Hydrobiologia
https://doi.org/10.1007/s10750-019-3917-8

PRIMARY RESEARCH PAPER

# Effects of macroconsumers on benthic communities across a gradient of vegetation loss in tropical karst streams

**Elaine Cristina Corrêa · Fabio de Oliveira Roque · Ryan Michael Utz · William Marcos da Silva · Francisco Severo-Neto · Keith Bryant Gido**

Received: 2 November 2017 / Revised: 14 February 2019 / Accepted: 15 February 2019

**Abstract** Though many studies have demonstrated top-down control by macroconsumers on benthic communities and ecosystem processes in tropical streams, few have simultaneously addressed such effects across a gradient of riparian vegetation loss. Here, we investigated if potential top-down effects induced by macroconsumers interact with native vegetation changes of tropical karst streams in Brazil. We experimentally excluded macroconsumers (e.g., fish and shrimp) from benthic habitats of seven streams with a range of forest cover from 20% to 100% and examined the effects on benthic invertebrate and periphyton communities. Across sites, the absence of macroconsumers had no effects on mean chlorophyll-*a* concentrations, total dry mass or abundance of benthic invertebrates. However, the periphyton community significantly differed between control and treatment replicates. Overall, experimental exclusion of macroconsumers resulted in weak or negligible effect on benthic communities, which contrasts a significant proportion of related literature conducted elsewhere. Such top-down effects have been poorly studied in tropical karstic streams to date.

Handling editor: Marcelo S. Moretti

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s10750-019-3917-8) contains supplementary material, which is available to authorized users.

E. C. Corrêa (✉) · F. de Oliveira Roque
Laboratório de Ecologia, Instituto de Biociências,
Universidade Federal de Mato Grosso do Sul, Cidade
Universitária s/n, Campo Grande, MS 79070-900, Brazil
e-mail: elaineccorrea@yahoo.com.br

R. M. Utz
Falk School of Sustainability, Chatham University, 6035
Ridge Road, Gibsonia, PA 15044, USA

W. M. da Silva
Laboratório de Ecologia, Câmpus do Pantanal,
Universidade Federal de Mato Grosso do Sul, Corumbá,
MS 79304-902, Brazil

F. Severo-Neto
Laboratório de Zoologia, Instituto de Biociências,
Universidade Federal de Mato Grosso do Sul, Cidade
Universitária s/n, Campo Grande, MS 79070-900, Brazil

K. B. Gido
Division of Biology, Kansas State University, 106 Ackert
Hall, Manhattan, KS 66506, USA

**Keywords** Electric exclusion experiment · Consumer exclusion · Riparian vegetation · Macroinvertebrates · Top-down control · Periphyton

## Introduction

Top-down ecological effects in streams, as mediated by macroconsumers, can influence the abundance, biomass and/or productivity of their prey and lower trophic levels (Paine, 1980; Pace et al., 1999). However, the strength of top-down control depends on a variety of factors, including prey edibility and vulnerability, disturbance regimes, abiotic variables, nutrient enrichment, and composition, and functional organization of the communities (e.g., Leibold, 1989; Power et al., 2008; Peckarsky et al., 2013). Thus, attempting to identify and predict in which ecological contexts top-down regulation are pervasive in freshwater food webs is of major theoretical and practical importance given the current loss of biodiversity in streams, particularly in tropical regions (Dudgeon et al., 2006).

Loss of macroconsumers can result in dramatic changes to community structure and ecosystem functioning across aquatic and terrestrial ecosystems (Estes et al., 2011). However, the ability of macroconsumers to elicit a trophic cascade appears to be context-specific. For example, in temperate streams, predatory largemouth and spotted bass [Centrarchidae: *Micropterus salmoides* (Lacepède, 1802) and *M. punctulatus* (Rafinesque, 1819)] suppress herbivorous fish, resulting in a strong cascading effect on the benthic algae assemblages (Power et al., 1985). In the tropics, some studies (e.g., Flecker, 1996; Pringle & Hamazaki, 1998) showed that experimental exclusion of macroconsumers increased the number of insects without a decrease in primary producer abundance, which is contrary to expectations based on cascading interactions. Thus, trophic cascades depend on the diet of macroconsumers, the presence of predatory invertebrates, length of the food chain, trophic diversity, and complexity of food webs in species rich ecosystems (Polis & Strong, 1996), as well as on the interaction between the top-down and bottom-up effects (e.g., nutrient cycling) (Power, 1992; Flecker et al., 2002; Lourenço-Amorim et al., 2014). Most top-down control studies in tropical streams have shown large effects (e.g., Moulton et al., 2004; Lourenço-Amorim et al., 2014), but some have found weak effects of macroconsumers (e.g., Pringle & Hamazaki, 1998). In such studies, a lack of effect was attributed to the presence of omnivorous macroconsumers (feeding on more than one trophic level) that are able to suppress abundance of prey from multiple trophic levels below their own (e.g., Pringle & Hamazaki, 1998). However, a few studies have simultaneously tested the effects of native vegetation loss or land-use change around streams and the consequences of macroconsumer loss on trophic interactions (Schofield et al., 2008; Wilson et al., 2016).

The conversion of native grasslands and forests to human-modified landscapes may result in prevalent modifications of biological communities (Haddad et al., 2015), particularly in stream ecosystems. In streams draining agricultural regions, pollutants and sediments are elevated, potentially reducing macroconsumer abundances (Schofield et al., 2004; Vörösmarty et al., 2010), which can result in a substantial loss of species (Dudgeon et al., 2006). Similarly, modifying and/or reducing riparian zones tend to increase irradiation, algal production, and macroconsumer effects (Wellnitz & Ward, 1998). Although the physical and chemical effects associated with land use in aquatic systems are well known, the effects of native vegetation loss on the dynamic of biological communities still remain controversial and can be context dependent (Allan, 2004). Understanding such effects is fundamental to elucidating ecosystem properties, especially in tropical regions where intensive modification of native forest to agriculture is a widespread environmental problem (Foley et al., 2011).

Streams in karstic watersheds of the Neotropics are particularly threatened by landscape conversion (Kresic, 2013). Such enhanced vulnerability occurs due to the thin limestone soils and rapid connection of the surface water to the aquifer, providing minimal filtration to remove pollutants/sediments (Van Beynen & Townsend, 2005). Furthermore, a disproportionate degree of landscape change in the tropics often occurs on land adjacent to streams, creating habitats with reduced environmental integrity and forest cover (Vörösmarty et al., 2010; Laurance et al., 2014). The karstic streams of the Bodoquena Plateau, a region of Central-West Brazil, support high diversity of species with 164 taxa of macroinvertebrates (Valente-Neto et al., 2018), many omnivorous groups such as shrimp (e.g., *Macrobrachium*) and more than 36 fish species (Casatti et al., 2010), including endemic and endangered species (e.g., Loricariidae: *Ancistrus formoso* Sabino & Trajano, 1997 and Trichomycteridae: *Trichomycterus dali* Rizzato, Costa, Trajano & Bichuette, 2011) (Sabino & Trajano, 1997; Cordeiro et al., 2014). These streams have complex patterns of hydrologic connectivity and high levels of calcium carbonate ($CaCO_3$) (Sallun-Filho & Karmann, 2007; Corrêa et al., 2018) that can influence the primary production as observed in other karstic streams (Corman et al., 2016). Stream biodiversity is threatened by recent decline of native vegetation primarily for agricultural purposes and pastures (Roque et al., 2016). Previous studies conducted in the region reported that the aquatic and terrestrial insects responded idiosyncratically to a gradient of riparian vegetation removal (Roque et al., 2017) and that fish communities did not vary between streams with watersheds dominated by pasture cover compared to those that flow though reference areas with native vegetation (Casatti et al., 2010). Understanding if native vegetation loss around streams can influence food web structure is an important avenue of research for ecosystems facing increasing anthropogenic pressures such as tropical karst streams.

The purpose of our study was to investigate whether macroconsumers control benthic communities and if such a potential top-down control interacts with the loss of native vegetation in tropical karst streams of Brazil. The loss of macroconsumers associated with the loss and fragmentation of native vegetation should result in shorter food chains (e.g., Hagen et al., 2012). Accordingly, top-down control in these systems is predicted to decrease with the loss of forest cover. However, riparian degradation impairs substrate suitability for biofilm production and also could cause bottom-up effects through food webs (Walser & Bart, 1999) by in-filling of interstitial habitat that harms crevice-occupying invertebrates (Henley et al., 2000) and reducing stream habitat heterogeneity (Sutherland et al., 2002). Consequently, the simultaneous loss of vegetation and macroconsumers may have interactive effects on benthic communities. To test the interaction between macroconsumers and forest cover, we experimentally excluded macroconsumers from the benthic zones of seven streams that varied along a gradient of forest cover and examined the effects of exclusion on benthic invertebrates and periphyton.

## Materials and methods

### Study area and site selection

Our study was conducted for 10 days, between 23 May and 12 June 2015, in streams of the Bodoquena Plateau, an elevated region in southwestern Mato Grosso do Sul, Brazil (Fig. 1). The plateau represents one of the most extensive continuous karst aquatic systems in Brazil (Sallun-Filho & Karmann, 2007) and spans the transition between Cerrado and Atlantic Rainforest ecoregions, both considered hotspots of biodiversity (Myers et al., 2000). A contiguous 770 $km^2$ of the western Bodoquena Plateau was conserved in a mostly natural state following the designation of Parque Nacional da Serra da Bodoquena (PNSB) in 2000. Forests surrounding the park are fragmented by cattle ranching and monocultures of soy and corn, resulting in a mosaic of land cover that ranges from dense riparian vegetation to deforested pasture. Native vegetation in the study area is composed of deciduous and semi-deciduous Cerrado biome vegetation with riparian forests dominated by leguminous (Fabaceae) and myrtle (Myrtaceae) trees (Baptista-Maria et al., 2009).

We selected study sites on seven second- or third-order streams with riparian zones spanning a landscape gradient from mostly forested to mostly agricultural (Table S1 in Online Resource). All sites drain karstic watersheds into the Formoso River, a tributary of the Upper Paraguay River basin that includes the Pantanal wetland complex. Substrate composition across the sites was mostly composed of sand- to cobble-sized inorganic particles, with some isolated areas of silt cover. Prior biological surveys ensured that all sites supported aquatic communities with similar trophic structure and composed of three broadly defined trophic levels: periphyton, invertebrates such as insect larvae, and macroconsumers represented by shrimp and fish.

With respect to vegetation-cover gradient, our site-selection process followed a standardized procedure adopted by the PNSB Long Term Ecological Research program (LTER) that evaluates the effects of land-use changes on terrestrial and aquatic ecological networks,

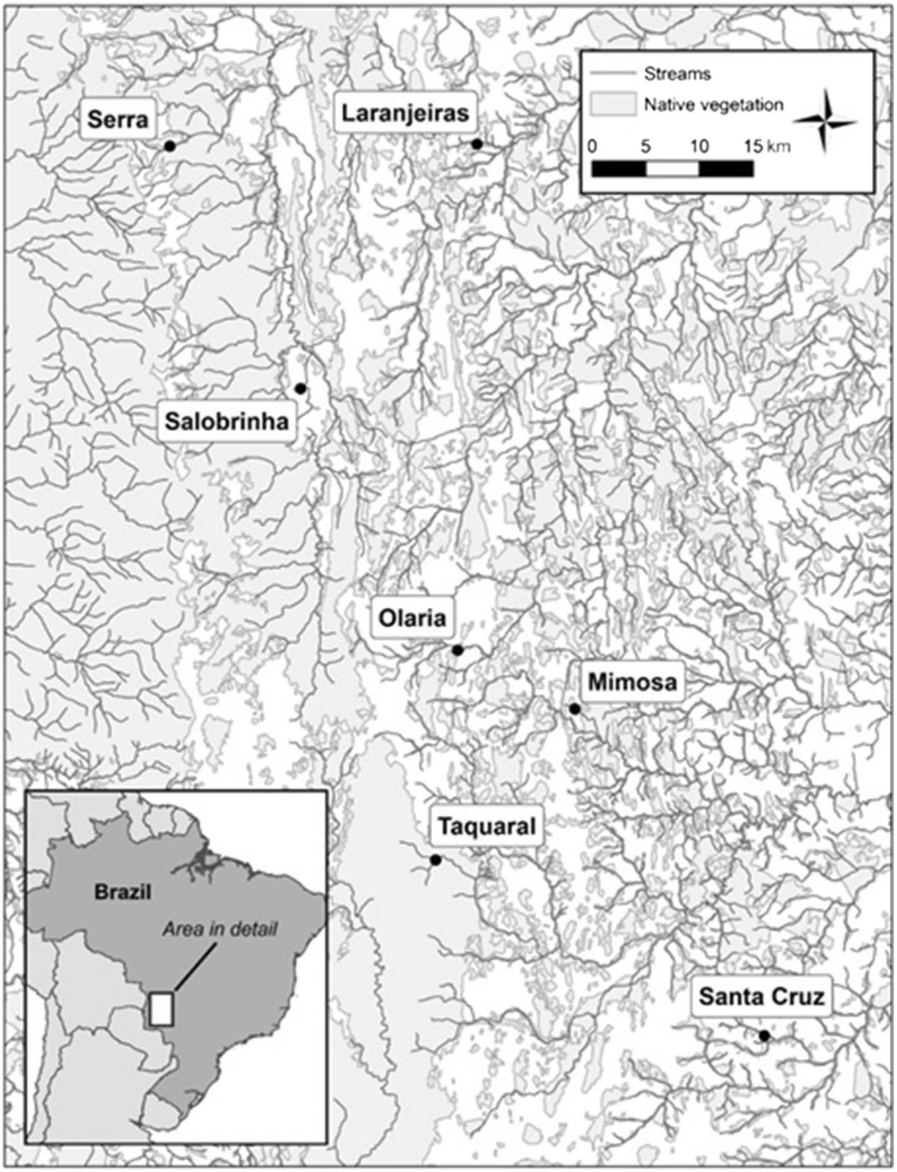

**Fig. 1** Map showing the seven study sites and surrounding land cover in the study area located in the Bodoquena Plateau in southwestern Mato Grosso do Sul, Brazil

and conducts land-use analysis at 360, 5000 ha hexagonal sites throughout the Bodoquena Plateau (Fig. S1 in Online Resource). Sites chosen spanned a forest-cover gradient as measured within the 5000-ha area surrounding the stream (Fig. S2).

In this study, the total percentage of forest cover at each site (i.e., within each hexagonal region) was re-calculated using a buffer of 250 m radius from the middle of the experimental reach. This buffer radius was chosen according to other studies that examined the influence of forest-cover loss near the streams on aquatic Odonata communities in the Bodoquena Plateau (Rodrigues et al., 2016; Valente-Neto et al., 2016). In addition, Odonata was suggested as a bioindicator of human impact, such as the degradation of riparian vegetation near the streams (Valente-Neto et al., 2016). To validate the amount of forest cover in the buffer zone of each site, we also used the Channel and Environmental Integrity (RCE) index based on Petersen (1992) and adapted by Nessimian et al. (2008) to measure physical integrity of each riparian zone, and afterward, we related the RCE scores to forest cover ($R^2 = 0.66$; $P = 0.03$). We calculated the percentage of forest cover using ArcGIS (version 10.1 ESRI, Redlands, California, USA).

## Stream attributes and vertebrate fauna surveys

Multiple physical and chemical parameters of all study sites were recorded during the experiment to characterize each stream (Table S1). Wetted width and depth were measured along the 30 m reach where experimental trials were conducted. Water-quality parameters, including temperature, conductivity, salinity, pH, and dissolved oxygen, were measured with a multiparameter water-quality meter (HI 9828 Hanna Instruments, USA) for 5 days in each site during the experiment. Total nitrogen (TN), phosphorus (TP), and turbidity were also recorded once at the end of the experiment. TN was measured using persulfate methods and cadmium reduction, while TP was measured using a persulfate digestion with stannous chloride; both were measured colorimetrically on a spectrophotometer (APHA, 1998).

Voucher specimens of fish were collected during June 2015 to characterize the macroconsumer assemblage at each site. The downstream ends of the 100 m sample reaches were blocked with a 5 × 2 m, 5-mm mesh block net and fish were subsequently collected with a 3 × 2 m, 5-mm mesh seine net (Castro et al., 2004; Casatti et al., 2010). Collected fish were euthanized using clove oil and preserved in 10% formaldehyde, transferred to 70% alcohol, and identified following published taxonomic keys (Britski et al., 2007).

## Experimental trials

An electrical exclusion technique was used to manipulate the access of macroconsumers to patches of benthic habitat. This method is widely employed (e.g., Pringle & Blake, 1994; Lourenço-Amorim et al., 2014; Andrade et al., 2017) to manipulate the presence of aquatic organisms occupying different trophic niches while allowing benthic invertebrates and periphyton access to substrates. Ten paired substrate baskets, five electrified and five controls, were deployed in a single, long pool in each stream. Basket dimensions were 20 × 20 × 10 cm with a 50 mm mesh opening (as previously recommended for use in the U.S. National Science Foundation's STREON program in the National Ecological Observatory Network) (Utz et al., 2013, 2017). Iron rings were affixed to the top of the baskets using plastic zip ties. An alligator clip was used to attach electrical fence chargers to the rings (model residential and commercial electric fence; LHR Manutenção e Montagem Ltd. Ribeirão Preto, São Paulo, Brazil), rated at 1.2 J, 110 µs of duration, and 1.3 amperes, with power supplied by one 12 V battery (Corrêa et al., 2018). However, the electrical properties could be variable when applied underwater (Landeiro et al., 2008).

All baskets were filled with 20–30 similarly sized (approximately 40 $cm^2$), round limestones to promote organism colonization. Stones placed in the basket were acquired from a commercial source to standardize the replicates and ensure no prior biological colonization. Basket positions within each stream were installed with a minimum distance between baskets of 1 m. In preliminary laboratory and field experiments, we tested the potential for electricity to affect fish and shrimp by observing their behavior around the basket in each stream prior to the experimental trials. A snorkeling observer positioned 1 m from the basket waited quietly for 5 min after arriving at the site, a period deemed long enough for aquatic organisms to resume normal activities following a disturbance (Reznick et al., 2001; Marshall et al., 2012). We recorded efficacy of exclosure for a total of 288 min in control and 368 min for electrified basket at all sites. Snorkeling observation confirmed that the electrical exclusion technique was effective in excluding fishes with different feeding habits: for example, *Ancistrus* sp., *Synbranchus marmoratus* Bloch, 1795 (Synbranchidae), *Xenurobrycon macropus* Myers & Miranda Ribeiro, 1945 (Characidae), and shrimp [e.g., Palaemonidae: *M. brasiliense* (Heller, 1862)] from foraging on benthic substrata across sites. No fish were observed entering electrified treatments. Macroconsumer, *Macrobrachium* sp. shrimp occasionally entered treatment units, but they attempted to exit immediately. In addition, many individual fishes [e.g., *Ancistrus* sp., *Characidium zebra* Eigenmann, 1909 (Crenuchidae), *Hypostomus* sp.] were observed feeding within control replicates during the same period.

## Field and laboratory processing of benthic ecological parameters

Primary producer and benthic invertebrate samples were collected from baskets at the end of the trial period. Due to the logistical challenges and time constraints associated with travel to each site, the experiments only lasted 10 days. We assumed this was an adequate amount of time to detect a treatment effect (i) because benthic invertebrates colonization and life cycles are extremely rapid (Flecker & Feifarek, 1994; Flecker, 1996; Rosemond et al., 1998); (ii) in our pilot experiment (10-days), we collected most groups of benthic invertebrates that occur in the region (e.g., Annelidae, Gastropoda, Diptera, Ephemeroptera, and Trichoptera larvae) including different feeding groups and top predators (Megaloptera and Odonata larvae); and (iii) we also collected some benthic algae such as *Cladophora* sp., which is known to require considerable time to colonize substrate (Hillebrand & Kahlert, 2001).

To collect primary producers, all stones in each basket were scraped and washed within a bucket to create a 500 ml slurry. A 40 ml subsample was taken from the slurry for periphyton analysis. Periphyton sample jars were covered with aluminum foil and transported to the lab for quantification of dry mass and chlorophyll-*a*. To collect benthic invertebrates, baskets were extracted from deployment sites by hand with a 0.5-mm mesh kick net positioned immediately downstream to catch any organisms that may have escaped during extraction. Sample substrata were deposited in plastic containers and preserved in 80% ethanol for subsequent invertebrate identification.

In the laboratory, half of each periphyton sample (20 ml) was preserved in 9% Lugol's solution for algal composition analysis and the other half filtered onto two pre-ashed glass fiber filters (0.45 µm porosity, 47 mm diameter). One filter was used to determine dry mass, and the other was used for chlorophyll-*a* analysis. Sediment filters were dried for 24 h at 105°C to obtain dry mass. Chlorophyll-*a* was extracted from each filter in 10 ml of 80% ethanol for 12 h in a freezer in the absence of light (Nusch, 1980), and extract concentrations of chlorophyll-*a* were measured using a spectrophotometer (model: Hach Dr 6000, Loveland, Colorado USA). The values of chlorophyll-*a* within each treatment and sites were determined from the equation: Cha ($\mu g/cm^2$) = $11.79 \times (BA'' - BA') \times VE \times VF/VE \times 2)/(\text{Basket area})$, where $(BA'' - BA')$ was the before acidification measured at different wavelengths: 665 and 664 nm, respectively. VE is the volume extracted, and VF is the volume filtered (Nusch, 1980).

An aliquot (0.5 ml) of the subsample preserved for identification was used to identify periphytic algae. We identified algal taxa as diatoms, green algae (Chlorophyceae), and blue-greens (Cyanophycea) following Bicudo & Menezes (2005). Benthic invertebrates were picked from the substrate and initially classified as insects, snails, and oligochaetes. Insects were identified to the lowest practical level, usually genus, using taxonomic keys and original descriptions (Domínguez & Fernández, 2009; Hamada et al., 2014).

## Statistical analyses

Physical and chemical parameters were compared among streams using one-way analysis of variance (ANOVA) models with stream identity as independent variable. The distribution of residuals for all tested variables approximated normality. If a model suggested that the parameter was statistically different among streams, post hoc comparisons using Tukey's honest significant differences test was applied to determine how streams compared to one another. Additionally, we tested if TN or TP values were significantly correlated with the forest-cover gradient.

We assessed the effect of macroconsumer exclusion on chlorophyll-*a* (measured as $\mu g/cm^2$), dry mass of sediments ($g/cm^2$) and benthic invertebrate abundances ($n \times 100\ cm^{-2}$) using linear mixed models (LMMs) with ln-response ratios (LRRs; natural log of the treatment to control ratio) of the parameters serving as dependent data. LRRs were calculated for each of the five paired replicates per site. The final LMM model included the stream identity as a random block factor and the proportion of forest cover as an independent variable. We also calculated the degree of correlation between the proportion of forest cover and LRRs to determine if any parameters appeared to be independently related to the forest-cover gradient using the Pearson product moment correlation test.

Multivariate analyses of the periphyton and benthic invertebrate communities were also conducted to determine if macroconsumer exclusion and forest cover affected community structure. Permutational multivariate analyses of variance (PERMANOVA) models with 1000 permutations were applied to test community-scale differences between control and treatment assemblages and relationships with the proportion of forest cover. Each PERMANOVA model included the experimental treatment, forest-cover gradient, and interaction between these two variables as model terms. Stream identity was also included as a random block factor. To visually depict community-scale differences when PERMANOVA models revealed statistically significant findings, non-metric multidimensional scaling (nMDS) derived from Bray–Curtis distance matrices was created to assess differences in community structure among samples. We also used indicator species analysis (ISA) (Dufrêne & Legendre, 1997) to determine if any invertebrate taxa were associated with control or electrified treatments.

All analyses were performed in open-source software R (R Core Team, 2015), using lmerTest package for LMM models (Kutznetsova et al., 2018), vegan package for ordination and PERMANOVA tests (Oksanen et al., 2017), and indicspecies package (Cáceres, 2013) for ISA.

## Results

### Abiotic factors

Most physical and chemical parameters were similar among sites (Tables S1, 1), with the exception of mean salinity, which was substantially lower at Santa Cruz, and pH, which was not found to be significantly different between pairs of sites following post hoc comparisons. Contrary to our expectations, TN (1.87–0.85 μg/l), TP (0.179–0.102 μg/l), and turbidity (80–100 NTU) were not correlated with the forest-cover gradient ($P = 0.38$, 0.47, and 0.63, respectively).

**Table 1** Parameters of ANOVA models comparing physical and chemical differences among sites. All models possessed 6 degrees of freedom

| Parameter | *F* | *P* |
|---|---|---|
| Water temp (°C) | 1.0 | 0.432 |
| Conductivity (μS cm$^{-1}$) | 0.9 | 0.535 |
| Salinity (ppt) | 14.4 | < 0.001 |
| pH | 2.5 | 0.044 |
| Dissolved oxygen (mg l$^{-1}$) | 1.8 | 0.140 |

### Macrofauna survey

The fish community composition and overall abundance varied among streams (Table S2; Fig. S3). Most encountered fishes were insectivores, including several dominant species such as *X. macropus* that feed primarily on either aquatic insect larvae (Graciolli et al., 2010) or *Astyanax asuncionensis* Géry, 1972 (Characidae) that feed on drifting terrestrial insects (Borba et al., 2008). Omnivorous and algivorous species were collected in all but two sites, although no site supported more than ten individuals per 100 m of stream. Three larger invertebrate species, including an omnivorous shrimp (*M. brasiliense*), crab (Trichodactylidae: *Sylviocarcinus australis* Magalhães & Turkay, 1996), and alderflies (*Corydalus* sp.), were collected during the faunal surveys, but these organisms comprised less than 3% of the total macrofauna assemblage. The mean size of fish and shrimp surveyed at sites was relatively small, ranging from 1.2 cm (± 0.93 cm, standard deviation [SD]) to 12 cm (± 2.43 cm SD).

### Primary producers

We recorded 13 taxa of primary producers, of which Chlorophyceae was dominant (Fig. 3). Most sites supported a mix of green algae and epiphytic diatoms among treatments.

Parameters associated with total primary producer mass did not respond to either experimental treatment or the interaction with forest cover. The LRR values of both chlorophyll-*a* and dry mass did not indicate a significant treatment effect (i.e., model intercept was near zero) nor an interaction of the treatment with forest cover, though mean chlorophyll-*a* values were lower in treatment replicates compared to control replicates in six out of seven sites (Table 2; Fig. 2). Chlorophyll-*a* values independent of the experimental treatment were significantly and positively correlated with the forest-cover gradient ($t = 3.3$, $df = 61$, $P = 0.0016$). Dry mass values were not found to be correlated with the forest-cover gradient ($t = 1.1$, $df = 65$, $P = 0.2648$).

PERMANOVA results suggested that the periphyton community differed between control and treatment samples, though not along the forest-cover gradient (Fig. 3; Table 3). An nMDS system (stress = 0.06) revealed that the periphyton assemblages in

**Table 2** Results of linear mix models that assessed the effects of exclosure treatment and the interaction with forest cover on benthic- and invertebrate-associated metrics

| Parameter | Variable | *t*-value | *P* value |
|---|---|---|---|
| Periphyton | | | |
| Chlorophyll-*a* | Exclosure treatment | 0.14 | 0.896 |
| | Treatment × forest cover | 0.86 | 0.426 |
| Dry mass | Exclosure treatment | 0.10 | 0.918 |
| | Treatment × forest cover | 0.11 | 0.916 |
| Benthic invertebrates | | | |
| All benthic invertebrates | Exclosure treatment | 0.31 | 0.761 |
| | Treatment × forest cover | 0.15 | 0.886 |

Each model assessed the ln-response ratio of the exclosure to control data as a dependent variable and included stream identity as a random block factor. All models listed below include 31 degrees of freedom

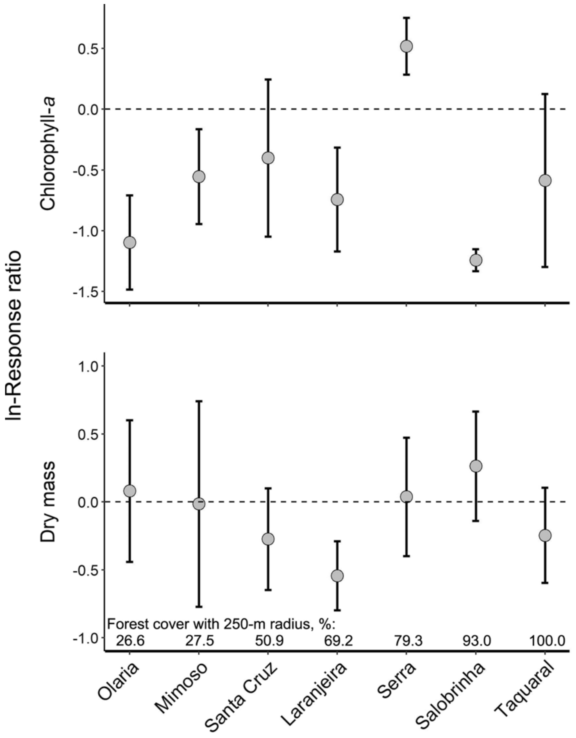

**Fig. 2** Site-specific ln-response ratios (LRRs) of chlorophyll-*a* and DM with respect to the experimental macroconsumer exclosure and forest-cover gradient. Shown are the means of treatment divided by control values ± 1 standard error. Sites are ordered from the least to most forest cover

macroconsumer-excluded baskets were dominated by green algae *Stigeoclonium* and Chlorophyceae (Fig. 3), the latter of which was present in 93% of electrified replicates. Twenty of the electrified replicates were represented solely by Chlorophyceae and one taxon, *Stigeoclonium*, was present only in electrified treatments. In contrast, the three taxa, *Enteromorpha*, *Nostochopsis*, and *Scenedesmus* were present only in control replicates and a fourth (*Trentophila*) was five times more common in control replicates compared to treatment replicates.

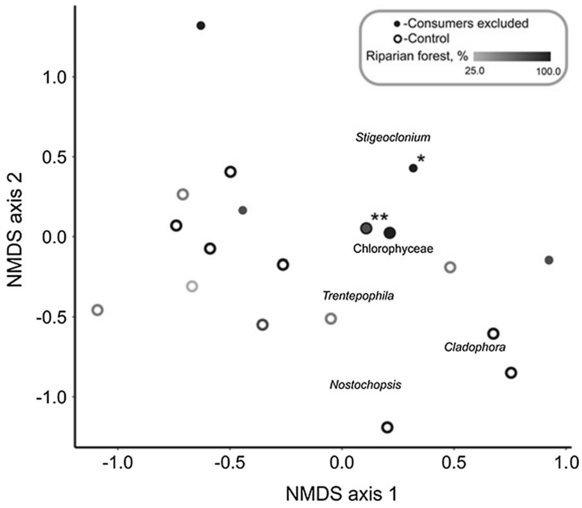

**Fig. 3** Non-metric multidimensional scaling systems for primary producers. Each point represents a basket and the shade of gray shown reflects the percentage of forest cover in the riparian zone. The coordinates for the top five most common primary producer species are also provided. Two sets of sample coordinates shown more than five replicates: the coordinates noted with a "single asterisk" represents treatment baskets, and those with "double asterisk" represent 14 control and 20 treatment baskets

**Table 3** Parameters from PERMANOVA models comparing periphyton and benthic invertebrate assemblages with respect to the treatment effect and forest-cover gradient

| Assemblage and parameter | $F$ | $R^2$ | $P$-value |
|---|---|---|---|
| Benthic invertebrates | | | |
| Exclosure treatment | 0.6 | 0.01 | 0.608 |
| Forest cover | 3.8 | 0.05 | 0.950 |
| Treatment × forestcover | 0.5 | 0.01 | 0.776 |
| Periphyton | | | |
| Exclosure treatment | 11.0 | 0.13 | $< 0.001$ |
| Forest cover | 6.7 | 0.08 | 0.978 |
| Treatment × forest cover | 2.4 | 0.03 | 0.897 |

Residuals for each model possessed 64 degrees of freedom

### Benthic invertebrates

We observed 2521 individuals from the benthic invertebrate baskets representing 30 families. Total abundance varied among sites with a maximum of 602 individuals observed (control: 324 and exclosure treatment: 278) at the Serra site. The invertebrate community was dominated by insects (85.31%) followed by Gastropoda (7.14%). The two most common families from the benthic samples were Leptophlebiidae and Chironomidae.

Total benthic invertebrate abundance was neither related to macroconsumer exclusion nor did the effects of the macroconsumer exclusion vary along the forest-cover gradient (Table 3; Fig. 4). Macroinvertebrate community composition was unrelated to the exclosure treatment, forest gradient, or the interaction between the exclosure treatment and forest gradient (Table 3). No indicator taxa were identified as significant indicators of control versus electrified sample types using ISA (all $P$ values $> 0.05$).

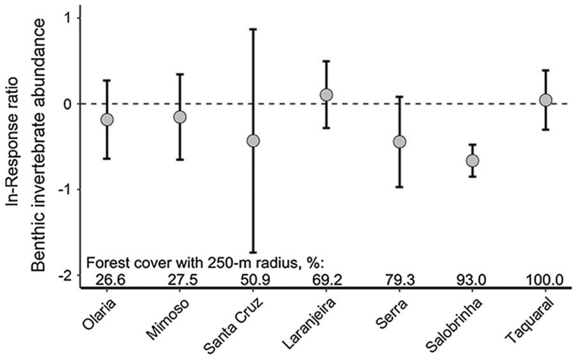

**Fig. 4** Site-specific ln-response ratios (LRRs) of total invertebrates abundance with respect to the experimental macroconsumer exclosure and forest-cover gradient. Shown are the means of treatment divided by control values ± 1 standard error. Sites are ordered from the least to most forest cover

## Discussion

Our findings offer no evidence of top-down ecological effects on primary producer biomass or benthic invertebrate assemblages across a gradient of forest cover in karstic tropical streams of the Bodoquena Plateau. However, the species composition of periphytic algae shifted with the absence of macroconsumers, as macroconsumer-excluded baskets supported less-diverse assemblages of primary producers.

The limited top-down response of algal biomass to macroconsumer exclusion was in contrast to other studies showing that the occurrence of fish and shrimp are of vital importance for the increasing rates of periphyton growth in streams (March et al., 2001; Baker et al., 2017). In addition, macroconsumers can significantly affect their prey behavior (Flecker, 1992; McIntosh & Townsend, 1996). For example, scraping mayflies commonly reduce foraging in the presence of predatory fish (e.g., McIntosh & Townsend, 1995; Schneider et al., 2014). In our study, macroconsumer exclusion may have promoted more grazing by scrapers, such as mayflies, which in turn changed algal composition across sites but did not influence algal biomass. Again, this is in contrast to Souza et al. (2007), who observed that periphyton biomass increased when mayflies (Baetidae) were experimentally excluded. A possible explanation for shifts in algal composition in exclosure treatments is related to the activity of insects associated to karstic biogenesis (Drysdale, 1999; Paprocki et al., 2003). Some insects that play a role in the deposition and erosion of travertines (e.g., hydropsychids, chironomids) may have responded to the absence of predators by constructing retreats with silken capture nets more freely inside the baskets. These nets may have become important substrates for $CaCO_3$ deposition, causing changes the substrates and altering biofilm growth.

Despite low chlorophyll-*a* density in the periphyton across our experiment, sites with diminished forest cover exhibited lower periphyton biomass, which is contrary to what would be expected with increased light availability. This discrepancy could be attributable to increasing sediment concentrations in impacted streams that impair substrate suitability for biofilm production. Furthermore, the short duration of the experiment would have contributed to the low density of chlorophyll-*a* from periphyton samples taken from the streams.

The exclusion of macroconsumers had no detectable effects on abundance of benthic invertebrates across sites, contradicting the general expectation that predators cause holistic effects on stream food webs (Williams et al., 2003). Such findings have precedence, as a lack of effect was observed when predatory fish were removed from patches within pools in tropical streams of Hong Kong (Ho & Dudgeon, 2015). In our study, such a lack of response could reflect several unique ecological attributes of our system, such as context dependency (Garcia et al., 2015). In tropical streams, including those of the Bodoquena Plateau, fish exhibit high trophic diversity and overlapping niches that are typically occupied by scraping and shredding insects (Winemiller et al., 2008; Moulton et al., 2010). The availability of resources and diverse benthic taxa such as terrestrial insects (Borba et al., 2008) and fruits from riparian vegetation (Reys et al., 2009; Correa & Winemiller, 2018), could have contributed to the limited top-down effect of macroconsumers on benthic invertebrates that colonized baskets. In addition, many insects may seek refuge between or under stones to avoid predation (Flecker & Allan, 1984; Flecker, 1992; Rosenfeld, 2000; Fairchild & Holomuzki, 2005). Studies from similar systems have shown that scouring water velocity may have a stronger impact on the macroinvertebrates than the presence or absence of macroconsumers (Baker et al., 2017). Moreover, the short duration of the experiment would also have limited the incubation time and potentially contributed to the lack of macroconsumers effect on benthic invertebrate community across sites.

Physical, chemical, and biological parameters were similar across the forest loss gradient, which contrasts with the tendency of streams with disturbed watersheds to exhibit strong environmental change relative to pristine sites. For example, total phosphorus was high and overlapped the upper ranges for unpolluted water (Brasil, 2012). Water temperature and conductivity also did not increase with diminished forest cover, which is contrary to other studies of how vegetation loss affects streams (Allan, 2004; Walsh et al., 2005). In addition, benthic invertebrate assemblages included both sensitive (e.g., Ephemeroptera, Plecoptera and Trichoptera) and tolerant (e.g., larval Chironomidae, Hydropsychidae, and Oligochaeta) taxa (Paul & Meyer, 2001; Allan, 2004; Walsh et al., 2005) across all sites along the forest-cover gradient. Therefore, the mosaic of vegetation and recent conversion of vegetation in the Bodoquena Plateau did not appear to have an effect on measured variables. Furthermore, previous studies of multitaxa communities in Bodoquena streams also did not find detectable responses between terrestrial and aquatic insects across a riparian-cover gradients (Roque et al., 2017), and comparisons of fish communities along of land-cover gradient also demonstrated weak or absent effects (Casatti et al., 2010). The landscape of the Bodoquena Plateau is presumably characterized by mosaics of vegetation such as savannah, deciduous, and semi-deciduous forests, which may maintain functional connectivity avoiding biodiversity loss. Much of the apparent usefulness of assessing forest-cover buffers or watersheds around streams arises from the general prediction that water quality, and consequently of the biota, reflects the characteristics of the land cover (Omernik & Bailey, 1997). However, as in other karstic systems, the watershed or forest-cover delimitation is particularly challenging in the Bodoquena Plataeu because surface water does not drain directly into surficial channels. Such hydrogeomorphic settings likely leads to decoupled effects of landscape degradation from instream processes, which might explain part of our findings. It is particularly challenging to test the importance of underground water flow because of the very limited availability of maps for and information on karstic tropical systems. Although the sampling of only seven streams likely restricted our ability to provide a general understanding, we believe that if the effect of the vegetation loss was strong, it would have exhibited a clear response in our dependent variables. Therefore, our results do not support the idea of a clear, ubiquitous effect of vegetation loss as a predictor of top-down control in streams.

Another possible confounding factor that might limit our ability to detect a top-down effect of macroconsumers was that our study was undertaken during the transition between wet season and dry season, which causes these streams to change drastically on abiotic and biotic factors. In the dry season, water temperatures are seasonally cool for the region (15–20°C during the study period). Macroconsumers may have had been foraging less during our study period than during the warmer wet season, such as was observed by Mantel & Dudgeon (2004) and Yang et al. (2009).

To conclude, manipulating the presence of macroconsumers did not induce effects on stream primary producer biomass and benthic invertebrate across sites representing a range of forest cover. Rather, experimental exclusion of macroconsumers resulted in a weak or negligible effect on benthic communities. However, further evaluation of these food web dynamics across different seasons or for extended periods of time will greatly improve our understanding of trophic dynamics and biotic interactions in a world increasingly severely modified by human activities, especially in tropical regions.

**Acknowledgements** We thank Waldeir Dias, Bruno Martínez, Guilherme Dalponti, Jonas Corrêa, Debora Moreira, and Emanuele Moura for their generous help in the field and laboratory. We are indebted to the Universidade Federal do Mato Grosso do Sul (Campus de Bonito), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) for the logistic support. Dr. Timothy Moulton and Dr. Walter Dodds provided insightful comments on earlier drafts of the manuscript. The research was supported by Planalto da Bodoquena: redes de interações em longo Prazo (PELD) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) by a doctoral scholarship and CAPES, FUNDECT/PAPOS (processo 23/200.638/2014). Finally, Chatham University and Kansas State University generously provided logistic supports for visiting scholarship.

## References

Allan, J. D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257–284.

Andrade, C. M., V. Neres-Lima & T. P. Moulton, 2017. Differentiating the roles of shrimp and aquatic insects in leaf processing in a Neotropical stream. Marine and Freshwater Research 68: 1695–1703.

APHA, 1998. Standard methods for the examination of water and wastewater. American Public Health Association, New York.

Baker, K., M. A. Chadwick, R. A. Wahab & R. Kahar, 2017. Benthic community structure and ecosystem functions in above- and below-waterfall pools in Borneo. Hydrobiologia 787: 307–322.

Baptista-Maria, V. R., R. R. Rodrigues, G. Damasceno-Junior, F. S. Maria & V. C. Souza, 2009. Composição florística de florestas estacionais ribeirinhas no estado de Mato Grosso do Sul, Brasil. Acta Botanica Brasilica 23: 535–548.

Bicudo, C. E. M. & M. Menezes, 2005. Gêneros de algas de águas continentais do Brasil: chave para identificação e descrições. Rima, Brasil.

Borba, C. S., R. Fugi, A. A. Agostinho & G. C. Novakowski, 2008. Dieta de *Astyanax asuncionensis* (Characiformes, Characidae), em riachos da bacia do rio Cuiabá, Estado do Mato Grosso. Acta Scientiarum Biological Sciences 30: 39–45.

Brasil, 2012. Ministério do Meio Ambiente. Conselho Nacional do Meio Ambiente. In Resolução 357. Brasília, IBAMA.

Britski, H. A., K. Z. S. Silimon & B. S. Lopes, 2007. Peixes do Pantanal: manual de identificação, 2nd ed. EMBRAPA, Brasil.

Cáceres, M. D., 2013. How to use the indicspecies package. http://cran.r-project.org/packages=indicspecies.

Casatti, L., R. M. Romero, F. B. Teresa, J. Sabino & F. Langeani, 2010. Fish community structure along a conservation gradient in Bodoquena Plateau streams, Central West of Brazil. Acta Limnologica Brasiliensia 22: 50–59.

Castro, R. M. C., L. Casatti, H. F. Santos, A. L. A. Melo, L. S. F. Martins, K. M. Ferreira, F. Z. Gibran, R. C. Benine, M. Carvalho, A. C. Ribeiro, T. X. Abreu, F. A. Bockmann, G. Z. Pelição, R. Stopiglia & F. Langeani, 2004. Estrutura e composição da ictiofauna de riachos da bacia do Rio Grande no estado de São Paulo, sudeste do Brasil. Biota Neotropica 4: 01–39.

Cordeiro, L. M., R. Borghezan & E. Trajano, 2014. Subterranean biodiversity in the Serra da Bodoquena karst area, Paraguay River basin, Mato Grosso do Sul, Southwestern Brazil. Biota Neotropica 14: 1–28.

Corman, J. R., E. K. Moody & J. J. Elser, 2016. Calcium carbonate deposition drives nutrient cycling in a calcareous headwater stream. Ecological Monographs 86: 448–461.

Correa, S. B. & K. Winemiller, 2018. Terrestrial–aquatic trophic linkages support fish production in a tropical oligotrophic river. Oecologia 189: 1069–1078.

Corrêa, E. C., F. O. Roque, R. M. Utz, J. S. Correa, F. L. Souza & A. P. Covich, 2018. Effects of macroconsumers on benthic communities: rapid increases in dry-season accrual of calcium in a tropical karst stream. PLoS ONE 13: e0209102.

Domínguez, E. & H. Fernández, 2009. Macroinvertebrados bentónicos sudamericanos, sistemática y biología. Tucumán, Argentina.

Drysdale, R. N., 1999. The sedimentological significance of hydropsychid caddis-fly larvae (Order: Trichoptera) in a travertine-depositing stream: Louie Creek, Northwest Queensland, Australia. Journal of Sedimentary Research 69: 145–150.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. Prieur-Richard, D. Soto, M. L. J. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81: 163–182.

Dufrêne, M. & P. Legendre, 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen & D. A. Wardle, 2011. Trophic downgrading of planet Earth. Science 333: 301–306.

Fairchild, M. P. & J. R. Holomuzki, 2005. Multiple predator effects on microdistributions, survival, and drift of stream hydropsychid caddisflies. Journal of the North American Benthological Society 24: 101–112.

Flecker, A. S., 1992. Fish predation and the evolution of invertebrate drift periodicity: evidence from Neotropical streams. Ecology 2: 438–448.

Flecker, A. S., 1996. Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology 77: 1845–1854.

Flecker, A. S. & J. D. Allan, 1984. The importance of predation, substrate and spatial refugia in determining lotic insect distributions. Oecologia 64: 306–313.

Flecker, A. S. & B. Feifarek, 1994. Disturbance and the temporal variability of invertebrate assemblages in two Andean streams. Freshwater Biology 31: 131–142.

Flecker, A. S., B. W. Taylor, E. S. Bernhardt, J. M. Hood, W. K. Cornwell, S. R. Cassatt, M. J. Vanni & N. S. Altman, 2002. Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. Ecology 83: 1831–1844.

Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman & D. P. M. Zaks, 2011. Solutions for a cultivated planet. Nature 478: 337–342.

Garcia, E. A., S. A. Townsend & M. M. Douglas, 2015. Context dependency of top-down and bottom-up effects in a Northern Australian tropical river. Freshwater Science 34: 679–690.

Graciolli, G., M. A. Azevedo & F. A. G. Melo, 2010. Comparative study of the diet of Glandulocaudinae and Tetragonopterinae (Ostariophysi: Characidae) in a small stream in Southern Brazil. Studies on Neotropical Fauna and Environment 38: 95–103.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D. X. Song & J. R. Townshend, 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1: e1500052.

Hagen, M., W. D. Kissling, C. Rasmussen, M. A. M. De Aguiar, L. E. Brown, D. W. Carstensen, I. A. Dos Santos, Y. L. Dupont, F. K. Edwards, J. Genini, P. R. Guimarães Jr., G. B. Jenkins, P. Jordano, C. N. Kaiser-Bunbury, M. E. Ledger, K. P. Maia, F. M. D. Marquitti, Ó. Mclaughlin, L. P. C. Morellato, E. J. O'Gorman, K. Trøjelsgaard, J. M. Tylianakis, M. M. Vidal, G. Woodward & J. M. Olesen, 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Advances in Ecological Research 46: 89–210.

Hamada, N., J. L. Nessimian & R. B. Querino, 2014. Insetos aquáticos na Amazônia brazileira: taxonomia, biologia ecologia. INPA, Manaus.

Henley, W. F., M. A. Patterson, R. J. Neves & A. D. Lemly, 2000. Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. Reviews in Fisheries Science 8: 125–139.

Hillebrand, H. & M. Kahlert, 2001. Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. Limnology and Oceanography 46: 1881–1898.

Ho, B. S. K. & D. Dudgeon, 2015. Are high densities of fishes and shrimp associated with top-down control of tropical benthic communities? A test in three Hong Kong streams. Freshwater Biology 61: 57–68.

Kresic, N., 2013. Water in karst: management, vulnerability, and restoration. McGraw-Hill, New York.

Kutznetsova, A., P. B. Brockhoff & R. H. Bojesen, 2018. Tests in linear mixed effects models (package lmerTest). https://cran.r-project.org/web/packages/lmerTest/index.html.

Landeiro, V. L., N. Hamada & A. S. Melo, 2008. Responses of aquatic invertebrate assemblages and leaf breakdown to macroconsumer exclusion in Amazonian "terra firme" streams. Fundamental and Applied Limnology/Archiv Für Hydrobiologie 172: 49–58.

Laurance, W. F., J. Sayer & K. G. Cassman, 2014. Agricultural expansion and its impacts on tropical nature. Trends in Ecology & Evolution 29: 107–116.

Leibold, M. A., 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. The American Naturalist 134: 922–949.

Lourenço-Amorim, C., V. Neres-Lima, T. P. Moulton, C. Y. Sasada-Sato, P. Oliveira-Cunha & E. Zandonà, 2014. Control of periphyton standing crop in an Atlantic Forest stream: the relative roles of nutrients, grazers and predators. Freshwater Biology 59: 2365–2373.

Mantel, S. K. & D. Dudgeon, 2004. Growth and production of a tropical predatory shrimp, *Macrobrachium hainanense* (Palaemonidae), in two Hong Kong streams. Freshwater Biology 49: 1320–1336.

March, J. G., J. P. Benstead, C. M. Pringle & M. W. Ruebel, 2001. Linking shrimp assemblages with rates of detrital processing along an elevational gradient in a tropical stream. Canadian Journal of Fisheries and Aquatic Sciences 58: 470–478.

Marshall, M. C., A. J. Binderup, E. Zandonà, S. Goutte, R. D. Bassar, R. W. El-Sabaawi, S. A. Thomas, A. S. Flecker, S. S. Kilham, D. N. Reznick & C. M. Pringle, 2012. Effects of consumer interactions on benthic resources and ecosystem processes in a Neotropical stream. PLOS ONE 7: e45230.

McIntosh, A. R. & C. R. Townsend, 1995. Impacts of an introduced predatory fish on mayfly grazing in New Zealand streams. Limnology and Oceanography 40: 1508–1512.

McIntosh, A. R. & C. R. Townsend, 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? Oecologia 108: 174–181.

Moulton, T. P., M. L. Souza, R. M. L. Silveira & F. A. M. Krsulović, 2004. Effects of ephemeropterans and shrimps on periphyton and sediments in a coastal stream (Atlantic forest, Rio de Janeiro, Brazil). Journal of the North American Benthological Society 23: 868–881.

Moulton, T. P., S. A. P. Magalhães-Fraga, E. F. Brito & F. A. Barbosa, 2010. Macroconsumers are more important than specialist macroinvertebrate shredders in leaf processing in urban forest streams of Rio de Janeiro, Brazil. Hydrobiologia 638: 55–66.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. Fonseca & J. Kent, 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nessimian, J. L., E. M. Venticinque, J. Zuanon, P. D. Marco, M. Gordo, L. Fidelis, J. D. Batista & L. Juen, 2008. Land use, habitat integrity, and aquatic insect assemblages in Central Amazonian streams. Hydrobiologia 614: 117.

Nusch, E. A., 1980. Comparison of different methods for chlorophyll and pheopigment determination. Archives of Hydrobiology Bulletin (Ergebnisse der Limnologie) 14: 14–36.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs & H. Wagner, 2017. Community ecology package. https://cran.r-project.org, https://github.com/vegandevs/vegan.

Omernik, J. M. & R. G. Bailey, 1997. Distinguishing between watersheds and ecoregions. Journal of the American Water Resources Association 33: 935–949.

Pace, M. L., J. J. Cole, S. R. Carpenter & J. F. Kitchell, 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14: 483–488.

Paine, R. T., 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49: 667–685.

Paprocki, H., R. W. Holzenthal & C. Cressa, 2003. A new species of *Smicridea* McLachlan (Trichoptera: Hydropsychidae) from Venezuela and its role in travertine biogenesis. Journal of the North American Benthological Society 22: 401–409.

Paul, M. J. & J. L. Meyer, 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32: 333–365.

Peckarsky, B. L., A. R. McIntosh, M. Alvarez & J. M. Moslemi, 2013. Nutrient limitation controls the strength of behavioral trophic cascades in high elevation streams. Ecosphere 4: 110.

Petersen, R. C., 1992. The RCE: a Riparian, channel, and environmental inventory for small streams in the agricultural landscape. Freshwater Biology 27: 295–306.

Polis, G. A. & D. R. Strong, 1996. Food web complexity and community dynamics. The American Naturalist 147: 813–846.

Power, M. E., 1992. Top-down and bottom-up forces in food webs: do plants have primacy. Ecology 73: 733–746.

Power, M. E., W. J. Matthews & A. J. Stewart, 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66: 1448–1456.

Power, M. E., M. S. Parker & W. E. Dietrich, 2008. Seasonal reassembly of a river foods, droughts, and impacts of fish. Ecological Monographs 78: 263–282.

Pringle, C. M. & G. A. Blake, 1994. Quantitative effects of Aytid shrimp (Decapoda: Atyidae) on the depositional environment in a tropical stream: Use of electricity for experimental exclusion. Canadian Journal of Fisheries and Aquatic Sciences 51: 1443–1450.

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

R Core Team, 2015. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna.

Reys, P., J. Sabino & M. Galetti, 2009. Frugivory by the fish *Brycon hilarii* (Characidae) in western Brazil. Acta Oecologica 35: 136–141.

Reznick, D., M. J. Butler, I. V. H. Rodd & A. E. D. Schluter, 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. The American Naturalist 157: 126–140.

Rodrigues, M. E., F. O. Roque, J. M. O. Quintero, J. C. C. Pena, D. C. Sousa & P. M. Junior, 2016. Nonlinear responses in damselfly community along a gradient of habitat loss in a Savanna landscape. Biological Conservation 194: 113–120.

Roque, F. O., J. Ochoa-Quintero, D. B. Ribeiro, L. S. M. Sugai, R. Costa-Pereira, R. Lourival & G. Bino, 2016. Upland habitat loss as a threat to Pantanal wetlands. Conservation Biology 30: 1131–1134.

Roque, F. O., E. C. Corrêa, F. Valente-Neto, G. Stefan, G. Schulz, P. R. B. Souza, C. M. Motta, L. L. O. Bavutti, E. Colzani, M. F. Demétrio, S. C. Escarpinati, R. Silvestre, F. Z. Vaz-de-Mello, T. Siqueira & J. M. O. Quintero, 2017. Idiosyncratic responses of aquatic and terrestrial insects to different levels of environmental integrity in riparian zones in a karst tropical dry forest region. Austral Entomology 56: 459–465.

Rosemond, A. D., C. M. Pringle & A. Ramírez, 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. Freshwater Biology 39: 515–523.

Rosenfeld, J., 2000. Effects of fish predation in erosional and depositional habitats in a temperate stream. Canadian Journal of Fisheries and Aquatic Sciences 57: 1369–1379.

Sabino, J. & E. Trajano, 1997. A new species of blind armoured catfish, genus *Ancistrus*, from caves of Bodoquena region, Mato Grosso do Sul, southwestern Brazil. Revue Française d'Aquariologie 24: 73–78.

Sallun Filho, W. & I. Karmann, 2007. Geomorphological map of the Serra da Bodoquena karst, west-central Brazil. Journal of Maps 3: 282–295.

Schneider, J., S. Worischka, C. Hellmann, J. Benndorf & C. Winkelmann, 2014. Flexibility in feeding periodicity of a grazing mayfly in response to different concentrations of benthivorous fish. Limnologica: Ecology and Management of Inland Waters 45: 24–32.

Schofield, K. A., C. M. Pringle & J. L. Meyer, 2004. Effects of increased bedload on algal and detrital-based stream food webs: experimental manipulation of sediment and macroconsumers. Limnology and Oceanography 49: 900–909.

Schofield, K. A., C. M. Pringle, J. L. Meyer & E. Rosi-Marshall, 2008. Functional redundancy of stream macroconsumers despite differences in catchment land use. Freshwater Biology 53: 2587–2599.

Souza, M. L., T. P. Moulton, R. M. L. Silveira, F. A. M. Krsulovic & E. F. Brito, 2007. Responses of Chironomidae

(Diptera; Insecta) to the exclusion of shrimps and Ephemeroptera in a coastal forest stream, Rio de Janeiro, Brazil. Brazilian Journal of Biology 67: 47–51.

Sutherland, A. B., J. L. Meyer & E. P. Gardiner, 2002. Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. Freshwater Biology 47: 1791–1805.

Utz, R. M., M. R. Fitzgerald, K. J. Goodman, S. M. Parker, H. Powell & C. L. Roehm, 2013. The national ecological observatory network: an observatory poised to expand spatiotemporal scales of inquiry in aquatic and fisheries science. Fisheries 38: 26–35.

Utz, R. M., S. D. Cooper, K. B. Gido & J. R. Stewart, 2017. Exclusion of fish and invertebrates from benthic patches of artificial aquatic environments across water conductivity levels using high-frequency (10 Hz) pulses and adjustable electrical settings. Freshwater Science 36: 151–161.

Valente-Neto, F., F. O. Roque, M. E. Rodrigues, L. Juen & C. M. Swan, 2016. Toward a practical use of Neotropical odonates as bioindicators: testing congruence across taxonomic resolution and life stages. Ecological Indicators 61: 952–959.

Valente-Neto, F., M. E. Rodrigues & F. O. Roque, 2018. Selecting indicators based on biodiversity surrogacy and environmental response in a riverine network: bringing operationality to biomonitoring. Ecological Indicators 94: 198–206.

Van Beynen, P. & K. Townsend, 2005. A disturbance index for karst environments. Environmental Management 36: 101–116.

Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. Nature 467: 555–561.

Walser, C. A. & H. L. Bart, 1999. Influence of agriculture on in-stream habitat and fish community structure in Piedmont watersheds of the Chattahoochee River System. Ecology Freshwater Fish 8: 237–246.

Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman & R. P. Morgan, 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24: 706–723.

Wellnitz, T. A. & J. V. Ward, 1998. Does light intensity modify the effect mayfly grazers have on periphyton? Freshwater Biology 39: 135–149.

Williams, L. R., C. M. Taylor & M. L. Warren, 2003. Influence of fish predation on assemblage structure of macroinvertebrates in an intermittent stream. Transactions of the American Fisheries Society 132: 120–130.

Wilson, M. C., X. Y. Chen, R. T. Corlett, R. K. Didham, P. Ding, R. D. Holt, M. Holyoak, G. Hu, A. C. Hughes, L. Jiang, W. F. Laurance, J. Liu, S. L. Pimm, S. K. Robinson, S. E. Russo, X. Si, D. S. Wilcove, J. Wu & M. Yu, 2016. Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology 31: 219–227.

Winemiller, K. O., A. A. Agostinho & P. Caramaschi, 2008. Fish ecology in tropical streams. Academic Press, London.

Yang, G. Y., T. Tang & D. Dudgeon, 2009. Spatial and seasonal variations in benthic algal assemblages in streams in monsoonal Hong Kong. Hydrobiologia 632: 189–200.