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DINÁMICA TRÓFICA DE LOS MACROINVERTEBRADOS BENTÓNICOS EN ARROYOS TROPICALES DE LA SUBCUENCA DEL RÍO LACANTÚN

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PRESENTA:
DANIELA CORTÉS GUZMÁN

TUTOR PRINCIPAL:
DR. JAVIER ALCOCER
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNAM
COMITÉ TUTOR:
DR. FERNANDO ÁLVAREZ
INSTITUTO DE BIOLOGÍA, UNAM
DR. ATILANO CONTRERAS
INSTITUTO DE BIOLOGÍA, UNAM

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Índice

Resumen

La estacionalidad tropical influye en la hidrología de los arroyos, la cual, a su vez, podría modificar la disponibilidad de la materia orgánica, con consecuencias para la estructura de la red trófica. En arroyos tropicales boscosos de primer orden, se espera una variación estacional en la fuente de energía, es decir, un aumento de la ruta energética autotrófica en la temporada de secas y un aumento de la ruta energética basada en detritos en la temporada de lluvias; sin embargo, dicha variación ha sido poco estudiada. En este estudio, nuestro objetivo fue definir la estructura trófica de los macroinvertebrados bentónicos y su dinámica anual relacionada con la disponibilidad estacional de recursos autotróficos y detritos en dos arroyos tropicales boscosos de primer orden de la subcuenca del Río Lacantún en México. Evaluamos la variación estacional en los almacenes y aportes de materia orgánica y su relación con el metabolismo ecosistémico. También evaluamos la dinámica de los grupos funcionales tróficos (GFT), su relación con la variación estacional de recursos tróficos y los rasgos ecosistémicos derivados de las proporciones de los GFT. Finalmente, identificamos la ruta energética de la red trófica de macroinvertebrados y la variación estacional de la estructura trófica. Encontramos una variación estacional en los almacenes y aportes de materia orgánica relacionada a la estacionalidad tropical. La materia orgánica disuelta y el seston aumentaron en la temporada de lluvias, mientras que los productores primarios bentónicos y la hojarasca aumentaron en la temporada de secas. La producción primaria bruta aumentó en la temporada de secas, mientras que la respiración ecosistémica no varió estacionalmente. La biomasa de los GFT varió estacionalmente. La biomasa de los GFT herbívoros incrementó en la temporada de secas correlacionada con el aumento en la disponibilidad de recursos autotróficos y la asimilación global de recursos tróficos autotróficos aumentó en la misma temporada. La biomasa de los GFT detritívoros no se correlacionó con la disponibilidad de detritos y la asimilación global de los detritos no varió estacionalmente. Los rasgos ecosistémicos —autotrofía/heterotrofia, interacción con el ambiente ribereño, estabilidad del sustrato, control por depredación— no variaron estacionalmente, asociado a la dominancia de los raspadores, trituradores y depredadores durante todo el año. La red trófica de los macroinvertebrados bentónicos presentó cuatro niveles, una estructura por tallas poco desarrollada y una frecuencia alta de omnivoría. Concluimos que la estacionalidad definida por el patrón de precipitación y su efecto en la hidrología de los arroyos son los principales factores que influyen en la dinámica de la materia orgánica en arroyos tropicales. La variación estacional de los recursos tróficos, a su vez, influye en la red trófica de los macroinvertebrados, la cual se basa principalmente en recursos autotróficos. La importancia relativa de los autótrofos en la red trófica es alta comparada con los detritos, debido a que una menor biomasa de algas sostiene igual o mayor biomasa de macroinvertebrados, especialmente en la temporada de secas. Sin embargo, la frecuencia alta de omnivoría reduce los cambios estacionales en la estructura trófica. Nuestros resultados sugieren que la materia orgánica autotrófica tiene un papel importante para mantener la red trófica de macroinvertebrados en arroyos tropicales boscosos de primer orden. Los modelos ecológicos clásicos desarrollados en arroyos templados y que sugieren que los arroyos de primer orden se basan principalmente en detritos no se pueden extrapolar directamente a los arroyos tropicales. Finalmente, cambios en el clima que modifiquen la hidrología de los arroyos y la disponibilidad de los recursos tróficos autotróficos podrían afectar de forma importante las redes tróficas de metazoos.

Abstract

Tropical seasonality influences stream hydrology, which in turn, modifies the availability of organic matter, with consequences for the food web structure. In tropical first-order forest streams, a seasonal alternation in the energy source, i.e., an increase in the autotrophic energy source in the dry season and an increase in the detrital energy source in the rainy season, is expected but remains unclear. In this study, we aimed to define the trophic structure of the benthic macroinvertebrates and their annual dynamics related to the seasonal availability of autotrophic and detrital food resources in two tropical first-order forest streams in the Lacantun River subbasin in Mexico. We assessed the seasonal variation of the organic matter stock and input and its relationship with stream metabolism. We also assessed the functional feeding group (FFG) dynamics, their relationship with the seasonal availability of food resources, and the ecosystem traits surrogated from the FFG ratios. Finally, we identified the trophic pathway of the benthic macroinvertebrate food web and the seasonal variation of the trophic structure. We found seasonal variation in organic matter stock and input related to tropical seasonality. Dissolved organic matter and seston increased in the rainy season, while benthic primary producers and leaf litter increased in the dry season. Gross primary production increased in the dry season, while ecosystem respiration did not differ between seasons. FFG biomass varied seasonally. The biomass of herbivore-FFG increased in the dry season correlated to their autotrophic food resources, and the overall assimilation of the autotrophic pathway increased in the dry season. The biomass of detritivore-FFG did not correlate to the detrital food resources, and the overall assimilation of the detrital pathway did not differ between seasons. Stream ecosystem traits —autotrophy/heterotrophy, interaction with the riparian environment, substrate stability, and top-down control— did not differ between seasons and were associated with a dominance of scrapers, shredders, and predators throughout the year. The benthic macroinvertebrate food web had four levels, a poorly developed size structure, and an important degree of omnivory in both streams and both seasons. We concluded that seasonality defined by the rainfall pattern and its effect on stream hydrology are the main drivers of organic matter dynamics in tropical streams. The seasonal variation of food resources influences the benthic macroinvertebrate food web, which relies significantly on autotrophic food resources. The relative importance of autotrophs on the food web in higher than detritus since a much lower algal biomass sustained equal or higher macroinvertebrate biomass, particularly in the dry season. However, the high frequency of omnivory reduced the seasonal changes in the food web structure. Our results suggest that the autotrophic organic matter plays an important role in maintaining the benthic macroinvertebrate food web in tropical first-order forest streams. The classical ecological stream models that suggest first-order temperate streams rely on detrital food resources do not directly extrapolate to tropical stream ecosystems. Instead, climate changes that may modify the hydrology of streams and the availability of autotrophic food resources are expected to greatly affect metazoan food webs.

Introducción general

Los procesos de flujo de materia y energía regulan el funcionamiento y determinan la dinámica de los ecosistemas acuáticos. El paisaje geomorfológico terrestre y las características particulares del ecosistema influyen en las interacciones bióticas que integran las comunidades acuáticas, que a su vez expresan los flujos por medio de las redes tróficas. A escala regional, los patrones climáticos y la geomorfología de la cuenca son los factores principales que influyen en los procesos de flujo de materia y energía (Barnes y Minshall 1983).

Los ecosistemas fluviales tropicales se encuentran dominados principalmente por los patrones de precipitación y temperatura (Lewis 2008). La irradiancia en la zona tropical es mayor que en las zonas templadas y polares, pero la variación anual de la temperatura es reducida. Por el contrario, la precipitación presenta patrones estacionales que determinan los procesos de escorrentía, el almacenamiento en los suelos y depósitos subterráneos, y el caudal de los ríos (Likens 2009). Los patrones estacionales de precipitación dentro de la zona tropical se pueden explicar por la circulación de las celdas de Hadley y la migración de la Zona de Convergencia Intertropical (Syvitski et al. 2014).

La geomorfología y la geología de la cuenca influyen en la química del agua, las características del sustrato, los contornos batimétricos, la velocidad del agua y el transporte de materiales (Wetzel 2001). El flujo del agua, en particular, modifica las características del hábitat para la biota, por lo cual influye directamente en la presencia, abundancia y distribución espacial y temporal de los organismos (Likens 2009). La química del agua y el transporte de materiales distribuyen los nutrientes disponibles en el ecosistema, influyendo a su vez en la producción primaria (Likens 2009). Los contornos batimétricos y las características del bosque ribereño determinan las interacciones y el flujo de materiales con el ambiente terrestre (Naiman et al. 2005).

Las redes tróficas son fundamentales para describir los flujos de materia y energía entre las comunidades (Douglas et al. 2005). Las redes de los sistemas lóticos tienden a ser complejas (gran cantidad de enlaces), anchas y cortas (pocos niveles tróficos) (Shurin et al. 2006, Thompson et al. 2007). Tradicionalmente, se ha sugerido que dicha estructura se debe a la dependencia de los organismos de los ríos en los detritos, lo que deriva en una baja eficiencia de transferencia energética (Vannote et al. 1980, Briand 1985). La noción de que los ríos de primeros órdenes (1-3) son predominantemente heterotróficos y dependientes de los detritos alóctonos está relativamente bien establecida para latitudes templadas. Por el contrario, los estudios de ríos en zonas tropicales sugieren que las relaciones tróficas difieren de las templadas en que, al parecer, tienen un aporte autóctono significativo (Douglas et al. 2005, Dudgeon et al. 2010, Frauendorf et al. 2013).

Los estudios realizados en ríos han derivado en el desarrollo de modelos conceptuales que, de forma general, abarcan los principales patrones de funcionamiento de estos cuerpos de agua. El *Concepto del Río Continuo* ("The River Continuum Concept", Vannote et al. 1980) plantea cambios en la proporción de grupos funcionales tróficos de invertebrados y peces, así como en el balance metabólico del ecosistema en el eje longitudinal del río. Para los ríos de primeros órdenes (1-3) se propone un metabolismo fuertemente heterotrófico, pues son sistemas que dependen principalmente de las entradas de materia orgánica del bosque ribereño. Así pues, las redes tróficas en estos sistemas serían anchas y cortas, con baja eficiencia en la transferencia energética.

Posteriormente, el *Concepto del Pulso de Inundación* ("The Flood Pulse Concept", Junk et al. 1989) se enfoca en la interacción de los ríos con su planicie de inundación, que se convierte en la fuente de materia orgánica principal para los ecosistemas acuáticos. Bajo esta propuesta, los ríos de primeros órdenes sostienen redes cortas y simples, pues están sujetos a pulsos de descargas de agua cortos e impredecibles que impiden la adaptación de los organismos y, asimismo, generan ambientes pobres en nutrientes. Estos disturbios restablecen el ambiente físico y biológico, lo que obliga a los organismos a permanecer en la zona central del canal más que en la zona de transición acuática/terrestre donde ocurren la mayoría de las transferencias de energía y materia.

Una perspectiva distinta frente al funcionamiento de los ríos se propuso con la *Síntesis del Ecosistema Fluvial* ("The Riverine Ecosystem Synthesis", Thorp et al. 2006). En este modelo se plantea que un río está compuesto por numerosos "parches" dinámicos de distinta composición y tamaño, que están regulados por factores de variabilidad temporal y del flujo. Las comunidades biológicas reflejan la naturaleza de estos procesos funcionales, de forma que, en los ríos de primeros órdenes, la fuente de energía principal que soporta la red trófica de metazoos parece ser una combinación de producción primaria autóctona y entradas alóctonas.

Finalmente, el *Concepto de Onda del Río* ("The River Wave Concept", Humphries et al. 2014) propone que los procesos funcionales del río dependen de las condiciones dinámicas del flujo, similar al comportamiento de una onda. En congruencia con el modelo de la *Síntesis del Ecosistema Ribereño*, se propone que en condiciones de flujo base, la red trófica de metazoos se basa en una combinación de producción primaria autóctona y entradas alóctonas. Por el contrario, durante las temporadas de flujo alto, las entradas alóctonas predominan y soportan de forma exclusiva la red trófica.

En ecosistemas lóticos tropicales, los fuertes cambios del nivel del agua (temporadas de lluvias y estiaje) generan cambios importantes en la disponibilidad de hábitat, en las fuentes de producción primaria y en la abundancia y composición de los recursos y los consumidores (Douglas et al. 2005). Por consiguiente, se esperaría que la estructura de las redes tróficas presentara una dinámica estacional asociada a la dinámica hidrológica. Los productores primarios en arroyos de primeros órdenes se ven afectados por las fluctuaciones en las variables ambientales y, por consiguiente, deben adaptarse a un ambiente particularmente inestable. En regiones tropicales y subtropicales las temporadas con menos precipitación son las de mayor diversidad, abundancia y crecimiento de los productores primarios lóticos macroscópicos, especialmente las macroalgas (Branco et al. 2014), lo que implica una variación estacional en la disponibilidad de estos organismos como recurso para los consumidores de la red trófica.

Las entradas de materia orgánica terrestre —alóctona— a los arroyos también varían estacionalmente, pues dependen del clima, del tipo de vegetación, de la fenología de las especies dominantes (Zhang et al. 2014), de la edad de los árboles y de la morfología del canal, entre otros (Lisboa et al. 2015). La proporción y disponibilidad de las fuentes de detritos alóctonos —materia orgánica terrestre— y autotróficas autóctonas —productores primarios acuáticos— de carbono presente en el ecosistema controlan la estructura de las comunidades acuáticas.

Los estudios comparativos de redes tróficas usualmente emplean información “estática”, que integra especies y enlaces sin un contexto temporal específico. Sin embargo, las redes tróficas son dinámicas y sus taxones, enlaces y estructura cambian en el tiempo (Woodward et al. 2005). A pesar de que estos aspectos son clave para responder preguntas específicas, por ejemplo, la respuesta de las propiedades de las redes tróficas a las perturbaciones

(Thompson et al. 2012), aún no son bien entendidos. Los estudios temporalmente puntuales no logran incorporar los efectos potenciales de la variabilidad climática, que son especialmente críticos en ambientes con una alta variabilidad inter e intra-anual en los recursos tróficos y los consumidores (García et al. 2017).

Algunos estudios realizados en arroyos de primeros órdenes de zonas boscosas tropicales han encontrado una prevalencia de los detritos alóctonos como base de las redes tróficas (Cheshire et al. 2005, Tomanova et al. 2007, Masese et al. 2014, Neres-Lima et al. 2017, Aguiar et al. 2018). Sin embargo, estos estudios se realizaron con base en análisis de contenidos estomacales, que evalúa el consumo y no directamente la asimilación de los recursos. Por otro lado, otro grupo de estudios en arroyos tropicales han encontrado que la producción primaria autóctona es la fuente principal de materia orgánica en la red trófica de metazoos (March y Pringle 2003, Brito et al. 2006, Li y Dudgeon 2008, Dudgeon et al. 2010, Neres-Lima et al. 2016). Estos últimos se realizaron con base en el análisis de isótopos estables, por lo cual evalúan efectivamente la asimilación de recursos. A pesar de lo anterior, éstos no tienen en cuenta la variación estacional, pues se realizaron solamente en temporada de secas o flujo bajo. Por lo anterior, la variación estacional de las fuentes de materia orgánica en arroyos tropicales de primer orden sigue sin evaluarse a fondo.

Los invertebrados acuáticos son los componentes principales “ideales” para entender la estructura trófica en los ríos de primeros órdenes (Cummins 1973). Los macroinvertebrados (>500 μm) en particular, porque son altamente diversos en los arroyos y porque la mayoría son bentónicos. Su diversidad taxonómica incluye cinco filos de organismos: platelmintos, nemátodos, anélidos, moluscos y artrópodos, de los cuales éstos últimos muestran una diversidad particularmente alta en los ríos. También presentan una diversidad funcional alta, que se ha expresado mediante la designación de grupos funcionales tróficos —GFT—

(Cummins 1974), una aproximación que clasifica a los macroinvertebrados en función de sus estrategias tróficas. Estos organismos representan un enlace fundamental entre las fuentes de materia orgánica y los vertebrados acuáticos (Hauer y Resh 2017). En parte por su diversidad y su ubicuidad, y en parte por su importancia ecológica, los macroinvertebrados bentónicos forman parte central de la ecología fluvial (Cummins 1974, Giersch et al. 2015).

El objetivo principal del presente estudio fue definir la estructura de la red trófica de macroinvertebrados bentónicos y su dinámica anual en relación con la variación estacional (épocas de secas y lluvias) en la disponibilidad de recursos autotróficos autóctonos y detritos alóctonos en dos arroyos tropicales de primer orden de la subcuenca del Río Lacantún, Chiapas, México.

Se plantearon los siguientes objetivos específicos con sus respectivas hipótesis:

1. Cuantificar los almacenes y entradas de materia orgánica alóctona y autóctona, su variación estacional y su relación con el metabolismo ecosistémico

I. La materia orgánica se correlacionará con la estacionalidad tropical. La biomasa de los productores primarios bentónicos y la hojarasca en el canal aumentará en la temporada de secas correlacionada con una disminución en el caudal y la turbidez del agua. La materia orgánica disuelta, el seston y los aportes de hojarasca aumentarán en la temporada de lluvias correlacionada con las lluvias de alta intensidad y la escorrentía.

II. El metabolismo ecosistémico (producción primaria bruta, PPB, y respiración ecosistémica, RE) reflejarán los cambios en la disponibilidad de materia orgánica. La PPB se correlacionará con la abundancia de productores primarios bentónicos en la temporada de secas, mientras que la RE reflejará los cambios en la hojarasca del canal que incrementa en la temporada de secas.

2. Evaluar la dinámica anual de los grupos funcionales tróficos (GFT) de los macroinvertebrados bentónicos, su relación con la variación estacional en la disponibilidad de recursos autotróficos y detritos, y la variación en los rasgos ecosistémicos derivados de las proporciones de los GFT.

I. Los GFT herbívoros constituirán la biomasa dominante en la temporada de secas, correlacionado con el aumento en los productores primarios bentónicos. Los GFT detritívoros constituirán la biomasa dominante en la temporada de lluvias, cuando los recursos autotróficos se encuentran en menor disponibilidad y dominan los detritos.

II. Los rasgos ecosistémicos variarán estacionalmente. En la temporada de secas, la dominancia de herbívoros indicará autotrofia, la interacción con el ambiente ribereño será débil, y predominará la materia orgánica particulada fina bentónica. En temporada de lluvias, la dominancia de detritívoros indicará heterotrofia, la interacción con el ambiente ribereño se fortalecerá y predominará la materia orgánica particulada fina en transporte.

3. Identificar la ruta trófica dominante, autotrófica o detritívora, su variación estacional y su efecto sobre la estructura trófica de la comunidad de macroinvertebrados bentónicos.

I. En la temporada de secas, aumentará la biomasa de macroinvertebrados soportada por la ruta autotrófica, cuando aumenta la biomasa de productores primarios bentónicos. El aumento en la asimilación de recursos autotróficos resultará en un mayor número de niveles tróficos (máxima posición trófica), un mayor desarrollo de la estructura por tallas y una mayor frecuencia de omnivoría, comparado con la temporada de lluvias.

Las metas se abordaron, de forma correspondiente, en los siguientes capítulos:

Capítulo 1: Estacionalidad de la materia orgánica y metabolismo ecosistémico en dos arroyos tropicales de primer orden (*Organic matter seasonality and ecosystem metabolism in two tropical first-order streams*)

Capítulo 2: Macroinvertebrados bentónicos de arroyos tropicales: diversidad funcional trófica del Río Lacantún, México (*Benthic macroinvertebrates of tropical streams: functional and trophic diversity of the Lacantún River, Mexico*)

Capítulo 3: Los autótrofos contribuyen de forma importante a la red trófica de macroinvertebrados bentónicos en dos arroyos tropicales boscosos de primer orden (*Autotrophs are important contributors to benthic macroinvertebrate food webs in two tropical fist-order forest streams*)

Discusión general

Capítulo 1: Estacionalidad de la materia orgánica y metabolismo ecosistémico en dos arroyos tropicales de primer orden

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Organic matter seasonality and ecosystem metabolism in two tropical first-order streams

Daniela Cortés Guzmán[1], Javier Alcocer[2,*], José Daniel Cuevas Lara[1], Ismael Soria Reinoso[1], Luis A. Oseguera[2] and Martín Merino-Ibarra[3]

[1] Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Universidad 3000, Ciudad de México 04510, México.
[2] Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Estado de México 54090, México.
[3] Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Universidad 3000, Ciudad de México 04510, México.

[*] Corresponding author: jalcocer@unam.mx

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ABSTRACT

Organic matter seasonality and ecosystem metabolism in two tropical first-order streams

Dissolved and particulate organic matter are the energy source for secondary production in forested streams. Cycling of organic matter and stream ecosystem functioning are linked to organic matter input and storage capacity and timing. This study assessed the seasonal variation (dry and rainy seasons) of environmental parameters, organic matter stock and input, and stream metabolism in two first-order tropical streams in the Selva Lacandona, Mexico. We also aimed to identify the drivers of organic matter and stream metabolism seasonality. We found seasonal variation in organic matter stock and input correlated with tropical seasonality. Dissolved organic matter and seston increased in the rainy season, while benthic primary producers and leaf litter stock and input increased in the dry season correlated with lower water discharge. Gross primary production increased in the dry season, while ecosystem respiration did not differ between seasons. Seasonality defined by the rainfall pattern and its effect on stream hydrology is the main driver of organic matter dynamics in tropical streams. However, environmental parameters and organic matter stock and input were not good predictors of stream metabolism.

Key words: particulate organic matter, dissolved organic matter, standing stocks, organic matter inputs, Lacandona rainforest, Mexico

RESUMEN

Estacionalidad de la materia orgánica y el metabolismo ecosistémico en dos arroyos tropicales de primer orden

La materia orgánica, tanto particulada como disuelta, es la fuente de energía principal para la producción secundaria en arroyos de zonas boscosas. El reciclaje de la materia orgánica y el funcionamiento de los ecosistemas lóticos están asociados con la magnitud y estacionalidad de la acumulación y los aportes de materia orgánica. El objetivo de este estudio fue evaluar la variación estacional (temporadas de secas y lluvias) de los parámetros ambientales, la acumulación y aportes de materia orgánica y el metabolismo ecosistémico en dos arroyos tropicales de primer orden, en la Selva Lacandona, México. Asimismo, se buscó identificar los factores que controlan esta estacionalidad. Se encontró que la variabilidad en la acumulación y aportes de materia orgánica se correlacionaron con la estacionalidad tropical. La materia orgánica disuelta y el seston aumentaron en la temporada de lluvias, mientras que los productores primarios bentónicos y los aportes y cantidad de hojarasca aumentaron en la temporada de secas, correlacionado con la disminución del caudal. La producción primaria bruta incrementó en la temporada de secas, mientras que la respiración ecosistémica no difirió. La estacionalidad definida por el patrón de lluvias y su efecto en la hidrología de los arroyos son los principales factores que controlan la dinámica de la materia orgánica en arroyos tropicales. Sin embargo, los parámetros ambientales y la acumulación y aportes de materia orgánica no fueron buenos predictores del metabolismo ecosistémico.

Palabras clave: *materia orgánica particulada, materia orgánica disuelta, acumulación de materia orgánica, aportes de materia orgánica, Selva Lacandona, México*

INTRODUCTION

Low-order streams represent the most significant proportion of rivers' length and drain ample landscape areas (Benson & Pearson, 2020). More importantly, they significantly contribute to organic matter processing due to the large amounts of materials they receive and their high retentive capacity (Tonin et al., 2017). Dissolved and particulate organic matter is the energy source for secondary production in stream food webs (Tonin et al., 2017). Particulate organic matter stocks also contribute to channel stability, reduce erosion, increase retentiveness, and serve as a habitat for organisms (Molinero, 2019; Tonin et al., 2017; Wetzel, 2001).

In forested tropical streams, organic matter stock and input vary temporally related to multiple factors, and their seasonal patterns are difficult to predict (Rios Touma et al., 2009). Allochthonous leaf litter input depends on rainfall (Tonin et al., 2017), phenology and composition of the riparian forest, bank slopes, litter humidity, overland flow and wind (Bambi et al., 2017; Carvalho & Uieda, 2010; Molinero, 2019; Tonin et al., 2017). Macrophytes and benthic algae are controlled by light availability, rainfall, and stream hydrology, i.e., low and high flow seasons (Davies et al., 2008; Douglas et al., 2005). Dissolved and suspended organic matter usually increased in the high flow periods, but their quantity, quality, and timing depend on the link between the headwater production, downstream reaches and riparian forest (Minshall et al., 2000; Richardson et al., 2009; Vannote et al., 1980).

Ecosystem metabolism is an integrated measure of organic matter production and consumption (Demars et al., 2015; Odum, 1956). Several factors at different scales control ecosystem metabolism, including hydrology, climate, light availability, temperature, nutrient concentration, organic matter supply, canopy cover, stream orientation and substrate (Garcia et al., 2015; Ortiz-Zayas et al., 2005; Tank et al., 2010). At a local scale, organic matter is a proximal factor driving ecosystem metabolism (Gawne et al., 2007; Ortiz-Zayas et al., 2005; Staehr et al., 2012). However, this relationship is less studied than the relationship between metabolism and light availability or nutrient concentrations (e.g., Bernot et al., 2010; Garcia et al., 2015; Saltarelli et al., 2018). The role of proximal and distal factors driving metabolism has been primarily evaluated in temperate streams (e.g., Bernot et al., 2010; Fuß et al., 2017). Tropical streams are expected to differ in their metabolism from temperate streams because of their higher temperatures and higher and constant irradiance (Ortiz-Zayas et al., 2005). Studies in tropical streams have evaluated the role of nutrients, light and land-use changes in metabolism (Gücker et al., 2009; Saltarelli et al., 2018), but none have assessed organic matter seasonality in stream metabolism.

The present study aims to assess the seasonal variation of the organic matter stock and input in two tropical first-order streams and its role as a driver of ecosystem metabolism. We addressed the following specific objectives: 1) to assess the seasonal (rainy season vs. dry season) variation in environmental conditions, organic matter stocks and inputs (dissolved organic matter —DOM—, seston, leaf litter, and benthic primary producers), and ecosystem metabolism; 2) to identify environmental drivers of organic matter and metabolism seasonality; 3) to assess the role of organic matter stocks and inputs as drivers of ecosystem metabolic rates. We hypothesized that: 1) organic matter abundance correlates with stream seasonality, i.e., dry and rainy seasons. Benthic primary producers and leaf litter stock increase in the dry season correlated with the decrease in water discharge and turbidity. DOM, seston, and leaf litter inputs increase in the rainy season correlated with high-intensity rainfall and water runoff. 2) Stream metabolism, i.e., gross primary production (GPP) and ecosystem respiration (ER) reflect changes in organic matter seasonality. GPP correlates with the abundance of benthic primary producers in the dry season, while ER reflects changes in leaf litter stock increasing in the dry season.

MATERIALS AND METHODS

Study site

This study was performed in two first-order streams, José and Mario, tributaries of the Lacantún River in the Lacandona rainforest, Chiapas, Mexico (Fig. 1). The Lacantún River subbasin belongs to the hydrological region N° 30 Grijalva-Usumacinta, the most extensive river system in Mexico (Muñoz-Salinas & Castillo, 2013). The subbasin covers 12 526 km^2 and has an elevation of 200 m a.s.l. Geological formations are mainly limestones, and the most common soils are lithosols, which have low organic matter content and are prone to weathering (Saavedra Guerrero et al., 2015).

The climate in the region is warm and rainy, with mean annual temperature of 27 °C and mean annual rainfall of 3190 mm (García, 2004). The rainfall pattern mainly defines seasonality (Fig. 2). The rainy season lasts from May to October, with two peaks in June and October. Average rainfall per month ranges between 96.4 and 338.0 mm, mean monthly temperature between 23.2 and 25.7 °C, mean solar radiation between 253 and 310 W/m^2, and mean wind speed between 2.3 and 3.2 km/h. The dry season lasts from November to May, with a small rainfall peak in February. Average rainfall per month ranges between 26.8 and 116.4 mm, mean monthly temperature between 19.2 and 23.2 °C, mean solar radiation between 214 and 339 W/m^2, and mean wind speed between 2.3 and 18.1 km/h (Servicio Meteorológico Nacional, "Montes Azules" weather station, 16° 48' 43" N, 91° 31' 29" W, 625 m a.s.l.).

The dominant vegetation in the region is the tropical evergreen rainforest, a diverse ecosystem with more than 267 species per hectare (Saavedra Guerrero et al., 2015). The tree species dominating the riparian zones are *Ampelocera hottlei* (Ulmaceae), *Croton schiedeanus* (Euphorbiaceae), and *Protium copal* (Burseraceae; Meli et al., 2015).

Streams in the Lacantún River subbasin are warm, low-mineralized, neutral, well-oxygenated and with low quantities of suspended solids (Álvarez-Porebski et al., 2015). José and Mario are 7.1 km apart from each other. The José stream (16° 6' 50" N, 90° 56' 10" W) is surrounded by

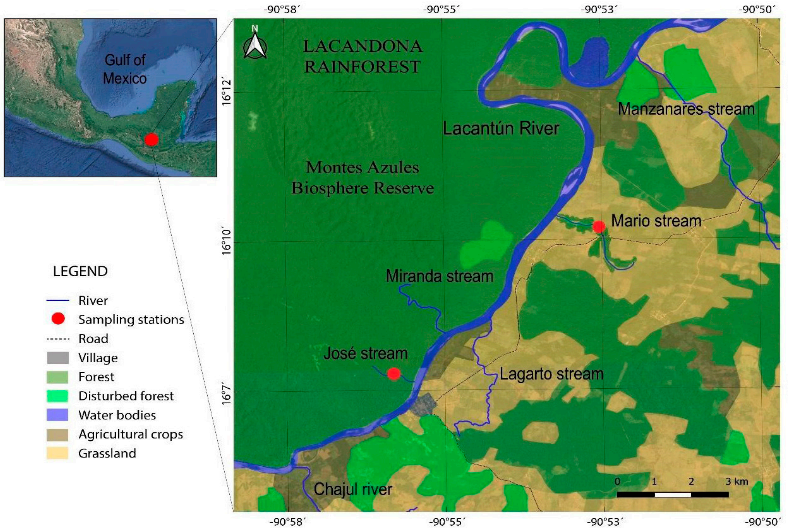

Figure 1. Location of the José and Mario streams. *Ubicación de los arroyos José y Mario.*

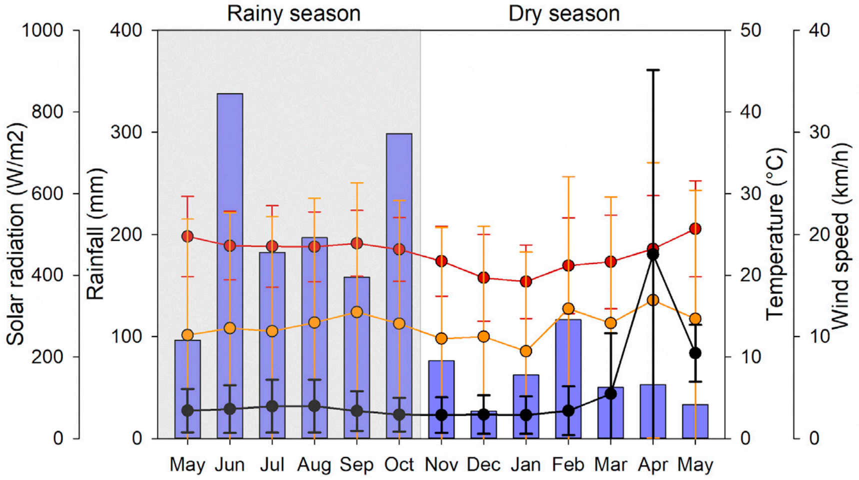

Figure 2. Mean (± standard deviation) monthly temperature (red line), wind speed (black line), solar radiation (orange line) and accumulated monthly rainfall (blue bars) during the study period (May 2018- May 2019). Data from the "Montes Azules" weather station. *Promedio (± desviación estándar) mensual de temperatura (línea roja), rapidez del viento (línea negra), radiación solar (línea naranja) y precipitación mensual acumulada (barras azules) durante el periodo de estudio (mayo 2018- mayo 2019). Datos de la estación meteorológica "Montes Azules".*

rainforest, 92 % shaded and well-preserved. The Mario stream (16° 8' 10" N, 90° 54' 27" W) is surrounded by rainforest in approximately 80 % of its length, 78 % shaded and showed minor disturbance degree (pasture-land use).

Environmental variables

The streams were sampled bi-monthly: three times in the rainy season (June, September, and October 2018) and three times in the dry season (January, March, and May 2019). We selected a 100 m long segment in each stream that included ponds, riffles, and various substrate types. The coverage of the different substrates along the 100 m segments was estimated using a 1 m^2 frame. Substrate types were gravel-boulders (2.1 - 64.0 mm), sand (0.05 - 2.0 mm), and silt (0.002 - 0.04 mm). We measured the morphometric (width and depth), physical, and chemical variables at three points (¼, ½, and ¾ of the stream width) every 20 m in the 100 m segments. The water velocity was measured using a Swoffer 3000 current meter at half the maximum depth at each point. The water discharge was calculated by multiplying the water velocity by the stream cross-section area. A multiparameter water quality probe (Hydrolab DS5) was used to measure water temperature, dissolved oxygen, pH, conductivity and turbidity.

Water samples were collected for chlorophyll-*a* and nutrient concentrations. First, we passed the water sample through a 100 µm filter to remove larger particles. Chlorophyll-*a* concentration in water followed the EPA 445.0 method (Arar & Collins, 1997). Between 40 and 100 ml of the sample were filtered through a glass fiber filter (GF/F; 0.7 µm). The chlorophyll-*a* was extracted with acetone (90 %) for 24 hours and stored in dark and cold. We measured the chlorophyll-*a* concentration with a digital fluorometer Turner Designs 10-AU. Nutrients were analyzed in a segmented flow autoanalyzer Skalar San Plus System. Total dissolved nitrogen and phosphorus were determined through oxidation at high pressure and high temperature with potassium persulfate (Valderrama, 1981). We followed Pujo-Pay & Raimbault (1994) to determine nitrogen and phosphorus particulate organic fractions. 60 ml of water were filtered through nitrocellulose filterers (0.22 and 0.45 µm) to measure ammonium and nitrate concentration (Kirkwood, 1994; Strickland & Parsons, 1972).

Dissolved organic matter (DOM) input

DOM was measured as dissolved organic carbon (DOC) concentration. We took a water sample and filtered it through a 100 µm filter to remove larger particles. Then, we filtered three replicates of 40 ml samples through a GF/F filter previously combusted (550 °C, 4h) and preserved with 40 % H_3PO_4. Finally, samples were analyzed in a Shimadzu TOC-L analyzer.

Particulate organic matter (POM) input

We quantified POM inputs as seston, direct litterfall, lateral leaf litter input (Bambi et al., 2017; Colón-Gaud et al., 2008), and transported leaf litter input from upstream (drift) (Pozo et al., 2009; Carvalho & Uieda, 2010) at each stream. Seston includes all the organic and inorganic suspended materials, and it could be used as a proxy of fine particulate organic matter in transport (Hutchens et al., 2017). We used between 250 and 1200 ml of pre-filtered (100 µm) water. Samples were filtered again through GF/F previously combusted (550 °C, 4 h) and weighed. Then, we acidified filters with HCl 10 % to eliminate the inorganic carbon (Seyler et al., 2005). Finally, the filters were dried (60 °C, 48 h) and weighed again. Seston was analyzed by triplicate. Direct litterfall was quantified using six 0.045 m^2 frames attached with a 1 mm mesh size screen. We distributed the traps throughout the 100 m segments and installed them above and perpendicularly to the channel, supported by synthetic ropes tied to trees. Lateral inputs were measured with another six frames with the same characteristics as those for the direct litterfall. We installed the traps along the stream banks in areas with a gentle slope down to the streams. Transported inputs were measured using drift nets (0.4 m^2) of 1 mm mesh size. We installed three drift nets in the upper section of the 100 m segment and left them for 1 hour.

Materials from direct and lateral traps were collected every two months and stored in the cold to further analysis in the laboratory. Materials were dried (60 °C, 48 h), weighed, combusted (550 °C, 4 h), and weighed again to obtain the ash-free dry mass (AFDM). To express the inputs in the same units (g AFDM m^{-2} d^{-1}), we applied the equations from Pozo et al. (2009). We divided the AFDM into the traps sampling area and the time between sample dates for direct inputs. For lateral inputs, we divided the AFDM into the trap width and the time between sample dates; then, we multiplied the result by two and divided it by the mean width of the channel to express the results per area of the river channel. To calculate transported inputs, we divided the AFDM into the amount of water passing through the drift net (water velocity x area of drift net submerged), then multiplied it by the water discharge, and the time elapsed divided it into the cross-channel section.

POM standing stock

We classified the POM standing stock into two categories: a) benthic primary producers, including the benthic algae and macrophytes, and b) the coarse particulate organic matter, composed mainly by leaf litter. We estimated the total coverage as the percentage of the substrate covered by each one along the 100 m segments using a 1 m^2 frame. Six aleatory replicates of leaf litter samples were manually sampled using a 0.13 m^2 frame. Three aleatory replicates of benthic algae were collected by scraping the surface of rocks; we then registered the rock area covered by the algae. Three aleatory replicates of macrophytes samples were manually sampled using a 0.13 m^2 frame. Benthic primary producers were determined to genus level and confirmed by experts. Samples of benthic primary producers and leaf litter were dried (60 °C, 48 h), weighed, combusted (550 °C, 4 h) and weighed again to obtain the AFDM.

Stream metabolism

We employed the open diel oxygen method in a single station to measure the ecosystem metabolism (Demars et al., 2015; Odum, 1956) with a Hobo U26 oxygen probe coupled with a thermistor (dissolved oxygen resolution: 0.02 mg/L, accuracy ± 0.2 mg/L up to 8 mg/L; ± 0.5 mg/L from 8 to 20 mg/L; temperature resolution 0.02 °C, accuracy 0.2 °C). The probe was installed submerged at 0.5 m (≈ half the mean depth) and left for 24-hour cycles. Dissolved oxygen and temperature readings were recorded every 5 minutes.

Logistic problems prevented measuring in January 2019.

We applied the equations from Grace & Imberger (2006) to calculate the gross primary production (GPP) and ecosystem respiration (ER) from the dissolved oxygen (DO) measurements. For each time measurement, we calculated the following variables:

The 100 % DO saturation at any temperature (T in Kelvin):

$$ln\,(100\%DO) \;=\; -139.34411 + \frac{1.575701*10^5}{T} - \frac{6.642308*10^7}{T^2} + \frac{1.2438*10^{10}}{T^3} - \frac{8.621949*10^{11}}{T^4}$$

The DO deficit (D):

$$D = 100\%\; DO\; (mg\; O_2\, L^{-1}) - measured\; DO\; (mg\; O_2\, L^{-1})$$

The reaeration coefficient (K_{O2}) standardized at 20 °C:

$$K_{O2\,(20°C)} = 50.8\; (water\; velocity\; (cm/s^{-1})^{0.67})(depth\; (cm)^{-0.85})$$

The temperature corrected K_{O2} for temperature at each time measurement:

$$K_{O2\,(Ti)} = \; K_{O2\,(20°C)} * 1.0241^{(Ti-20°C)}$$

The reaeration flux:

$$RF\; (mg\; O_2\; L^{-1}m^{-1}) = \;(K_{O2(Ti)} * D)\; /\; time\; interval\; (min)$$

The night-time respiration rate:

$$NRR\; (mg\; O_2\; L^{-1}min^{-1}) = \frac{(\Delta DO - K_{O2\,(Ti)} * D)}{time\; interval\; (min)}$$

The average of all NRR:

$$Rnight = \Sigma NRR\; (mg\; O_2\; L^{-1}min^{-1})/n$$

The day-time respiration rate:

$$DRR\; (mg\; O_2\; L^{-1}min^{-1}) = R_{night} * 1.072^{Ti-Tnight}$$

The GPP flux:

$$GPP_{flux}(mg\; O_2\; L^{-1}min^{-1}) = \frac{\Delta DO - K_{O2\,(Ti)} * D}{time\; (min) + \; R_{night} * 1.072^{Ti-Tnight}}$$

Daily GPP:

$$GPP\; (mg\; O_2\; L^{-1}d^{-1}) = \Sigma GPP_{flux} * time$$

$$GPP\; (mg\; O_2\; m^{-2}d^{-1}) = GPP\; (mg\; O_2\; L^{-1}d^{-1}) * depth_{(mean)} * 1000$$

Daily ecosystem respiration:

$$EC\; (mg\; O_2\; L^{-1}d^{-1}) = \frac{\Sigma DRR + \;\Sigma NRR}{time}$$

$$ER\; (mg\; O_2\; m^{-2}d^{-1}) = ER\; (mg\; O_2\; L^{-1}d^{-1}) * depth_{(mean)} * 1000$$

We tested for differences in environmental parameters, OM stocks and inputs, GPP and ER among seasons and streams using two-way ANOVA followed by Holm Sidak *post hoc* pairwise comparisons performed in SigmaPlot 14.0. We evaluated the correlation between environmental parameters, OM stocks and inputs, GPP, and ER using a principal component analysis performed in PRIMER 7.

RESULTS

Environmental parameters

The José and Mario streams are warm, well-oxygenated, from slightly acid to slightly basic and with low electrical conductivity (Table 1). The José stream had higher pH ($F = 63.2002, p < 0.001$), conductivity ($F = 647.608, p < 0.001$) and water discharge ($F = 7.481, p = 0.026$) than the Mario stream. Temperature ($F = 2.313, p = 0.167$), dissolved oxygen ($F=1.488, p = 0.257$), turbidity ($F = 1.203, p = 0.305$) and chlorophyll-*a* ($F = 1.601, p = 0.241$) were not significantly different between streams. Nutrient concentrations were low (i.e., oligotrophic) and not significantly different between streams (Table 1, NH_4 $F = 2.130, p = 0.183$; NO_3^- $F=1.264, p = 0.293$; DIN: $F = 0.512, p = 0.494$; TP $F = 0.055, p = 0.821$). The substrate is coarse in both streams, composed mainly of sands (35 - 44 %) and gravel-boulders (24 - 38 %).

Table 1. Physical and chemical parameters (mean ± s.d., n = 18) of the José and Mario streams. *Parámetros fisicoquímicos (promedio ± d.e., n = 18) de los arroyos José y Mario.*

Parameter	José stream		Mario stream	
	Rainy season	Dry season	Rainy season	Dry season
Total lenght (m)	1321		3280	
Mean width (m)	4.0 ± 1.1		3.1 ± 1.6	
Mean depth (m)	0.40 ± 0.25	0.41 ± 0.25	0.30 ± 0.23	0.39 ± 0.31
Water discharge (m/s^3)	0.29 ± 0.03	0.18 ± 0.04	0.16 ± 0.15	0.04 ± 0.01
Temperature (°C)	22.2 ± 0.6	23.2 ± 1.5	25.5 ± 0.7	24.7 ± 1.9
Dissolved oxygen (mg/L)	7.5 ± 0.7	7.7 ± 1.2	7.1 ± 0.6	6.2 ± 1.7
pH	8.1 ± 0.3	7.9 ± 0.1	6.9 ± 0.3	6.5 ± 0.2
Conductivity (µS/cm)	959 ± 8	1069 ± 96	73 ± 21	63 ± 23
Turbidity (NTU)	12 ± 14	3 ± 12	30 ± 38	18 ± 38
Chlorophyll-*a* (µg/L)	0.24 ± 0.08	0.25 ± 0.12	0.43 ± 0.15	0.24 ± 0.17
Ammonium (NH_4) (µMol/L)	0.8 ± 0.4	1.3 ± 1.0	1.1 ± 0.5	3.2 ± 1.9
Nitrate (NO_3^-) (µMol/L)	13.1 ± 7.6	11.8 ± 6.0	10.3 ± 1.8	8.1 ± 3.5
Total inorganic dissolved N (DIN) (µMol/L)	14.6 ± 7.5	13.3 ± 7.0	11.7 ± 1.8	11.5 ± 5.2
Total phosphorus (TP) (µMol/L)	1.5 ± 0.6	4.0 ± 4.6	1.4 ± 0.1	3.1 ± 3.3
DIN:TP	9.7	3.3	8.4	3.7

Table 2. Abundance (mean ± s.d.) of the organic matter stock and input and metabolism estimations in the José and Mario streams (DOM: dissolved organic matter, GPP: gross primary production, ER: ecosystem respiration). *Abundancia (promedio ± d.e.) de los diferentes almacenes y entradas de materia orgánica y estimaciones de metabolismo en los arroyos José y Mario (DOM: materia orgánica disuelta, GPP: producción primaria bruta, ER: respiración ecosistémica).*

Stream	Season	DOM	Seston	Leaf litter				Benthic primary producers	GPP	ER
				Direct input	Lateral input	Transported input	Stock			
		mg/L	mg/L	g AFDM m^{-2} d^{-1}	g AFDM m^{-2} d^{-1}	g AFDM m^{-2} d^{-1}	g AFDM/m^2	g AFDM/m^2	g O_2 m^{-2} d^{-1}	g O_2 m^{-2} d^{-1}
José	Rainy	3.1 ± 0.4	3.9 ± 2.2	21.1 ± 9.5	9.4 ± 4.9	20.2 ± 10.3	46.3 ± 17.4	0.01 ± 0.01	0.6 ± 0.5	19.3 ± 8.8
	Dry	4.1 ± 1.3	2.5 ± 0.8	96.0 ± 28.9	115.7 ± 89.5	32.1 ± 26.7	125.5 ± 10.5	0.06 ± 0.04	12.6 ± 4.7	24.5 ± 4.2
	Annual	3.5 ± 1.0	3.2 ± 1.7	58.6 ± 45.3	62.5 ± 81.3	26.1 ± 20.5	85.9 ± 45.3	0.04 ± 0.04	7.8 ± 7.4	21.4 ± 7.2
Mario	Rainy	8.0 ± 2.0	26.0 ± 15.8	32.5 ± 39.7	45.8 ± 34.9	39.4 ± 21.7	53.2 ± 34.6	0.05 ± 0.04	0.3 ± 0.2	23.0 ± 11.6
	Dry	3.0 ± 0.8	10.6 ± 5.9	65.0 ± 24.1	194.6 ± 91.2	56.5 ± 31.5	253.7 ± 17.4	0.16 ± 0.03	1.6 ± 2.0	34.0 ± 24.8
	Annual	5.8 ± 3.0	18.1 ± 15.0	52.0 ± 31.6	135.1 ± 105.4	47.9 ± 27.7	166.0 ± 112.5	0.11 ± 0.07	0.8 ± 1.2	27.4 ± 16.0

Water discharge ($F = 9.771$, $p = 0.014$) and turbidity ($F = 5.360$, $p = 0.040$) were higher in the rainy season than in the dry season in the streams. Temperature ($F = 0.714$, $p = 0.423$), dissolved oxygen ($F = 0.440$, $p = 0.526$), pH ($F = 3.247$, $p = 0.109$), conductivity ($F = 2.124$, $p = 0.183$), chlorophyll-*a* ($F = 0.100$, $p = 0.760$) and nutrients did not significantly differ between seasons (NH_4 $F = 3.394$, $p = 0.103$; NO_3^- $F = 0.068$, $p = 0.800$; DIN: $F = 0.009$, $p = 0.925$; TP $F = 0.792$, $p = 0.400$).

Organic matter

Organic matter stock and input amply varied in both streams (Table 2, Fig. 3). DOM ranged between 0.5 and 10.2 mg/L, while seston ranged between 0.002 and 0.02 mg/L. Leaf litter inputs ranged between 5.9 and 255.6 g AFDM m^{-2} d^{-1} and were mainly represented by the lateral input. Leaf litter stock was the most abundant particulate organic matter stock, ranging between 20.4 and 357.8 g AFDM/m^2, while benthic primary producers ranged between 0.01 and 0.19 g AFDM/m^2. Benthic primary producers were dominated by the green algae *Cladophora*, the diatoms *Surirella*, *Girosigma*, *Navicula*, *Coconeis*, *Ulnaria*, *Pinnularia*, *Flagilaria*, *Gomphonema*, *Amphora*, and *Diploneis*, and an undetermined Characeae.

DOM ($F = 16.184, p = 0.004$), transported leaf litter ($F = 7.709, p = 0.024$) and benthic primary producers ($F = 14.748, p = 0.005$) were significantly higher in the Mario stream than in the José stream. Seston ($F = 0.666, p = 0.438$) and leaf litter lateral input ($F = 2.351, p = 0.164$), direct input ($F = 0.506, p = 0.497$) and stock ($F = 1.848, p = 0.211$) did not significantly differ between streams.

DOM was higher in the rainy season in the Mario stream but did not differ between seasons in the José stream (*Season* $F = 15.899, p = 0.004$, *stream x season* $F = 38.300, p < 0.001$, *Holm-Sidak for José* $t = 1.557, p = 0.158$). Similar-

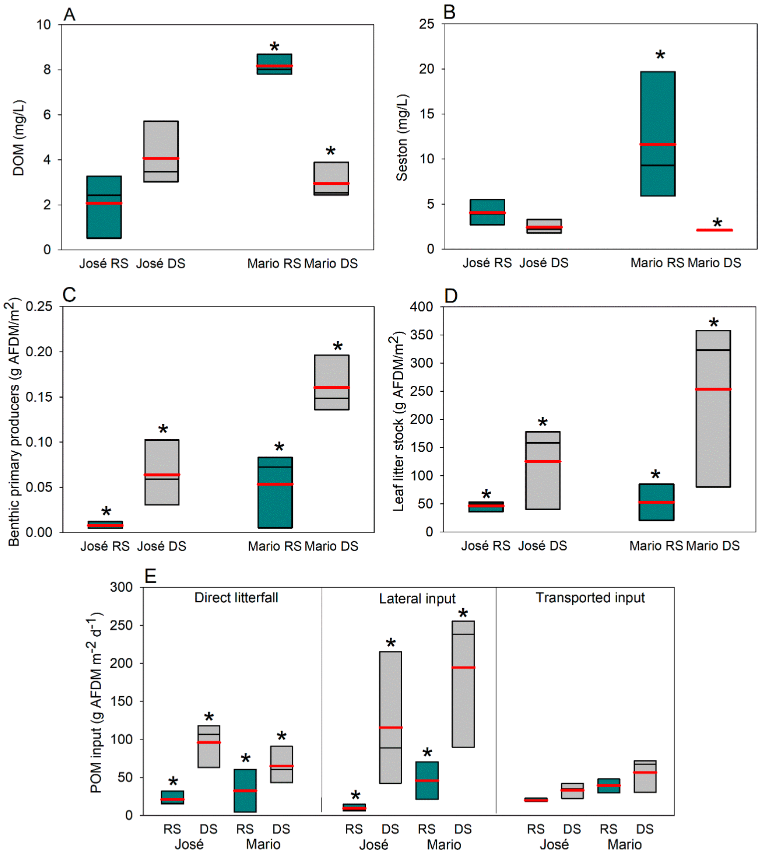

Figure 3. Seasonal variation (RS: rainy season, DS: dry season) of the different organic matter stocks and inputs in the José and Mario streams. A: DOM (n = 3), B: seston (n = 3), C: benthic primary producers (n = 6), D: leaf litter stocks (n = 6), E: leaf litter inputs (n = 6) Mean: red lines, median: black lines. * indicates significant differences. *Variación estacional (RS: temporada de lluvias, DS: temporada de secas) de los diferentes almacenes y entradas de materia orgánica en los arroyos José y Mario. A: DOM (n = 3), B:seston (n = 3), C: productores primarios bentónicos (n = 3), D: hojarasca almacenada (n = 6), E: aportes de hojarasca (n = 6). Promedio: líneas rojas, mediana: líneas negras). * indica diferencias significativas.*

ly, seston was higher in the rainy season in the Mario stream but did not differ between seasons in the José stream (*Season* $F = 14.098, p = 0.004$, *stream x season* $F = 25.697, p < 0.001$, *Holm-Sidak for José* $t = 0.452, p = 0.293$). Leaf litter direct input ($F = 15.065, p = 0.005$), lateral input ($F = 11.502, p = 0.009$), stock ($F = 7.936, p = 0.023$) and benthic primary producers ($F = 19.392, p = 0.002$) were higher in the dry than in the rainy season in both streams. Transported leaf litter ($F = 3.875, p = 0.085$) did not differ between seasons in the streams.

Stream metabolism

GPP in the José stream ranged between 0.25 and 15.77 g O_2 m^{-2} d^{-1}. In Mario, it ranged between 0.15 and 3.09 g O_2 m^{-2} d^{-1}. It significantly differed between streams and seasons, but the interaction was significant (*stream x season* $F = 21.523, p = 0.002$). GPP was significantly higher in the rainy season than in the dry season in José ($t = 5.911, p < 0.001$), but it did not differ between seasons in Mario ($t = 0.650, p = 0.534$). It was also significantly higher in José than in Mario only in the rainy season ($t = 6.049, p < 0.001$, Table 2).

ER in José ranged between 9.69 and 27.53 g O_2 m^{-2} d^{-1}. In Mario, it ranged between 9.61 and 51.52 g O_2 m^{-2} d^{-1}. ER did not differ between seasons or streams (*stream* $F = 0.701, p = 0.427$, *season* $F = 4.042, p = 0.079$, *stream x season* $F = 0.324, p = 0.585$, Table 2).

The first two components of PCA explained 50.6 % of the variation (Fig. 4). PC1 explained 33.7 % and was positively correlated to leaf litter stock (0.321), lateral input (0.235) and benthic primary producers (0.337), and negatively correlated to water discharge (-0.334). PC2 explained 16.9 %, was positively correlated to GPP (0.284), and negatively correlated to DOM (-0.353), direct litterfall (-0.321) and ER (-0.248).

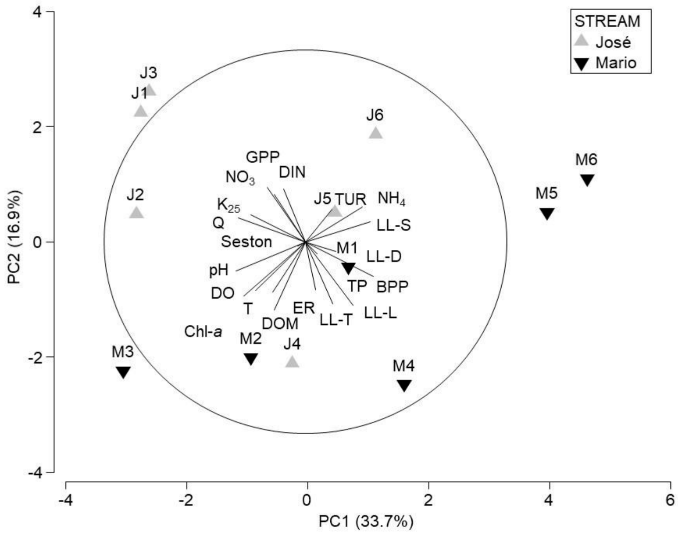

Figure 4. PCA between environmental parameters, organic matter stocks and inputs, and stream metabolism. Q: water discharge, T: temperature, DO: dissolved oxygen, K_{25}: conductivity, TUR: turbidity, Chl-*a*: chlorophyll-*a*, NH_4: ammonium, NO_3: nitrate, DIN: total inorganic dissolved nitrogen, TP: total phosphorus, DOM: dissolved organic matter, BPP: benthic primary producers, LL-S: leaf litter stock, LL-D: direct litterfall, LL-L: leaf litter lateral input, LL-T: leaf litter transported input, GPP: gross primary production, ER: ecosystem respiration. *PCA entre parámetros ambientales, almacenes y aportes de materia orgánica y metabolismo ecosistémico. Q: caudal, T: temperatura, DO: oxígeno disuelto,* K_{25}*: conductividad, TUR: turbidez, Chl-*a*: clorofila-*a*,* NH_4*: amonio,* NO_3*: nitrato, DIN: nitrógeno disuelto inorgánico total, TP: fósforo total, DOM: materia orgánica disuelta, BPP: productores primarios bentónicos, LL-S: almacén de hojarasca, LL-D: caída directa de hojarasca, LL-L: aporte lateral de hojarasca, LL-T: aporte transportado de hojarasca, GPP: producción primaria bruta, ER: respiración ecosistémica.*

DISCUSSION

Organic matter variation

The magnitude of organic matter input and stock measured in our study was low compared to other tropical low-order streams (e.g., Bambi et al., 2017; Dudgeon et al., 2010; García et al., 2016; Li & Dudgeon, 2008; Mantel et al., 2004; Molinero, 2019; Tonin et al., 2017).

DOM and seston significantly increased in the Mario stream in the rainy season, as reported in temperate and tropical streams and rivers (Atkinson et al., 2009; Wiegner et al., 2009). On the contrary, DOM and seston did not differ between seasons in the José stream.

The abundance of benthic primary producers increased in the dry season in both streams negatively correlated to water discharge. Increased discharge in the rainy season imposes two adverse effects on benthic algae in tropical streams. Faster currents might flush algae out from the channel, particularly at the beginning of the rainy season (Bleich et al., 2015). Moreover, rainfall favors the riparian vegetation growth, which increases the shade above the channel and limits the benthic algae development (Bleich et al., 2015).

Leaf litter standing stocks in the José and Mario streams increased in the dry season negatively correlated to water discharge, as reported in other tropical streams (Bambi et al., 2017; Colón-Gaud et al., 2008; Molinero, 2019). In low order streams, in-stream retention decreases with flooding or increasing water discharge in the rainy season, even in zones with high litter inputs (Colón-Gaud et al., 2008). In Ecuadorian streams, at the beginning of the rainy season, high amounts of leaf litter were transported downstream due to a lack of in-stream retention structures (Molinero, 2019). Large wood debris in the José and Mario streams covered less than 10 % of the channels; therefore, the scarcity of retention structures favored the downstream transport of leaf litter during the rainy season.

Direct litterfall and lateral input in the José and Mario streams also increased in the dry season, while transported input did not significantly differ between seasons. A litterfall peak in the dry season is typical in tropical forests (Benson & Pearson, 1993; Colón-Gaud et al., 2008; Mohan Kumar & Deepu, 1992; Molinero, 2019; Tonin et al., 2017; Wieder & Wright, 1995), often as a consequence of water stress on terrestrial vegetation (Bambi et al., 2017; Tonin et al., 2017). Lateral transport increases in the dry season since dry leaves are more easily transported by wind (Tonin et al., 2017). Wind velocity increases in the dry season in the study region, which likely increases the transportation of dry leaves.

Stream metabolism variation

GPP and ER values in the José and Mario streams were within the range of values reported from other tropical streams (GPP: 0.1–16.2 g O_2 m^{-2} d^{-1}, ER: 0.6–42.1 g O_2 m^{-2} d^{-1}; Gücker et al., 2009; Bernot et al., 2010; Saltarelli et al., 2018). Moreover, ER values exceeded GPP values in each sampling date, suggesting heterotrophy in the streams.

GPP increased in the dry season in the José stream, while there were no statistically significant differences between seasons in the Mario stream. Nonetheless, there was no significant correlation between GPP and benthic macroalgae abundance, although they both increased in the dry season. Lower water discharge and lower turbidity likely favored microorganism activity (not measured) in the dry season, leading to higher GPP (Douglas et al., 2005; García et al., 2016; Townsend & Douglas, 2014).

ER did not differ between seasons in either stream. The principal component explaining the ER variation explained a low percentage (< 20 %) and included direct litterfall and DOM along with ER. In forested streams, leaf litter and DOC are the primary drivers contributing to the ER and decomposition process (Bernot et al., 2010; Saltarelli et al., 2018; Vannote et al., 1980). However, ER did not reflect the leaf litter increase in the dry season in both streams, nor the DOM increase in the rainy season in the Mario stream. This lack of correlation might be related to a) the leaf litter stock was highly abundant in both seasons and b) seasonal DOM changes were not significant enough to modify the stream metabolism.

Drivers of stream metabolism

The organic matter stocks and inputs explained a low percentage of stream metabolism variation. The lack of such correlation could be related to the metabolic activity of the smallest standing stocks of organic matter, i.e., microorganisms, that tend to be the most metabolically active components (Gawne et al., 2007). Moreover, when most organic matter in a stream is of allochthonous origins, like in the José and Mario streams, metabolism does not usually correlate with autochthonous producer biomass, and GPP and ER are rather uncoupled (Ortiz-Zayas et al., 2005). In streams with uncoupled GPP and ER, distal factors, like land use, influence metabolism more strongly than organic matter (Bernot et al., 2010).

GPP and ER in José and Mario streams did not correlate with nutrient concentrations, which is most likely associated with the oligotrophic status of the streams. The oligotrophic status, in turn, plays a major role in limiting the primary producer biomass. Low dissolved N:P ratios indicate N is strongly limiting GPP (Cotner et al., 2006; Hamilton & Lewis, 1990). The N:P < 8 found in the José and Mario streams revealed that N plays a significant role in controlling the in-stream primary productivity (Redfield, 1958). In streams with strong nutrient limitation, GPP does not correlate with nutrient concentrations probably because any increased loading of nutrients is rapidly consumed (Cotner et al., 2006; Garcia et al., 2015; Townsend et al., 2011). In addition, in N-limited streams, other nutrients, like phosphorous, do not correlate with GPP because its role is likely masked by other factors (Bernot et al., 2010).

CONCLUSION

The José and Mario streams displayed a seasonal variation in organic matter stock and input. The organic matter timing and quantity correlated to tropical seasonality and its effect on stream hydrology. Although several factors likely influence organic matter inputs and in-stream retention, the seasonality defined by the rainfall pattern is probably the main driver of organic matter dynamics in tropical streams. On the contrary, stream metabolism was not explained by tropical seasonality. Environmental parameters and organic matter stocks and inputs were not good predictors of stream metabolism. The high amount of leaf litter probably masked the role of primary producers on GPP, while its constant supply resulted in relatively constant ER values in both seasons. Nutrients were not good predictors of stream metabolism since they were at very low concentrations.

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Capítulo 2: Macroinvertebrados bentónicos de arroyos tropicales: diversidad funcional trófica del Río Lacantún, México

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RESEARCH PAPER

Benthic macroinvertebrates of tropical streams: functional and trophic diversity of the Lacantún River, Mexico

Daniela Cortés-Guzmán[1] · **Javier Alcocer**[2] · **Kenneth W. Cummins**[3]

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Abstract
The differences between temperate and tropical seasonality suggest that ecological models developed for temperate streams do not necessarily apply to tropical streams. While detritus is the base of the temperate zone stream food webs, we expected a seasonal alternation in the energy source in tropical streams (i.e., increase in the autochthonous energy source in the dry season, and an increase in the allochthonous energy source in the rainy season). We sought to evaluate the annual dynamics of the benthic macroinvertebrate functional feeding group (FFG) communities, the availability of their food resources, and the use of FFG ratios as surrogates for stream ecosystem traits in two first-order, tropical streams in Chiapas, Mexico. We found an increase in the biomass of herbivore-FFGs correlated to their autochthonous food resources in the dry season. The detritivore-FFGs biomass did not correlate to the abundance of the allochthonous food resources. Stream ecosystem traits were similar between seasons and were associated with a dominance of scrapers, shredders, and predators throughout the year. We concluded that the temperate classical ecological stream models that suggest allochthonous resources almost entirely support food webs do not directly extrapolate to tropical stream ecosystems. Instead, tropical stream food webs significantly rely on autochthonous food resources.

Keywords Aquatic insects · Functional feeding groups (FFG) · Headwater streams · Lacandona rainforest · Chiapas

Introduction

Many ecological theories and models concerning lotic ecosystems are based on forested, temperate zone, low-order streams. Energy pathways in macroinvertebrate food webs in low order streams are described as short, nutrient-poor, and populated with macroinvertebrate functional feeding groups (FFG) that are dependent upon allochthonous food resources derived from the riparian streamside (e.g., River Continuum Concept by Vannote et al. 1980; Flood Pulse Concept by Junk et al. 1989). Temperate zone seasonality exhibits detritus-based food webs during autumn–winter seasons, when the input of allochthonous leaf litter provides the food resource for FFG detrital shredders. Mechanical and biological break down of the leaf litter provides fine particulate organic matter (FPOM) food resource for FFG collectors, including other seasons of the year (Vannote et al. 1980). An increase in the relative importance of the autochthonous resources is expected in spring–summer seasons (Minshall 1978). However, primary production is typically limited by shading in forested streams in the temperate zone. In tropical streams, rainfall seasonality (rainy and dry seasons) produces significant differences in the structure of the benthic macroinvertebrate stream communities (Boulton et al. 2008; Boyero et al. 2009). In the tropics, the supply of leaf litter organic matter is usually from evergreen trees in the riparian (streamside) zone. Evergreen leaf litter is processed much more slowly than the deciduous litter from most temperate

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✉ Javier Alcocer
jalcocer@unam.mx

Daniela Cortés-Guzmán
dacortesgu@comunidad.unam.mx

[1] Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Av. Universidad 3000, Alcaldía Coyoacán, 04510 Ciudad de México, México

[2] Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes Iztacala, CP 54090 Tlalnepantla, Estado de México, México

[3] Michigan State University, Kellogg Biological Station, Hickory Corners, USA

forests trees. The relative importance of autochthonous resources is generally greater in tropical streams (Brito et al. 2006; Dudgeon et al. 2010; García et al. 2016; Lau et al. 2009; March and Pringle 2003; Mantel et al. 2004).

Precipitation regime characterizes tropical seasonality. There are two seasons: one with high-intensity rainfall (rainy season) and the other with low-intensity rainfall (dry season) (Lewis 2008). Tropical seasonality affects stream hydrology. Intense rainfall produces higher water discharge and turbidity and lower conditions in the dry season (Syvitski et al. 2014). Primary producers in tropical streams, micro- and macroalgae, and aquatic vascular plants, increase in the dry season related to the decrease in water turbidity, lower flows Lau et al. 2009; Thorp et al. 2002), and shade by the evergreen riparian forest cover that sheds half of their leaves in the dry season, allowing more light to reach the stream surface. The resulting primary production provides a high-quality nutritional resource for scrapers and herbivore shredders to different degrees by season. Although the amount of autochthonous food resources may be limited, its quality is significantly higher per gram than that of the detritus (Branco et al. 2017; Frauendorf et al. 2013). Macroinvertebrate herbivore consumers depend on algal (scrapers) or macrophytes (herbivore shredders) food resources. Benthic macroinvertebrate food webs that shift from detritus-based to primary production-based status likely respond to a significant change in the general quality of the autochthonous food resource. As yet, this prediction has not been adequately studied in tropical stream ecosystems.

Dynamic food web influences on stream ecosystem ecological functions can be described by several ecological traits (Townsend and Hildrew 1994). Among these, feeding strategies are adaptations of macroinvertebrate taxa that reflect environmental conditions and the characteristics of available food resources. This allows for the taxonomic composition of functional feeding groups (FFGs) to be used to evaluate stream communities (Merritt et al. 2017, 2019; Statzner et al. 2001).

The FFGs approach that links a limited number of taxonomically based feeding strategies to a limited number of food resource categories can be used as an indicator of stream ecosystem traits (Cummins 1974; Cummins and Klug 1979; Merritt et al. 2017, 2019). Examples are: (1) the relative importance of autotrophic vs. heterotrophic ecosystem function, (2) the availability of coarse particulate organic matter (CPOM) detritus, (3) the availability of fine particulate organic matter (FPOM) in transport (TFPOM) vs benthic storage (BFPOM) on or in the sediments, (4) the stability of the stream bottom substrates, and (5) the relative dominance of predators (e.g., Merritt et al. 2017, 2019). Because ecosystem traits are difficult to measure directly and to integrate over spatial and temporal dimensions, macroinvertebrate FFGs can serve as surrogates for stream ecosystem traits integrated over the longer and spatially extensive scales of their life cycles (Table 1) (Cummins et al. 2005; Merritt et al. 2002). Furthermore, benthic macroinvertebrates are likely the most diverse and well-studied organisms in lotic environments and show predictable responses to environmental changes (Brasil et al. 2014; Egler et al. 2012; Merritt et al. 2017, 2019; Shimano et al. 2013).

Information concerning macroinvertebrates from tropical regions, particularly the tropical rainforest in Mexico, is scarce (e.g., Bond et al. 2014; Bueno-Soria y Barba-Álvarez 2011; Bueno-Soria et al. 2005; Castillo et al. 2018). Available tropical macroinvertebrate studies have been primarily taxonomic. The few studies on FFGs in tropical streams have focused on spatial differences among substrate types or microhabitats and do not account for temporal differences (Boyero 2005; Oliveira and Nessimian 2010).

Tropical seasonality (i.e., cold/dry and warm/rainy seasons) differs from the temperate zone four seasons (spring, summer, autumn, winter). The temperature differences in tropical streams are usually very subtle (≈ 10 °C), while in temperate zones, stream temperatures range seasonally between 0 and 25 °C. A key question is whether tropical benthic macroinvertebrate communities (taxonomic composition, richness, and FFGs) are driven by the seasonality through the contrasting (rainy and dry seasons) hydrological regimes (temperature, water levels, and discharge). Because the hydrological environment influences the functional composition of a stream benthic macroinvertebrate communities, changes in hydrology will be reflected in patterns of the FFGs that can serve as surrogates for the hydrological ecosystem traits.

Our study evaluated the dry and rainy seasonal variation in the taxonomic and trophic (FFGs) diversity of the benthic macroinvertebrate communities of the first-order streams Jose and Mario. These changes in macroinvertebrate communities were also evaluated relative to the seasonal availability of the autochthonous vs. allochthonous food resources for the FFGs in these tropical Mexican streams in the Lacandona rainforest. Lacandona is an evergreen tropical rainforest. The phenology of the tree species that are the source of the litter in the streams involves a complex set of interactions (Cummins et al. 1989; Saavedra Guerrero et al. 2015). The leaf litter allochthonous food resource is available all year around, but litter conditioning is necessary to be consumed by detrital shredders. By contrast, the autochthonous food resources were expected to be available mainly during the low flow dry season, when environmental conditions favor aquatic primary productivity.

In this study, we investigated three hypotheses: (1) The relative availability of different food resources for the benthic macroinvertebrates changes seasonally in response to tropical hydrodynamics. (a) Benthic algae and macrophytes autochthonous food resources abundance increase in the dry

Table 1 Ecosystems traits based on the benthic macroinvertebrate FFGs biomass (*B*) and abundance (*N*) in the José and Mario streams Lacantún River, Chiapas

Ecosystem traits	FFG ratios for traits	Suggested thresholds for surrogated ratios	Calculated surrogated ratios							
			José stream				Mario stream			
			RS		DS		RS		DS	
			B	*N*	*B*	*N*	*B*	*N*	*B*	*N*
Autotrophy to heterotrophy (P/R)	SC + HSH/DSH + GC + FC	> 0.75	0.96	0.47	0.89	0.81	8.82	0.84	4.55	1.09
Coarse particulate organic matter to fine particulate organic matter (CPOM/FPOM)	DSH/GC + FC	Rainy season > 0.25 Dry season 0.50	0.80	0.42	0.76	0.42	0.74	0.13	0.86	0.20
FPOM in transport (suspended) to FPOM storage in sediments (TFPOM/BFPOM)	FC/GC	> 0.50	0.09	0.32	0.08	0.22	0.12	1.15	0.08	0.99
Channel bottom stability (stable stream bottom / unstable stream bottom)	SC + FC + HSH/DSH + GC	> 0.50	1.08	0.78	0.98	1.06	9.34	2.52	4.83	2.67
Top–down predator control	P/SC + DSH + HSH + GC + FC	0.10–0.20	0.63	0.33	0.84	0.33	0.22	0.24	0.33	0.21

Ecosystems traits surrogates according to Cummins et al. (2005), Merritt et al. (2017, 2019)

RS rainy season, *DS* dry season, *GC* gathering collectors, *FC* filtering collectors, *SC* scraper, *HSH* herbivore shredders, *DSH* detrital shredders, *P* predators (engulfers + piercers)

season compared to leaf litter allochthonous resources. (b) The abundance of leaf litter increases in the rainy season, when other resources are less available. (2) Benthic macroinvertebrate community structure would track the availability of their food resources. (a) The herbivore-FFGs, scrapers feeding on periphyton, and herbivore shredders, feeding on macrophytes, constitute the dominant biomass in the dry season. (b) Detritivore-FFGs, detrital shredders, feeding on CPOM leaf litter together with filtering and gathering collectors, feeding on FPOM detritus, dominates macroinvertebrate biomass in the rainy season. (3) Stream ecosystem traits, predicted by ratios of benthic macroinvertebrate FFGs that serve as surrogates for those traits, would change seasonally. In the dry season: (a) the dominance of scrapers and herbivore shredders indicating autotrophy prevails. (b) Detrital shredder dominance indicating interaction with the riparian environment weaken. (c) Gathering collector's dominance, indicating the predominance of BFPOM, is greater. In the rainy season: (d) heterotrophy prevails. (e) The interaction with the riparian evergreen forest cover is greater. (f) TFPOM is greater than BFPOM.

Materials and methods

Study area

Tropical streams José and Mario are first-order tributaries of the Lacantún River sub-basin (16° 08′ N, 90° 54′ W, 200 m a.s.l.), a tributary of the Usumacinta River in Chiapas state, Mexico (Fig. 1). The Lacantún River sub-basin comprises 12,526 km^2 of hydrological region No 30 Usumacinta–Grijalva, the most important river system in Mexico in terms of length (~ 1100 km) and discharge (~ 2678 m^3 s^{-1}, Muñoz-Salinas and Castillo 2015). The climate in the region is warm and rainy, with a mean annual temperature of 27 °C and mean annual precipitation of 3,190 mm (García 2004). The inter-tropical convergence zone determines the seasonality of the region. Trade winds generate tropical storms from the southern and southeastern Caribbean Sea. This produces a May–October warmer and wetter rainy season. Antitrade winds produce a November to April colder and drier dry season (Grodsky and Carton 2003). This seasonality is an important determinant of the lotic ecosystem dynamics of the José and Mario study streams.

The "Montes Azules" Biosphere Reserve (MABR) in the Lacantún River subbasin is an important section (≈ 15%) of the Lacandona rainforest. Although anthropogenic activities have disturbed the Usumacinta River Basin, the José and Mario study streams are within or near the Reserve (MABR) where there are fewer human impacts (Álvarez-Porebski et al. 2015). The evergreen tropical rainforest surrounding the streams is a diverse ecosystem, with more than 267 plant

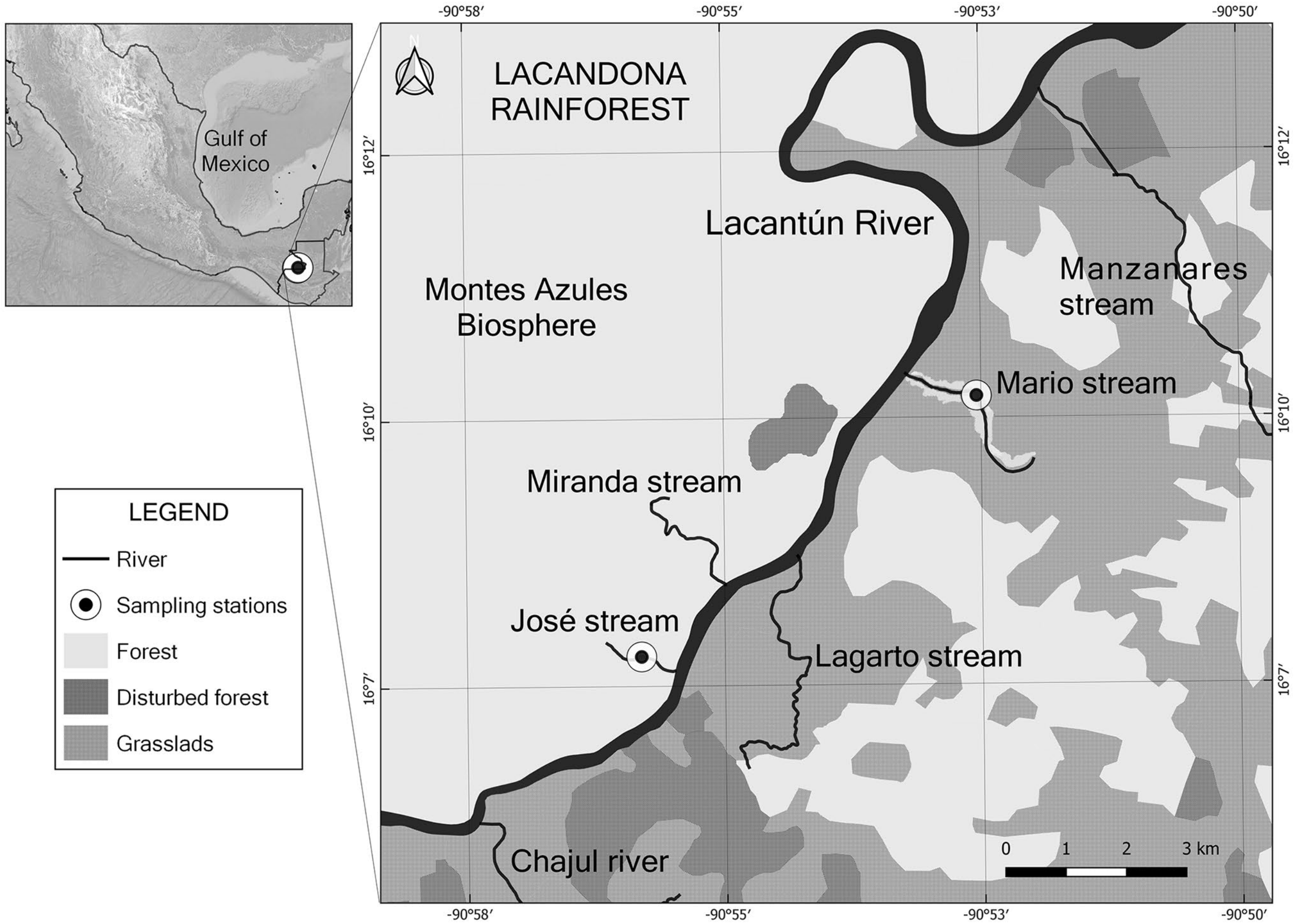

Fig. 1 Location of the José and Mario streams, Lacantún River, Chiapas, Mexico

species per ha, 75% of which are evergreen species with constant leaf drop throughout the year (Saavedra Guerrero et al. 2015). Main tree species in the riparian forest are *Ampelocera hottlei* (Ulmaceae), *Croton schiedeanus* (Euphorbiaceae), and *Protium copal* (Burseraceae) (Meli et al. 2015).

The study streams are 7.1 km apart. Rainforest surrounds the 1321 m long José stream (Fig. 1). The stream's mean width is 4.0 ± 1.1 m with a mean depth of 0.4 ± 0.2 m. The 3280 m long Mario stream flows just outside the MABR, where some degree of pasture-land use disturbance occurs; yet, approximately 80% of its riparian forest is conserved (Fig. 1). The stream has a mean width of 3.1 ± 1.6 m, and a mean depth of 0.4 ± 0.3 m.

Sampling design

The study streams were sampled six times: three times in the rainy season, June, September, and October in 2018, plus three times in the dry season, January, March, and May in 2019. The precipitation regime characterizes the two contrasting seasons of the region. The "Montes Azules" weather station reported rainy season conditions from May to October 2018 (with two peaks in June and October) and dry season conditions from late October 2018 to May 2019. Monthly precipitation ranged between 158.0 and 298.8 mm in the rainy season and from 26.8 to 116.4 mm in the dry season. The temperature showed little variation throughout the year. Monthly temperatures ranged from 23.2 to 25.7 °C in the rainy season and from 19.2 to 23.2 °C in the dry season. Humidity ranged from 78.2 to 90.8%.

To estimate the percentage of shadow over the channels, we used Hobo UA-002-64 sensors. We installed one sensor on a high roof, in a clear zone without trees that served as the 100% reference. Then, two additional sensors were installed in each stream, at the water surface to estimate the light reaching the channels. Sensors were left for a 24 h period.

We selected a 100 m long segment in each stream that represented stream heterogeneity: riffles, pools, backwaters, and different substrate types (e.g., Rodríguez-Capítulo et al. 2009). Environmental variables were measured at three points (the center and both sides, 1/3 of the stream width away from the shore) every 20 m in each 100 m segment. A multiparameter water quality sonde (Hydrolab DS5) was used to measure temperature (T), dissolved oxygen (DO), pH, electric conductivity standardized to 25 °C (K_{25}), and turbidity (Tur) at the three points. At the same stream margin points, current velocity was measured at half the maximum depth with a Swoffer 3000 current meter. Water velocity, mean width, and depth were used to calculate the water discharge (Q) (Elosegui et al. 2009). Seasonal differences in environmental and morphometric variables were evaluated through a two-tailed t-test in SigmaPlot 14.0.

Percent cover of the stream substrate types along each 100 m segment was estimated using a 1 m^2 frame demarked with a 0.01 m^2 grid. To determine the sediment type we followed Elosegui and Díez (2009). The sediment types were coarse sediments, gravel-boulders (2.1–64.0 mm), sand (0.05–2.0 mm), and silt (0.002–0.05 mm); to differentiate sand and silt, we used a 0.05 mm filter. We estimated the total availability of food resources for the benthic macroinvertebrate FFGs in the two streams as the percentage stream substrate covered by each of four categories: benthic algae, macrophytes, leaf litter, and benthic fine particulate organic matter (BFPOM). Benthic algae, macrophytes, and leaf litter were manually sampled using a frame of 0.13 m^2, and the amounts of each category were extrapolated to estimates of coverage in the 100 m segments (García et al. 2016). BFPOM was assumed to be represented by the stream bottom sediments that were not covered by the other food types and consisted of FPOM on and in the substrate. Estimation of the FPOM in suspension and transported in the current (TFPOM) was obtained through the suspended solids measurements from composite water samples collected along the stream segments. We passed a known stream water volume through a 100 µm filter to remove fragments of coarse particulate matter. Then, 30–100 ml of water were filtered through a glass fiber filter (GF/F) of 0.7 µm previously combusted (at 550 °C for 48 h) and weighted. TFPOM was obtained through the difference in the weight of the filter before and after filtration (Hutchens et al. 2017). Seasonal differences in resources abundance were evaluated through a two-tailed *t* test; when equal variances criterium was not met, we applied a Mann–Whitney rank sum test. Analyses were performed in SigmaPlot 14.0.

A D-frame net (0.5 mm mesh) was used to collect composite benthic macroinvertebrates samples representing all habitats along each 100 m segment. This collection method was standardized by 1-min sweeps in a 1 m^2 area (Chiasson 2009); the area was visually estimated, and the same group of researchers did the sampling on the six sample dates. The macroinvertebrates were sorted in the field, preserved in cold (− 10 °C), identified to genus and classified into FFGs using studies from tropical streams when the information was available (Domínguez and Fernández 2009; Dudgeon 1989; Spies et al. 2006; Tomanova et al. 2006; Oliveira and Nessimian 2010) and the classification from North American aquatic insects when tropical studies were not available (Merritt et al. 2019). FFGs were categorized into three main groups: (i) herbivores, including scrapers (SC) and herbivore shredders (HSH), (ii) detritivores, including detritivore shredders (DSH), gathering collectors (GC) and filtering collectors (FC), and (iii) predators (P), including piercer predators (PP) and engulfer predators (EP) (Merritt et al. 2017, 2019). The limited taxonomic knowledge of neotropical macroinvertebrates prevented the identification of immatures to the species level. However, research has shown that identification to the species level is usually not required for determining functional diversity (FFGs) (e.g., Cummins and Klug 1979; Dolédec et al. 2000; Gayraud et al. 2003; Tomanova et al. 2006; Merritt et al. 2017, 2019).

The benthic macroinvertebrates were counted and then oven-dried at 60 °C for 48 h and weighed collectively by FFG (morpho/taxa) on a mass comparator Mettler Toledo (precision 0.1 µg) to obtain their dry biomass. These FFG biomass values, expressed as surrogated ratios, were used to calculate five ecosystem traits (Table 1) (Cummins et al. 2005, Merrit et al. 2017). These ratios are dimensionless and essentially independent of sample size. Traits differences between seasons and streams were evaluated through a two-way ANOVA in SigmaPlot 14.0, with an orthogonal design, the random factor “stream” and the fixed factor “season”.

Seasonal differences in the FFGs abundance and biomass were evaluated through a parametric ANOVA. We performed a principal components analysis (PCA) to test if the environmental variables explained the food resource availability. To test the effect of the type and quantity of food resources on the macroinvertebrate community structure, we used linear regression analyses between the expected food resource and the FFGs biomass. SC biomass was tested against benthic algae, HSH against macrophytes, GC against BFPOM, FC against TFPOM, DSH against leaf litter, and P against all other FFGs summed. The two streams were treated as replicates, and data were transformed ($\log_{10}$) to achieve normality. The ANOVA and linear regressions were performed in SigmaPlot 14.0. The PCA was performed in PRIMER 7.

Results

Water column and substrate

Overall characteristics of the two streams were similar. The streams are warm, well-oxygenated, neutral to slightly basic, and with low conductivity (Table 2). José had higher pH ($t = 7.404$, 10 *d.f.*, $p < 0.001$) and conductivity ($t = 22.013$, 10 *d.f.*, $p < 0.001$) than Mario, while the other parameters

Table 2 Physical and chemical parameters of the José and Mario streams, Lacantún River, Chiapas

	José stream						Mario stream					
	T (°C)	DO (mg L^{-1})	pH	K_{25} (µS cm^{-1})	Tur (NTU)	Q (m^3 s^{-1})	T (°C)	DO (mg L^{-1})	pH	K_{25} (µS cm^{-1})	Tur (NTU)	Q (m^3 s^{-1})
RS												
X	22.2	7.5	8.1	959	12	0.29	25.5	7.1	6.9	73	30	0.16
SD	0.6	0.7	0.3	8	14	0.03	0.7	0.6	0.3	21	38	0.15
Min	23.3	6.9	7.8	922	0	0.25	24.5	6.3	6.4	49	0	0.06
Max	24.8	8.6	8.6	998	34	0.32	26.6	8.4	7.8	90	107	0.33
DS												
Mean	23.2	7.7	7.9	1069	3	0.18	24.7	6.2	6.5	63	18	0.04
SD	1.5	1.2	0.1	96	12	0.04	1.9	1.7	0.2	23	38	0.01
Min	21.2	6.4	7.8	949	0	0.12	21.6	3.6	6.0	45	1	0.02
Max	25.1	9.4	8.1	1188	82	0.20	28.5	8.8	7.0	96	209	0.05

RS rainy season, *DS* dry season, *T* temperature, *DO* dissolved oxygen, K_{25} conductivity, *Tur* turbidity, *Q* water discharge, *X* mean, *SD* standard deviation, *Min* minimum, *Max* maximum, samples (N) = 18

(water discharge, temperature, dissolved oxygen, and turbidity) were similar between streams (Table 2). Seasonality was confirmed through the water discharge ($t=2.504$, 10 *d.f.*, $p=0.03$) and turbidity ($t=2.224$, 10 *d.f.*, $p=0.04$), which were higher in the rainy season in both streams.

José is 92% shaded, while Mario is 78% shaded. Gravel-boulders (33–38% in José, 24–30% in Mario) and sands (43–44% in José, 35–39% in Mario) dominated the bottom of both streams. Silt coverage was higher in Mario than José (4–5% in José, 19% in Mario).

Total allochthonous food resources (leaf litter and FPOM) were three orders of magnitude more abundant than the autochthonous food resources (benthic algae and macrophytes) in both streams and seasons (Table 3). Autochthonous food resources (José stream $t=-4.027$, 4 *d.f.*, $p=0.016$; Mario stream $t=-5.246$, 4 *d.f.*, $p=0.006$) and leaf litter (José stream $t=-6.749$, 4 d.f., $p=0.002$; Mario stream $t=-8.960$, 4 *d.f.*, $p<0.001$) in both streams were more abundant in the dry season than in the rainy season, probably due to dislodgement during high flows. Estimated BFPOM was up to 10% more abundant than TFPOM in both streams and seasons. However, in Mario and contrasting to the other food resources, FPOM—both benthic and transported—was more abundant in the rainy season than in the dry season ($U=1.0$, $p=0.004$). FPOM in José was similar between seasons ($U=7.0$, $p=0.093$) (Table 3).

The first three principal components explained 86.7% of the variation of food resources (Fig. 2). The first component (PC1) explained 43.4% of the variation and included the benthic algae (0.470) and the macrophytes (0.470) negatively correlated to the precipitation (−0.489). The second component (PC2) explained 25.0% of the variation and included the leaf litter (0.575) negatively correlated to the water discharge (−0.550). The third component (PC3) explained 18.3%, included the BFPOM (−0.562) and TFPOM (−0.587), positively correlated to the turbidity (−0.464).

Biota

We collected 63 genera of benthic macroinvertebrates from 39 families and ten orders (Table 4, Table S1). Of those, 24 genera (40%) have been previously reported from the Usumacinta River basin (Castillo et al. 2018 and references within), and 39 genera (60%) constitute new reports for the

Table 3 Food resources abundance in the José and Mario streams, Lacantún River, Chiapas

Stream	Season	Autochthonous		Allochthonous		
		Benthic algae (g dry mass m^{-2})	Macrophytes (g dry mass m^{-2})	Leaf litter (g dry mass m^{-2})	TFPOM (g l^{-1})	BFPOM (g l^{-1})
José	RS	0.003 ± 0.001	0.005 ± 0.002	41.28 ± 5.28	0.004 ± 0.002	0.054 ± 0.030
	DS	0.021 ± 0.012	0.043 ± 0.024	216.85 ± 187.14	0.002 ± 0.001	0.038 ± 0.019
Mario	RS	0.018 ± 0.014	0.036 ± 0.028	137.48 ± 104.7	0.010 ± 0.006	0.132 ± 0.138
	DS	0.053 ± 0.011	0.107 ± 0.021	246.8 ± 118.3	0.002 ± 0.001	0.026 ± 0.008

RS rainy season, *DS* dry season

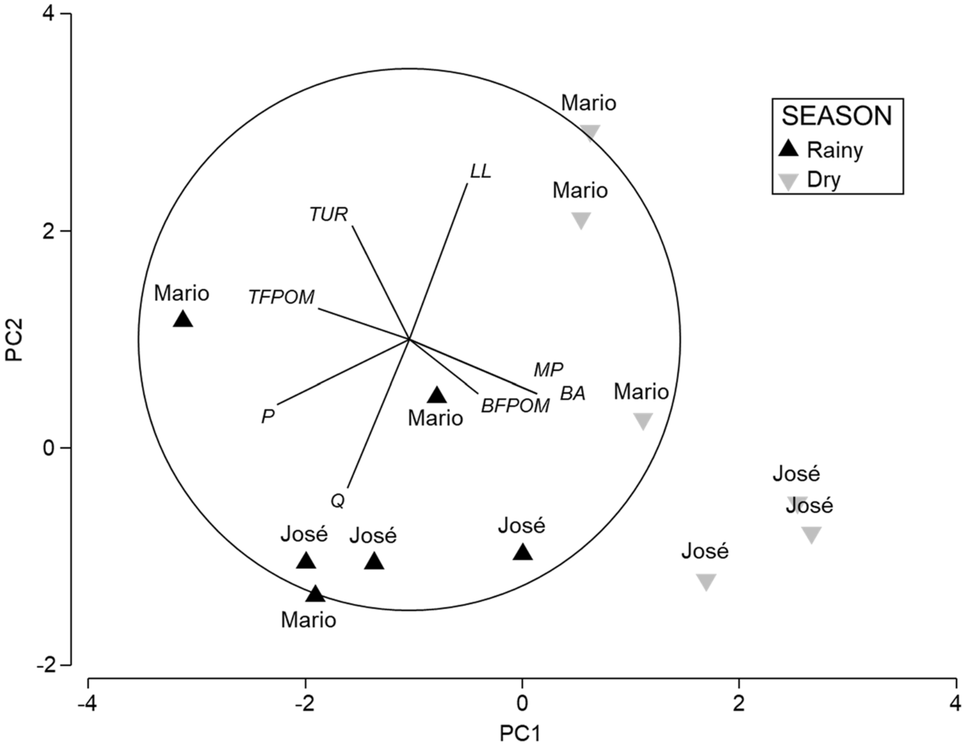

Fig. 2 Principal components analysis between the abundance of food resources (*BA* benthic algae, *MP* macrophytes, *LL* leaf litter, *TFPOM* transported fine particulate organic matter, *BFPOM* benthic fine particulate organic matter) and the environmental parameters (*P* precipitation, *Q* water discharge, *TUR* turbidity) throughout the year in the José and Mario streams, Lacantún River, Chiapas

Table 4 Number of genera summarized by order collected in the José and Mario streams, Lacantún River, Chiapas in both seasons

Orders	José stream		Mario stream		No. total genera
	No. genera	%	No. genera	%	
Mesogastropoda	1	2	1	1.6	1
Decapoda	2	3	1	1.6	2
Ephemeroptera	4	6	5	7.9	5
Odonata	12	19	12	19	14
Plecoptera	1	2	1	1.6	1
Hemiptera	3	5	3	4.8	3
Megaloptera	1	2	1	1.6	1
Coleoptera	15	24	13	20.6	18
Trichoptera	9	14	11	17.5	11
Diptera	6	10	5	7.9	7
Total	54	86	53	84.1	63

region. Odonata and Coleoptera had the highest taxonomic richness, with 14 and 18 genera, respectively, while Plecoptera, Megaloptera, and Mesogastropoda had just one genus each. Of the 63 genera, 44 (70%) inhabited both streams, while ten genera (16%) were found only in José, and nine genera (14%) were found only in Mario. The taxonomic richness was characterized by 54 genera in José and 53 in Mario.

A total of 27 (43%) genera were assigned to a single FFG; that is, they were obligate taxa dependent on a single food resource category, and 36 (57%) genera were facultative and assigned to more than one FFG. A total of 28 genera were predators, 26 engulfer predators and four piercer predators, 21 gathering collectors, 20 scrapers, 12 herbivore shredders, eight filtering collectors, and seven detrital shredders.

The taxonomic richness in the José stream was characterized by 27 ± 7 genera in the rainy season and 33 ± 3 genera in the dry season. The Mario stream's taxonomic richness was characterized by 27 ± 8 genera and 32 ± 2 genera in the rainy and dry seasons, respectively. This taxonomic richness was similar in both seasons and in both streams. In both streams, abundance in the rainy season (461 ± 267 ind in José, 404 ± 249 ind in Mario) was half of the abundance in the dry season (803 ± 29 ind in José, 707 ± 145 ind in Mario).

Both abundance and biomass values were highly variable (Table 5) as reflected in the variation coefficients. High variance is common in benthic macroinvertebrates studies because of the well-known clumped (negative binomial) distribution of stream benthic macroinvertebrates.

The FFG total abundance was higher in the dry season ($F = 16.581$, $p < 0.001$). Detritivores had higher abundance than herbivores and predators ($F = 6.277$, $p = 0.005$), but there was no difference between streams ($F = 0.062$, $p = 0.805$, Table 5). In the José stream, GC, SC, and PE had the highest abundances. In the Mario stream, SC, GC, and FC were the most abundant. HSH and PP were the least abundant in both streams (Fig. 3).

The FFG biomass of both streams varied seasonally (Fig. 3). All the FFGs showed a higher taxonomic richness in the dry season than in the rainy season. The PE in the

Table 5 Mean (±SD) values and variation coefficients (%) of the benthic macroinvertebrate biomass (B, mg C m^{-2}) and abundance (N, ind) per FFG in the José and Mario streams, Lacantún River, Chiapas

FFG	Proxy	José stream		Mario stream	
		RS	DS	RS	DS
GC	*B*	47.8±23.7	139.0±50.7	31.9±36.2	101.3±43.9
		50%	37%	113%	43%
	N	26.1±15.4	38.2±7.9	17.7±13.5	31.2±21.6
		59%	21%	76%	69%
FC	*B*	5.0±4.6	13.7±15.4	3.6±3.4	7.9±2.7
		92%	112%	94%	34%
	N	8.3±4.5	8.1±4.7	19.8±14.5	27.8±16.6
		54%	58%	73%	59%
DSH	*B*	40.8±17.0	112.4±37.6	28.1±33.0	94.0±39.6
		42%	33%	117%	42%
	N	14.7±9.5	18.3±4.5	2.9±1.9	11.4±7.1
		65%	25%	66%	62%
Total detritivores	*B*	49.9±25.1	147.4±46.7	33.4±36.2	105.7±42.1
		50%	32%	108%	40%
	N	30.1±19.9	49.6±8.2	24.5±16.7	43.4±21.7
		66%	16%	68%	50%
SC	*B*	64.1±78.0	141.5±69.4	159.4±123.0	313.6±260.3
		122%	49%	77%	83%
	N	19.7±12.2	33.2±7.3	23.6±16.9	43.6±16.4
		62%	22%	72%	37%
HSH	*B*	55.7±74.5	83.0±23.9	155.1±119.1	291.5±244.5
		134%	29%	77%	84%
	N	5.1±6.8	18.9±8.0	7.7±4.9	16.9±5.3
		133%	42%	64%	31%
Total herbivores	*B*	65.7±80.7	144.8±66.3	159.4±123.0	313.7±260.4
		123%	46%	77%	83%
	N	19.9±12.7	37.6±10.9	23.6±16.9	44.0±15.8
		63%	29%	72%	36%
PP	*B*	18.5±18.3	41.2±22.5	5.3±1.9	13.3±16.6
		99%	54%	36%	125%
	N	6.0±3.6	4.5±1.8	1.6±0.7	1.3±0.3
		59%	41%	41%	22%
PE	*B*	78.3±28.4	416.9±373.4	67.4±47.4	239.2±122.7
		36%	90%	70%	51%
	N	16.4±6.9	33.1±7.4	12.2±6.8	21.8±5.6
		42%	22%	55%	25%
Total predators	*B*	96.8±44.7	458.1±392.9	72.6±49.1	252.5±113.4
		46%	86%	68%	45%
	N	22.4±10.5	37.6±7.9	13.8±7.2	23.1±5.3
		47%	21%	52%	23%

RS rainy season, *DS* dry season, *GC* gathering collectors, *FC* filtering collectors, *SC* scraper, *HSH* herbivore shredders, *DSH* detrital shredders, *PP* piercer–predator, *PE* predator–engulfer

José stream had the highest biomass during both seasons, followed by the SC and HSH in the rainy season and SC and GC in the dry season. In contrast, the SC in the Mario stream had the highest biomass during both seasons, followed by the HSH and PE (Table 5).

In the José stream, the total biomass of herbivore-FFGs (SC and HSH) was similar to the total biomass of detritivore-FFGs (GC, FC, and DSH) in both seasons ($F = 0.628$, $p = 0.550$). In the Mario stream, the herbivores biomass was higher than the detritivores biomass in both seasons

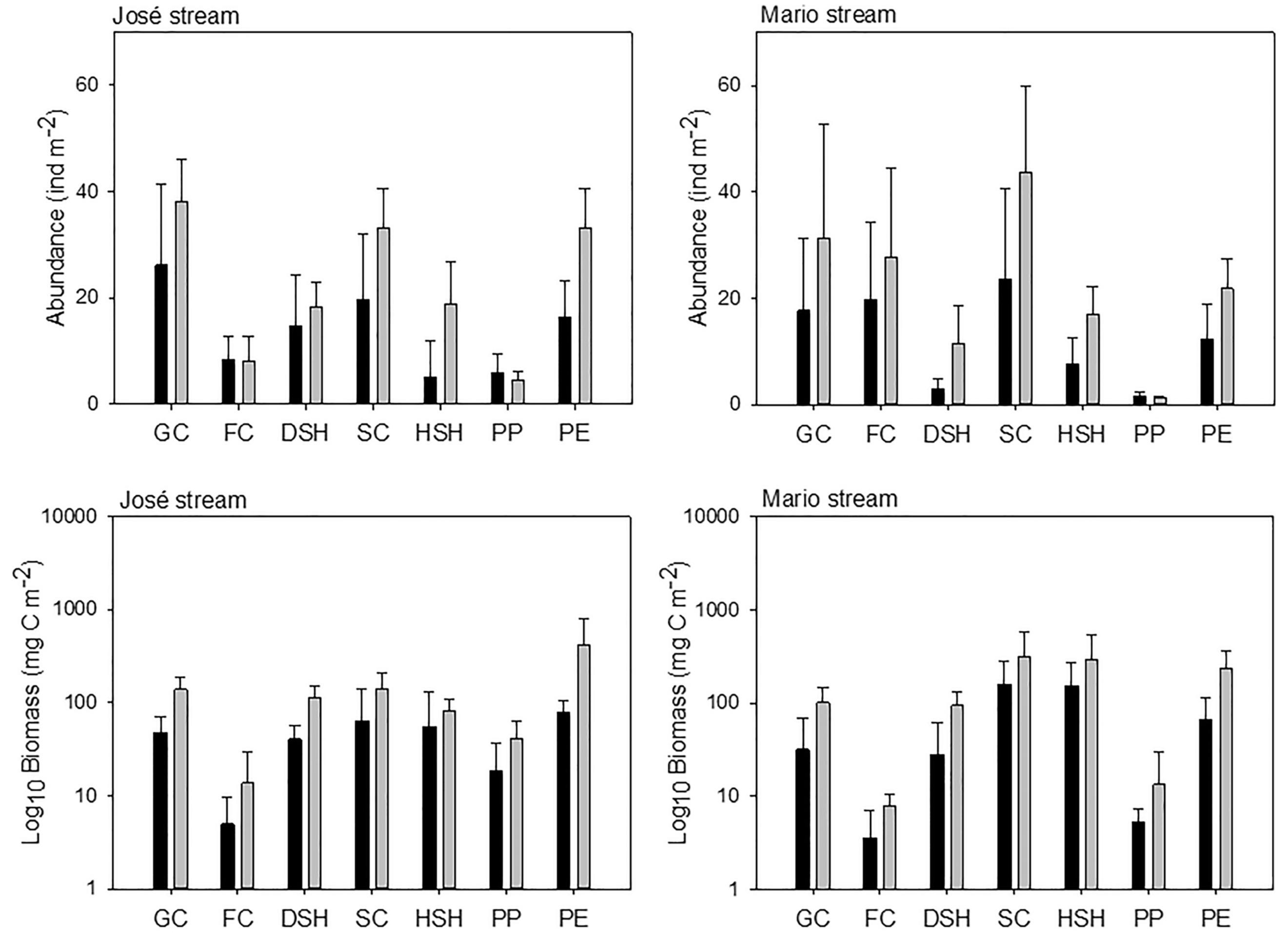

Fig. 3 Mean (± standard deviation) of the benthic macroinvertebrate abundance (up) and biomass (down) per FFG in the José and Mario streams. (*SC* scraper, *HSH* herbivore shredders, *GC* gathering collectors, *FC* filtering collectors, *DSH* detrital shredders, *PP* piercer–predators, *PE* engulfer–predators)

Table 6 Linear regression output performed with the FFGs biomass and food resources abundances of the José and Mario streams, Lacantún River, Chiapas, in both seasons

Equation	r^2 adjusted	Standard error	*P*
SC = 3.24 + (0.64 * Benthic algae)	0.52	0.36	0.005
HSH = 3.09 + (0.74 * Macrophytes)	0.46	0.45	0.009
GC = 0.50 – (0.93 * BFPOM)	0.48	0.31	0.008
FC = – 1.21 – (0.95 * TFPOM)	0.37	0.37	0.021
DSH = 1.45 + (0.12 * leaf litter)	0.09	0.46	0.765
P = 0.20 + (0.77 * total prey)	0.45	0.3	0.010

($F=6.150$, $p=0.029$). Moreover, the herbivores biomass in Mario was twice the herbivores biomass in José, but the detritivores biomass was similar in both streams (Table 5).

Linear regressions showed a relationship between FFGs and their expected food resources, except DSH, which did not correlate with the leaf litter abundance (Table 6). Herbivore (SC and HSH) and predator (PP and PE) FFGs showed positive correlations with their expected food resources in both streams and seasons. On the contrary, detritivores had either a negative correlation (GC and FC) or no correlation (DSH) with their expected food resources (Fig. 4).

The biomass distribution of FFGs indicated a predominantly autotrophic metabolism in both streams, and significantly higher in Mario ($F=7.984$, $p=0.022$, Table 1). The CPOM to FPOM ratio showed a high detrital shredder association linked to the riparian zone, without differences between streams ($F=0.279$, $p=0.612$). TFPOM was lower than the BFPOM storage in the sediments in both streams ($F=0.509$, $p=0.496$), and the stability of the channel bottom was high in Mario and marginally low in José ($F=7.930$, $p=0.023$). The predator control (top-down control) was higher in José than in Mario ($F=7.870$, $p=0.023$, Table 1). All the ecosystem traits were similar between seasons in both streams (P/R $F=0.288$, $p=0.606$; CPOM/

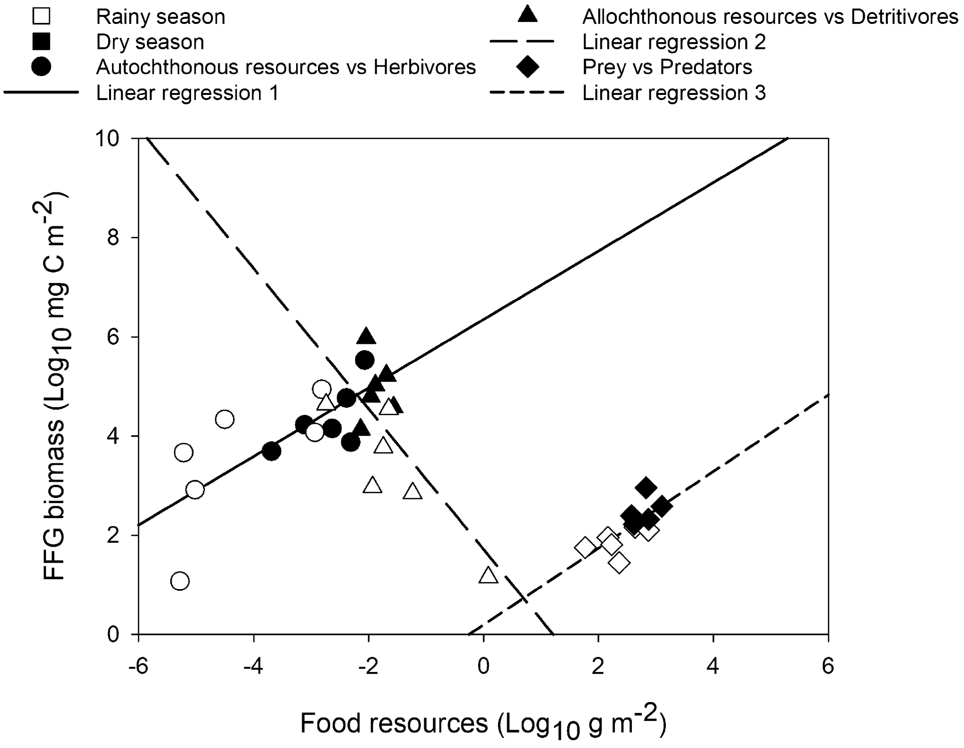

Fig. 4 Linear regressions between the FFGs and their expected trophic resources in the José and Mario streams, Lacantún River, Chiapas, in both seasons. Herbivores include SC and HSH, detritivores include GC, FC, and DSH, predators include PP and PE, autochthonous resources include benthic algae and macrophytes, allochthonous resources include leaf litter and FPOM, and prey include all FFGs except for predators

FPOM $F=0.809$, $p=0.395$; TFPOM/BFPOM $F=0.691$, $p=0.430$; Substrate stability $F=0.349$, $p=0.571$; Top-down control $F=0.920$, $p=0.366$).

The surrogate FFG ratios for stream ecosystem traits indicated some differences between the numerical ratios and the biomass ratios (Table 1). Based on numerical abundance, both streams were autotrophic in the dry season, but only Mario was autotrophic in the rainy season. The numerical abundance also showed a dominance of FPOM in Mario in both seasons, and in José just in the dry season. The numerical TFPOM to BFPOM ratio and the substrate stability ratio were similar to the biomass ratios. The top–down predator control was closer to the suggested ratio thresholds (i.e., 0.10–0.20) but lower than the ratio based on biomass (Table 1).

Discussion

Taxonomic diversity

The observed benthic macroinvertebrate taxonomic richness (30 ± 5 taxa in José, 29 ± 6 taxa in Mario) is within the range of 13–70 taxa reported for other tropical streams (e.g., Al-Shami et al. 2014; Buss et al. 2004; Parreira de Castro et al. 2016; García et al. 2016). Richness is also similar to that previously found for the region (33 ± 30, 2–103 taxa) (Bueno-Soria et al. 2005).

The most diverse orders found in the José and Mario streams were Coleoptera (18 genera) and Odonata (14 genera). Castillo et al. (2018) found 26 Coleoptera genera and 21 Odonata genera in the nearby Usumacinta River. It is not surprising that Odonata was highly diverse in the José and Mario streams because the neo-tropical region holds the highest diversity for this order, as Balian et al. (2008) reported. In addition, Coleoptera, along with Diptera and Trichoptera, are highly diverse in freshwater environments. They represent between 15 and 43% of the total species richness of aquatic insects worldwide (Balian et al. 2008).

The benthic macroinvertebrate taxonomic richness did not change significantly between seasons in the José and Mario streams, although the heavy rainfalls had selectively flushed out some taxa (Baptista et al. 2001; Buss et al. 2004). Many species have been shown to resist being flushed out by environmental disturbances through refuge-seeking behavior (Scrimgeour and Winterbourn 1989).

Trophic dynamics

In tropical streams, the abundance of algae increases during the dry season (Douglas et al. 2005) as was the case for José and Mario streams. This led to an increase in herbivore biomass in both streams. In contrast, in the rainy season, the higher water discharge increased turbidity and limited the light availability for primary producers. An increase in the transportation of sediment particles was a consequence of heavy runoff. These transported particles are composed mainly of inorganic material and they need to be coated with bacteria to represent a suitable nutritional resource for FFG collector benthic macroinvertebrates (Cummins et al. 2005).

Herbivore biomass was higher in Mario (236.5 ± 20.8 mg C m^{-2}) than in José (105.2 ± 78.9 mg C m^{-2}). This pattern was associated with the higher benthic algae and macrophyte abundance in Mario, which was less shaded than José (78% vs. 92%). We also found significantly more leaf litter on the stream bottom of both streams in the dry season than in the rainy season. It is probable that even if rainfall increased the amount of leaf litter carried into the streams, the increased current rapidly washed out the leaves and reduced their availability (Cummins et al. 2005). We could not relate the leaf litter abundance to the DSH biomass in either of the two streams (Table 6), despite DSH biomass and leaf litter abundance both increased in the dry season compared to the rainy season. DSH select CPOM leaf litter that has been preconditioned by hyphomycete fungi and bacteria (e.g., Arsuffi and Suberkropp 1989; Cargill et al. 1985). Phenology of tree species in the evergreen, tropical rainforest is complex (Saavedra Guerrero et al. 2015). Even though a peak in leaf drop could occur in the rainy season (Wantzen et al. 2008), leaf litter would not be suitable as a food resource for DSH until it was conditioned. Moreover, freshwater crabs are usually important DSH in tropical streams, and standard benthic sampling methods tend to overlook crabs (Boulton et al. 2008); therefore, we could be underestimating the DSH biomass and its relationship with the leaf litter.

Gathering collectors (GC) was the most abundant FFG in the José stream and the second most abundant in Mario. GC biomass was one of the lowest in both streams and seasons related to the small average body size per individual (e.g., *Traverella*, *Leptohyphes*). The opposite was true for shredders that had high biomass but low abundance. Abundant GC and sparse DSH is a common condition in tropical streams (e.g., Brasil et al. 2014; Ferreira et al. 2017; Graça et al. 2015; Tomanova et al. 2006; Oliveira and Nessimian 2010; Ono et al. 2020). GC and DSH are very abundant in North American streams (Table 7). Biomass of GC and DSH are not usually measured in North American stream studies, making comparisons with tropical streams difficult. Biomass is usually a better indicator of a trophic condition than abundance (Cummins et al. 2020). Taxonomic richness of DSH in the José and Mario streams was very low compared to the number of taxa found in North American streams (Table 7). This difference is likely related to the deciduous trees and shrubs present in the riparian zone that borders North American first-order streams and supports diverse DSH populations (e.g., Grubbs and Cummins 1996). The riparian evergreen forest bordering the José and Mario streams contains few deciduous tree species.

Filtering collectors (FC) constituted the lowest biomass (< 13%) in both streams and both seasons. However, their taxonomic richness was more than 20% of the total benthic

Table 7 Comparison of Mexican and North American headwater stream ecosystem traits and benthic macroinvertebrates

Ecosystem traits and benthic macroinvertebrate traits	Mexican streams						North American streams		
	José			Mario					
First order stream width	4.0 ± 1.1 m			3.1 ± 1.6 m			0.5–2.0 m		
Human disturbance	Minimal			Minor pasture			Minimal		
Substrate	Gravel to boulders with scarce large wood						Gravel to cobbles with abundant large wood		
	No. families	No. genera		No. Families	No. genera		No. families	No. genera	
		O	F		O	F		O	F
SC	2	5	15	3	6	14	24	24	59
HSH	5	1	11	5	1	11	12	35	43
DSH	1	1	6	1	1	6	17	35	43
GC	9	15	9	8	12	9	35	3	167
FC	1	6	3	1	6	3	15	33	12
P	14	26	2	12	26	2	49	211	12
Total	32	54	46	30	52	45	152	341	336

José and Mario after Table 4. North American data from ecological tables in Merritt et al. (2019) under habitat entries for streams in general plus small head water streams or spring brooks; for FG entries under a taxon, obligate (O) signifies the only choice available and facultative (F) entries, the first in the list was used to designate the FFG, based on the preponderance of the literature listed (Mexican, Table 4, this paper, North American, ecological tables in Merritt et al. (2019). José and Mario are first order streams. The North American data are for first to third order streams

SC scrapers, *DSH* detrital shredders, *HSH* herbivore shredders, *GC* gathering collectors, *FC* filtering collectors, *P* predators macroinvertebrate community. The low FC biomass was associated with the reduced average size per individual of these collectors. The rapid shift between seasonal high-quality food items eroded into the water column (benthic algae and macrophyte fragments) and the more continuously available low-quality mineral particles and TFPOM allochthonous food resources favors higher taxonomic richness and abundance of collectors. Collectors exhibit opportunistic feeding strategies typical of facultative FFGs (Covich 1988; Wantzen and Wagner 2006).

Both GC and FC had a negative correlation with their expected food resources (Fig. 2). The biomass of the collectors depends on the quality of their food resources. FPOM is abundant and comes from the breakdown of CPOM leaf litter and macroinvertebrate feces that are available all year round (Cummins 1974). Evergreen foliage is processed slowly by microbes and DHS but it is continuously available throughout the year (Ferreira et al. 2017). The slow processing of this organic matter is in large part due to the presence of many humic compounds that are recalcitrant and require organisms with specialized enzymes to processing (Li et al. 2009). This results in low-quality FPOM from low-quality evergreen CPOM (Cummins et al. 1989) and restricts the growth of collectors in tropical streams (Ramírez et al. 2014).

Finally, the predator biomass was high during both seasons in both streams. The taxonomic composition of the macroinvertebrates in both José and Mario streams (Table 7) showed that active and ambush predators had a good supply of prey taxa. A high degree of flexibility in the life histories and mobility of neotropical lotic predators is conducive to the exploitation of their prey food resource (Covich 1988; Gebrehiwot et al. 2017; Tomanova et al. 2006). Greater mobility of active predators increases their foraging range and facilitates the location of suitable prey food patches (Graça et al. 2001). Large predator biomass can only be sustained by large proportions of rapid turnover prey taxa, known as the Allen's paradox (Allen 1951, 1958).

Ecosystem traits

Changes in biomass of FFG macroinvertebrates related to the relative importance of the José and Mario stream ecosystems energy pathways and serve as environmental dynamics indicators (Ellison et al. 2005). Contrary to our hypothesis, stream ecosystem traits were not significantly different between the rainy and dry seasons and there was no change in the dominance of FFGs between seasons. SC and HSH FFGs had the higher biomass throughout the year, although there was a clear increase in the biomass of all the FFGs during the dry season.

Autotrophic herbivory food web pathways were found in both streams but were more prevalent in Mario. However, allochthonous food resources (CPOM leaf litter and FPOM) were abundant in both streams. The ratio of DSH to total collectors (CG and FC) indicated a strong relationship with leaf litter inputs and DSH macroinvertebrates in both streams. The consumption of CPOM leaf litter frequently has been related to the low nutritional FPOM (Cummins et al. 2005). FPOM was sparse in both streams and seasons and supported only small populations of collectors, especially filtering collectors dependent on TFPOM (e.g., Mattingly et al. 1981; Ward and Cummins 1979). A low ratio of transported to benthic FPOM (TFPOM/BFPOM) based on the ratio of filtering collectors to gathering collectors indicated that a larger portion of the FPOM was benthic FPOM settled on/in the stream bottom sediments.

The higher biomass of the gathering collectors compared to filtering collectors in the both streams was likely due to the availability of higher quality microbially colonized FPOM, on and in the bottom sediments (Cummins et al. 2005). Both streams in both seasons had adequate stable substrates that allowed scrapers and filtering collectors to maintain in their feeding locations in the current. This explained the constancy of the number of FFGs and taxonomic richness of the macroinvertebrate fauna through both seasons. The high biomass of predators in both streams and seasons supported the low density on prey populations that was observed.

Aquatic food webs are frequently size-structured, reflecting a correspondence between trophic position and body size (Potapov et al. 2019; Shurin et al. 2006). Large predators were Odonata, Megaloptera (*Corydalus*), and Plecoptera (*Anacroneuria*) in the food webs characteristic of the José and Mario streams. Prey taxa had low biomass compared to their predators as shown by the ratio of predator to prey FFGs. This condition is normal in stream ecosystems and supports the required rapid turnover rates of prey biomass to support the greater predator biomass (Allen 1958; Shurin et al. 2006). The FFG ratio of predators to prey was well above the proposed threshold expected for top–down control in both streams and seasons (Tables 1 and 7). However, we also observed correspondence between the biomass of FFGs and the abundance of their food resources. The conclusion is that bottom–up (food resource limitation) and top–down (predator regulation) control can occur together. Nery and Schmera (2016) demonstrated that a combination of bottom–up and top–down controlled macroinvertebrates communities in headwater streams could occur. They also showed that bottom–up forces had a stronger effect on macroinvertebrate abundance and biomass, but top-down effects were also indicated by large predator biomass. Both bottom-up and top–down effects likely affected the FFG macroinvertebrates that were documented in the José and Mario streams.

The ecosystems traits surrogated from FFGs proportions are likely to change in response of land-use change, which is one of the main threats to freshwater ecosystems (Dudgeon et al. 2006). Changes in trophic interactions, resource use, and feeding behavior are among the primary responses to land-use changes (Allan 2004; Price et al. 2019). Changes in the riparian vegetation directly influence the autotrophy to heterotrophy ratio by modifying the nutrient budget and the autochthonous production, and the strength of the relationship with the riparian environment, thereby affecting the relative contribution of allochthonous and autochthonous resources (Parreira de Castro et al. 2016; Price et al. 2019). Moreover, it has been observed that land-use change oversimplifies the macroinvertebrate food webs by homogenizing the energy pathway, removing specialized taxa, and reducing the trophic redundancy, which negatively affects the functioning of the entire stream ecosystem (Parreira de Castro et al. 2016; Price et al. 2019). First-order, forested streams, like José and Mario, with a strong relationship with the riparian environment, and a combination of bottom–up and top–down controls, are particularly susceptible to land-use change.

This study measured the seasonal, intra-annual, variation in the benthic macroinvertebrate trophic dynamics. Long-term studies to evaluate the inter-annual variability in food resources and the associated macroinvertebrate responses would contribute significantly to the study of trophic dynamics in first-order, tropical streams. More information is needed because freshwater ecosystems are among the most threatened worldwide (Dudgeon et al. 2006). Changes in climatic patterns will undoubtedly affect riparian forests cover along streams, seasonal hydrologic patterns, and affect availability of macroinvertebrate food resources and, consequently, alter their food webs.

Conclusions

The hydrodynamics and environmental characteristics of the José and Mario streams differed between seasons. However, we did not find significant differences in the taxonomic diversity of the streams between seasons nor between streams.

Our results supported the first hypothesis that food resource availability changed between seasons. Autochthonous primary producers and allochthonous leaf litter increased in the dry season, correlated to the tropical hydrodynamics. Benthic macroinvertebrate biomass differed between seasons; it was higher during the dry season than during the rainy season in both streams.

The second hypothesis was partially supported by the data. There was an increase in SC and HSH biomass in the dry season in both streams. This increase in biomass was consistent with an increase in the benthic algae and macrophyte food resources supported by lower flows and greater transparency in the dry season. This accompanied an increase in the biomass of DSH, FC and GC in the dry season, but was negatively or not correlated to the abundance of their food resources. The latter was likely related to the low quality of the recalcitrant CPOM from the evergreen riparian forests cover that led to the generation of low-quality FPOM.

Finally, the third hypothesis was not supported by our results. The stream ecosystem traits predicted by FFG ratios did not change seasonally in either stream. This was probably associated to the dominance of scrapers and shredders biomass throughout the year.

Our study supports the proposal that tropical seasonality affects the biomass of benthic macroinvertebrate FFGs and the abundance of their food resources. In tropical streams, low flow in the dry season favors the development of primary producers that support herbivore food webs. The low diversity and abundance of detrital shredders (DSH), and gathering (GC) and filtering (FC) collectors did not match the timing of evergreen leaf drop into the stream riparian zone. A possible explanation is likely due to the time require for the microorganisms to condition the recalcitrant evergreen leaves which delays rendering their palatability for detrital shredders. In temperate zone streams the timing between the deciduous leaf dropping and the abundance of DSH is tightly coupled.

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Capítulo 3: Los autótrofos contribuyen de forma importante a la red trófica de macroinvertebrados bentónicos en dos arroyos tropicales boscosos de primer orden

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Autotrophs are important contributors to benthic macroinvertebrate food webs in two tropical first-order forest streams

Daniela Cortés-Guzmán[1], Javier Alcocer[2], Dolores Planas[3]

[1]Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, México

[2]Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Ciudad de México, México

[3]Centre de recherche en géochimie et en géodynamique GEOTOP, IUQAM-McGILL, Montreal, Canada

Correspondence: Javier Alcocer. FES Iztacala, Universidad Nacional Autónoma de México. Av. de los Barrios 1, Los Reyes Iztacala, C. P. 54090, Tlalnepantla, Estado de México, México. jalcocer@unam.mx. Phone: 525556231333.

Keywords: autotrophic pathway, detrital pathway, stable isotopes, omnivory, trophic structure

Abstract

1. In tropical first-order streams, the availability of basal resources changes according to tropical seasonality, i.e., dry and rainy seasons, with consequences for the food web structure. However, the seasonal variation in autotrophic and detrital pathways remains unclear. In this study, we aimed to establish whether the dominant pathway

of the benthic macroinvertebrate food web in two tropical first-order streams in the Lacandona rainforest, Mexico, relies on autotrophic or detrital food resources.

2. We evaluated the assimilation of autotrophic and detrital food resources through carbon (C) and nitrogen (N) stable isotope ($\delta^{13}C$ and $\delta^{15}N$) analysis. We included the biomass of the macroinvertebrates sustained by the autotrophic and detrital pathways and the food web structure—trophic position, size structure, and degree of omnivory.

3. The biomass sustained by the detrital pathway remained similar throughout the year in both streams. In contrast, the biomass sustained by the autotrophic pathway was higher in the dry season than in the rainy season. The benthic macroinvertebrate food webs had four levels, a poorly developed size structure, and an important degree of omnivory in both streams and in both seasons. It is likely that omnivory was a response to high resource variability and a strategy to reduce intraguild competition.

4. Autotrophs had a relatively higher importance than detritus since a much lower algae biomass sustained an equal or higher macroinvertebrate biomass, particularly in the dry season when the biomass of autotrophs increased. Seasonality influenced the macroinvertebrate food web by modifying the food resource availability and transference to higher trophic levels. However, the high frequency of omnivory reduced the seasonal changes in the food web structure.

5. Our results suggest that the autotrophic pathway plays an important role in maintaining the benthic macroinvertebrate food web in tropical streams, and its relative importance is associated with seasonality. Therefore, changes in climate that

may modify the hydrology of streams are expected to greatly affect metazoan food webs.

Introduction

Food webs that are based on detritus are usually shorter (Briand, 1985; Pimm et al., 1991) and less size-structured (Blanchard et al., 2009; Potapov et al., 2019) than those based on primary production. Detritus-based food webs are expected to sustain few trophic levels due to their dependency on low-quality food resources and low energy efficiency (Blanchard et al., 2009). In contrast, the highly nutritious base of primary producers is expected to sustain several trophic levels (McGarvey et al., 2016). Furthermore, food webs that are exclusively dependent on detritus are characteristic of low-productivity ecosystems that cannot sustain omnivorous interactions—individuals feeding on more than one trophic level (Wootton, 2017). Primary production-based food webs are found in intermediately productive ecosystems that can support several omnivorous interactions without excluding the weaker competitor (Wootton, 2017).

Traditional riverine ecological models (e.g., Vannote et al., 1980) suggest that food webs are mainly based on allochthonous detritus, which is well supported by the high diversity and abundance of shredders and collector detritus feeders in temperate first-order streams (Merritt et al., 2019). In contrast, autotrophic algal carbon seems to support the metazoan food web in tropical first-order streams, particularly during low-flow—dry season—conditions (Thorp et al., 2006; Humphries et al., 2014).

The relative availability of autotrophic and detrital food resources in tropical streams is related to the hydrological—rainy and dry—seasonality (Davies et al., 2008, Wantzen et al., 2008). Micro and macroalgae in tropical streams increase in abundance during the low-flow dry seasons (Thorp and Delong 2002; Lau et al., 2009), temporarily providing a higher quality resource than the more permanent, but low-quality, detritus (Wantzen et al., 2008). The enhanced nutritional quality of algae and periphyton compared with detritus is well known (Frauendorf et al., 2013; Guo et al., 2016; Branco et al., 2017), but the effects of food resource seasonality on the food web structure are poorly studied in tropical regions.

Studies in first- to third-order, forested, protected, shaded, tropical streams have evaluated food assimilation through stable isotope analysis (SIA) in the dry season and found a prevalence of autotrophic food resources (e.g., Li and Dudgeon, 2008; Dudgeon et al*.,* 2010). Other investigations performed in the rainy season found that both autotrophic and detrital resources support food webs (March and Pringle, 2003; Brito et al*.,* 2006; Neres-Lima et al*.,* 2016, 2017). These analyses suggest that the relative contributions of the different food resources vary between seasons in tropical streams, however this remains understudied. While these studies evaluated the relative contributions of different sources, they did not assess resource assimilation in relation to the biomass of the consumers.

Assessing food resource assimilation contributes to the understanding of metabolic pathways and stream ecosystem functioning (Thorp et al., 2006). Some studies have suggested that most of the organic matter transferred to higher trophic levels is primarily autotrophic, even in net heterotrophic rivers with high inputs of detritus (Lewis et al., 2001; Thorp and Delong, 2002; Thorp et al., 2006). High amounts of this allochthonous detritus directly enter the detrital pathway, increasing microbial respiration rates, but partially disengaging the metazoan and microbial food webs (Cotner et al., 2006). The connectivity between the metazoan and microbial food webs can be estimated through an analysis of food resource assimilation.

SIA has advantages in that it reveals the trophodynamics (i.e., “the dynamics of nutrition or metabolism” as proposed by Lindeman, 1942) of streams as (a) a relatively low fractionation during the trophic transfers makes $\delta^{13}C$ a good indicator of food sources (France, 1996); (b) the $\delta^{13}C$ of aquatic primary producers is usually more enriched than the terrestrial producers’ signal

(Finlay et al., 1999); (c) the $\delta^{13}C$ of consumers incorporates the signal of the source for relatively long periods (Finlay, 2001); and (d) the significant fractionation on each trophic transfer of the $\delta^{15}N$ may be used to indicate the trophic position; therefore, top predators are enriched in $\delta^{15}N$ compared with the consumers at the base of the food web (Jepsen and Winemiller, 2002). Although the limitations of SIA and mixing models are recognised (Caut et al., 2009; Kilham et al., 2009; Bunn et al., 2013), the method is extensively used in the reconstruction of the food web from streams and rivers.

In this study, our primary goal was to determine the seasonal dynamics of the energy source and pathway of the benthic macroinvertebrate food web in two tropical first-order streams. For this purpose, we addressed the following research questions: (i) Which basal food resources, aquatic primary producers or detritus, sustain the benthic macroinvertebrate food web? (ii) Does the energy pathway differ seasonally? (iii) Does the food web structure change according to the dominant energy pathway? We expected an increment in the biomass of the benthic macroinvertebrates sustained by the autotrophic pathway in the dry season when the biomass of aquatic primary producers. Increased assimilation of the autotrophic resources results in a higher number of trophic levels (i.e., a higher maximum trophic position), a more developed size structure, and a higher degree of omnivory sustained by the more nutritious autotrophic pathway.

Methods

Study site

José and Mario (16°08' N, 90°54' W, 200 m a.s.l.) are first-order streams that are tributaries of the Lacantún River in Chiapas, southern Mexico (Figure 1). The Lacantún River watershed comprises 12,526 km^2 of the Mexican hydrological region No 30 Usumacinta-Grijalva, the largest fluvial system in Mexico (Muñoz-Salinas and Castillo, 2013). The watershed is in the Lacandona rainforest and includes the "Montes Azules" Biosphere Reserve (MABR). The Lacandona rainforest is the most diverse ecosystem in Mexico, supporting a high number of endemic species. Limestones dominate the lithology of the Lacandona rainforest, where the dissolution of magnesium and calcium carbonate shapes the landscape (Carabias-Lilo et al*.*, 2000). The dominant vegetation type is the evergreen tropical rainforest. The climate is tropical, warm (annual mean temperature of 27 °C), and rainy (annual precipitation of 3190 mm; García, 2004).

The “Montes Azules” weather station reports two well-defined seasons, the rainy season from May to October, with two peaks in June and October, and the dry season from late October to May. Monthly precipitation averages 211.7 ± 90.3 mm (158.0–298.8 mm) in the rainy season and 59.7 ± 30.0 mm (26.8–96.4 mm) in the dry season. Monthly temperature averages 23.8 ± 0.5 °C (23.2–25.7 °C) in the warmer rainy season and 21.8 ± 2.2 °C (19.2–23.2 °C) in the colder dry season. Humidity fluctuates from 78% to 91% (SMN, 2019). The streams are 7.1 km apart from each other. José is west of the Lacantún River (Figure 1), in a forested watershed. Mario is east of the Lacantún River (Figure 1), and its watershed exhibits some degree of perturbation related to land-use change from forest to pastures. Nonetheless, approximately 80% of its riparian forest is preserved, and ≈50 m off each riverbank is covered with native trees.

Environmental variables

Details on the environmental measurements are given in Cortés-Guzmán et al*.* (2021 in press). The streams were sampled three times in the rainy season (June, September, and October 2018) and three times in the dry season (January, March, and June 2019). We selected a 100 m reach at each stream where the percentage of shadow and the physical and chemical variables were measured.

The percentage of shadow over the channels was estimated using Hobo UA-002-64 temperature and light data loggers. One logger was installed on a high roof and used as 100%

reference, and two additional loggers were installed at the water surface to record light intensity for 24 hours. The main substrates (i.e., gravel, sand, silts) along the reaches were visually estimated using a 1 m^2 frame demarked with a 0.01 m^2 grid.

The physical and chemical variables were measured every 20 m at ¼, ½, and ¾ of the channel width along each reach. We measured temperature, dissolved oxygen, pH, conductivity (standardised at 25 °C), and turbidity using a Hydrolab DS5 multiparameter water quality probe. We measured mean width and mean depth along the reaches and the water velocity at half of the channel width and half of the maximum depth with a Swoffer 3000 current meter to calculate the water discharge (Elosegui et al., 2009). The seasonal differences in the environmental variables were assessed using a two-way ANOVA.

Benthic macroinvertebrates

Following the multi-habitat sampling approach, a D-frame net of 0.5 mm mesh was used to collect composite samples of benthic macroinvertebrates over the selected 100 m reaches at each stream. Substrates were sampled in proportion to their overall availability in the reach so that the substrates covering 20% of the reach composed approximately 20% of the samples (Gerth and Herlihy, 2006; Hughes and Peck, 2008). The method was standardised in time (1-minute sweeps) and area (1 m^2) according to Chiasson (2009). Organisms were left in filtered stream water for 12 hours to allow gut clearance (Lau et al*.*, 2009). Macroinvertebrates were identified at the genus level (Wiederholm, 1983; Merritt et al*.*, 2008; Hamada et al., 2018). Organisms were oven-dried (60° C, until constant weight), and all individuals from a given genus were weighed to obtain the dry mass as the biomass estimation. The number of individuals in each sample was counted to estimate the dry mass per individual. Only the most frequent genera (>30%, or two or more sampling dates) contributing to the largest biomass (>5% per sampling date) were considered for SIA. Samples of whole animals were grounded to a fine powder in an agate mortar to obtain approximately 1.0 mg for further SIA.

Food resources

Three types of food resources (autochthonous benthic algae, autochthonous macrophytes-epiphytes complex, and allochthonous leaf litter) were evaluated at each 100 m reach, where the macroinvertebrates were collected. We collected three replicates of macrophytes and three replicates of leaf litter using a 0.13 m^2 frame and removed them manually from the streambed. Benthic algae mainly covered the rocks; thus, we scratched three replicates using a toothbrush and measured the rock area covered. The percentage coverage area of the potential food resources along the reach was estimated using a 1 m^2 frame demarked with a 0.01 m^2 grid. Benthic algae, macrophytes, and their associated epiphytic algae were examined under optic and stereoscopic microscopes to identify and obtain clean samples of the three resources before being oven-dried (60 °C, until constant weight) and weighed. Each sample was grounded to a fine powder in an agate mortar for elemental (C and N) SIA analyses. The dry mass and the estimated coverage area were used to calculate the total biomass at each reach (García et al., 2016).

Elemental and stable isotope analysis

Elemental content analysis and SIA were performed at GEOTOP, Université du Québec à Montréal, Canada. Sub-samples of benthic algae, macrophytes, and leaf litter sources were analysed for carbon (C) and nitrogen (N) content in a standard elemental analyser (Carlo Erba NC 2500). The sources and benthic macroinvertebrates samples from each sampling date were weighed in tin cups to obtain the same amount of CO_2 and N_2 for all samples and reference materials. The samples were analysed in a continuous flow model with a Micromass Isoprime 100 isotope ratio mass spectrometer coupled to an Elementar Vario MicroCube elemental analyser.

For carbon isotopes ($\delta^{13}C$), two internal reference materials ($\delta^{13}C = -28.73 \pm 0.06‰$ and –11.85

± 0.04‰) were used to normalise the results on the NBS19-LSVEC scale. A third reference material ($\delta^{13}C$ = –17,04 ± 0.11‰) was analysed as an unknown to assess the normalization's exactness. The results are given in delta units (δ) in ‰ vs. VPDB. The overall analytical uncertainty (1s) is better than ±0.1‰. For nitrogen isotopes ($\delta^{15}N$), two internal reference materials ($\delta^{15}N$ = –0.10 ± 0.24‰ and +14.95 ± 0.09‰) were used to normalise the results on the AIR (IAEA-N1, IAEA-N2, and IAEA-N3) scale. A third reference material ($\delta^{15}N$ = –0,1 ± 0.15‰) was analysed as an unknown to assess the normalization's exactness. The results are given in delta units (δ) in ‰ vs. AIR. The overall analytical uncertainty (1s) is better than ±0.2‰.

Data analysis

We applied a Bayesian mixing model in the MixSIAR software (Stock et al., 2018) to obtain each source's contribution to the macroinvertebrates' diet. Subsequently, each source's percentage contribution was weighted by the consumers' biomass to calculate the biomass sustained by each trophic pathway. We used trophic fractionation values of 0.1 ± 2.2‰ for $\Delta^{13}C$ and 2.6 ± 2.0‰ for $\Delta^{15}N$ (Brauns et al., 2018).

To obtain the benthic macroinvertebrate trophic position or trophic level (TP), we used as a baseline ($\delta^{15}N_{baseline}$) the value of the taxon with the lowest $\delta^{15}N$ for each season and stream (Vander Zanden and Rasmussen, 1999; Post, 2002) and a 2.6 ± 2.0‰ value of trophic fractionation ($\Delta^{15}N$) (Brauns et al., 2018) applied to the following equation:

$$\text{Trophic position (TP)} = \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{\Delta^{15}\text{N} + 2}$$

This method corrects the variation in the $\delta^{15}N$ baseline using the value of a primary consumer instead of the more variable basal source, and is sensitive to omnivory (Vander Zanden and Rasmussen, 1999, 2001). Taxa occurring in any class centred on an interval (e.g., 1.9–2.1, 2.9–

3.1) were considered to occupy a discrete TP (Thompson et al., 2007; Schmidt et al., 2017). Taxa occurring in a non-integer value were considered omnivorous, and the decimal fraction was used as the degree of omnivory (Lampert and Sommer, 2007; Lau et al*.,* 2009). To determine the contribution of basal resources and prey to the carnivores' diet, we applied the mixing model using macroinvertebrates above TP 3 as predators and macroinvertebrates below TP 3 as potential prey. We compared all organisms' body mass to their trophic position through linear regression to evaluate each stream and season's size structure.

We performed a two-tailed paired t-test to assess the differences between the dry and rainy season resources biomass. Next, we performed a two-tailed paired t-test to assess the differences between the average assimilation of autotrophic and detrital food resources, including all the sampling dates. Finally, we performed a one-tailed paired t-test between the dry and rainy season assimilation of autotrophic and detrital food resources, based on the assumption that the autotrophic resources would increase in the dry season (one-directional hypothesis). Analyses were performed using IBM SPSS Statistics.

Results

Environmental parameters

The José stream is 1321 m long, 4.0 ± 1.1 m wide, 0.4 ± 0.2 m deep, and 92% shaded. Mario is 3280 m long, 3.1 ± 1.6 m wide, 0.4 ± 0.3 m deep, and 78% shaded. The substrate is mainly coarse in both streams, composed of 35% to 44% of sands (0.05–2.0 mm) and 24% to 38% of gravel boulders (2.1–64.0 mm). Retention structures, such as large logs and rocks, cover less than 10% of each channel.

José and Mario are warm (21.2–28.5 °C), generally well-oxygenated (6.2–9.4 mg L^{-1}), and from slightly acid to slightly basic (6.05–8.54, Table 1). Compared with Mario, José has significantly higher conductivity (F = 647.608, p < 0.001) and pH (F = 63.200, p < 0.001), while the other physical and chemical variables are similar between streams. The streams have similar nutrient concentrations (i.e., ammonium, nitrates, dissolved inorganic nitrogen, phosphates, and total phosphorous (Cortés-Guzmán et al. 2021 in press). A higher water discharge (F = 9.771, p = 0.014) and turbidity (F = 5.360, p = 0.040) during the rainy season confirms the tropical seasonality of the streams.

Benthic macroinvertebrates: composition

The benthic macroinvertebrate community was composed of 63 genera, 54 in José and 53 in Mario. Based on their high frequency (>30%, or two sampling dates) and biomass (>5% per sampling date) contributions, we selected 24 genera from 20 families and 10 orders (Table 2). All these taxa were present in both streams except for *Pseudotelphusa,* which was only found in José. In the José stream, 22 genera were present in the rainy season and 24 in the dry season, while in the Mario stream, 21 were present in the rainy season and 23 in the dry season.

Food resources

The dominant benthic algae in the José stream included the green algae *Cladophora* and the diatoms *Surirella*, *Gyrosigma*, *Navicula*, *Cocconeis*, *Ulnaria,* and *Pinnularia*. The green algae *Cladophora* and the diatoms *Flagilaria*, *Gomphonema*, *Navicula*, *Amphora*, *Diploneis*, and *Pinnularia* dominated the benthic algae in the Mario stream community. The dominant macrophyte was an undetermined Characeae species in both streams. The detrital food resources were allochthonous leaf litter from different riparian forest trees. The principal tree species of the riparian ecosystems in the region are *Ampelocera hottlei* (Ulmaceae), *Croton schiedeanus* (Euphorbiaceae), and *Protium copal* (Burseraceae) (Meli et al., 2015).

The largest available biomass in both streams and seasons was leaf litter, which was up to five orders of magnitude higher than the autotrophic food resources (Table 3) and represented 99% of the potential food resources. Benthic algae showed the lowest biomass (<0.04%). The autotrophic food resources were comparatively higher in the dry than in the rainy season (José stream: $t = –4.027$, 4 d.f., $p = 0.016$; Mario stream: $t = –5.246$, 4 d.f., $p = 0.006$), while the detrital food resources also increased in the dry season (José stream: $t = –6.749$, 4 d.f., $p = 0.002$; Mario stream: $t = –8.960$, 4 d.f., $p < 0.001$) compared with the rainy season.

Benthic algae displayed the lowest C:N ratio in both seasons, suggesting a higher nutritional value than the other food resources (Figure 2). Leaf litter displayed the highest C:N ratio, suggesting the lowest nutritional value. In the José stream, the macrophyte C:N ratio was higher in the rainy season than in the dry season; while in the Mario stream, the macrophyte C:N ratio was similar between seasons (Figure 2).

The three food resources differed in their isotopic ($\delta^{13}C$) signatures. In the José stream, the macrophytes displayed the most depleted values in the rainy season, while the benthic algae had the most enriched values. In contrast, the macrophytes displayed the most enriched values in the dry season, while the leaf litter exhibited the most depleted values (Figure 2). In the Mario stream, the leaf litter showed the most depleted values in both seasons, while the macrophytes had the most enriched values (Figure 2), which is likely to be associated with the presence of epiphytes.

Resource assimilation

The total contribution from the autotrophic pathway (67%) to the benthic macroinvertebrate biomass was double that of the detrital pathway (33%) in the José stream ($t = 3.33$, d.f. = 47, $p = 0.002$). The autotrophic pathway contribution, including both benthic algae and macrophytes, increased in the dry season relative to the rainy season ($t = 2.201$, d.f. = 23, $p = 0.038$) and constituted 69.7% of the total biomass of benthic macroinvertebrates, highlighting the importance of the autotrophic food resources in the food web in this stream (Table 4). The contribution of the detrital food resource to the macroinvertebrate biomass was not significantly different between seasons (t = 0.577, d.f. = 23, p = 0.567).

In the Mario stream, the total contribution to the macroinvertebrate biomass from autotrophic (52.3%) and detrital (47.7%) pathways were not significantly different (t = 0.963, d.f. = 35, p = 0.342). Even though the differences were not statistically significant, the autotrophic pathway seems to be an important energy source for the macroinvertebrates in the Mario stream.

Food web structure: trophic position and omnivory

The $\delta^{13}C$ isotopic signature of the macroinvertebrates ranged from –31.65‰ to –25.66‰ in José, and from –37.83‰ to –27.41‰ in Mario. The $\delta^{15}N$ isotopic signature ranged from 1.26‰ to 7.41‰ in José, and from 2.03‰ to 9.19‰ $\delta^{15}N$ in Mario (Figure 3).

In José, the TP ranged between 1.99 and 3.80 in the rainy season, and *Macrobrachium* (Palaemonidae, Decapoda) had the maximum TP (Table 2). In the dry season, the TP ranged between 2.00 and 3.99, and *Palaemnema* (Platystictidae, Odonata) had the maximum TP. In Mario, the TP ranged between 2.00 and 4.21 in the rainy season and between 2.00 and 3.86 in the dry season. *Palaemnema* (Platystictidae, Odonata) had the maximum TP in both seasons (Table 2).

The macroinvertebrates from both streams displayed a high degree of trophic omnivory; they fed on more than one trophic level. The degree of omnivory was similar between streams and seasons, and it had an average value between 44 ± 26% and 46 ± 22%, but with an ample range of between 10% and 87%.

In José, the number of taxa classified as omnivorous exceeded the taxa occurring at a discrete TP (Table 2). During the rainy season, 19 taxa were omnivorous, while 5 taxa occurred at a discrete TP. In the dry season, 15 taxa were omnivorous, and 9 taxa occurred at a discrete TP. Macroinvertebrates above TP 3 fed mainly on animal tissue (47 ± 13% in the rainy season, 37 ± 10% in the dry season) and autotrophic resources (36 ± 15% in the rainy season, 49 ± 14% in the dry season). Leaf litter represented a minor contribution to their diets (16 ± 11% in the rainy season, 14 ± 6% in the dry season).

In Mario, the number of taxa occurring at a discrete TP was similar in both seasons (Table 2). In the rainy season, 11 taxa were omnivorous and 10 occurred at a discrete TP. In the dry season, 12 taxa were omnivorous and 11 taxa occurred at a discrete TP. Macroinvertebrates above TP 3 fed mainly on animal tissue (67 ± 18% in the rainy season, 69 ± 8% in the dry season), followed by autotrophic resources (28 ± 18% in the rainy season, 18 ± 7% in the dry season), while leaf litter represented a lower contribution to their diets (6 ± 4% in the rainy season, 12 ± 8% in the dry season).

We did not find a correlation between the TP and body mass of individual macroinvertebrate taxa in either stream or season (body mass = 0.918 + 0.3 * trophic position, $r^2 = 0.01$, $p = 0.098$, Figure 4).

Discussion

Seasonal variation of basal food resources

Seasonal hydrology strongly influences the biomass availability of potential food resources in the streams. The total biomass of allochthonous detrital food resources (99%) was higher than the autochthonous autotrophic food resources (1%) in both seasons and in both streams. The biomass of aquatic primary producers—benthic algae and macrophytes—increased in the dry season (from 0.009 to 0.128 g m^{-2}) compared with the range in the rainy season (from 0.002 to 0.064 g m^{-2}) in both streams, when the water discharge and turbidity were lower, as reported in other tropical streams (Douglas et al., 2005; Lau et al., 2009; Branco et al., 2017). The biomass of detrital food resources—leaf litter—was also higher in the dry season than in the rainy season in both streams. In evergreen tropical forests, a leaf drop peak occurs in the dry season associated with water stress (Bambi et al., 2017; Tonin et al., 2017). Similarly, faster water velocity and a lack of retention structures in the channel, such as in the case of José and Mario, during the rainy season wash out part of the leaf litter. Hence, a higher water flow reduces the leaf litter accumulation at the bottom of a channel (Cummins et al., 2005), while litter retention increases in the dry season.

Resources assimilation: does the energy pathway differ seasonally?

In the José stream, the autotrophic pathway sustained 55–70% of the macroinvertebrate biomass, increasing from 54.6% in the rainy season to 69.7% in the dry season. In Mario, both pathways contributed to the macroinvertebrate biomass in both seasons in similar proportions (≈50%). Despite the lower biomass of the autotrophic food resources available in both streams (≈1%), its contribution to the macroinvertebrate biomass was high. The shallow water columns of José and Mario (0.4 m mean depth) combined with warm temperatures (21.2–28.5 °C) are likely to promote rapid benthic algal growth rates. Algae have proven to be the main food resource assimilated by macroinvertebrates in several tropical streams, even where its availability is limited (Townsend and Douglas, 2014; Schmidt et al., 2017), and particularly in the dry, low-flow season (Salas and Dudgeon, 2001; Lau et al., 2009; Frauendorf et al., 2013; Jardine 2014). A high selectivity for algae is likely to be associated with its higher nutritional value (low C:N ratio, and probably fatty acid composition, Guo et al., 2016) compared with the recalcitrant components of low nutritional value (high C:N ratio) leaf litter (Neres-Lima et al., 2016). Macrophyte consumption was low (4.9–23.7%), as was the case in other tropical streams where its consumption is minimal (March and Pringle, 2003; Brito et al., 2006).

The available biomass of detrital and autotrophic food resources was higher in Mario than in José. However, in Mario, the macroinvertebrate biomass sustained by autotrophic food resources was lower and not significantly different from the biomass sustained by detrital food resources. This suggests, as has been observed in other tropical streams (Jardine, 2014), that in the Mario stream, large but scarce omnivores, such as *Pomacea* (Gastropoda), derive a higher biomass from detrital (57–75%) rather than autotrophic food resources. In contrast, other abundant but smaller taxa (e.g., *Antocha*, *Cylloepus*) preferentially consume algae (53–78%). Ultimately, it transpired that the global consumption in Mario was similar between the autotrophic and detrital food resources. The contribution of larger invertebrates (low ratios of annual production to biomass) feeding on detritus (e.g., *Pomacea*) may be overestimating the importance of the detrital trophic pathway in the Mario stream. Small-body invertebrates, mainly insects, have a higher turnover and production rates (Jardine, 2014), and rely mainly on autochthonous food resources.

The macroinvertebrate biomass supported by the detrital pathway (30% and 55%) remained similar in both seasons and both streams, and it was close to the maximum values reported in other tropical stream studies using stable isotopes (Li and Dudgeon, 2008; Dudgeon et al., 2010; Jardine, 2014; García et al., 2016). The consumption of leaf litter is associated with increasing conditioning (Abelho, 2001), mainly mediated by algae, hyphomycetes, and bacteria, which are common in tropical streams and increase leaf litter palatability (Wantzen et al., 2008; Guo et al., 2016). Conditioned litter is more easily consumed by shredders, such as decapods, mayflies, and caddisflies, that can be frequent in tropical streams (Cheshire et al., 2005; Yule et al., 2009). In the José and Mario streams, the shredders *Traverella* (Leptophlebiidae, Ephemeroptera) and *Phylloicus* (Calamoceratidae, Trichoptera) were abundant (up to 360 individuals) and may be contributing to the breakdown of the leaf litter. It is likely that the presence of shredders, hyphomycetes, and conditioned leaves explains the relatively high assimilation of leaf litter in the José and Mario streams, however this requires further investigation.

Trophic structure: does the food web structure change according to the seasonal differences in food resource availability?

The maximum TP was higher in the Mario stream than in the José stream. In José, it was similar between seasons, while in Mario, it was higher in the rainy season than in the dry season. Although TP quantification was difficult due to a lack of replication in our study, the maximum TP was similar to those reported in tropical streams in Hong Kong (Lau et al., 2009). In the Hong Kong streams, the maximum TP did not change between seasons if shaded (3.93–3.97), but it was higher in unshaded streams (4.39), particularly in the rainy season (5.13). Isotopic enrichment could be associated with a lower canopy coverage leading to increased light penetration (Lau et al., 2009), as seems to be the case in Mario (78% shaded) compared with José (92% shaded).

Omnivory was dominant in the José and Mario streams, as reported in other tropical streams (Mantel et al., 2004; Tomanova et al., 2006; Lau et al., 2009). It has been hypothesised (e.g., Wantzen and Wagner, 2006; Guo et al., 2016) that omnivory is more common in tropical streams than in temperate streams because it allows shifts between the temporal, sparse, high-quality algal resources and the more permanent, abundant, low-quality detrital resources (Covich, 1988; Jepsen and Winemiller, 2002; Wantzen and Wagner, 2006; Frauendorf et al., 2013).

In the José and Mario streams, macroinvertebrates showed a high degree of omnivory due to the assimilation of basal resources with different δ^{15}N values (benthic algae: 3.2–4.3‰; macrophytes: 2.6–4.5‰; and detritus: 0.4–1.2‰). Omnivory is usually an adaptive response of the organisms to nutritional limitations (Jepsen and Winemiller, 2002; Wootton, 2017), which explains the omnivory in the primary consumers in the José and Mario streams. A flexible feeding strategy (e.g., feeding on both primary producers and detritus) is expected in tropical streams (Frauendorf et al., 2013) as the temporal variability in environmental conditions and resources is high relative to the life span of the organisms (Digel et al., 2011). Thus, in the studied streams, the primary consumers complemented their diets by consuming the abundant, low-nutritious, allochthonous food resources and the scarce, but highly nutritious, autochthonous food resources.

Consumers above TP 3 in the José and Mario streams fed mainly on animal tissue and benthic algae. The probability of trophic omnivory increases with trophic position (Thompson et al., 2007; Wootton, 2017); therefore, a high degree of omnivory can be found in predators (Frauendorf et al., 2013). Omnivory in predators may reduce the competition for prey with the predators feeding on a suboptimal resource (i.e., algal resources) (Eubanks and Denno, 1999). The study streams show a strong top-down control through the high abundance of predators compared with their potential prey (Cortés-Guzmán et al., 2021). Omnivory may be a strategy to reduce competition at the highest TP in the José and Mario streams.

We did not find a correlation between TP and body mass in the José and Mario streams. Although scarce, some taxa (e.g., large crustaceans, gastropods, and odonates) contributed significantly to the biomass and occupied a low-to-intermediate TP, which resulted in a less developed food web size structure. Furthermore, large body-sized taxa, such as *Macrobrachium*, *Pseudothelphusa*, and *Pomacea*, are unlikely to be preyed upon by other invertebrates, weakening the relationship between body size and trophic position (Jardine, 2014).

Conclusions

In relation to our two first objectives, we found that the principal energy pathway of the benthic macroinvertebrate food webs in the tropical José and Mario streams is autotrophic (45–70%). Nonetheless, the detrital pathway also constitutes an important source (30–55%). Autotrophic food resources have a disproportionately larger significance, when compared with the more abundant detrital food resources, as the much lower algae biomass that is available sustains an equal or higher macroinvertebrate biomass, particularly during the dry season when the autotroph biomass increased.

Regarding the third objective, the macroinvertebrate food webs are characterised by abundant omnivores and a lack of size structure. It is likely that omnivory is a flexible feeding strategy associated with resource variability and competition. Tropical seasonality influences the benthic macroinvertebrate food web by modifying the availability of food resources and their transference to higher trophic levels. However, the high frequency of omnivory reduces the seasonal changes in the food web structure.

Our results suggest that autotrophs play an important role in maintaining the benthic macroinvertebrate food webs, however their importance varies with seasonality and its effect on hydrology. Therefore, the changes in climate that may modify the hydrology of streams are expected to greatly affect metazoan food webs.

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Author contributions

D.C-G.: conceptualization, methodology, sample processing, formal analysis, writing—draft, and writing—review and editing; J.A.: conceptualization, methodology, funding acquisition, writing—draft, and writing—review and editing; and D.P.: sample processing, writing—draft, and writing—review and editing.

ORCID

Daniela Cortés Guzmán: https://orcid.org/0000-0001-6683-0224.

Javier Alcocer: https://orcid.org/0000-0002-0535-7936.

Dolors Planas: https://orcid.org/0000-0003-0901-2887.

Data Availability Statement

Data are available from the authors upon reasonable request.

Conflict of Interest Statement

The authors have no conflicts of interest to declare.

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Table 1. Physical and chemical variables of the José and Mario streams, Lacantún River, Chiapas, Mexico (T: temperature; DO: dissolved oxygen; K_{25}: electric conductivity; Tur: turbidity; Q: water discharge; $\overline{x}$: mean; s.d.: standard deviation).

	José stream				**Mario stream**			
	Rainy season		**Dry season**		**Rainy season**		**Dry season**	
	$\overline{x}$ ± s.d.	**Range**	**$\overline{x}$ ± s.d.**	**Range**	**$\overline{x}$ ± s.d.**	**Range**	**$\overline{x}$ ± s.d.**	**Range**
T (°C)	22.2 ± 0.6	23.3 – 24.8	23.2 ± 1.5	21.2 – 25.1	25.5 ± 0.7	24.5 – 26.6	24.7 ± 1.9	21.6 – 28.5
DO (mg L^{-1})	7.5 ± 0.7	6.9 – 8.6	7.7 ± 1.2	6.4 – 9.4	7.1 ± 0.6	6.3 – 8.4	6.2 ± 1.7	4.4 – 8.8
pH	8.1 ± 0.3	7.8 – 8.5	7.9 ± 0.1	7.8 – 8.1	6.9 ± 0.3	6.4 – 7.8	6.5 ± 0.2	6.0 – 7.0
K_{25} (µS cm^{-1})	959 ± 8	922 – 998	1069 ± 96	949 – 1188	73 ± 21	49 – 90	63 ± 23	45 – 96
Tur (NTU)	12 ± 14	0 – 34	3 ± 12	0 – 82	30 ± 38	0 – 107	18 ± 38	1 – 209
Q (m^3 s^{-1})	0.29 ± 0.03	0.25 – 0.32	0.18 ± 0.04	0.12 – 0.20	0.16 ± 0.15	0.06 – 0.33	0.04 ± 0.01	0.02 – 0.05

Table 2. Abundance and trophic position of the benthic macroinvertebrates contributing to the highest frequency and biomass in the José and Mario streams, Lacantún River, Chiapas, Mexico (RS: rainy season; DS: dry season; TP: trophic position).

Genus	José stream				Mario stream			
	RS	TP	DS	TP	RS	TP	DS	TP
Mesogastropoda: Ampullaridae								
Pomacea	16	2.28	3	2.00	17	2.50	22	2.00
Decapoda: Palaemonidae								
Macrobrachium	6	3.80	28	3.33	49	3.92	136	3.59
Decapoda: Pseudothelphusidae								
Pseudothelphusa	13	2.84	16	2.90	0		0	
Ephemeroptera: Leptohyphidae								
Leptohyphes	168	2.57	71	2.22	0		132	2.00
Ephemeroptera: Leptophlebiidae								
Traverella	178	2.31	89	2.40	301	2.00	481	2.16
Odonata: Calopterygidae								
Hetaerina	40	3.58	87	3.01	52	3.30	14	2.94
Odonata: Coenagrionidae								
Argia	11	3.44	83	3.14	6	3.05	51	3.34
Telebasis	15	3.43	91	3.17	66	3.48	196	3.29
Odonata: Gomphidae								
Phyllocycla	5	3.34	78	3.36	7	2.36	32	3.03
Progomphus	86	3.27	30	3.10	30	3.54	12	3.19
Odonata: Libellulidae								
Perithemis	27	3.19	174	2.81	70	3.02	85	2.75
Odonata: Platystictidae								

Palaemnema	12	3.54	42	3.99	6	4.21	32	3.86
Plecoptera: Perlidae								
Anacroneuria	167	3.47	181	3.51	12	3.67	57	3.45
Hemiptera: Belostomatidae								
Abedus	1	3.79	9	3.35	0		2	3.00
Hemiptera: Naucoridae								
Cryphocricos	58	3.02	81	2.97	35	3.50	28	3.12
Limnocoris	122	2.88	41	2.80	14	3.03	10	3.08
Megaloptera: Corydalidae								
Corydalus	37	3.38	88	3.14	30	3.26	38	3.12
Coleoptera: Elmidae								
Cylloepus	4	2.96	83	2.50	4	3.00	9	2.76
Macrelmis	78	2.24	113	2.02	24	2.00	33	2.00
Coleoptera: Scirtidae								
Elodes	16	2.00	36	3.00	4	2.00	3	2.08
Trichoptera: Calamoceratidae								
Phylloicus	36	2.48	189	2.12	3	2.05	12	2.05
Trichoptera: Hydropsychidae								
Leptonema	31	1.99	133	2.78	137	3.03	294	2.96
Diptera: Chironomidae								
Stenochironomus	9	2.03	6	2.08	24	2.00	80	2.00
Diptera: Tipulidae								
Antocha	8	3.38	14	3.30	12	3.58	22	3.49

Table 3. Basal food resource biomass in the José and Mario streams, Lacantún River, Chiapas, Mexico (RS: rainy season; DS: dry season).

		Autochthonous				**Allochthonous**	
	Season	**Benthic algae**		**Macrophytes complex**		**Leaf litter**	
		(g dry mass m^{-2})	**%**	**(g dry mass m^{-2})**	**%**	**(g dry mass m^{-2})**	**%**
José stream	RS	0.003 ± 0.001	0.006	0.005 ± 0.002	0.011	46.28 ± 17.42	99.983
	DS	0.021 ± 0.012	0.017	0.043 ± 0.024	0.034	125.52 ± 10.49	99.949
	Average	0.012 ± 0.013	0.014	0.024 ± 0.026	0.028	85.90 ± 45.27	99.958
Mario stream	RS	0.018 ± 0.014	0.034	0.036 ± 0.028	0.068	53.23 ± 34.62	99.899
	DS	0.053 ± 0.011	0.021	0.107 ± 0.021	0.042	253.67 ± 17.40	99.937
	Average	0.036 ± 0.022	0.022	0.071 ± 0.045	0.043	166.0 ± 112.49	99.936

Table 4. Biomass of benthic macroinvertebrates (mean ± s.d.) sustained by autotrophic and detrital food resources and contribution (%) of the pathways to the total biomass of benthic macroinvertebrates in the José and Mario streams, Lacantún River, Chiapas, Mexico (RS: rainy season; DS: dry season).

		Autochthonous						**Allochthonous**	
	Season	**Benthic algae**		**Macrophytes complex**		**Total autochthonous**		**Leaf litter**	
		(g C m^{-2})	**%**	**(g C m^{-2})**	**%**	**(g C m^{-2})**	**%**	**(g C m^{-2})**	**%**
José stream	RS	0.73 ± 0.54	49.7	0.07 ± 0.01	4.9	0.40 ± 0.05	54.6	0.72 ± 0.06	45.4
	DS	2.35 ± 0.20	46.0	1.36 ± 0.14	23.7	1.85 ± 0.13	69.7	1.50 ± 0.10	30.3
	Average	1.54 ± 1.34	45.7	0.72 ± 1.06	21.3	1.13 ± 1.23	67.0	1.11 ± 0.78	33.0
Mario stream	RS	1.02 ± 0.68	46.5	0.38 ± 0.02	17.3	0.70 ± 0.06	63.8	0.83 ± 0.65	36.2
	DS	2.02 ± 1.48	40.0	0.25 ± 0.02	5.2	1.14 ± 0.14	45.2	2.51 ± 1.18	54.8
	Average	1.51 ± 1.17	43.3	0.32 ± 0.20	9.0	0.92 ± 1.02	52.3	1.67 ± 1.26	47.7

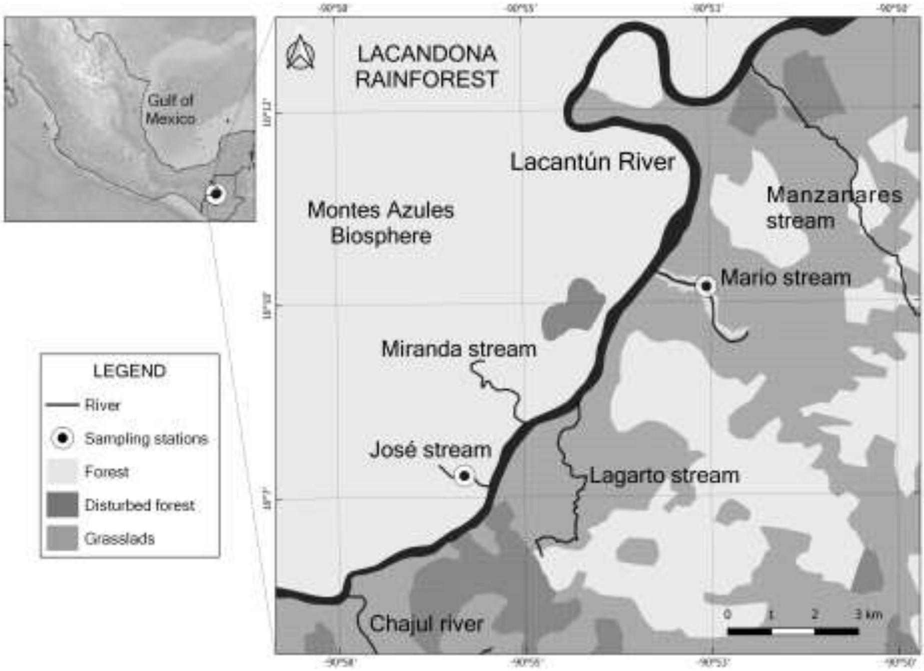

Figure 1. José and Mario first-order streams (black dots), Lacantún River, Chiapas, Mexico (Cortés-Guzmán et al. 2021).

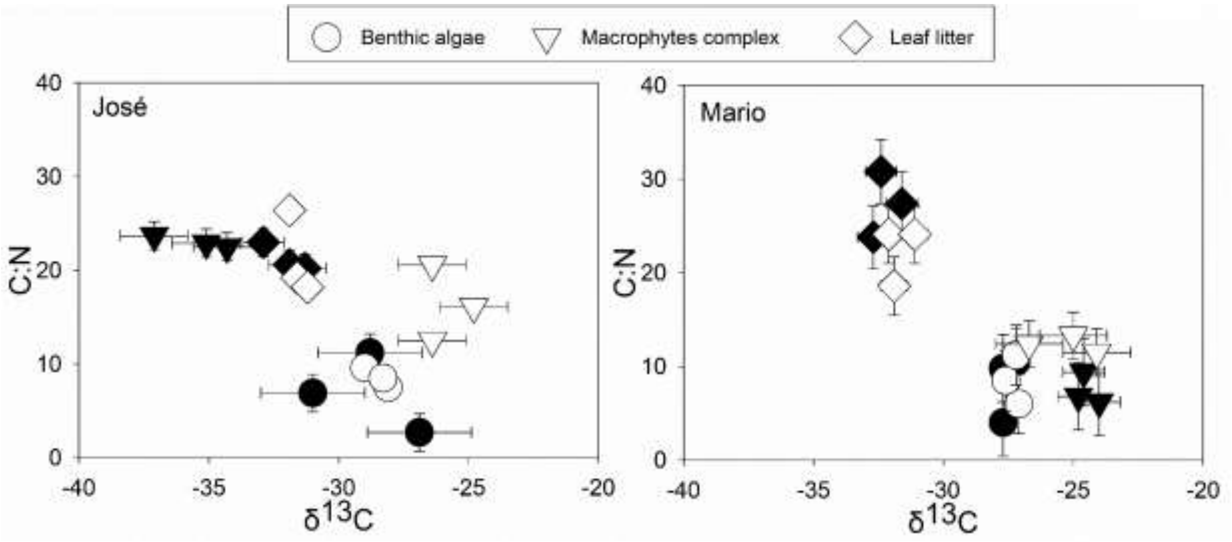

Figure 2. Average (± standard deviation) C:N ratio and $\delta^{13}C$ of the basal food resources for the benthic macroinvertebrate food webs in the José and Mario streams, Lacantún River, Chiapas, Mexico, in the rainy (black symbols) and dry (white symbols) seasons.

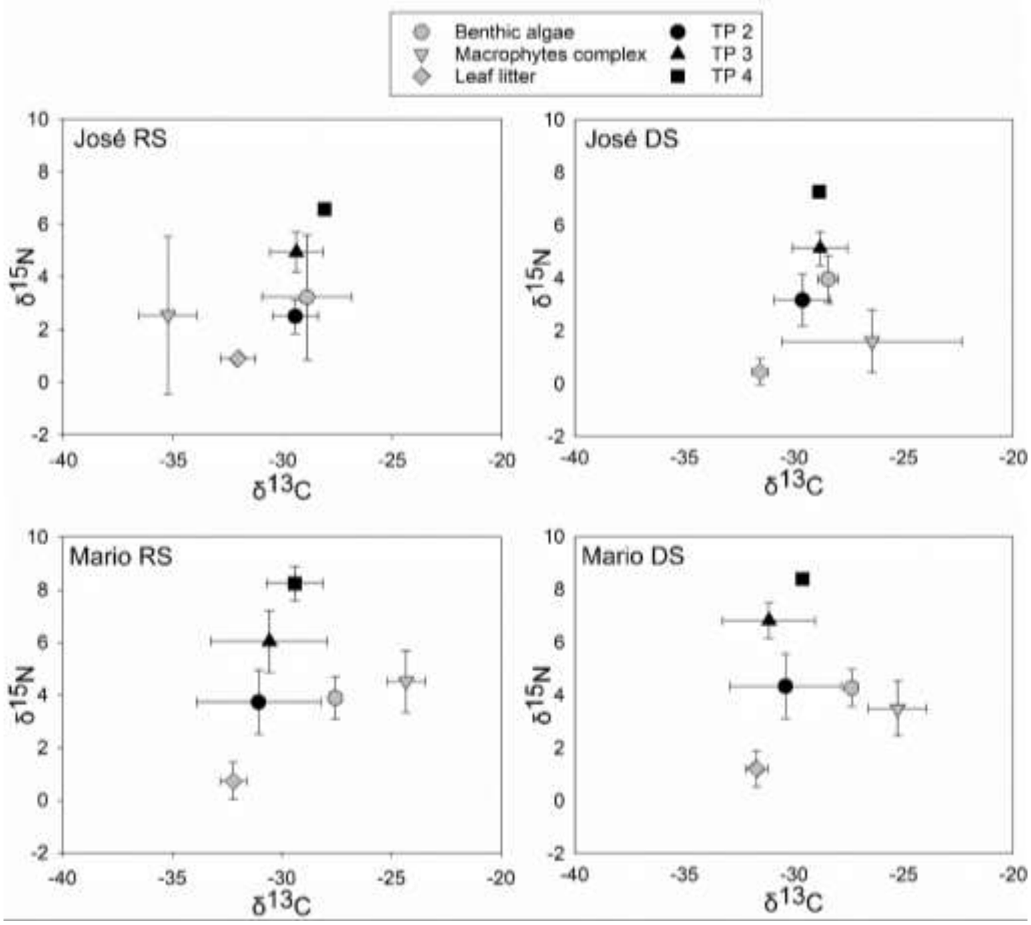

Figure 3. Distribution of the isotopic signature of the benthic macroinvertebrates and the basal food resources in the José and Mario streams, Lacantún River, Chiapas, Mexico, in both seasons (RS: rainy season; DS: dry season; TP 2: primary consumers; TP 3: secondary consumers; TP 4: tertiary consumers).

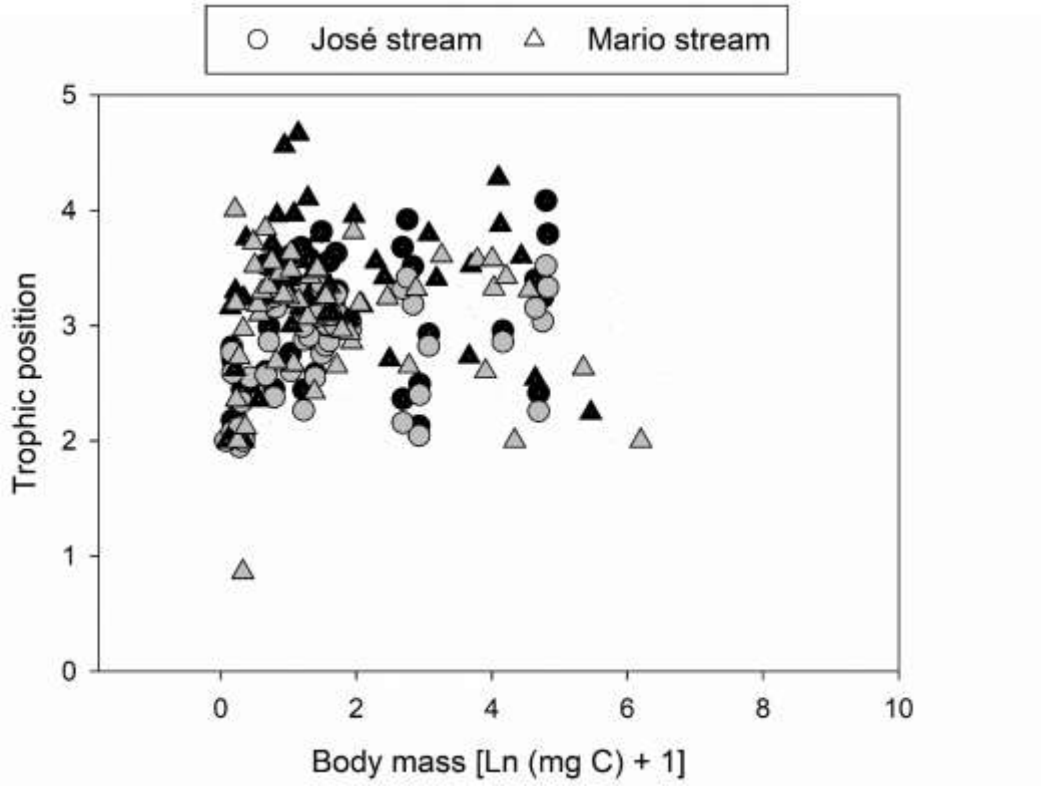

Figure 4. Linear regression between the individual body mass of the benthic macroinvertebrates and their trophic position measured through $\delta^{15}N$ (black figures: rainy season; grey figures: dry season). Body mass = 0.918 + 0.3 * trophic position, $r^2 = 0.01$, $p = 0.098$.

Discusión general

El objetivo principal del presente estudio fue definir la estructura de la red trófica de los macroinvertebrados bentónicos en dos arroyos tropicales de primer orden de la subcuenca del Río Lacantún, Chiapas, México, así como su dinámica anual en relación con la variación estacional (lluvias y secas) en la disponibilidad de recursos autotróficos y detritos. Se cuantificaron los almacenes y aportes de materia orgánica autotrófica autóctona y detritos alóctonos en los dos arroyos, se analizó su variación estacional y se compararon con las estimaciones de metabolismo ecosistémico. Se evaluó la dinámica estacional de los grupos funcionales tróficos (GFT) de los macroinvertebrados bentónicos, se analizó su relación con la disponibilidad de los recursos alimenticios y se analizaron los rasgos ecosistémicos derivados de las proporciones de los GFT. Se identificó la ruta trófica dominante de la red trófica de los macroinvertebrados bentónicos, así como su dinámica estacional asociada a la variación de los recursos tróficos dada por la hidrodinámica y su efecto en la estructura trófica de la red.

Cuantificación de la materia orgánica y del metabolismo ecosistémico

Los almacenes y aportes de materia orgánica en los dos arroyos estudiados variaron estacionalmente asociados a los cambios en la hidrología de los arroyos derivados de la estacionalidad tropical y expresado en el patrón de precipitación (épocas de secas y lluvias). La materia orgánica particulada gruesa (MOPG), incluyendo hojarasca, algas bentónicas y macrófitas, aumentaron en abundancia en la temporada de secas, como consecuencia de la disminución en la precipitación pluvial y el caudal. El aumento del caudal en la temporada de lluvias representa dos efectos adversos para los productores primarios autóctonos. Las corrientes rápidas pueden desprender las algas del canal y las lluvias favorecen el crecimiento de la vegetación ribereña, que aumenta la sombra sobre el canal (Bleich et al.

2015).

La abundancia de la materia orgánica disuelta (MOD) y particulada fina (MOPF) aumentó en la temporada de lluvias debido al aumento en la precipitación y con ésta, la turbidez, tal como se ha reportado en ríos y arroyos tropicales y templados (Atkinson et al. 2009, Wiegner et al. 2009). Los aportes directos (caída vertical desde los árboles en las orillas) y laterales (arrastre desde la zona de ribera) de hojarasca aumentaron en la temporada de secas debido al incremento en la caída de las hojas por el estrés hídrico de las plantas y por el transporte eólico de hojas secas (Tonin et al. 2017).

La producción primaria bruta (PPB) incrementó en la temporada de secas, mientras que la respiración ecosistémica (RE) no difirió entre temporadas. El incremento de la PPB en temporada de secas no se correlacionó con la biomasa de los productores primarios. La respuesta a esta falta de correlación puede deberse a que la PPB esté relacionada con la actividad microbiana (Douglas et al. 2005), que no fue medida en este estudio, más que con la producción dada por los productores primarios macroscópicos. La RE tampoco se correlacionó con la abundancia de detritos, a pesar de que la hojarasca y la MOD suelen ser factores importantes en los procesos de descomposición en ríos (Bernot et al. 2010). Probablemente la abundancia constante de los detritos durante todo el año explica la falta de correlación con las variaciones en la RE.

La estacionalidad, definida por el patrón de precipitación y su efecto en la hidrología de los arroyos son los principales factores que controlan la dinámica de la materia orgánica en arroyos tropicales. Sin embargo, los parámetros ambientales y los almacenes de materia orgánica no fueron buenos predictores del metabolismo ecosistémico.

Dinámica estacional de los grupos funcionales tróficos (GFT) de macroinvertebrados

bentónicos

La biomasa de los GFT de los macroinvertebrados bentónicos en los arroyos varió estacionalmente. La biomasa de los GFT herbívoros, raspadores y trituradores, aumentó en la temporada de secas asociada al incremento en la abundancia de los recursos autóctonos, algas bentónicas y macrófitas. La abundancia de los productores primarios en arroyos tropicales aumenta en temporadas de flujo bajo debido a las condiciones favorables de luz y caudal (Douglas et al. 2005). La biomasa de los GFT detritívoros, trituradores y colectores, también aumentó en la temporada de secas, pero no se correlacionó o lo hizo negativamente con la abundancia de los recursos alimenticios. La hojarasca, recurso principal de los detritívoros trituradores, no se correlacionó con la biomasa de los macroinvertebrados probablemente asociado a que este recurso presenta una alta abundancia todo el año, además de que su consumo depende principalmente del grado de acondicionamiento que tenga (Arsuffi y Suberkropp 1989). La MOPF, recurso principal de los colectores, mostró una baja abundancia durante todo el año y probablemente constituyó un recurso de baja calidad nutricional (Cummins et al. 2005). Por consiguiente, la comunidad de colectores en los arroyos presentó baja biomasa, correlacionada negativamente con la abundancia del recurso.

Los rasgos ecosistémicos, definidos con base en las proporciones de los GFT, mostraron predominancia de la autotrofia en ambos arroyos y en ambas temporadas, expresada por la dominancia de los herbívoros. Sin embargo, la biomasa alta de los trituradores detritívoros comparada con la de los colectores, indicó una interacción fuerte con el ambiente ribereño y con sus recursos alóctonos. La comunidad asociada a la MOPF bentónica (depositada en los sedimentos) dominó con relación a la MOPF suspendida o en transporte en ambas temporadas, lo cual probablemente está relacionado con la presencia de microorganismos en los sedimentos que facilitan el consumo de la materia orgánica (Cummins et al. 2005). Ambos arroyos presentaron sustratos estables, que permitieron la presencia de raspadores y filtradores en ambas temporadas. Los depredadores presentaron una biomasa alta, lo cual indicó un fuerte control descendente en la comunidad. Esto sugiere que las presas están presentando tasas altas de recambio para sostener la biomasa alta de los depredadores (Allen 1958)

Ruta trófica dominante y estructura de la red trófica de macroinvertebrados bentónicos

La ruta trófica dominante en los arroyos estudiados fue la autotrófica, basada principalmente en algas bentónicas, ya que sustentó el 60% de la biomasa de los macroinvertebrados bentónicos. La biomasa de los macroinvertebrados basada en detritos no varió estacionalmente, probablemente asociado a la disponibilidad alta de detritos alóctonos, principalmente hojarasca, durante el año. La biomasa de macroinvertebrados basada en recursos autotróficos aumentó en la temporada de secas, asociado al aumento en la abundancia de los recursos. En varios arroyos tropicales se ha encontrado una alta asimilación de algas, incluso cuando su disponibilidad es limitada (Schmidt et al. 2017).

La estructura trófica, evaluada mediante la posición trófica máxima, la estructura por tallas y el nivel de omnivoría, no varió estacionalmente. La posición trófica máxima fue mayor en Mario (4.21) que en José (3.99). En José fue similar entre temporadas, mientras que en Mario fue mayor en la temporada de lluvias que en la de secas. Este patrón fue similar al encontrado en arroyos tropicales de Hong Kong, donde se asoció al grado de sombra sobre el canal y al consecuente enriquecimiento isotópico (Lau et al. 2009).

La omnivoría fue la estrategia trófica predominante en ambos arroyos y temporadas. Se ha hipotetizado que la omnivoría es común en arroyos tropicales debido a que es una estrategia que permite el intercambio entre los recursos tróficos abundantes de baja calidad nutricional con los recursos tróficos escasos de alta calidad (Wantzen y Wagner 2006). La red trófica no se estructuró por tallas, es decir, no encontramos una correlación lineal entre la masa corporal y la posición trófica. Algunos taxones, como crustáceos y gasterópodos, contribuyeron de forma importante a la biomasa, pero ocuparon posiciones tróficas intermedias, lo cual debilitó la estructura por tallas. Además, estos organismos de gran tamaño difícilmente son depredados por otros invertebrados (Jardine 2014), lo cual resultó en una estructura por tallas poco desarrollada.

Dinámica anual de la red trófica de macroinvertebrados bentónicos en relación con la variación estacional en la disponibilidad de recursos autóctonos y alóctonos

La variación estacional de los almacenes y aportes de materia orgánica de los arroyos influyó en la dinámica de la red trófica de los macroinvertebrados bentónicos. Los productores primarios bentónicos aumentaron en la temporada de secas, asociados a la disminución de la precipitación y por consiguiente del caudal. Los flujos bajos y el aumento de la transparencia del agua característicos de la temporada de secas favorecieron el desarrollo y abundancia de las algas bentónicas, como se ha observado en otros arroyos tropicales (Douglas et al. 2005, García et al. 2016).

Asociado al incremento en la disponibilidad de algas, la biomasa de los grupos funcionales tróficos raspadores, que se alimentan de algas bentónicas, y trituradores herbívoros, que se alimentan de macrófitas, incrementó en la temporada de secas. Mientras que el porcentaje de biomasa de macroinvertebrados producida por la vía autotrófica aumentó en la temporada de secas en el arroyo José, en el arroyo Mario no se observó la misma tendencia.

La ruta trófica autotrófica resultó ser de gran importancia en la red trófica de los macroinvertebrados bentónicos en estos dos arroyos tropicales de primer orden. Los recursos autotróficos soportaron entre el 45 y el 70% de la biomasa de los macroinvertebrados bentónicos. La importancia de la ruta trófica autotrófica resalta aún más teniendo en cuenta que la biomasa de los productores primarios es muy baja (1%) comparada con la biomasa de los detritos (99%).

Los aportes de hojarasca ya sea por caída directa o por transporte (arrastre) lateral aumentaron en la temporada de secas en los dos arroyos, producto del máximo de caída de hojas de los árboles ribereños debido al estrés hídrico impuesto por la sequía, así como por el transporte eólico de las hojas secas. Los almacenes de hojarasca aumentaron en la temporada de secas, favorecidos por el flujo bajo. En la temporada de flujo bajo se favoreció la retención de la materia orgánica. Por el contrario, durante la temporada de lluvias los fuertes flujos sumados a la falta de estructuras de retención (p.ej., troncos caídos, grandes rocas) arrastraron la hojarasca del canal impidiendo su depósito y disminuyendo así los almacenes de ésta.

En la temporada de secas aumentó la biomasa de los detritívoros trituradores, macroinvertebrados que se alimentan principalmente de detritos en forma de hojarasca. Sin embargo, su abundancia no se correlacionó con la abundancia de su recurso alimenticio. Más aún, el porcentaje de biomasa producida por la vía detritívora alóctona no varió estacionalmente. Es probable que la abundancia alta de detritos permitiera que los macroinvertebrados lo consumieran de forma constante sin modificar de forma apreciable su disponibilidad, a diferencia de los recursos autotróficos que sólo están disponibles temporalmente. Se sabe (Casotti et al. 2019, Wantzen et al. 2008) que el grado de acondicionamiento de las hojas facilita su consumo y asimilación por parte de los macroinvertebrados, lo cual resulta ser más importante que la abundancia en sí misma y constituye el factor que finalmente determina su disponibilidad.

La MOPF aumentó en la temporada de lluvias y se correlacionó con el aumento de la precipitación y turbidez del agua. La biomasa de los GFT que se alimentan de MOPF, colectores recolectores y filtradores, estuvo negativamente correlacionada con la abundancia del recurso, pues aumentó en la temporada de secas. Así como la abundancia de la MOPF fue el recurso menos abundante, la biomasa de los colectores fue la más baja de todos los GFT en los arroyos. Gran parte de la MOPF usualmente proviene del fraccionamiento de la hojarasca (MOPG), la cual suele ser de baja calidad nutricional en arroyos tropicales (Cummins et al. 2005). Durante el fraccionamiento se reduce, aún más, la calidad del recurso, pues aumenta proporcionalmente el contenido de lignina y celulosa (Tank et al. 2010). El resultado es un recurso alimenticio de muy baja calidad y en baja cantidad, que limita fuertemente el desarrollo de la comunidad de colectores que dependen de éste.

Tres aspectos de la estructura trófica de los macroinvertebrados fueron evaluados: la posición trófica, el grado de omnivoría y la estructura por tallas. La posición trófica máxima fue similar entre temporadas en José, pero aumentó en temporada de lluvias en Mario. Ambas rutas tróficas, autotrófica y detritívora, contribuyeron a sostener la biomasa de todos los niveles tróficos, aunque la vía autotrófica soportó mayor biomasa de macroinvertebrados.

El porcentaje de omnivoría en las redes tróficas fue importante (30-40%) y no varió estacionalmente. La omnivoría se presentó en todos los niveles de consumidores, probablemente como una estrategia flexible de alimentación (Wootton 2017). A los consumidores primarios les permite explotar los detritos abundantes, aunque de baja calidad nutricional y los recursos autotróficos, escasos temporalmente, pero de mayor calidad nutricional. Para los consumidores secundarios es una estrategia que permite reducir la competencia intragremial al alimentarse de presas animales y de recursos basales. Esta estrategia resulta especialmente importante en los arroyos estudiados, donde existe un alto control descendente por la abundancia alta de depredadores.

Las redes tróficas acuáticas suelen estar estructuradas por talla, por lo cual presentan una estructura de pirámide invertida (Shurin et al. 2006). Sin embargo, la presencia de organismos de gran tamaño corporal en los arroyos estudiados, como crustáceos (*Macrobrachium*) y moluscos (*Pomacea*)**,** con niveles tróficos bajos o intermedios, disrumpió la estructura de tallas de la red en los arroyos estudiados. Por lo anterior, la red trófica de macroinvertebrados en los arroyos no se estructuró por tallas. Más aun, la presencia de organismos de gran tamaño, que se alimentan principalmente de detritos, podría llevar a sobreestimar la importancia de esa vía trófica (Jardine 2014). Los insectos, de menor tamaño, pero usualmente con mayor tasa de producción secundaria, se alimentaron principalmente de recursos autotróficos.

A pesar de las variaciones en la biomasa de macroinvertebrados basada en los dos tipos de recursos, autotróficos y detritos, los tres aspectos evaluados de la estructura trófica no variaron estacionalmente. La alta frecuencia de omnívoros entre los macroinvertebrados probablemente mantuvo la estructura de la comunidad estable, a pesar de las variaciones en la abundancia de recursos.

Nuestros resultados sugieren que la ruta autotrófica tiene una función importante en las redes tróficas de metazoos en arroyos tropicales y su importancia está relacionada con la estacionalidad. No obstante, los procesos de respiración predominaron en los arroyos. La aparente paradoja entre un metabolismo heterotrófico neto y la red trófica de metazoos basada principalmente en producción primaria autóctona sugiere que el circuito microbiano y la red de metazoos están pobremente acoplados (Cotner et al. 2006), aunque esto permanece sin estudiarse aún.

Conclusiones

El presente es uno de los primeros estudios enfocados en describir la variación temporal de las redes tróficas de macroinvertebrados bentónicos en zonas tropicales. Se comprobó que la abundancia de los recursos basales autotróficos y detritos de la red trófica de macroinvertebrados varía estacionalmente, principalmente en función de los patrones de precipitación que determinan el caudal de los arroyos y con ello, las características ambientales y biológicas. Esta variación tiene un efecto en la red trófica de los macroinvertebrados. El aumento en la abundancia de los recursos autotróficos en temporada de secas se refleja en la biomasa de los grupos funcionales tróficos que los consumen como su principal fuente de alimento, así como en un aumento general de la biomasa de macroinvertebrados sustentada por la vía autotrófica. Los detritos alóctonos también variaron estacionalmente, pero aparentemente no tienen un efecto directo sobre la biomasa de macroinvertebrados, probablemente porque el grado de acondicionamiento bajo de la hojarasca tiene un mayor efecto sobre el consumo por parte de los macroinvertebrados, que la abundancia misma del recurso. Otros aspectos de la estructura trófica (posición trófica, grado de omnivoría, estructura por tallas) no variaron estacionalmente, sino que se presentaron como características fijas de la estructura de la red trófica. Finalmente, se comprobó que la vía autotrófica representa la mayor contribución a la producción secundaria de los macroinvertebrados, especialmente en temporada de secas, en estos dos arroyos tropicales de primer orden, incluso cuando éstos presentan producción primaria baja y metabolismo neto heterotrófico.

Nuestros resultados sugieren que los modelos ecológicos tradicionales (p.ej., *Concepto del Río Contínuo, Concepto del Pulso de Inundación*) no representan adecuadamente las redes tróficas de los arroyos tropicales boscosos de primer orden. Aunque los recursos alóctonos constituyen la biomasa dominante dentro de los arroyos, las redes tróficas animales no están basadas principalmente en estos recursos. Por el contrario, la producción primaria, aunque limitada, representa el principal recurso que sostiene la red trófica. Los modelos ecológicos propuestos posteriormente (*Síntesis del Ecosistema Fluvial, Concepto de Onda del Río*) representan más acertadamente lo encontrado en el presente estudio. La importancia relativa de los recursos tróficos autotróficos y detritos varía en función de la configuración del ecosistema y principalmente, en función de la estacionalidad climática e hidrológica. El cambio climático a nivel global podría modificar la hidrología de los arroyos afectando significativamente las redes tróficas de macroinvertebrados bentónicos.

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