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Ecosystem metabolism in tropical streams and rivers: a review and synthesis

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Abstract

Ecosystem metabolism of freshwater ecosystems has been studied for several decades, with theory and synthesis largely derived from temperate streams and rivers in North America and Europe. Advances in sensor technology and modeling have opened a wider range of streams to be included to test theories beyond temperate streams. In this paper, we review and synthesize ecosystem metabolism data from tropical streams and rivers to determine to what extent the constraints of metabolism measured in temperate streams are similar in tropical streams. We compiled 202 measurements of gross primary productivity (GPP) and ecosystem respiration (ER) from 83 tropical streams spanning 22.2°S to 18.4°N. Overall, tropical streams were heterotrophic (ER > GPP), with GPP ranging from 0.01 to 11.7 g O_2 m^{-2} d^{-1} and ER ranging from –0.2 to –42.1 g O_2 m^{-2} d^{-1}, similar on average to rates reviewed from temperate streams, but with higher maximum ER in tropical streams. Gross primary productivity increased with watershed area; a result also observed in temperate streams. ER decreased with elevated phosphorus and higher annual rainfall. We constructed a structural equation model that explained greater variation of ER (74%) than GPP (26%), and reflects similar drivers, such as land-use and watershed area, as in temperate streams. We conclude that tropical stream ecosystem metabolism has similar drivers as temperate streams, and a warmer and wetter climate and human use of tropical lands will influence metabolic rates in streams.

For over six decades, measuring and estimating primary productivity and ecosystem respiration in freshwater ecosystems (i.e., streams, rivers, lakes, and wetlands) has been a complex theoretical and empirical task (Odum 1956). Beneath the theoretical and data collection approach first developed by Odum (1956) is a complex interaction of climate, hydrologic, geologic, and terrestrial influences on in-stream processes. The basic stream ecosystem metabolism calculation is an oxygen mass balance that informs carbon (C) fixation and mineralization within the stream ecosystem in terms of oxygen concentration in the water:

$$\frac{dO_2}{dt} = G + R + D$$

where the change in O_2 (g m^{-3}) is a balance of production during photosynthesis (G) during day light hours, consumption during aerobic heterotrophic respiration (R), and O_2 diffusion exchange based on the O_2 partial pressure gradient between water and atmosphere (D). Each of these volumetric O_2 fluxes (G, R, D) are scaled to the area of benthos for a particular time period, and estimates of gross primary productivity (GPP), ecosystem respiration (ER), and net ecosystem production (NEP) are derived using a variety of quantitative approaches (Marzolf et al. 1994; Holtgrieve et al. 2010; Grace et al. 2015; Hall and Hotchkiss 2017; Appling et al. 2018). Data collection for stream ecosystem metabolism depends on O_2 sensor quality and accurate understanding of gas exchange (Raymond et al. 2012; Hall and Ulseth 2020). Each component driving the oxygen mass balance is mediated by a variety of geomorphological and hydrological factors, and the existing methods and theory have been developed primarily from temperate streams in North America and Europe.

There have been persistent arguments discussing what fundamental differences, or lack thereof, exist between tropical and temperate ecosystems (Hawkins 2001), including streams and rivers (Boulton et al. 2008; Dodds et al. 2019). Tropical streams, defined here as streams between 0° and 23.5° North and South latitude, experience a different climatic regime than temperate streams, which potentially influences metabolism in freshwaters (Lewis 2008). Tropical forests experience diverse climate, geology, and high taxonomic diversity of organisms (Townsend et al. 2008). For example, canopy cover and

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Additional Supporting Information may be found in the online version of this article.

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temporal availability of light to the stream bed are more variable in temperate stream ecosystems than tropical ecosystems (Davies et al. 2008; Dodds et al. 2019). In forested temperate streams, canopy closure following seasonal spring leaf-out resulted in reduced GPP due to light limitation, and canopy opening due to leaf abscission stimulated ER from leaf material inputs in the fall (Roberts et al. 2007), whereas tropical streams and rivers can have closed canopies year-round. In tropical streams, the seasonal variation of canopy closure may not be as strong or canopy closure may persist year-round, leaving streams light limited and with high continuous inputs of terrestrial organic matter (Townsend et al. 2011). In tropical streams where light availability to the benthos is high, GPP is among the highest rates measured, up to 10-times greater than comparable temperate streams (Davies et al. 2008). However, no previous reviews or syntheses of tropical stream metabolic rates has allowed for a comparison to their temperate counter parts.

Seasonal temperature variation in the tropics span a narrower range than that of temperate streams (Janzen 1967). Temperature regulates biological metabolism (Brown et al. 2004) and infrequent low temperatures in tropical streams, particularly in the lowland tropics, should drive higher respiration year-round (Song et al. 2018). Temperature variability due to elevation are stronger than temporal variation in tropical streams compared to temperate streams (Janzen 1967; 2018). At the organismal level, the response of heterotrophic metabolism to increases in temperature is exponential for terrestrial tropical taxa (Dillon et al. 2010), suggesting that increases in metabolism per unit temperature increase will be higher in the tropics. As a result, faster metabolic rates at the organismal level due to warming temperatures associated with climate change should result in elevated rates at the ecosystem level in the tropics (Dillon et al. 2010). However, warmer water has lower gas solubility, and combined with high metabolic rates, can lead to low dissolved oxygen and difficulties in estimating stream ecosystem metabolism (Lewis 2008). Further, temperature patterns vary across elevation and land-use types, and the responses of ecosystem metabolism to temperature will vary depending on a suite of climatic and site specific characteristics (Dodds et al. 2019). An improved understanding of how temperature affects both GPP and ER in tropical streams will help forecast possible feedbacks to climate change associated with a warmer world.

In addition to temperature differences between temperate and tropical streams and their effects on stream metabolism, a range of abiotic drivers are of interest in tropical streams. Generally, rainfall is greater in the tropics due to the inter-tropical convergence zone (ITCZ), which distributes heat and water across the tropics. Increased rainfall causes greater solid and solute fluxes through streams and rivers from weathered soils (Lewis 2008), structures the stream benthos and primary producer assemblages (Pringle and Hamazaki 1997), and delivers terrestrial organic matter and nutrients downstream to the ocean (Mayorga et al. 2010). Seasonal flooding associated with rainfall contributes to higher turbidity, which attenuates light penetration to the benthos and in water column. Flooding can also structure primary producer assemblages, shifting dominance from diatoms and blue-green algae in headwater streams (Pringle and Hamazaki 1997) and transporting producers from upstream reaches in larger rivers and their floodplains (Lewis 1988).

Nutrients also influence biological processes in streams. Nitrogen (N) and phosphorus (P) are limiting elements in freshwaters (Dodds and Smith 2016; Paerl et al. 2016) and their availability in tropical streams may regulate both GPP and ER. Increased N and P can result in small increases in both GPP and ER across different stream types and latitudes (Mulholland et al. 2001; Bernot et al. 2006, 2010). Specific to the effects of phosphorus in the tropics, a number of studies have reported increased heterotrophic activity (microbes, macroinvertebrates, and fungi) with elevated P (Rosemond et al. 2002; Ramírez et al. 2003; Ardón et al. 2006), suggesting a stimulatory effect of P on ER. Studies from streams across nutrient gradients have concluded light limitation is a stronger effect on GPP than nutrients (Pringle et al. 1986; Paaby and Goldman 1992), and as is reported in temperate streams (Hill et al. 2001; Roberts et al. 2007; Finlay 2011). However, greater study of the combined effects of limitations from light and nutrients on primary producers and the food webs they support is needed.

In this paper, we review and synthesize stream ecosystem metabolism measurements made in the tropics. Reviews on C processing in streams, rivers, lakes, and estuaries (Bernot et al. 2010; Marcarelli et al. 2011; Hoellein et al. 2013) and on whole stream metabolism (Finlay 2011) have been completed, though focused on temperate ecosystems. Greater number of studies of freshwater metabolism from streams and rivers is part of a growing literature in tropical ecology (Ramírez et al. 2015; Riveros-Iregui et al. 2018) and an important contribution to the field as there are increasing threats to tropical freshwater ecosystems, including reduced hydrologic connectivity, pollution, hydropower development, and biodiversity loss (Encalada et al. 2019). Specifically, we evaluated the effect of watershed area, nutrients, rainfall, and temperature on stream ecosystem metabolism, evaluated potentially associated physical and chemical parameters, and use a structural equation model to explore how multiple variables control GPP and ER. We hypothesized that (1) as watershed area increases and incident light increases in wider rivers, GPP will increase due to alleviation of light limitation; (2) streams with higher nutrient concentrations will have greater GPP and ER due to nutrient stimulation of photosynthesis and respiration; (3) streams that receive higher rainfall will have lower GPP and ER as a result of scouring and elevated turbidity; and (4) GPP and ER will be greater in streams with warmer temperatures. Further, we also explored the upscaling of daily metabolic estimates to annual C fluxes and light mediation of GPP and ER.

Methods

Data selection and extraction

Our review began with a literature search in Web of Science, using key words "tropical" in each search, either "stream" or "river", and "gross primary producti*", "ecosystem respiration", or "metabolism" as different search words, yielding a total of 257 articles published before September 2019. Each of these papers was assessed for inclusion of (1) stream location identified by latitude and longitude; (2) text, graphical, and/or tabular presentation of GPP and ER, and (3) open channel methods used to measure metabolism (e.g., single station or two-station), and (4) dates of the measurements, resulting in 18 articles with available data. Graphically presented data were extracted using WebPlotDigitizer for each measurement (Rohatgi 2019). We amended the dataset from published research with unpublished data from our own research in Costa Rica and from publicly available metabolism data from Rio Icacos and Quebrada Sonadora in Puerto Rico through the StreamPULSE project (Appling et al. 2018; Vlah and Berdanier 2020). The data in this study are found in Data S2.

We expanded the data extraction from each reference for relevant hydrological, geomorphological, physical, and chemical parameters (Table 1). Metabolism estimates are integrative at the ecosystem level and influenced by climate, geology, hydrology, chemistry, and biota; therefore, we compiled parameters relevant to each of these potential drivers. Units were standardized to those shown in Table 1 and conversions of stream ecosystem metabolism expressed as g C m^{-2} d^{-1} were converted to units of O_2 using a 1 : 1 M respiratory quotient (Demars et al. 2016). Dissolved inorganic nitrogen (DIN), if not explicitly reported, was calculated as the sum of nitrate (NO_3^--N) and ammonium (NH_4^+-N). In studies where GPP was low, many authors report GPP as < 0.01 g O_2 m^{-2} d^{-1}, and we report those data as 0.01 g O_2 m^{-2} d^{-1} as a minimum threshold; studies that quantitatively report GPP < 0.01 g O_2 m^{-2} d^{-1} are compiled as reported.

Climate data collection

Rainfall was collected as total annual rainfall for the year of the GPP and ER measurements. If not reported in the papers, location and date specific annual rainfall totals were extracted from the TerraClimate dataset (Abatzoglou et al. 2018), which yields total annual rainfall within a 4000 m buffer around a given location (i.e., the coordinates of the stream extracted from the paper). Incident downward radiation was extracted using the CFS Reanalysis dataset (Saha et al. 2014), specific to the coordinates and year of the metabolism estimates. We extracted mean daily radiation (W m^{-2}) for the year of the measurements. Radiation values were converted to PAR fluxes following Sager and McFarlane (1997). Each of the climate datasets were accessed through the Climate Engine data portal (Huntington et al. 2017).

Table 1. Parameters extracted from each reference, if available, with associated units and percentage of whole-stream metabolism measurements for each parameter.

Parameter	Units	% of measurements filled
Latitude	Decimal degree	99.1
Longitude	Decimal degree	99.1
Elevation	Meters above sea level	43.6
Annual rainfall*	mm	100
%For	% forested area in watershed	84.7
%Ag	% agricultural area in watershed	84.7
%Urb	% urban area in watershed	84.7
Canopy†	Categorical: Open, closed	83.0
Canopy cover	% canopy cover	62.9
PAR	μmol m^{-2} s^{-1}	100
Strahler order	Integer	72.3
Stream width	m	82.7
Stream depth	m	50
Velocity	m s^{-1}	46
Slope	m m^{-1}	44.1
Watershed area	km^2	74.8
Discharge	m^3 s^{-1}	79.7
Temperature	°C	77.7
DO	mg L^{-1}	30.7
pH	Unit	39.6
Conductivity	μS cm^{-1}	48.5
NO_3^--N	μg L^{-1}	55
NH_4^+-N	μg L^{-1}	21.3
Dissolved inorganic nitrogen (DIN)	μg L^{-1}	24.3
Total nitrogen (TN)	μg L^{-1}	23.3
Total phosphorus (TP)	μg L^{-1}	23.3
Soluble reactive phosphorus (SRP)	μg L^{-1}	60.9
TN : TP	Molar	23.3
DIN : SRP	Molar	10.4
Gas exchange (K_{600})‡	d^{-1}	86.6
GPP	g O_2 m^{-2} d^{-1}	100
ER	g O_2 m^{-2} d^{-1}	100

*If not reported in the study, annual rainfall at the given coordinates was extracted from the TerraClimate dataset.

†"Closed" canopy is classified as %canopy cover ≥ 70% or ≥ 90% forested land-cover; "Open" is %canopy cover < 50% or stream width > 5 m.

‡Standardized all reported gas exchange coefficients to a Schmidt number of 600, following Raymond et al. (2012).

Analysis and synthesis

Based on our hypotheses and the availability of data collected in the review, we examined the drivers of GPP and ER from tropical streams and rivers. We evaluated metabolic space to visualize patterns in productivity, similar to previous studies (Odum 1956; Hoellein et al. 2013). We used Student's *t*-test to evaluate GPP and ER under closed or open canopies. We used linear regression to evaluate the effects of watershed area, soluble reactive phosphorus (SRP), rainfall (mm), and stream temperature (°C), which were $\log_{10}$ transformed to meet assumptions of normality and better visualize the variation across the range of conditions represented in our dataset.

For parameters that were not commonly reported in our review (less than 50% in Table 1), we used a pairwise correlation matrix for chemical and geomorphological variables. We evaluated correlation of incomplete data using the Kendall tau statistic, using only complete pairs in our limited dataset, which is a rank-based measure of association and are more robust for datasets with few complete cases.

We constructed a structural equation model (SEM) to better understand multiple controls of GPP and ER in tropical streams and rivers. These models allow for testing of causal hypotheses and evaluation of multiple, simultaneous influences. There are many drivers of both GPP and ER, often with high co-linearity, and the SEM approach allows for a priori evaluation of a potentially interrelated drivers and is more robust compared to other multivariate approaches (Bernot et al. 2010; Lefcheck 2019). Using the SEM in Bernot et al. (2010) as a template to evaluate controls of GPP and ER within a hierarchy, we constructed an a priori meta-model based on the data we compiled (Fig. S1). Our model incorporated hierarchical structure, attempting to separate drivers at the regional (watershed area, land cover, rainfall) and local (temperature, discharge, SRP, DIN, width, and depth) levels. We hypothesized that correlated errors would exist at the two levels. At regional level, we modeled temperature and rainfall with correlated errors, as warmer temperatures correlate with wetter conditions (Collins et al. 2013). At the local level, we correlated errors between SRP and DIN to reflect nutrient increases particularly from non-forested lands (Allan 2004), and between width and depth which increase predictably with stream size (Raymond et al. 2012).

To provide close approximation to daily metabolism estimates, rainfall in the SEM was converted to mean daily rainfall by dividing annual rainfall by 365. The SEM was fit with $\log_{10}$ transformed metabolic and chemical data and arcsin transformed land cover data, averaged for each stream, using the psem() function in the piecewiseSEM R package (Lefcheck 2016). The psem() function returns standardized and unstandardized path coefficients (*ß*) for all pathways and coefficient of determination (r^2) for endogenous variables. We evaluated the goodness of fit of the SEM using the Fisher's C statistic, which assess the fit of the data to the model structure and ensures no missing paths were excluded. Fisher's C is χ^2 distributed with degrees of freedom equal to two times the number of independence claims and a model-wide p value can be determined where $p > 0.05$ indicates the data support the model structure. Further details on SEM methods are in Data S1.

Light influence on annual GPP and ER

We upscaled median GPP and ER from each stream to annual rates of C fixation and respiration (g C m^{-2} y^{-1}). Metabolic rates were converted from O_2 to C using a molar respiratory quotient of 1 : 1 (Demars et al. 2016). As temperatures in the tropics are less variable over time and space (Janzen 1967), we hypothesize the upscaling of metabolic rates to annual rates is less dependent on changes in temperature than similar estimates from temperate and Arctic streams and represent changes as a result seasonality driven by rainfall. Annual estimates of GPP and ER from tropical streams will be useful in understanding the importance of in-stream processes in the tropics.

Using upscaled annual rates, we evaluated the dependence of fixation and respiration on mean daily light availability. We evaluated annual metabolic rates as a function of PAR assuming linear and nonlinear (e.g., logarithmic, logistic, or

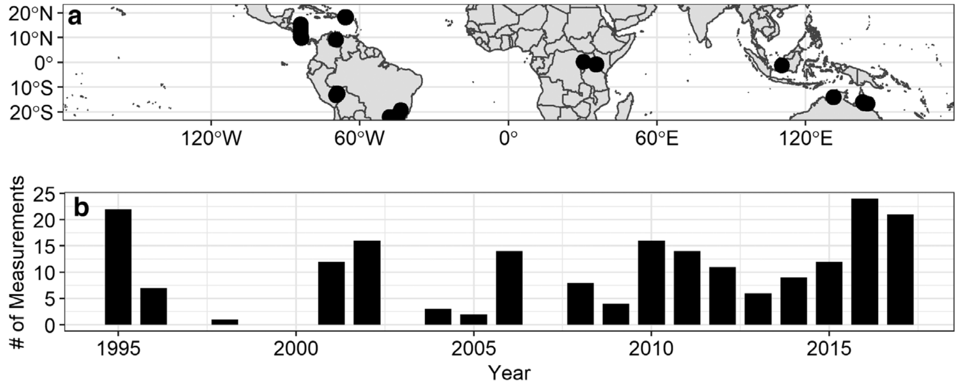

Fig. 1. (**a**) Map of the tropics (|latitude| ≤ 23.5°) and metabolism measurements in this study; (**b**) number of metabolism measurements made by year compiled in this review.

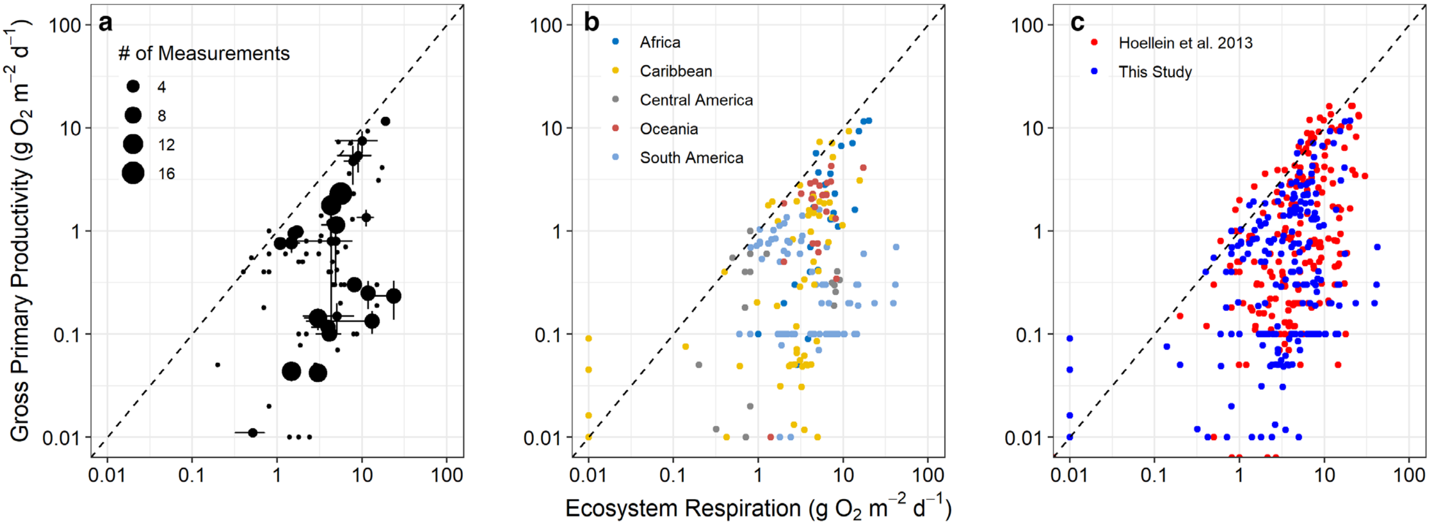

Fig. 2. (**a**) Median GPP and ER from each stream, with error lines showing 95% confidence intervals; (**b**) all metabolic rates collected in the review, colored by global region; (**c**) all GPP and ER data compiled in this review (blue) plotted against stream data reviewed in Hoellein et al. (2013) (red). Point size in a) is scaled by the number of measurements in each stream. The dashed black lines are 1 : 1 lines in all panels. Note log axes.

Michaelis–Menten) saturation equations. Linear and logarithmic models were fit using lm() in R (R Core Team 2019). Logistic and Michaelis–Menten models were fit using the drc R package (Ritz et al. 2015), using the L.3() and MM.2() self-starter functions, respectively, within the drm() function. The four models for each GPP and ER were compared using AIC and AIC weights, w_i. Comparing model fits allows interpretation of the effect of light directly on GPP and indirectly on ER, through GPP.

Results

From the published studies and publicly available data, we extracted 202 GPP and ER measurements from 83 streams and rivers across the global tropics (Figs. 1a, 2a). Metabolism data publicly available through the StreamPULSE data portal (https://data.streampulse.org/) provided continuous data for 11 months in two streams in Puerto Rico (Rio Icacos and Quebrada Sonadora) and our own unpublished data from Costa Rica (Taconazo) were the three sources of continuous

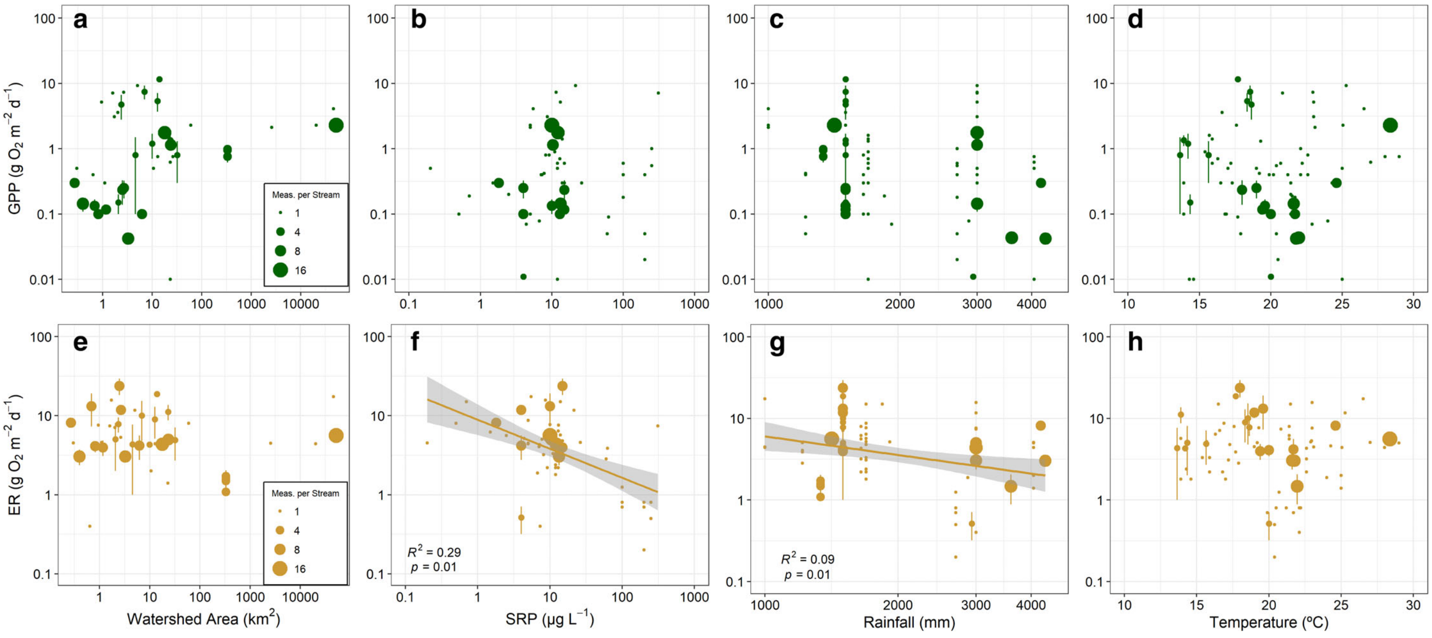

Fig. 3. Predicted drivers of mean GPP (**a–d**) and mean ER (**e–h**) in each stream. Point size in each panel shows the number of metabolism measurements from a single stream contributing to calculate the average. Error bars are standard error. Lines represent best-fit lines with 95% confidence intervals. Note $\log_{10}$ transformation of *y*-axes and *x*-axes in **a**, **b**, **c**, **e**, **f**, and **g**.

Table 2. Results of linear regression between GPP and ER, and the hypothesized drivers. Values in parentheses for intercept and estimate are 95% confidence intervals.

Rate	Driver	Intercept	Estimate	*F* value	*p* value	R^2
$\log_{10}$ (GPP)	$\log_{10}$ (Area)	−0.22 (−0.50 to 0.05)	0.14 (– 0.02–0.30)	$F_{1,41} = 3.30$	0.08	0.07
$\log_{10}$ (GPP)	$\log_{10}$ (SRP)	−0.49 (−0.84 to −0.14)	0.04 (– 0.23–0.32)	$F_{1,59} = 0.11$	0.75	<0.01
$\log_{10}$ (GPP)	$\log_{10}$ (Rainfall)	1.69 (−1.37–4.75)	−0.62 (– 1.55–0.31)	$F_{1,81} = 1.76$	0.19	0.02
$\log_{10}$ (GPP)	Temperature	−0.85 (−1.76–0.06)	0.02 (– 0.02–0.07)	$F_{1,75} = 1.11$	0.29	0.01
$\log_{10}$ (ER)	$\log_{10}$ (Area)	0.73 (0.59–0.88)	−0.02 (– 0.11–0.06)	$F_{1,41} = 0.34$	0.56	0.01
$\log_{10}$ (ER)	$\log_{10}$ (SRP)	0.95 (0.75–1.14)	−0.37 (– 0.52 to −0.22)	$F_{1,59} = 23.6$	<0.01	0.29
$\log_{10}$ (ER)	$\log_{10}$ (Rainfall)	3.06 (1.32–4.79)	−0.76 (– 1.29 to −0.23)	$F_{1,81} = 8.23$	0.01	0.09
$\log_{10}$ (ER)	Temperature	0.69 (0.16–1.22)	−0.01 (– 0.03–0.02)	$F_{1,75} = 0.18$	0.68	<0.01

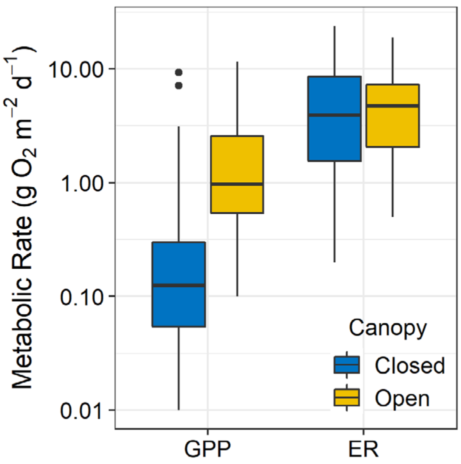

Fig. 4. Metabolic rates, GPP (in green) and ER (tan), under open and closed canopies. Boxplots show the median, 25th and 75 quartiles, with outliers at > 90 and < 10 percentiles. Note log *y*-axis.

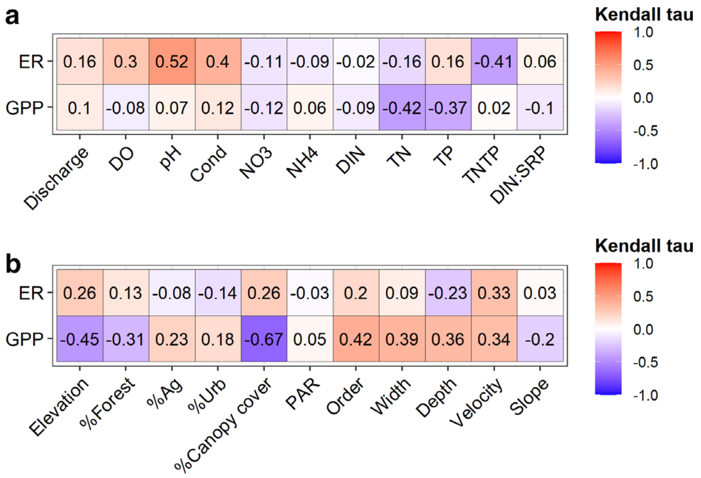

Fig. 5. Cross-correlation matrix of (**a**) chemical and (**b**) geomorphological drivers of GPP and ER. Values and colors in each box are Kendall tau, with stronger trends in richer colors and positive associations in red and negative associations in blue. Chemical and geomorphological drivers are described with units in Table 1.

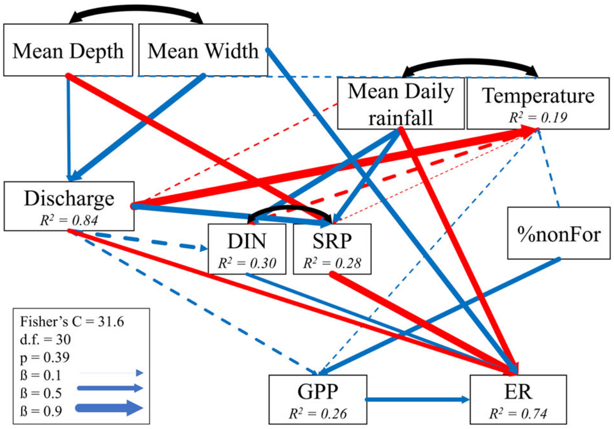

Fig. 6. Structural equation model examining the drivers of GPP and ER in tropical streams and rivers. Blue arrows indicate $ß > 0$ and red arrows $ß < 0$. Arrow size are proportional are standardized path coefficients, as indicated in the caption. Fisher C and *p* value refer to model-wide goodness of fit, where $p > 0.05$ indicates the data fit the model structure. Solid lines represent significant ($p < 0.05$) pathways and dashed lines refer to pathways with $p > 0.05$. See Table S1 for standardized and unstandardized coefficients, standard errors, sample size, and *p* values for each pathway.

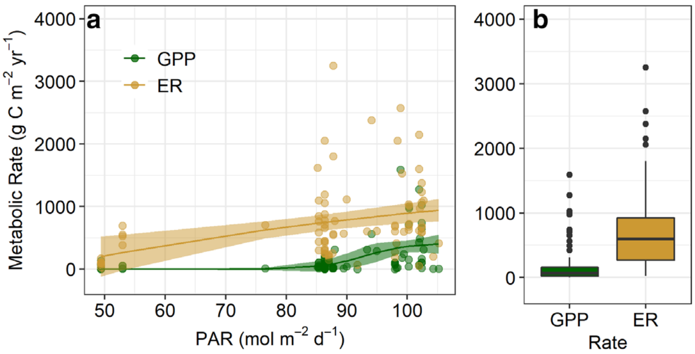

Fig. 7. (**a**) Scaled metabolic rates plotted against daily mean annual PAR for each stream in the review. Brown points are ER and green are GPP, both units as kg C m^{-2} yr^{-1}. Best fit lines represent the model with greatest AIC weight (Table 3), with 95% confidence intervals. (**b**) Boxplots of mean GPP and ER from each stream. Boxplots are median with IQR (25th to 75th percentile), and outliers are > 90th or < 10th percentiles.

Table 3. Saturation model fits for light on GPP and ER. Models are briefly summarized in each row and "Met" represents both GPP and ER as described by PAR. Models were selected by comparing AIC scores, via AIC weights. Asterisks (*) designate the best model for each GPP and ER.

	GPP		ER	
Model	**AIC**	w_i	**AIC**	w_i
Logistic: Met $\sim 1/(1 + e^{\text{PAR}})$	1169.5	0.98*	1299.5	0.13
Logarithmic: Met $\sim \log_{10}$(PAR)	1180.3	0.00	1297.4	0.38*
Linear: Met $\sim$ PAR	1178.3	0.01	1297.6	0.35
Michaelis–Menten: Met $\sim$ Met$_{\max}$PAR/PAR	1182.8	0.00	1299.3	0.14

data, in contrast to most articles that presented a few days of data for each stream. The most daily measurements came from the Daly River, Australia (n = 16), followed by two streams from Puerto Rico: Puente Roto (n = 12) and Quebrada Bisley (n = 10) (Fig. 2b), spanning multiple publications and study years. The most measurements were made in 1995 (n = 25) and 2016 (n = 24) (Fig. 1b). The majority of measurements were made in headwater or first order streams (54.9%), followed by third order (13.7%), fourth order (9.1%), and second order (5.1%); 17% of measurements did not report stream position data.

Streams were predominately heterotrophic (GPP < ER) across all regions and stream sizes (Fig. 2). Across all measurements, median GPP was 0.4 g O_2 m^{-2} d^{-1} (range 0.01--11.7 g O_2 m^{-2} d^{-1}) and median ER was –4.30 g O_2 m^{-2} d^{-1} (range –0.1 to –42.1 g O_2 m^{-2} d^{-1}). Only 13 measurements (6.3%) occurred where GPP : ER > 1. Ecosystem respiration significantly increased with GPP, but with little explanatory power ($R^2 = 0.05$, $p < 0.01$).

Hypothesized drivers explained some of the variation in GPP and ER. Watershed area was weakly related with GPP ($R^2 = 0.07$, $p = 0.08$) (Fig. 3a, Table 2), while ER showed no relation with watershed area ($R^2 = 0.01$, $p = 0.56$) (Fig. 3b, Table 2). Ecosystem respiration decreased at higher SRP ($R^2 = 0.29$, $p < 0.01$), while GPP showed no relationship ($R^2 < 0.01$, $p = 0.74$) (Table 2, Fig. 3b,f). Total annual rainfall showed no relationship with GPP ($R^2 = 0.02$, $p = 0.19$) but a negative relationship with ER ($R^2 = 0.07$, $p = 0.01$) (Fig. 3c,g, Table 2). Neither GPP ($R^2 = 0.01$, $p = 0.29$) nor ER ($R^2 < 0.01$, $p = 0.68$) were related with temperature (Fig. 3d,h). Gross primary productivity was 2.6-times greater under open (mean GPP = 2.09 g O_2 m^{-2} d^{-1}) canopies compared to closed (mean GPP = 0.57 g O_2 m^{-2} d^{-1}) canopies ($t = -4.7$, $p < 0.01$, Fig. 4), while ER in open (– 4.74 g O_2 m^{-2} d^{-1}) or closed canopies (– 6.33 g O_2 m^{-2} d^{-1}) showed less variation ($t = -1.77$, $p = 0.08$).

Less commonly reported variables reveal potential drivers of both GPP and ER as indicated by the Kendall τ correlation coefficient. Strongest physical and chemical relationships (Fig. 5a) for ER were pH ($\tau = 0.52$), TN : TP ($\tau = -0.41$), and conductivity ($\tau = 0.40$), while GPP had strongest associations with TN ($\tau = -0.42$), TP ($\tau = -0.37$), and NO_3^- ($\tau = -0.12$) (Fig. 5a). Geomorphological variables related (Fig. 5b) with ER were strongest with velocity ($\tau = 0.33$), canopy cover ($\tau = -0.26$), and elevation ($\tau = 0.26$), while GPP was associated with %canopy cover ($\tau = -0.67$), elevation ($\tau = -0.45$), and stream order ($\tau = 0.42$).

We explored both regional and site level controls of both GPP and ER with a structural equation model (Fig. 6). From the meta-model, a model was fit with strong support of the hypothesized structure with no missing pathways (Fisher's $C = 31.6$, $p = 0.39$). The model explained more variation in ER ($r^2 = 0.74$) than GPP ($r^2 = 0.26$). Strongest pathways, as measured by the standardized coefficient, for GPP was %non-forested land area ($ß = 0.51$) and discharge ($ß = 0.30$), whereas ER was driven by SRP ($ß = -0.76$) and GPP ($ß = 0.46$). Phosphorus ($r^2 = 0.46$) was linked to watershed area ($ß = 2.10$) and mean daily rainfall ($ß = -0.66$). The SEM explained most variation in discharge ($r^2 = 0.84$), and less for temperature ($r^2 = 0.19$), DIN ($r^2 = 0.30$), and SRP ($r^2 = 0.28$).

Annual estimates of ER ranged from 27.4 to 3250 g C m^{-2} yr^{-1} and GPP ranged from 1.4 to 1587.8 g C m^{-2} yr^{-1} (Fig. 7). Among the various models fitted, GPP was best explained by a logistic model ($w_i = 0.98$) and ER was best fit by a logarithmic ($w_i = 0.38$) and linear ($w_i = 0.35$) models (Table 3).

Discussion

Our main finding is the similarity of metabolic rates between tropical streams (Fig. 2c) and temperate streams (Finlay 2011; Marcarelli et al. 2011; Hoellein et al. 2013). Specifically, Hoellein et al. (2013) found 87% (189 of 217 measurements in that study) of streams with GPP : ER < 1, compared to 97% in tropical streams, based on our analyses. In tropical streams, GPP and ER were less related ($R^2 = 0.05$) than temperate streams ($R^2 = 0.23$, Hoellein et al. 2013), though regression equations had similar slopes and intercepts (this study: ER = 0.82GPP + 4.63; Hoellein et al. 2013: ER = 0.78GPP + 4.8). Streams are predominately heterotrophic, following theory that a majority of streams rely on allochthonous inputs to fuel heterotrophic food webs (Fisher and Likens 1973; Webster and Meyer 1997). Our synthesis across the tropics showed that open canopies above streams drove greater GPP (Fig. 4), as has been shown in Costa Rican streams (Ortega-Pieck et al. 2017) while ER was similar across open and closed canopy types. While the relationship between seasonal inputs of organic matter during the fall leaf abscission and ER in temperate streams has been established (Hill et al. 2001), exploration of this relationship in tropical streams is needed.

Temperature may also explain some of the differences between temperate and tropical streams. Our review spans a wide range of temperature (12.9–34°C) and warmer temperatures than from temperate streams (3.8–27.1°C, Hoellein et al. 2013). While there was no relationship between temperature and GPP or ER (Fig. 3d,h), the SEM revealed a positive effect of temperature on GPP ($ß = 0.16$) but no linkage between temperature and ER. The limited weak effect of temperature (Fig. 3h, $R^2 < 0.01$) is in contrast to biological theory (Brown et al. 2004; Yvon-Durocher et al. 2012; Williamson et al. 2016) and from a study reporting nonlinear increases as a result of warming temperatures on metabolic rates of tropical taxa (Dillon et al. 2010). In a cross-biome study of stream ecosystem metabolism, there was a weak pathway between ER and temperature (Bernot et al. 2010). The SEM identified a positive linkage between GPP and temperature ($ß = 0.16$). This relationship was not evaluated in other reviews (Bernot et al. 2010; Hoellein et al. 2013), but there is evidence for higher GPP as a result of higher N fixation caused by warmer stream temperature (Welter et al. 2015), and we suggest these indirect and multi-faceted interactions may be similarly true in tropical streams. Climate change predicts warmer stream temperatures in the tropics (0.9–3.3°C), and while we see no direct effect of temperature, there is growing evidence of shifts in productivity under warmer conditions (Padfield et al. 2017; Hood et al. 2018).

Watershed area did not drive increases in GPP as strongly as found in temperate streams (Finlay 2011; Hall et al. 2016). There was weak relationship of watershed area and GPP (Fig. 3a, Table 2). Further, the SEM identified a positive linkage of GPP to discharge ($ß = 0.30$), suggesting GPP increases with stream or river size and position downstream in a watershed, though regression analysis do not reflect this point (Fig. 3a). However, we reviewed data from primarily small streams and a few from large rivers (Fig. 3a). In temperate streams, Finlay (2011) and Hoellein et al. (2013) showed increasing GPP and ER with watershed area, across a similar range of watershed area (0.01–10,000 km^2) to this study (0.3–53,000 km^2). There were strong correlations with GPP from variables including elevation, stream order, channel width, depth, and water velocity (Fig. 5), which further support a causal relationship with river size and ecosystem metabolism, as hypothesized in the River Continuum Concept (Vannote et al. 1980) and shown empirically (Hall et al. 2016).

Stream hydrology explained some variation in GPP and ER. Annual rainfall was negatively related to ER and a negative pathway in the SEM ($ß = -0.65$), but not GPP (Fig. 3c,f). The SEM identified a strong linkage between mean daily rainfall to both discharge and temperature, as we expected. The linkage between discharge and GPP ($ß = 0.30$) may reflect the increase of GPP in larger rivers, also supported by the positive relationship between discharge and watershed area. However, these data are snapshots of measurements, and generally at low flows, when the data collection for stream ecosystem metabolism is easier. Metrics like days since last rainfall or short-term rainfall will capture rainfall driven processes (e.g., scouring, organic matter loading, turbidity) more accurately at the stream level and help resolve the relationship between rainfall and metabolism. Rainfall will likely have different effects on ecosystem metabolism depending on position in the watershed between mountainous streams (e.g., greater scouring) vs. lowland rivers (e.g., greater organic matter loading and turbidity). Turbidity was not collected in this review and is important to consider as it relates to light penetration of the water column of streams and rivers. Rainfall and precipitation regimes, including frequency and magnitude of extreme events, are expected to change under climate change, highlighting the need to better understand the relationships between rainfall, discharge, and stream ecosystem metabolism.

We did not find support for our second hypothesis that higher nutrients would lead to higher GPP and ER. First, we observed no relationship of GPP with SRP (Fig. 3b) and a negative relationship between SRP and ER (Fig. 3e). The highest SRP concentrations (250 $\mu g\ L^{-1}$) came from an agriculturally influenced streams in Costa Rica (Ortega-Pieck et al. 2017), where low ER (– 0.5 and – 0.8 $g\ O_2\ m^{-2}\ d^{-1}$) were measured relative to the overall mean ER ($ER = -6.01\ g\ O_2\ m^{-2}\ d^{-1}$) in this review. The negative relationship of ER and SRP counters research from lowland forested streams in Costa Rica, where SRP is a driver of microbial respiration (Ramírez et al. 2003), macroinvertebrate abundance (Rosemond et al. 2002), and leaf litter decomposition rates (Ardón et al. 2006) across similar hydrologic and light conditions. As each of these responses to SRP contribute to integrative ER, we would hypothesize ER to increase with SRP in these streams, but conflicts with results from agriculturally influenced streams (Ortega-Pieck et al. 2017). Decreased ER in streams with higher SRP may be the result of loading of agriculturally derived chemicals (e.g., pollutants, pesticides) and obscuring a presumed stimulatory effect of SRP. Further resolution of the relationship of SRP and ER is needed. Previous studies have had difficulty in relating stream ecosystem metabolism with nutrients (Mulholland et al. 2001; Bernot et al. 2010; Finlay 2011), in part due to small sample sizes and short temporal measurements. Empirical tests of the effects of nutrients on GPP and ER are needed in both tropical and temperate streams, and the rapid increase in the number of metabolism measurements should allow for resolution of this effect and the effects of nutrients compared to effects of hydrology and light. In a recent meta-analysis, integrated ecosystem responses (which include whole-stream measurements of GPP and ER, but also leaf decomposition rates) increased by 139% in response to N and P additions (Ardón et al. 2020).

Scaling of GPP and ER to annual rates of C fixation and respiration were similar to previous estimates from streams and rivers. The annual estimates of GPP are greater than reference streams compiled in Finlay (2011), where maximum GPP was ~ 100 g C m^{-2} d^{-1}, in contrast to the maximum GPP in tropical streams of 1600 g C m^{-2} d^{-1}, a 16-times increase. This increase is greater than the 10-fold difference between tropical and temperate stream GPP stated in Davies et al. (2008). In fact, the highest rates of GPP from tropical streams are greater than GPP reported from human-dominated (e.g., agricultural and urban) streams (~ 750 g C m^{-2} d^{-1}, Finlay 2011). Respiration followed a similar pattern, with tropical ER rates > 75th quartile (> 970 g C m^{-2} d^{-1}) from temperate streams and comparable to ER from human-dominated streams (> 1000 g C m^{-2} d^{-1}, Finlay 2011). Gross primary productivity was best explained using a logistic saturation model, whereas ER was best fit by a logarithmic model, though a linear model was similarly weighted (Table 3). This model indicates that high light conditions leads to GPP of around 550 g C m^{-2} yr^{-1} though several instances of GPP greater than this prediction are present in the data. Variance around the GPP-PAR curve is driven by site characteristics, including canopy shading of the stream surface, turbidity, nutrient limitation, and primary producer communities. The difference in model fits between GPP and ER reflect the influence of allochthonous material to fuel stream food webs. Light data in this study was collected as downward shortwave radiation and not PAR incident at the stream surface or benthos, similar to the approach of Savoy et al. (2019). Measuring light at these two scales is a fundamental difference to results from Finlay (2011), where a PAR had a linear relationship with GPP, and PAR was the main driver of GPP in those streams. While the upscaled annual rates are less dependent on differences in temperature, we note that seasonality in the tropics is dictated by rainfall, and predominance of field work during the dry season may bias our values towards those periods. Further, several streams only report 1 day of GPP and ER estimates and should further be extrapolated with caution.

While this review includes a wide range of stream measurements, large areas of the tropics remain unstudied or unpublished (Fig. 1a). Specifically, metabolism data from the Amazon basin is unrepresented, despite a large field of study on C fluxes in the Amazon (Richey et al. 2002). While this review focused on studies using the open channel methods using a one- or two-station approach, we acknowledge a wide literature of respiration estimates using bottle incubations and ^{18}O fractionation from the Amazon basin (Quay et al. 1995; Ward et al. 2013) and Australia (Bunn et al. 1999). Bunn et al. (1999) report a range of GPP (2.7–6.3 g O_2 m^{-2} d^{-1}) and ER (– 5.4 to – 12.2 g O_2 m^{-2} d^{-1}) that are similar to the estimates using open channel methods summarized in this study. Previous studies have measured CO_2 fluxes from headwater in the Amazon (Richey et al. 2002; Johnson et al. 2008), and a large fraction of CO_2 generated is from in-stream respiration (Mayorga et al. 2005), suggesting that ER in these sites could be a large flux. The threats to the Amazon basin from climate change, land use change, and dam construction in montane rivers (Anderson et al. 2018; Encalada et al. 2019) all have the potential to drive changes in ecosystem structure and function in the Amazon, and changes in metabolic rates can be potentially used as a monitoring diagnostic to indicate changes in freshwater ecosystems with greater understanding of the drivers of GPP and ER (Palmer and Febria 2012). Beyond the forested sites, more study from a broad range of urban, agricultural, montane, lowland, seasonally wet, and desert streams and rivers in the tropics will be valuable additions.

An interesting component to the studies in this review are the connection of whole-stream processes with animals. In several studies, the experimental removal of fishes and loss of tadpole populations due to fungal diseases had effects that manifested at the ecosystem level. The loss of tadpoles in headwater streams in Panama stimulated GPP 10× (0.001–0.012 g O_2 m^{-2} d^{-1}, though these values are near the measurement limits of GPP) while decreasing ER 50% (– 0.71 to – 0.32 g O_2 m^{-2} d^{-1}), and altered N uptake and cycling in the stream (Whiles et al. 2013). Experimental removal of a commonly harvested fish in Venezuela resulted in higher GPP and ER, but the increase in ER was greater than the increase in GPP and the ecosystem became more heterotrophic (Taylor et al. 2006). While these studies explicitly measured changes in metabolism due to the changes in stream biota, several studies have documented changes in C cycling and top-down control of benthic organic matter, nutrients, and algal communities in tropical streams (Pringle and Hamazaki 1997, 1998; Davies et al. 2008). We suggest merging metabolism measurements with consumer and food web studies can be a fruitful area of research (Rüegg et al. 2020), particularly in the tropics.

Our review suggests that tropical stream ecosystem metabolism is driven by similar processes as temperate streams and supports findings from previous reviews though have similar limitations of small sample sizes and coarse temporal resolution. Our data collection shows there is a growing body of metabolism data from the tropics including headwater streams to large rivers and should be included into global assessments of the effect of temperature. Climate change has the potential to affect metabolic rates in tropical streams. With predicted warmer temperatures from 0.9 to 3.3°C and wetter and more extreme seasonal rainfall in the tropics (Collins et al. 2013), it remains unclear how metabolic rates will respond. Our results suggest the rapid depletions in forest cover across the tropics in favor of open canopy agriculture or grazing land suggest faster C release (ER) compared to C capture (GPP) from tropical streams.

References

Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958-2015. Sci. Data **5**: 1–12. doi:10.1038/sdata.2017.191

Allan, J. D. 2004. Landscapes and Riverscapes: The influence of land use on stream ecosystems. Annu. Rev. Ecol. Evol. Syst. **35**: 257–284. doi:10.1146/annurev.ecolsys.35.120202.110122

Anderson, E. P., C. N. Jenkins, S. Heilpern, et al. 2018. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. Sci. Adv. **4**: 1–8. doi:10.1126/sciadv.aao1642

Appling, A. P., R. O. Hall, C. B. Yackulic, and M. Arroita. 2018. Overcoming equifinality: Leveraging long time series for stream metabolism estimation. J. Geophys. Res. Biogeo. **123**: 624–645. doi:10.1002/2017jg004140

Ardón, M., L. A. Stallcup, and C. M. Pringle. 2006. Does leaf quality mediate the stimulation of leaf breakdown by phosphorus in Neotropical streams? Freshw. Biol. **51**: 618–633. doi:10.1111/j.1365-2427.2006.01515.x

Ardón, M., L. H. Meglin, R. M. Utz, et al. 2020. Experimental nitrogen and phosphorus enrichment stimulates multiple trophic levels of algal and detrital-based food webs: A global meta-analyses from streams and rivers. Biol. Rev. doi:10.1111/brv.12673

Bernot, M. J., J. L. Tank, T. V. Royer, and M. B. David. 2006. Nutrient uptake in streams draining agricultural catchments of the midwestern United States. Freshw. Biol. **51**: 499–509. doi:10.1111/j.1365-2427.2006.01508.x

Bernot, M. J., D. J. Sobota, R. O. Hall, and others. 2010. Interregional comparison of land-use effects on stream metabolism. Freshw. Biol. **55**: 1874–1890. doi:10.1111/j.1365-2427.2010.02422.x

Boulton, A. J., L. Boyero, A. P. Covich, M. Dobson, S. Lake, and R. Pearson. 2008. Are tropical streams ecologically different from temperate streams? p. 257–284.*In* Tropical stream ecology. Elsevier.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**: 1771–1789.

Bunn, S. E., P. M. Davies, and T. D. Mosisch. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshw. Biol. **41**: 333–345.

Collins, M., R. Knutti, J. Arblaster, and others. 2013. Long-term climate change: Projections, commitments and irreversibility. *In* T. F. Stocker, D. Qin, G.-K. Plattner, et al. [eds.], Climate change 2013 the physical science basis: Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press.

Davies, P. M., S. E. Bunn, S. K. Hamilton, and D. David. 2008. Primary production in tropical streams and rivers, p. 23–42. *In* D. Dudgeon [ed.], Tropical stream ecology. Elsevier.

Demars, B. O. L., G. M. Gíslason, J. S. Ólafsson, J. R. Manson, N. Friberg, J. M. Hood, J. J. D. Thompson, and T. E. Freitag. 2016. Impact of warming on CO2 emissions from streams countered by aquatic photosynthesis. Nat. Geosci. **9**: 758–761.

Dillon, M. E., G. Wang, and R. B. Huey. 2010. Global metabolic impacts of recent climate warming. Nature **467**: 704–706. doi:10.1038/nature09407

Dodds, W. K., and V. H. Smith. 2016. Nitrogen, phosphorus, and eutrophication in streams. Inl. Waters **6**: 155–164. doi:10.5268/IW-6.2.909

Dodds, W. K., L. Bruckerhoff, D. Batzer, et al. 2019. The freshwater biome gradient framework: Predicting macroscale properties based on latitude, altitude, and precipitation. Ecosphere **10**: 1–33. doi:10.1002/ecs2.2786

Encalada, A. C., A. S. Flecker, N. L. Poff, and others. 2019. A global perspective on tropical montane rivers. Science **365**: 1124–1129. doi:10.1126/science.aax1682

Finlay, J. C. 2011. Stream size and human influences on ecosystem production in river networks. Ecosphere **2**: art87. doi:10.1890/es11-00071.1

Fisher, S. G., and G. E. Likens. 1973. Energy flow in bear brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecol. Monogr. **43**: 421–439.

Grace, M. R., D. P. Giling, S. Hladyz, V. Caron, R. M. Thompson, and R. Mac Nally. 2015. Fast processing of diel oxygen curves: Estimating stream metabolism with base (BAyesian single-station estimation). Limnol. Oceanogr. Methods **13**: 103–114. doi:10.1002/lom.10011

Hall, R. O., and E. R. Hotchkiss. 2017. Stream metabolism, p. 219–233.*In* G. A. Lamberti and F. R. Hauer [eds.], Methods in stream ecology, Vol. 2: Ecosystem function, 3rd ed. Academic Press Ltd-Elsevier Science Ltd.

Hall, R. O., and A. J. Ulseth. 2020. Gas exchange in streams and rivers. Wiley Interdiscip. Rev. Water **7**: e1391.

Hall, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems **19**: 73–86. doi:10.1007/s10021-015-9918-1

Hawkins, B. A. 2001. Ecology's oldest pattern? Trends Ecol. Evol. **16**: 470. doi:10.1016/s0169-5347(01)02197-8

Hill, W. R., P. J. Mulholland, and E. R. Marzolf. 2001. Stream ecosystem responses to forest leaf emergence in spring. Ecology **82**: 2306–2319.

Hoellein, T. J., D. A. Bruesewitz, and D. C. Richardson. 2013. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. Limnol. Oceanogr. **58**: 2089–2100. doi:10.4319/lo.2013.58.6.2089

Holtgrieve, G. W., D. E. Schindler, T. A. Branch, and Z. Teresa A'Mar. 2010. Simultaneous quantification of aquatic ecosystem metabolism and reaeration using a Bayesian statistical model of oxygen dynamics. Limnol. Oceanogr. **55**: 1047–1063. doi:10.4319/lo.2010.55.3.1047

Hood, J. M., J. P. Benstead, W. F. Cross, and others. 2018. Increased resource use efficiency amplifies positive response of aquatic primary production to experimental warming. Glob. Chang. Biol. **24**: 1069–1084. doi:10.1111/gcb.13912

Huntington, J. L., K. C. Hegewisch, B. Daudert, C. G. Morton, J. T. Abatzoglou, D. J. McEvoy, and T. Erickson. 2017.

Climate engine: Cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bull. Am. Meteorol. Soc. **98**: 2397–2410.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. Am. Nat. **101**: 233–249.

Johnson, M. S., J. Lehmann, S. J. Riha, A. V. Krusche, J. E. Richey, J. P. H. B. Ometto, and E. G. Couto. 2008. CO_2 efflux from Amazonian headwater streams represents a significant fate for deep soil respiration. Geophys. Res. Lett. **35**: L17401. doi:10.1029/2008gl034619

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. **7**: 573–579. doi:10.1111/2041-210X.12512

Lefcheck, J. S. 2019. Structural equation modeling in R for ecology and evolution.

Lewis, W. M. 1988. Primary production in the Orinoco River. Ecology **69**: 679–692.

Lewis, W. M. 2008. Physical and chemical features of tropical flowing waters, p. 1–21. *In* Tropical stream ecology. Academic Press.

Marcarelli, A. M., C. V. Baxter, M. M. Mineau, and R. O. Hall. 2011. Quantity and quality: Unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology **92**: 1215–1225.

Marzolf, E. R., P. J. Mulholland, and A. D. Steinman. 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole stream metabolism in small streams. Can. J. Fish. Aquat. Sci. **51**: 1591–1599.

Mayorga, E., A. K. Aufdenkampe, C. A. Masiello, A. V. Krusche, J. I. Hedges, P. D. Quay, J. E. Richey, and T. A. Brown. 2005. Young organic matter as a source of carbon dioxide outgassing from Amazonian rivers. Nature **436**: 538–541. doi:10.1038/nature03880

Mayorga, E., S. P. Seitzinger, J. A. Harrison, and others. 2010. Global nutrient export from WaterSheds 2 (NEWS 2): Model development and implementation. Environ. Model. Software **25**: 837–853. doi:10.1016/j.envsoft.2010.01.007

Mulholland, P. J., C. S. Fellows, J. L. Tank, and others. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshw. Biol. **46**: 1503–1517.

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. **1**: 102–117.

Ortega-Pieck, A., A. K. Fremier, and C. H. Orr. 2017. Agricultural influences on the magnitude of stream metabolism in humid tropical headwater streams. Hydrobiologia **799**: 49–64. doi:10.1007/s10750-017-3204-5

Paaby, P., and C. R. Goldman. 1992. Chlorophyll, primary productivity, and respiration in a lowland Costa Rican stream. Rev. Biol. Trop. **40**: 185–198.

Padfield, D., C. Lowe, A. Buckling, R. Ffrench-Constant, S. Jennings, F. Shelley, J. S. Ólafsson, and G. Yvon-Durocher. 2017. Metabolic compensation constrains the temperature dependence of gross primary production. Ecol. Lett. **20**: 1250–1260. doi:10.1111/ele.12820

Paerl, H. W., J. T. Scott, M. J. McCarthy, and others. 2016. It takes two to tango: When and where dual nutrient (N & P) reductions are needed to protect lakes and downstream ecosystems. Environ. Sci. Technol. **50**: 10805–10813. doi:10.1021/acs.est.6b02575

Palmer, M. A., and C. M. Febria. 2012. The heartbeat of ecosystems. Science **336**: 1393–1394. doi:10.1126/science.1223250

Pringle, C. M., and T. Hamazaki. 1997. Effects of fishes on algal response to storms in a tropical stream. Ecology **78**: 2432–2442.

Pringle, C. M., and T. Hamazaki. 1998. The role of omnivory in a Neotropical stream: Separating diurnal and nocturnal effects. Ecology **79**: 269–280.

Pringle, C. M., P. Paaby-Hansen, P. D. Vaux, and C. R. Goldman. 1986. In situ nutrient assays of periphyton growth in a lowland costa Rican stream. Hydrobiologia **134**: 207–213.

Polato, N. R., B. A. Gill, A. A. Shah, and others. 2018. Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. Proceedings of the National Academy of Sciences **115**: 12471–12476. doi:10.1073/pnas.1809326115

Quay, P. D., D. 0. Wilbur, J. E. Richey, A. H. Devol, R. Benner, and B. R. Forsberg. 1995. The 18O:16O of dissolved oxygen in rivers and lakes in the Amazon Basin: Determining the ratio of respiration to photosynthesis rates in freshwaters. Limnol. Oceanogr. **40**: 718–729. doi:10.4319/lo.1995.40.4.0718

R Core Team. 2019. R: A language and environment for statistical computer.

Ramírez, A., C. M. Pringle, and L. Molina. 2003. Effects of stream phosphorus levels on microbial respiration. Freshw. Biol. **48**: 88–97.

Ramírez, A., M. Ardón, M. Douglas, and M. Graça. 2015. Tropical freshwater sciences: An overview of ongoing tropical research. Freshw. Sci. **34**: 606–608.

Raymond, P. A., C. J. Zappa, D. Butman, and others. 2012. Scaling the gas transfer velocity and hydraulic geometry in streams and small rivers. Limnol. Oceanogr. Fluids Environ. **2**: 41–53. doi:10.1215/21573689-1597669

Richey, J. E., J. M. Melack, A. K. Aufdenkampe, V. M. Ballestter, and L. L. Hess. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature **416**: 617–620.

Ritz, C., F. Baty, J. C. Streibig, and D. Gerhard. 2015. Dose-response analysis using R. PLoS One **10**: e0146021.

Riveros-Iregui, D. A., T. P. Covino, and R. González-Pinzón. 2018. The importance of and need for rapid hydrologic assessments in Latin America. Hydrol. Process. **32**: 2441–2451. doi:10.1002/hyp.13163

Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems **10**: 588–606.

Rohatgi, A. 2019. WebPlotDigitizer.

Rosemond, A. D., C. M. Pringle, A. Ramírez, M. J. Paul, and J. L. Meyer. 2002. Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. Limnol. Oceanogr. **47**: 278–289.

Rüegg, J., C. C. Conn, E. P. Anderson, et al. 2020. Thinking like a consumer: Linking aquatic basal metabolism and consumer dynamics. Limnol. Oceanogr. Lett. 1–17. doi:10.1002/lol2.10172

Sager, J. C., and J. C. McFarlane. 1997. Radiation, p. 1–29. *In* R. W. Langhans and T. W. Tibbitts [eds.], Plant growth chamber handbook. Iowa State University.

Saha, S., S. Moorthi, X. Wu, and others. 2014. The NCEP climate forecast system version 2. J. Climate **27**: 2185–2208. doi:10.1175/JCLI-D-12-00823.1

Savoy, P., A. P. Appling, J. B. Heffernan, E. G. Stets, J. S. Read, J. W. Harvey, and E. S. Bernhardt. 2019. Metabolic rhythms in flowing waters: An approach for classifying river productivity regimes. Limnology and Oceanography **64**: 1835–1851. doi:10.1002/lno.11154

Song, C., W. K. Dodds, J. Rüegg, and others. 2018. Continental-scale decrease in net primary productivity in streams due to climate warming. Nat. Geosci. **11**: 415–420. doi:10.1038/s41561-018-0125-5

Taylor, B. W., A. S. Flecker, and R. O. Hall Jr. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. Science **313**: 833–836.

Townsend, A. R., G. P. Asner, and C. C. Cleveland. 2008. The biogeochemical heterogeneity of tropical forests. Trends Ecol. Evol. **23**: 424–431. doi:10.1016/j.tree.2008.04.009

Townsend, A. R., C. C. Cleveland, B. Z. Houlton, C. B. Alden, and J. W. C. White. 2011. Multi-element regulation of the tropical forest carbon cycle. Front. Ecol. Environ. **9**: 9–17. doi:10.1890/100047

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**: 130–137.

Vlah, M., and Berdanier. 2020. StreamPULSE: run stream metabolism models on StreamPULSE data.

Ward, N. D., R. G. Keil, P. M. Medeiros, and others. 2013. Degradation of terrestrially derived macromolecules in the Amazon River. Nat. Geosci. **6**: 530–533. doi:10.1038/ngeo1817

Webster, J. R., and J. L. Meyer. 1997. Organic matter budgets for streams: A synthesis. J. North Am. Benthol. Soc. **16**: 141–161.

Welter, J. R., J. P. Benstead, W. F. Cross, J. M. Hood, A. D. Huryn, P. W. Johnson, and T. J. Williamson. 2015. Does N_2 fixation amplify the temperature dependence of ecosystem metabolism? Ecology **96**: 603–610. doi:10.1890/14-1667.1

Whiles, M. R., R. O. Hall, W. K. Dodds, and others. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. Ecosystems **16**: 146–157. doi:10.1007/s10021-012-9602-7

Williamson, T. J., W. F. Cross, J. P. Benstead, G. M. Gíslason, J. M. Hood, A. D. Huryn, P. W. Johnson, and J. R. Welter. 2016. Warming alters coupled carbon and nutrient cycles in experimental streams. Glob. Chang. Biol. **22**: 2152–2164. doi:10.1111/gcb.13205

Yvon-Durocher, G., J. M. Caffrey, A. Cescatti, and others. 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature **487**: 472–476. doi:10.1038/nature11205

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Conflict of Interest

None declared.

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