrations were similar across streams with the only exception of the stream SMA(I) that presented a higher average of DOC (7.1 mg L^{-1}) (Tab. 2). ESP(P), FAZ(P), BRO(P) and SMA(I) showed predominance of organic carbon (OC): 63, 62, 87% and 75%, respectively, while CAN(I) and MIN(I) presented 57 and 52%, respectively, of inorganic carbon (IC).

Average canopy cover varied between 58 and 77% (Tab. 2), with no significant temporal, site or temporal*site (interaction) variation (all $P>0.500$) (Tab. 3). Average sestonic and benthic chlorophyll varied between 0.6-4.6 µg L^{-1} and 6.6-32.5 mg m^{-2}, respectively (Tab. 2), but just sestonic chlorophyll show defined patterns across impacted *versus* preserved streams and temporal effect ($P<0.05$, Tab. 3). The dominant substrata in the streams were sand [ESP(P), BRO(P), MIN(I)], rocks [CAN(I), SMA(I)] and leaves [FAZ(P)] (Tab. 2).

Average total phosphorus (TP) concentrations varied in impacted from 0.028 to 0.042 mg L^{-1} and in preserved streams from 0.009 to 0.038 mg L^{-1}, with no significant impact and temporal differences ($P>0.05$, Tab. 3) (Fig. 1A). The streams SMA(I) and BRO(P) had the lowest values of soluble reactive phosphorus but all other sites had similar concentrations (averages from 0.004 to 0.015 mg L^{-1}, Fig. 1B), and there was no difference across impacted *versus* pristine sites ($P>0.05$, Tab. 3). There were significant temporal differences in average nitrogen concentrations in the nitrogen forms ($P<0.05$, Tab. 3), but there were no significant differences between streams.

Streams presented daily variations in DO concentrations (see Supplementary Material for detailed dissolved oxygen plots) from 6.0 to 9.0 mg L^{-1} in BRO(P), CAN(I), MIN(I) and SMA(I), from 3.5 to 7.5 mg L^{-1} in ESP(P) and from 1.5 to 6.0 mg L^{-1} in FAZ(P). The stream BRO(P) had the lowest reaeration coefficient (k_{O2}, ~20 d^{-1}), followed by ESP(P) (~24 d^{-1}), FAZ(P) (~41 d^{-1}), CAN(I) (~99 d^{-1}), MIN(I) (~122 d^{-1}) and SMA(I) (~274 d^{-1}) (Tab. 2).

Gross primary production rates were always lower than 0.7 gO_2 m^{-2} d^{-1} in all streams. The ESP(P) stream had the greatest apparent GPP rates (0.1-0.7 gO_2 m^{-2} d^{-1}) and MIN(I) and SMA(I) had the lowest (0.1 and <0.1-0.1 gO_2 m^{-2} d^{-1}, respectively) (Tab. 4). Ecosystem respiration varied between 0.6 and 42.1 gO_2 m^{-2} d^{-1} in all the streams, with rates lower in impacted streams ($P<0.05$, Tab. 3).

Tab. 2. Characterization of the study streams [Espraiado - ESP(P), Fazzari - FAZ(P), Broa - BRO(P), Canchim - CAN(I), Mineirinho - MIN(I) and Santa Maria - SMA(I)] regarding hydrological, water, substrate variables as well as canopy vegetation: discharge (Q), water velocity (Vel), reaeration coefficient (k_{O2}) for 20°C, wetted width, water temperature (T), pH, conductivity, total suspended solids (TSS), turbidity, dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), canopy cover, sestonic and benthic chlorophyll (Chla) and relative importance of different materials (sand, silt, leaf, bark, root and rock) in the substrate. Averages±Standard Deviations are shown for each case (except for the substrate composition), considering six sampling periods (October and December 2015 and February, April, June and August 2016).

Variables	Preserved sites			Impacted sites		
	ESP(P)	FAZ(P)	BRO(P)	CAN(I)	MIN(I)	SMA(I)
Q (L s^{-1})	10.5±3.9	2.2±2.1	18.8±7.0	4.1±1.3	5.5±1.5	69.0±24.1
Vel (m s^{-1})	0.05±0.03	0.03±0.03	0.06±0.05	0.08±0.03	0.09±0.02	0.22±0.07
k_{O2} (d^{-1})	~24	~41	~20	~99	~122	~274
Wetted width (m)	0.6	1.3	0.8	1.2	1.2	1.4
T (°C)	18.0±2.7	19.6±1.5	19.0±2.5	19.4±1.8	20.0±2.5	21.7±3.5
pH	5.6±0.2	5.4±0.1	4.6±0.3	6.4±0.1	6.6±0.2	6.7±0.2
Conductivity (µS cm^{-1})	14±6	12±6	8±2	29±3	29±6	39±4
TSS (mg L^{-1})	5±3	4±1	1±1	6±6	7±5	4±1
Turbidity (NTU)	7±4	6±2	1±1	14±7	49±60	9±3
DOC (mg L^{-1})	3.8±3.1	3.0±1.4	3.7±4.0	2.3±1.2	2.0±0.4	7.1±9.4
DIC (mg L^{-1})	2.2±0.5	1.9±0.7	0.6±0.2	3.0±0.4	2.2±0.8	2.4±0.3
Canopy cover (%)	72±5	77±4	66±16	77±5	74±2	58±10
Sestonic Chla (µg L^{-1})	1.1±1.5	0.6±1.5	1.2±1.9	3.9±6.7	4.6±6.8	3.2±3.7
Benthic Chla (mg m^{-2})	6.6±3.7	11.6±5.2	14.4±5.9	32.5±14.1	14.3±7.4	7.4±5.0
Sand (%) in substrate	31	*	44	28	69	6
Silt (%) in substrate	21	14	29	18	*	*
Leaf (%) in substrate	14	51	6	*	*	*
Bark (%) in substrate	6	9	1	*	*	*
Root (%) in substrate	28	26	20	*	*	*
Rock (%) in substrate	*	*	*	54	31	94

**Below 0.5%.*

ESP(P) and FAZ(P) presented the highest values of ER varying from 10.4 to 42.1 and from 2.7 to 41.3 $gO_2\ m^{-2}\ d^{-1}$, respectively (Tab. 4). NEP rates were always lower than -0.5 $gO_2\ m^{-2}\ d^{-1}$ in all streams and showed that streams were heterotrophic (respiration exceeded gross primary production) in all sampling periods (Tab. 4).

NEP, ER and GPP showed significant variations across impacted *versus* preserved streams ($P<0.05$, Tab. 3) in relation to tested factors. Linear Mixed-Effect models (Tab. 5) showed that depth, discharge, velocity and total phosphorus were the most important predictors for GPP ($P<0.05$, AIC = -75.43 and -77.39, Tab. 5). ER was mostly driven by depth, velocity, and canopy cover ($P<0.05$, AIC = 59.89 and 60.74).

DISCUSSION

All streams were heterotrophic during the entire year of the experiment, presenting high ER and low GPP rates compared to most other studies (see Bernot *et al.,* 2010 and Hall and Beaulieu, 2013 for a comprehensive comparison). While there was no temporal variation on canopy cover, the riparian vegetation was a significant determinant of metabolism, not only by reducing solar radiation, but also by contributing with allochthonous organic material and determining different substrata characteristics. These two factors probably caused increases in ER and reduced GPP by light limitation. Also, total suspended solids can attenuate light affecting photosynthesis, as pointed by Lewis (2008) and observed by Young and Huryn (1996). However, in our study total suspend solids and turbidity were not correlated with GPP, probably because the streams are shallow and already light limited by canopy cover.

We note in the pristine/forested sites the possibility that apparent GPP rates may be an artifact of tree root respiration and diurnal patterns of evapotranspiration. This was reported by Dodds *et al.* (2017) in the Espraiado stream, ESP(P), where the authors measured the root

Tab. 3. Summary of mixed effects model results considering all studied variables (n = 36) and impact effects (land use types: impacted *versus* pristine sites), temporal effects (seasonality) and their interaction. Streams were set up as random factor. Significant effects at P<0.05 are in bold.

Variable	Impact effect	Temporal effect	Interaction (impact*temporal) effect
Temperature	P=0.16	**P<0.05**	**P<0.05**
pH	**P<0.05**	**P<0.05**	P=0.39
Turbidity	P=0.10	P=0.10	P=0.65
Dissolved oxygen	P=0.14	**P<0.05**	P=0.08
Electric conductivity	**P<0.05**	P=0.16	P=0.86
Total suspended solids	P=0.28	P=0.17	P=0.33
Inorganic suspended solids	P=0.20	P=0.60	P=0.18
Organic suspended solids	P=0.44	**P<0.05**	P=0.43
Total nitrogen	P=0.69	**P<0.05**	P=0.57
Total Kjeldahl nitrogen	P=0.30	**P<0.05**	P=0.60
Nitrate	P=0.41	**P<0.05**	P=0.29
Nitrite	P=0.68	**P<0.05**	P=0.22
Total phosphorus	P=0.24	P=0.07	P=0.60
Soluble reactive phosphorus	P=0.94	P<0.05	**P<0.05**
Dissolved inorganic carbon	P=0.18	**P<0.05**	P=0.70
Dissolved organic carbon	P=0.46	**P<0.05**	P=0.22
Seston chlorophyll	**P<0.05**	**P<0.05**	P=0.20
Benthic chlorophyll	P=0.54	P=0.85	P=0.07
Canopy cover	P=0.78	P=0.23	P=0.39
Discharge	P=0.69	**P<0.05**	P=0.33
Velocity	P=0.13	**P<0.05**	P=0.30
Gross primary production	**P<0.05**	P=0.18	P=0.20
Ecosystem respiration	**P<0.05**	P=0.63	P=0.22
Net ecosystem production	**P<0.05**	P=0.64	P=0.22

activity directly as it contributes to water DO concentration along the day/night cycle. During active transpiration in day, the trees remove low DO water, increasing DO concentrations observed in the stream channel. At night, the water is not moved up the plant vascular system and DO concentrations drop. This produced a DO pattern similar to that observed for the photosynthesis occurring in streams, with more DO concentration in the day time and reduced during the night. We were not able to directly measure root respiration in our study.

Average stream velocity presented a significant negative effect on GPP as noted also by other studies. Hydrological characteristics, such as discharge and average velocity, in fact can produce a temporal effect on the metabolism of streams, due to the scouring of stream biofilms (Hall, 2016). While we sampled all streams at base flow, stream average velocity was considered as an indicator that links to the seasonality of the study area (*i.e.*, rainy summers and dry winters, see Saltarelli, 2017) and therefore related to abrasion and disturbance of biofilms. Stated differently, although our measurements were made at base flow, those made in the rainy period were more likely to have been made on biofilms subject to recent high flow events. Current velocity can significantly influence the architecture and temporal dynamics of natural biofilms (Battin *et al.*, 2003) and thus aquatic metabolism. Discharge effects were also reported by Uehlinger *et al.* (2003), in experiments carried out in the Rio Spol (Swiss Alpes), located downstream of a reservoir. GPP was reduced by 64% and ER by 36% after flooding, and they were related to periphyton biomass reduction. On the other hand, Acuña *et al.* (2004) related the increase in GPP with an increase in discharge in a Spanish stream. In that case authors explained that discharge removed organic matter present in the periphyton, providing more light availability for the algal community.

The increase in phosphorus and nitrogen, essential for

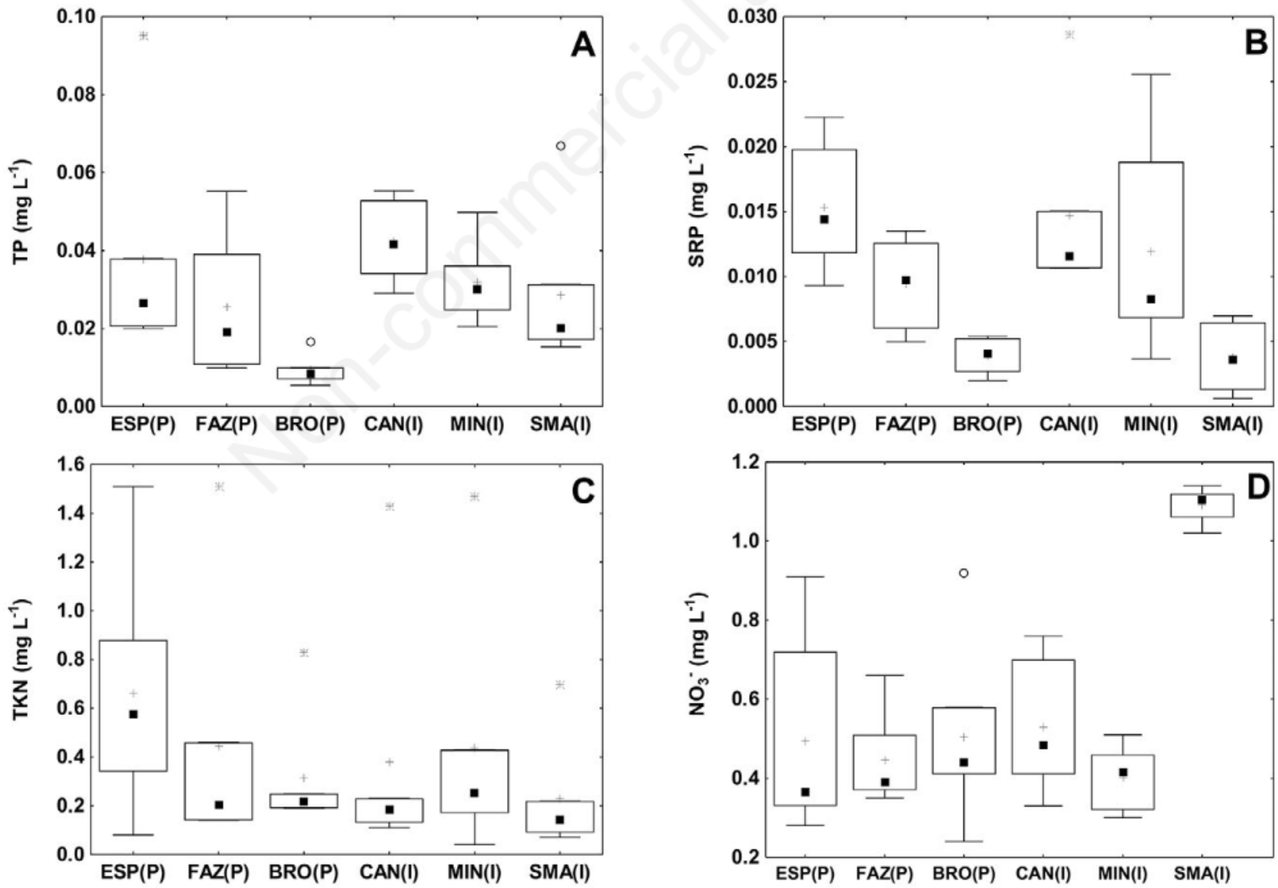

Fig. 1. Phosphorus and nitrogen concentrations across the studied streams [Espraiado - ESP(P), Fazzari - FAZ(P), Broa - BRO(P), Canchim - CAN(I), Mineirinho - MIN(I) and Santa Maria - SMA(I)]: A) total phosphorus (TP); B) soluble reactive phosphorus (SRP); C) total Kjeldahl nitrogen (TKN) and D) nitrate (NO$_3^-$). Boxplots show 25% quartile (┴), 75% quartile (┬), medians (■), means (+) and outliers (○) of the dataset for each stream.

algal and macrophyte growth, can also affect metabolic rates (Dodds, 2007). In our study, the relationships between metabolic rates and nutrients, especially phosphorus, were suggested by the Linear Mixed-Effect models (Tab. 5). However, there is still limited evidence on the relationships between nutrient availability and algal biomass accrual, especially for non-experimental studies (Bernhardt *et al*., 2018). These authors argued that anthropogenic impacts on streams (*e.g*., surface runoff or wastewater inputs) bring a myriad of changes not only in nutrient supply, but also in light availability and other disturbances, and this makes it more difficult to assess the effects on each individual factor on stream metabolism. In tropical streams impacted by agriculture, SRP concentrations (7.2 $\mu g\ L^{-1}$) were found to be related to higher GPP as in another study carried out in the Cerrado biome (Gücker *et al*., 2009). GPP also increased in a temperate river as a response to effluents from a wastewater treatment plant probably as a result of mixed effects from such effluents (Aristi *et al*., 2015). Silva-Junior (2016) summarized some metabolic responses across different biomes as a response of different land use stress.

Apparently, light and total phosphorus influenced GPP, as expected but depth and discharge were also important. We suspect this is not related to stimulation of respiration by primary producers, because ER rates were so much greater than GPP in most of our streams. Bott *et al*. (2006) reported that in Muscoot stream (New York), average nutrient concentrations were high (TN: 1.6 $mg\ L^{-1}$ and TP: 0.04 $mg\ L^{-1}$), and GPP was low (0.4 $gO_2\ m^{-2}\ d^{-1}$), suggesting light limited GPP and not nutrients. Bernot *et*

Tab. 4. Average temperature (°C), DO maximum amplitude ($mg\ L^{-1}$) and Net ecosystem production (NEP), Ecosystem respiration (ER) and Gross primary production (GPP) rates ($gO_2\ m^{-2}\ d^{-1}$) in the studied streams from October de 2015 to August 2016.

		Date	T (°C)	ΔDO ($mg\ L^{-1}$)	GPP ($gO_2\ m^{-2}\ d^{-1}$)	ER ($gO_2\ m^{-2}\ d^{-1}$)	NEP ($gO_2\ m^{-2}\ d^{-1}$)
Preserved sites	ESP(P)	Oct/15	19.8	0.8	0.2±0.1	39.0±0.1	-38.8
		Dec/15	20.9	0.5	0.7±0.1	42.1±0.1	-41.4
		Feb/16	21.3	0.3	0.1±0.0	10.4±0.0	-10.3
		Apr/16	16.4	0.6	0.1±0.0	13.6±0.0	-13.5
		Jun/16	16.9	0.4	0.1±0.0	14.0±0.0	-13.9
		Aug/16	17.3	0.5	0.2±0.0	23.5±0.0	-23.3
	FAZ(P)	Oct/15	20.5	1.0	0.1±0.0	14.6±0.0	-14.5
		Dec/15	21.6	1.2	0.1±0.0	8.6±0.0	-8.5
		Feb/16	22.0	0.3	<0.1±0.0	4.3±0.0	-4.3
		Apr/16	18.5	0.8	0.1±0.0	7.5±0.0	-7.4
		Jun/16	18.5	0.7	0.3±0.1	41.3±0.2	-41.0
		Aug/16	18.5	0.9	0.1±0.0	2.7±0.0	-2.6
	BRO(P)	Oct/15	21.6	0.4	0.2±0.0	12.1±0.0	-11.9
		Dec/15	21.9	0.3	0.3±0.0	14.3±0.0	-14.1
		Feb/16	22.0	0.1	<0.1±0.0	5.3±0.0	-5.3
		Apr/16	17.7	0.4	0.1±0.0	10.2±0.0	-10.1
		Jun/16	17.2	0.4	0.2±0.0	11.5±0.0	-11.3
		Aug/16	18.4	0.5	0.6±0.0	17.5±0.1	-16.9
Impacted sites	CAN(I)	Oct/15	21.2	0.8	0.2±0.0	6.8±0.0	-6.6
		Dec/15	21.2	0.5	0.1±0.0	6.3±0.0	-6.2
		Feb/16	20.6	0.2	<0.1±0.0	4.1±0.0	-4.1
		Apr/16	20.7	0.4	0.1±0.0	2.7±0.0	-2.6
		Jun/16	17.8	0.2	<0.1±0.0	1.9±0.0	-1.9
		Aug/16	17.0	0.5	<0.1±0.0	2.0±0.0	-2.0
	MIN(I)	Oct/15	21.8	0.9	0.1±0.0	6.6±0.1	-6.5
		Dec/15	21.7	0.4	0.1±0.0	2.1±0.0	-2.0
		Feb/16	22.1	0.3	0.1±0.0	4.4±0.0	-4.3
		Apr/16	18.9	0.4	0.1±0.0	4.4±0.0	-4.3
		Jun/16	16.6	0.6	0.1±0.0	2.5±0.0	-2.4
		Aug/16	18.6	0.5	0.1±0.0	4.6±0.0	-4.5
	SMA(I)	Oct/15	24.0	0.5	<0.1±0.0	1.7±0.0	-1.7
		Dec/15	24.4	0.4	0.1±0.0	0.6±0.0	-0.5
		Feb/16	24.5	0.6	<0.1±0.0	8.2±0.1	-8.2
		Apr/16	20.4	0.4	0.1±0.0	6.8±0.1	-6.7
		Jun/16	18.5	0.5	<0.1±0.0	6.9±0.1	-6.9
		Aug/16	21.2	0.6	<0.1±0.0	0.8±0.0	-0.8

al. (2010) studied 72 streams and observed that nitrate and ammonium concentrations were positively related to metabolic rates in US and Puerto Rico. Authors reported that riparian characteristics (*e.g.*, vegetation and soil) and land-use (agriculture and urbanization) influenced in stream nutrient concentrations. In some streams in Indonesia with palm cultivation (*Elaeis guineenses*), Carlson *et al.* (2014) reported an increase in ER (5.0 gO_2 m^{-2} d^{-1}) compared to more preserved areas (2.0 gO_2 m^{-2} d^{-1}) during dry season. The increase could have been driven by the increasing input of organic matter (*e.g.*, palm leaves). Our data suggest multiple limiting factors of GPP and ER can occur in tropical streams.

Following our initial hypothesis, all streams were heterotrophic with high ER and low GPP, and therefore, especially responsive to increases of organic matter inputs. This study suggests that human activities such as agricultural and land use alter stream ecosystem functioning, as highlighted from the Linear Mixed-Effect models that showed that changes in metabolic rates are explained by the variations in discharge, nutrients and canopy cover. Interestingly, ER was frequently higher in unaltered than altered sites (Tab. 4, maximum of 42.1 and 8.2 gO_2 $m^{-2}$$d^{-1}$, respectively). This suggests that inputs of natural allochthonous organic material in the more pristine sites had a more pronounced effect on ER rates in comparison to organic pollution and nutrient inputs in the impacted study sites. Also, while we just characterized the biofilms in terms of benthic chlorophyll, it is possible that biofilm community structure (*e.g.*, relative importance of algae, bacteria and fungi communities) was significantly different across sites, leading to different respiration rates. The biodiversity and the colonization sequences of different biological communities in the biofilms are subjected to multiple factors and can substantially influence stream metabolism (Artigas *et al.*, 2012; Besemer, 2015).

In order to protect streams in Brazil, it is important to adopt measures to maintain stream ecosystem health. Tromboni and Dodds (2017) pointed out that the implementation of sewage treatment plants as well as phosphate control is lacking and particularly urgent in Brazil, where urban areas are the major driver of nutrient concentration increases in streams, there are no bans on phosphorus-containing detergents, and water treatment is still not common. To mitigate environmental risks, governments in Western Europe and North America (Compton *et al.*, 2011) have enacted legislation to control livestock expansion, fertilizer application, riparian protection, other farm practices, and/or banning phosphate-containing laundry detergents. Such initiatives are still limited in Brazil as well as those for determining nutrient exports across watersheds with varying land uses.

Riparian protection is also important to maintain metabolic rates more similar to the reference natural condition, as highlighted by Silva-Junior (2016). Restoration techniques such as the increase of the hydraulic residence time and reduction of water velocity could increase GPP. With an increase of carbon production, an increase in the complexity of stream food webs could occur. Those changes could modify nutrient retention and exports in addition to restoring ecosystem

Tab. 5. Linear Mixed-Effects models of GPP and ER rates against discharge, velocity, nutrients, depth and canopy cover. β is the slope for the variables, SE is standard error and significant effects at P<0.05. AIC is the Akaike's Information Criterion.

Dependent variable	Independent variable	*β*	SE	P-value	AIC
GPP ($gO_2\,m^{-2}\,d^{-1}$)	Intercept	-0.122	0.067	*	-75.43
	Discharge	-0.050	0.013	P<0.05	
	Total phosphorus	0.056	0.017	P<0.05	
	Depth	0.908	0.088	P<0.05	
GPP ($gO_2\,m^{-2}\,d^{-1}$)	Intercept	-0.187	0.064	*	-77.39
	Velocity	-0.623	0.187	P<0.05	
	Total phosphorus	0.068	0.017	P<0.05	
	Depth	0.698	0.082	P<0.05	
ER ($gO_2\,m^{-2}\,d^{-1}$)	Intercept	-2.043	1.366	*	59.89
	Depth	5.608	0.712	P<0.05	
	Discharge	-0.240	0.130	0.09	
	Canopy cover	0.427	0.138	P<0.05	
	Soluble reactive phosphorus	0.047	0.161	0.77	
ER ($gO_2\,m^{-2}\,d^{-1}$)	Intercept	0.765	0.571	*	60.74
	Velocity	-4.159	1.745	P<0.05	
	Total phosphorus	0.297	0.154	0.06	
	Depth	3.931	0.759	P<0.05	

Discharge (L s^{-1}); velocity (m s^{-1}); depth (m); total phosphorus (µg L^{-1}); soluble reactive phosphorus (µg L^{-1}); canopy cover (%). Data were (ln^{+1}) transformed; **not calculated.*

services (Palmer *et al.*, 2014). Understanding stream ecosystem function can provide insights of the effects of the reduction of vegetation by the changes of the Native Vegetation Protection Law of Brazil ("Brazilian Forest Code") that recently reduced the width of the zone of protected riparian vegetation.

The results of this study are important because they provide reference metabolism characteristics of streams located in the understudied tropical Cerrado and information regarding its relation to biological and physico-chemical aspects. Such information is fundamental for classifying and modelling metabolic rates of lotic aquatic systems as well as guiding management and restoration efforts (Bernhardt *et al.*, 2018). Metabolism can be used as a functional indicator of stream health and anthropogenic impacts (Fellows *et al.*, 2006). The estimation of the metabolism over the years can indicate how drivers such as light availability, allochthonous inputs, and temperature have changed and are likely to change the metabolism (Bernhardt *et al.*, 2018). The use of functional indicators based on functional ecosystem processes has some advantages over structural ones because they encompass a wider variety of physical and biological factors across different habitats (Young *et al*., 2008; Gucker *et al*., 2009) allowing for comparisons among streams in different areas (Davies and Jackson, 2006).

CONCLUSIONS

The tropical streams we studied were influenced by the degree of human modification in their watersheds in relation to different environmental impacts (*e.g*., agricultural crops, urban areas, soil erosion/loss and fragmentation of riparian vegetation). The streams were net heterotrophic throughout the whole analyzed period, with respiration rates (maximum of 42.1 $gO_2\ m^{-2}\ d^{-1}$) higher than usually reported in most studies available in the literature, and low rates of gross primary production. Land use was not directly related to metabolic rates. Such rates usually present a natural day-to-day variability that can be not captured by limited measurements across different land uses. The light attenuation by the riparian vegetation was one of the most important predictors of the metabolic rates due to its role in restricting solar radiation availability by the shading effect. Also, discharge explained some variation on GPP, probably due to its effect on the reduction of biomass of primary producers by the abrasion caused by water velocity and turbulence, whose effect was probably greater in the rainy summer period in the studied streams. Metabolism has been used as a functional indicator of the level of disturbance and sensitivity to anthropogenic impacts in streams. Our study indicates that tropical streams can be vulnerable to deforestation, discharge alteration related to flow shifts under global climate changes, and alteration of organic matter loading leading to further dissolved oxygen consumption. Such influences at the base of the food web could have implications for ecosystem functioning and stream food webs.

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