Original Research Article

Macro-scale (biomes) differences in neotropical stream processes and community structure

Maria João Feio [a, *], Gustavo FM. Leite [b], Renan S. Rezende [c],
Adriana O. Medeiros [d], Lorena C. Cruz [d], Juliana AS. Dahora [d], Adolfo Calor [e],
Vinicius Neres-Lima [f], Monalisa Silva-Araújo [f], Marcos Callisto [g],
Juliana França [g], Isabela Martins [g], Marcelo S. Moretti [h], Juliana V. Rangel [h],
Maurício M. Petrucio [i], Aurea L. Lemes-Silva [i], Renato T. Martins [j],
Karina Dias-Silva [k], Galileu PS. Dantas [l], Yara Moretto [m], José F. Gonçalves Jr. [b]

[a] MARE – Centro Do Mar e Ambiente, Departamento de Ciências da Vida, Faculdade de Ciências e Tecnologia, Universidade de Coimbra, Portugal
[b] Aquariparia/Laboratorio de Limnologia, Departamento de Ecologia, Universidade de Brasília, Distrito Federal, Brazil
[c] Programa de Pós-graduação Em Ciências Ambientais, Universidade Comunitária da Região de Chapecó, Chapecó, Brazil
[d] Laboratório de Microbiologia Ambiental, Instituto de Biologia, Universidade Federal da Bahia, Brazil
[e] Laboratório de Taxonomia de Insetos Aquáticos, Instituto de Biologia, Universidade Federal da Bahia, Brazil
[f] Departamento de Ecologia, Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, Brazil
[g] Laboratório de Ecologia de Bentos, Departamento de Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil
[h] Laboratório de Ecologia de Insetos Aquáticos, Universidade Vila Velha, Espírito Santo, Brazil
[i] Progama de Pós-graduação em Ecologia, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil
[j] Programa de Pós-Graduação Em Ecologia e Evolução, Universidade Federal de Goiás, Goiânia, Brazil
[k] Faculdade de Ciências Biológicas, Campus Altamira, Universidade Federal do Pará, Brazil
[l] Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
[m] Universidade Federal Do Paraná - Setor, Departamento de Biodiversidade, Programa de Pós-graduação em Aquicultura e Desenvolvimento Sustentável, Palotina, Brazil

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ABSTRACT

The definition of conservation strategies and ecological assessment schemes requires understanding ecosystem patterns over multiple spatial scales. This study aimed to determine if macro-scale structural and functional (processes) patterns associated with stream ecosystems differed among three neotropical biomes (Cerrado, Amazon, Atlantic Forest). We compared the aquatic communities (benthic invertebrates and hyphomycetes) and processes (decomposition rates, primary production and biofilms growth and aquatic hyphomycetes reproduction rates-sporulation) of Cerrado stream sites (neotropical savannah) against those of stream sites in the connecting biomes of the Atlantic Forest and Amazon (rainforests). We expected that, contrary to the biome dependency hypothesis the community structure and processes rates of streams at the biome-scale would not differ significantly, because those ecosystems are strongly influenced by their dense riparian forests, which have a transitional character among the three biomes. Fifty-three stream sites were selected covering a wide range of geographic locations (Table 1), from near the Equator (2° S) in the Amazon, to intermediate latitudes in the Cerrado (12-19° S), and latitudes closer to the tropic of Capricorn in the Atlantic Forest (19°-25° S). We found that:

* Corresponding author.
  E-mail address: mjf@ci.uc.pt (M.J. Feio).

1) at the abiotic level, the aquatic ecosystems of the three biomes differed, which was mostly explained by large-scale factors such as temperature, precipitation and altitude; 2) functional and structural variables did not behave similarly among biomes: decomposition and sporulation rates showed larger differences among biomes than invertebrate and aquatic hyphomycete assemblages structure; 3) invertebrate assemblages structure differed between the rainforests and Cerrado but not between rainforests (Amazon and Atlantic Forest) whereas aquatic hyphomycetes were similar among all biomes; 4) biofilm growth and algae concentration in biofilms of artificial substrates were highly variable within biomes and not significantly different between biomes. Overall, aquatic ecosystem processes and community structure differed across biomes, being influenced by climatic variables, but the variation is not as pronounced as that described for terrestrial systems. Considering the potential use of these functional and structural indicators in national-wide ecological assessments, our results indicate the need to define different reference values for different biomes, depending on the variable used. The approach followed in this study allowed an integrative analysis and comparison of the stream ecosystems across three tropical biomes, being the first study of this kind. Future studies should try to confirm the patterns evidenced here with more sites from other areas of the three biomes, and especially from the Amazon, which was the least represented biome in our investigation.

1. Introduction

Large-scale studies across biomes provide important insights on natural variations of ecosystems (Boyero et al., 2011; 2012). Understanding their spatial patterns is essential for the definition of reference conditions, the basis of modern ecological assessment schemes and effective conservation strategies (Hughes et al., 1986; Rouget et al., 2006; Hawkins et al., 2010; Feio et al., 2014). Biomes are one of the large spatial-scale divisions of nature, which are classified by their predominant vegetation and additionally by their climatic or geographical characteristics, such as equatorial, tropical or boreal (Woodward et al., 2004). Compared to terrestrial environments, little research has focused on aquatic biomes and their biological patterns. Earlier studies defended the biome dependency theory (high similarity in sites within or among drainage basins of a single biome) by aquatic invertebrates (Ross, 1963; Corkum, 1991, 1992), associating this with the strong link between them and the terrestrial vegetation. In 1983, Minshall et al. investigated longitudinal and inter-biome differences in benthic organic matter, transported organic matter, community production and respiration and functional feeding groups, in rivers of North America. More recently, others explored functional aspects across biomes, such as stream' metabolism (Mulholland et al., 2001) or nitrogen uptake (Webster et al., 2003) in North America biomes.

Headwater streams can be considered meta-ecosystems composed of riparian and aquatic ecosystems, with obvious links between the structural and functional components (Gregory et al., 1991; Loreau et al., 2003; Gounand et al., 2017). These links occur via the process of decomposition of allochthonous organic matter, mainly in the form of leaves from the riparian vegetation that fall in the water and are a direct source of energy for the invertebrates, aquatic fungi and bacteria (Vannote et al., 1980; Graça et al., 2015). At the same time, primary production is usually reduced in these systems because of light limitation (Vannote et al., 1980; Danger et al., 2013). These processes have been widely studied in temperate streams, where headwater streams are called detritus-based ecosystems (Moore et al., 2004; Richardson and Danehy, 2007; Danger et al., 2013) and more recently also in tropical systems (e.g., Rezende et al., 2017a; Neres-Lima et al., 2016, 2017; Linares et al., 2018). Yet, the great diversity of vascular plants and their characteristics (e.g., leaf toughness, phenolic content) in tropical systems leads to a high variability in breakdown rates with recalcitrant species taking over a year to decompose while others decompose in few days (Wantzen et al., 2008; Graça et al., 2015; Rezende et al., 2017b). The relative importance of invertebrates and fungi in leaf decomposition also varies greatly within studies in the tropics, showing both low and high abundances of shredders and a more or less importance of microbial decomposition than by invertebrates (Alvim et al., 2014a,b, Graça et al., 2015, Sales et al., 2015, Neres-Lima et al., 2016). In addition, some studies found that autochthonous sources such as algae constitute an alternative relevant source of energy to tropical consumers, contrary to temperate models (Brito et al., 2006; Wantzen et al., 2008; Lau et al., 2009; Dudgeon et al., 2010; Neres-Lima et al., 2016).

Studying simultaneously the structural and functional components of these aquatic ecosystems can contribute to clarify these aspects, while providing useful insights to the construction of integrative ecological assessment schemes for streams. Despite recommendations (e.g., European Commission, 2000; Gessner and Chauvet, 2002; Young and Collier, 2009; Feio et al., 2010), there currently are no official Brazilian monitoring programs assessing the structural and functional components. In Brazil, the biological monitoring of freshwaters mandated in laws (e.g., CONAMA, 2005; COPAM/CERH-MG, 2008) and structural biological methods have been developed for fish, invertebrates, algae, or cyanobacteria (e.g., Melo et al., 2015; Macedo et al., 2016; Carvalho et al., 2017; Silva et al., 2017). Yet, functional approaches are also not officially used.

One of the predominant biomes in Brazil is the Cerrado, a neotropical savannah that covers most of the centre of the country and houses three of the largest catchments in South America (Strassburg et al., 2017). It is characterized by a dry

season between May and September and the vegetation is adapted to the periodic lack of water, with scattered trees and shrubs, small palms, and a ground layer of grasses (Quesada et al., 2008). The Atlantic Forest biome, composed of always-green dense forests, covers a large section of the Brazilian coast, but differently from the Cerrado, the high precipitation is distributed throughout the entire year (Joly et al., 2014). The Amazon, the largest biome of Brazil, covers ca. 40% of the country, and has permanently high humidity. This biome is highly diverse (Cheng et al., 2013; Castello and Macedo, 2016) and provides essential ecosystem services to the world (Fearnside, 2005).

In Cerrado watersheds, in spite of the surrounding sparse and low vegetation, most streams are enclosed by dense riparian forests, 50−200 m wide and with high plant diversity (Nóbrega et al., 2017). This vegetation has transitional characteristics between the Amazon forest, Atlantic forest, Pantanal and Caatinga (Silva Júnior, 2004; Felfili and Silva Júnior 2005; Bambi et al., 2017) leading to similarities in riparian vegetation structure and composition among those biomes. Mean annual temperatures, a factor known to affect litter decomposition rates, aquatic communities (e.g, Ferreira and Chauvet, 2011; Martínez et al., 2017) and primary production (Rasmunssen et al., 2011), are also similar among those biomes (Woodward et al., 2004).

In view of this, we expected that, contrary to the biome dependency hypothesis (Ross, 1963; Corkum, 1991, 1992), the structure and processes of least-disturbed small stream sites would not differ significantly among Cerrado, Amazon and Atlantic Forest biomes. To test this, we compared biological structural and functional patterns of Cerrado stream sites to those of Amazon and Atlantic Forest. We selected ecosystem variables that are also potential indicators of stream quality (Feio et al., 2010): benthic invertebrate and aquatic hyphomycete assemblage structure; as well as decomposition rates, biofilm primary production (Chla), biofilm growth, and aquatic hypomycete sporulation rate.

2. Methods

2.1. Study areas

We considered three Brazilian tropical biomes (Fig. 1): the Cerrado, Atlantic Forest and Amazon. The Cerrado biome has a typical Aw climate (humid tropical savannah) with two well-defined seasons: dry from May to September, and wet from October to April when 80% of the precipitation falls (Hunke et al., 2015). In the wet season, the average temperature is 22 (±1)ºC, rainfall of 197 ± 60 mm/month, with peaks between January and March. In the dry season, the average temperature is 20 (±1)ºC and rainfall of 2 ± 3 mm/month. Scattered trees and shrubs, small palms, and a ground layer of grasses characterize the area. The rainfall variability strongly influences the composition of vegetation, with grasses remaining dead or dormant during the dry season until the next wet season (Quesada et al., 2008). The Cerrado is a world biodiversity hotspot (Myers et al., 2000) because of the high level of endemism but is also one of worlds' most threatened biomes, because of the rapid deforestation since the 1980s (double than that in the Amazon, between 2008 and 2010) and replacement of natural vegetation with pasture and row crop agriculture, such as soybean, maize, cotton and sugarcane (Lambin et al., 2013; Redo et al., 2012; Hunke et al., 2015). Part of the study sites are located in an area of Chapada Diamantina mountain, which is located inside the large area of bioma Caatinga but is can considered an enclave of Cerrado due to its ecological characteristics, specially near the streams (Sales et al., 2015). The Atlantic Forest, according to Joly et al. (2014), is a continuum of tree species distributions composed of five main types of forest: dense ombrophilous, open ombrophilous, mixed ombrophilous, semi-deciduous seasonal and deciduous seasonal. The study sites are representative of dense ombrophilous forest and the Köoppen−Geiger climate classification includes: Af (tropical rainforest) in the states of Espírito Santo and Rio de Janeiro (mean annual temperatures of 23.2 °C and average annual precipitation of 1791 mm; Neres-Lima et al., 2016); and Cfa (humid subtropical; mean annual precipitation of 20.1 °C, average precipitation of 1462 mm) in the states of Santa Catarina and Paraná with high rainfall distributed evenly throughout the year. The always-green dense forest occurs in the tropical rainforest without a biologically dry period throughout the year and exceptionally with two months of scarce humidity (Colombo and Joly, 2010). The dense vegetation consists of tree species, shrubs, lianas, epiphytes and herbaceous species (Lisboa et al., 2015). This biome is one of 34 world hotspots for biodiversity being a priority for conservation (Ribeiro et al., 2009). Yet, currently, 11.4−16% of the original forest cover is made up of small fragments (<50 ha) with a high degree of isolation (Myers et al., 2000; Ribeiro et al., 2009). The climate can be classified as Af, Am or Aw (Peel et al., 2007). Specifically, in the Ducke Reserve, where study sites are located, the climate is Afi (tropical humid equatorial), with rainy (November−May) and dry (June−October) seasons. The mean annual precipitation is 2286 mm, and mean annual temperature is 26.7 °C (Mendonça et al., 2005). The mean monthly temperature is always greater than 18 °C (Lopes et al., 2014). The dominant vegetation in Duke reserve is of the type *terra firme*, which covers most of the Amazon region (65%) and is characterized by high richness and diversity of species (Silva et al., 2016). Only in the 10000 ha of Ducke reserve, ~1200 tree species were recorded (Costa et al., 2008). The Amazon aquatic systems have been highly altered by deforestation and construction of dams, and this region has suffered from increased droughts in recent decades because of climate change amplified by changes in land use (Malhi et al., 2008; Castello and Macedo, 2016).

2.2. Study sites

Fifty-three stream sites (11 in the Atlantic Forest, 3 in the Amazon and 39 in the biome of Cerrado) were selected for this study conducted in 2015, avoiding periods of high flow (dry season in Cerrado). The sites included in this study were
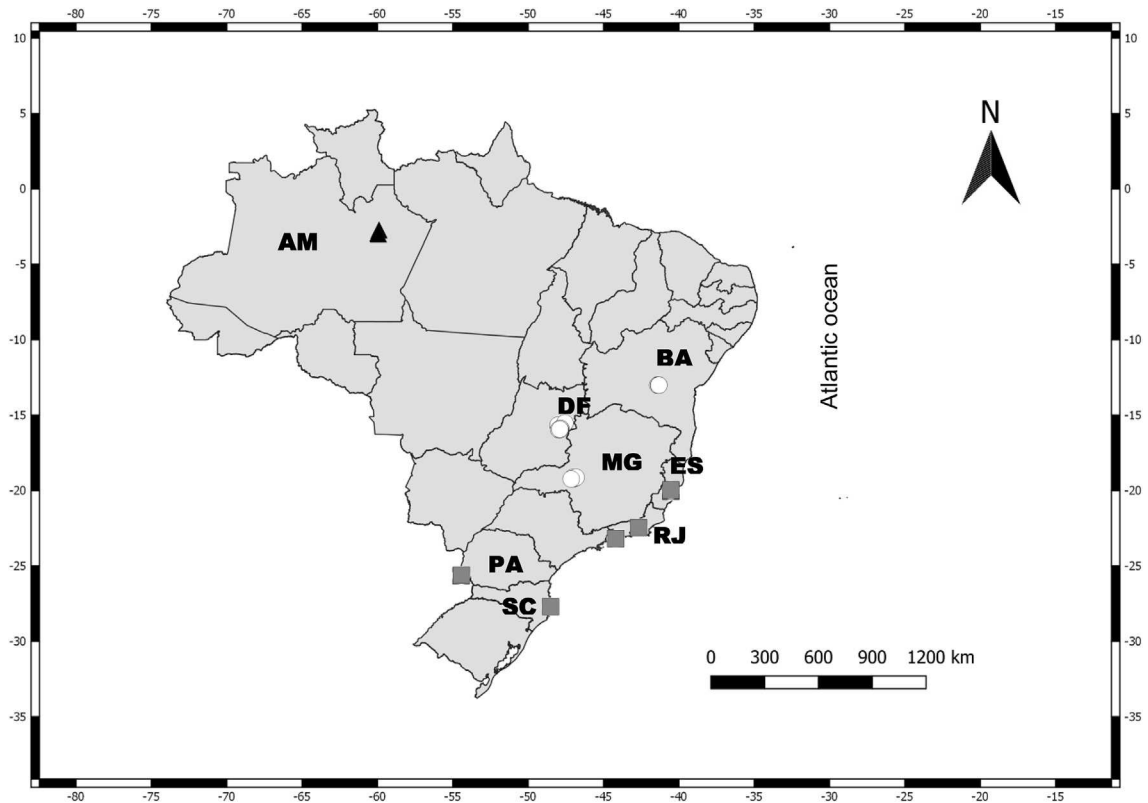
Fig. 1. Localization of the 53 study sites in the Brazil (at this scale many sites are seen superimposed) and their biomes: Cerrado (open circles), Atlantic Forest (grey squares) and Amazonia (black triangles). States where the sites are located are given by the codes AM (Amazon), BA (Bahia), Minas Gerais (MG), DF (Distrito Federal), ES (Espírito Santo), RJ (Rio de Janeiro), PA (Paraná), Santa Catarina (SC).

clearwaters with the exception of the Amazonian blackwater streams. They covered a wide range of geographic locations (Table 1, Fig. 1), from near the Equator (2° S) in the Amazon, to intermediate latitudes in the Cerrado (12-19° S), and latitudes closer to the tropic of Capricorn in the Atlantic Forest (19°-25° S). The site longitudes also vary, with the Atlantic Forest covering longitudes ranging between 40° and 54° W, the Cerrado sites ranging between 46 and 48° W and the Amazon sites at 59° W.

To select least-disturbed streams, all streams were analysed by experts of each region through an a priori classification system, with 8 categorical variables describing alterations in the segment (ca. 500 m, centred at the sampling site) and the site (ca. 50 m). This evaluation of streams was based on visual inspection and pre-existing information and knowledge. At the segment level were evaluated: 1) the natural connectivity (considering the presence of transversal barriers, dams, roads); 2) riparian vegetation (cuts and presence of exotic species); 3) land use (alterations to natural vegetation); 4) urban area (impervious surfaces and construction); and 5) the sediment load (related into turbidity). At the site level, the aspects evaluated were: 6) the morphology (instream habitats and modifications in the channel and margins); 7) toxic acidification of the water (alteration of pH or oxygenation); and 8) nutrients and organic contamination (adapted from Pont et al., 2006; Feio et al., 2009). One of 5 qualitative classes were attributed to each variable: 1 = no evidence of degradation/no alteration from natural condition; 2 = slight degradation (with no reflex on the aquatic communities); 3 = moderate degradation; 4 = evident degradation; 5 = strong degradation. The least-disturbed sites selected were those classified with only class 1 or 2 for all variables.

2.3. Abiotic characterization of sites

All streams were characterized using abiotic variables that could be related to ecological large-scale differences, such as biome (Cerrado, Atlantic Forest, Amazon rainforest − hereafter referred as Amazon), geographic location (latitude and longitude), lithology and water pH, climate (mean annual precipitation and air temperature), altitude, size (distance to source, km; stream order, Strahler system, Strahler, 1952; drainage area, km^2) and hydromorphological characteristics (valley form: flat, U or V shape; channel width, m; channel form: naturally contained, meandering) and canopy cover (% shading at zenith). Data was obtained in the field (coordinates, altitude, valley and channel form, canopy cover (% of shadow in the channel), lithology, pH), from Geographical Information Systems (with QGIS software; distance to source, stream order, drainage area)

Table 1

Characterization of the study sites by biome (average ± SD and predominant lithology, valley form and channel form).

Biome	Cerrado (n = 39)	Atlantic Forest (n = 11)	Amazon (n = 3)
Latitude (range)	12º-19ºS	19º-25ºS	2ºS
Longitude (range)	41-48ºW	40º-54ºW	59ºW
Mean annual precipitation (mm)	116 ± 23	897 ± 533	2438 ± 0
Mean annual air temperature (ºC)	23 ± 3	22 ± 3	25 ± 1
Water temperature (ºC)	20 ± 1	20 ± 1	25 ± 1
Stream order (min-max)	1−4	1−3	1
Distance to source (km)	3.5 ± 3.4	1.8 ± 1.0	0.7 ± 0.1
Altitude (m)	1005 ± 89	318 ± 238	79 ± 29
Lithology (dominant; clay = 1,sand = 2, schist = 3; granite = 4)	2.5 ± 0.8	3.0 ± 1.6	2.0 ± 0.0
Valley form (dominant; flat = 1, U shaped = 2, V shaped = 3)	1.5 ± 0.6	2.2 ± 1.1	1.0 ± 0.0
Channel form (dominant; meandering = 1, naturally contained = 2)	1.4 ± 0.5	1.6 ± 0.5	2.0 ± 0.0
Canopy cover (% shading at zenith)	67.2 ± 21.8	90.1 ± 9.8	100 ± 0.0
pH	7.6 ± 1.0	7.2 ± 0.9	4.2 ± 0.0

or local meteorological stations (climate). Table 1 presents the mean values found in the stream sites of each biome and the categories pre-defined for lithology, valley and channel form.

2.4. Functional and structural variables

2.4.1. Decomposition

Balsa-wood slabs were used as standard substrates for the measurement of decomposition in all stream sites. This substrate was successfully used to measure total decomposition in temperate streams (Ferreira et al., 2006; Ferreira and Graça, 2007). As its hardness is comparable or even inferior to tropical leaves this was considered a good standard substrate to measure invertebrates decomposition in the present experiment. The wooden slabs ($11 \times 15 \times 0.1$ cm) were incubated for 60 days in all sites inside litterbags with coarse (1 cm) and fine mesh (0.5 mm) for the measurement of total decomposition (by invertebrates and microorganisms - fungi and bacteria) and microbial decomposition (by microorganisms only), respectively (three replicates for each mesh size). After retrieving the bags from the streams, 5 wooden discs (18 mm Ø) were cut from each bag, dried for 72 h at 60 °C, and weighed (0.0001 g precision). Finally, the circles are ashed for 5 h at 550 °C and ashes were weighed to calculate ash free dry mass (AFDM). Decomposition was calculated based on the difference between the initial AFDM (given by control circles) and AFDM of circles of incubated wood. Decomposition rates were then converted into % of mass loss in 60 days and AFDM/d.

2.4.2. Biofilms growth and primary productivity

Biofilm growth (Gr; mg m^{-2} day^{-1}), and algae productivity (given by the concentration of Chlorophyll a - Chla; mg m^{-2}) were measured from biofilms grown on artificial substrates. Acetate sheets (20×15 cm) were used as substrates. The acetate sheets were submerged in streams for 60 days, tied to nylon lines. After retrieval, one circle (Ø4cm) was scraped from each sheet and the content transferred to a preweighed aluminum cap, dried at 60 °C for 72 h and weighed (dry mass). The biofilm was then ashed at 550 °C for 1 h and reweighed to calculate the AFDM. Growth rate (A.P.H.A., 1995) was calculated as: Gr = mean biofilm AFDM ca^{-1}t^{-1}; where ca is the area of the circle scraped (m^{-2}) and t is the number of incubation days. Another identical circle from each sheet was used to measure Chla on the biofilm. The second circle was scraped into a solution of ethanol (90%), absorbance was measured using a spectrophotometer, and the Chl a concentration calculated according to A.P.H.A. (1995).

2.4.3. Aquatic hyphomycetes and sporulation rates

Aquatic hyphomycetes associated with the wooden substrate placed in litter bags as well as the sporulation rates were obtained according to the standard methodology established in Barlöcher (2005). A set of 5 discs cut from the wooden substrate, from each fine and coarse mesh litterbags was introduced in Erlenmeyer flasks containing 30 mL of distilled water. The flasks were installed over an orbital shaker (100 rpm) for 48 h at 18 °C, in order to simulate the ideal conditions for sporulation. The suspensions containing the liberated spores were fixed with 4% formalin to avoid the fungal germination. Aliquots of each sample were filtered through a Millipore™ membrane filter (0.45 μm), stained with cotton blue in lactophenol and examined through an optical microscope (400x), for spore counting (sporulation rates expressed as spores/g of AFDM/day) and aquatic hyphomycetes identification to species level using Gulis (2005) and Fiuza et al. (2015, 2017).

2.4.4. Macroinvertebrates

Macroinvertebrates were sampled with a kick net with an opening of 30×30 cm and a mesh size of 0.5 mm. Each sample was composed of 3 sub-samples of 1 m long each, located over a transept covering the existing habitats at the stream site. Samples were washed over a 0.5 mm mesh sieve, sorted and animals preserved in alcohol. All individuals were counted and identified to family using Merritt and Cummins (1996), Cummins et al. (2005), Mugnai et al. (2010), and Hamada et al. (2014).

2.5. Data analyses

2.5.1. Abiotic

Principal Components Analysis (data transformed by log (x+1) and normalized) was used to assess the distribution of study sites across biomes based on Euclidean distance resemblance of multivariate data (Legendre and Legendre, 2012). Significant differences between biomes were assessed by a multivariate PERMANOVA (Permutational Multivariate Analysis of Variance; Euclidean distance; 999 permutations) (Anderson, 2001). The PERMANOVA main outputs are a distance-based pseudo-F value of the test, analogue to the F statistic for multi-factorial ANOVA and a significance p value given by an appropriate permutation procedure for each term (Anderson et al., 2008).

2.5.2. Processes patterns

Functional differences (considering all functional parameters) among biomes were assessed through a multivariate PERMANOVA (main test and pairwise tests), followed by the individual analysis of patterns in total and microbial decomposition, primary productivity, biofilm growth rates and sporulation rates across biomes with univariate PERMANOVA. Data were a priori transformed by log (x+1). A Canonical analysis of principal coordinates, CAP (Euclidean distance) was also performed to find axes through multivariate cloud of points that best discriminate among a priori defined groups and provide a visual distribution of sites (Anderson et al., 2008).

2.5.3. Assemblage structural patterns

Macroinvertebrate abundance data were pre-treated with log (x+1) to down weight the effect of abundant species and potential effects of differences in sampling effort between teams (in spite of common protocols). The hyphomycete assemblages were analysed for only 36 sites (25 Cerrado, 8 Atlantic Forest and 3 Amazon). The counts were transformed to relative abundances (% of species in the total spore production) and no further transformation was applied. Then, the invertebrate and fungi assemblages were compared by a CAP analysis and differences tested by a multivariate PERMANOVA (Bray-Curtis similarity coefficient). In addition, SIMPER - similarities percentage analysis was used to analyse the most contributive species within biomes. Diversity indices were also calculated to compare the number of taxa (S), Margalef richness index (d = (S - 1)/ ln N, where N = number of individuals) and equitability (J′, Pielou's evenness) between biomes.

3. Results

3.1. Abiotic characteristics

The largest differences among the studied sites of the three biomes were in precipitation (lower in Cerrado (115 ± 23 mm) and higher in Amazon (2438 ± 0 mm)); and in altitude (higher in Cerrado (1005 ± 89 m) and near sea level in Amazon (79 ± 29 m)). In addition, Amazon sites were acidic but mostly neutral in other biomes. The dominant site lithology was varied, from clay to granitic. The remaining characteristics were more homogenous: most sites had a dense canopy cover (>60%), small distance to source (<3 km), low stream order (<4), naturally constrained channels, and flat or U shaped valleys.

The Principal Components analysis (Fig. 2) based on abiotic parameters (except coordinates) explained 68.6% of sites variability in the first 3 axes (PC1 = 33.9%, PC2 = 19.2%, PC3 = 15.5%). Biomes are mostly discriminated over PC1, especially by temperature (eigenvector = 0.511) and precipitation (0.485) (being higher in Amazon and Atlantic Forest sites), and by altitude (0.444), (being higher in Cerrado sites). PC2 indicates a division in Cerrado sites by pH (0.654), corresponding to streams located in the state of Bahia, and those of Amazon and a group of Cerrado with a lower pH versus those in Atlantic Forest and remaining Cerrado sites. Flat channel form also distinguished Amazon sites and a group of Cerrado sites from the Atlantic Forest and most Cerrado sites on PC2 (−0.413). Finally, PC3 is better correlated with lithology (0.546) and channel form (0.511).

PERMANOVA confirmed that there are overall differences (Pseudo-F = 11.691, p = 0.001, 998 perm), and among all biomes, considering their abiotic characteristics (Pairwise tests: t = 3.152, p = 0.001, 998 perm: Atlantic Forest vs Cerrado; t = 2.220, p = 0.006, 278 perm: Atlantic Forest vs Amazon; t = 4.090, p = 0.001, 996perm: Cerrado vs Amazon).

3.2. Functional parameters

The overall functional variation (considering all functional parameters) between biomes was analysed based on data of 45 sites (excluding sites with missing data for any of the functional variables). PERMANOVA indicated that biomes were functionally different (Pseudo-F = 11.885, p = 0.001, 999perm). The MDS plot (Fig. 3) and pairwise tests show that these differences mainly resulted from differences between Amazon and Atlantic Forest (t = 4.554, p = 0.005, 164 perm) and between Amazon and Cerrado sites (t = 4.486, p = 0.001, 940 perm), whereas the Atlantic Forest and Cerrado sites were only approached significance (t = 1.682, p = 0.068).

Total decomposition rates were significantly different among all biomes for the 51 sites analysed (Pseudo-F = 10.898, p = 0.001, 998 perm; pairwise tests: t = 4.022, p = 0.011, 283 perm for Amazon vs Atlantic Forest; t = 4.072, p = 0.001, 951 perm for Amazon vs Cerrado; t = 2.114, p = 0.05, 994 perm for Atlantic Forest vs Cerrado). Microbial decomposition varied also among biome sites (Pseudo-F = 7.277, p = 0.003, 998 perm) but was only significantly different between Amazon and
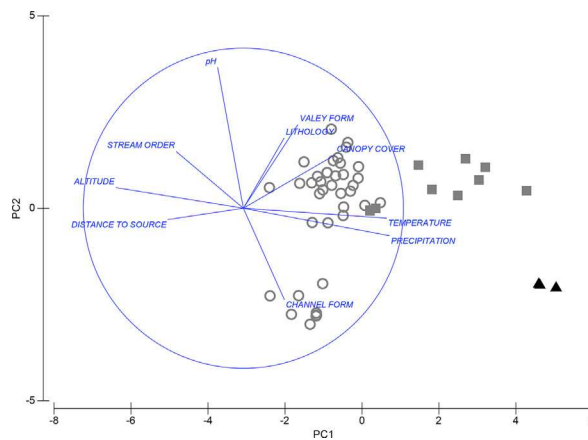
Fig. 2. Principal Components Analysis (data transformed by log x+1 and normalized) based on abiotic characteristics of Cerrado (grey open circles), Atlantic Forest (grey squares) and Amazonia (black triangles) biome sites.

Atlantic Forest (t = 3.258, p = 0.012, 335 perm) and Amazon and Cerrado (t = 3.442, p = 0.001, 953 perm) sites whereas no significant differences were found between the Atlantic Forest and Cerrado (t = 1.619, p = 0.109, 994 perm). Both total decomposition and microbial decomposition were lower in Cerrado sites ($15.1 \pm 12.9\%$ and $13.9 \pm 13.2\%$) and highest in Amazon sites ($47.0 \pm 15.2\%$ mass loss in 60 days, $41.6 \pm 10.1\%$, respectively), with intermediate values in the Atlantic Forest sites ($23.7 \pm 7.0\%$ and $21.5 \pm 9.3\%$) and (Fig. 4A).

The sporulation rates of aquatic hyphomycetes differed significantly between all biomes (Pseudo-F = 38.085, p = 0.001, 999 perm). Pairwise tests confirm differences between Amazon and Atlantic Forest (t = 3.407, p = 0.009, 165 perm), Amazon and Cerrado (t = 7.988 m p = 0.001, 937 perm) and between Cerrado and Atlantic Forest (t = 2.623, p = 0.017, 996 perm) sites. Lowest values were found in Cerrado (0.66 ± 0.57 conidia mgAFDM^{-1} d^{-1}) and Atlantic Forest (1.39 ± 1.23 conidia mgAFDM^{-1} d^{-1}) sites but substantially higher in Amazon sites (63.19 ± 56.79 conidia mgAFDM^{-1} d^{-1}) (Fig. 4B).

However, the parameters associated with biofilms on artificial substrates were not significantly different among biomes (Chla: Pseudo-F = 2.119, p = 0.146, 999 perm; biofilms growth: Pseudo F = 0.320, p = 0.293, 996 perm; 51 sites analysed) (Fig. 4C and D). Yet, the Chla showed a similar pattern of variation as decomposition, with lower values in Cerrado (0.0101 ± 0.0182 mg m^{-2} d^{-1}) and Atlantic Forest (0.0171 ± 0.0315 mg m^{-2} d^{-1}) sites and higher values in Amazon sites (0.0326 ± 0.0368 mg m^{-2} d^{-1}) (Fig. 4C). The biofilm growth rate was highly variable, especially in the Cerrado, where the highest values were reached (Fig. 4D).

3.3. Assemblages

3.3.1. Invertebrates

A total of seventy macroinvertebrate families (Table S1) were identified in the three biomes, with 15 (min) to 27 (max) families/sample (mean 19.3 ± 6.7) in Amazon sites, 5–27 (mean 21.7 ± 5.5) in the Atlantic Forest and 2–36 (13.2 ± 9.1) in Cerrado sites. The SIMPER analysis (Table 2) indicates that Cerrado and the Atlantic rainforest had a comparable within-biome similarity (i.e., similarity between assemblages found in sites of the same biome) regarding the invertebrates (32 and 29%, respectively), while the Amazonian samples were more alike (72%). Yet, the most representative families of the invertebrate assemblages were similar for the three biomes (e.g., Chironomidae, Elmidae, Ceratopogonidae, Leptoceridae, Hydropsychidae). Eight families were only representative of Cerrado sites, but had a low contribution to the within biome similarity (e.g., Calopterygidae, Coenagriodinae, Polycentropodidae and Pyralidae); seven families were representative of the Atlantic rainforest (e.g., Megapodagrionidae, Palaemonidae and Hyalellidae); and four representative of the Amazon rainforest (Palaemonidae, Dytiscidae, Glossossomatidae, Gerridae, and Scirtidae).

Macroinvertebrate assemblages were significantly different among biomes (Pseudo-F = 2.2328, p (perm) = 0.002, 997 perm). Pairwise tests showed that differences were significant between Cerrado and Amazon sites (t = 1.488, p = 0.025, 952 perm) and Cerrado and the Atlantic Forest (t = 1.533, p = 0.018, 998 perm), but only nearly significant between Amazon and Atlantic Forest sites (t = 1.342, p = 0.078, 275 perm). The CAP plot confirms these patterns (Fig. 5). In addition, it is clear that among biomes the geographic proximity (given by the state) is not necessarily associated with assemblages' similarity.

3.3.2. Fungi

Fourteen species of aquatic hyphomycetes were identified in this study (Table S2). The total number of species found in biomes varied between 4 in Amazon rainforest and 12 in Cerrado, with an intermediate value in Atlantic rainforest (9). The SIMPER analysis (Table 3) indicates that Cerrado and the Atlantic rainforest had again a comparable within-biome similarity
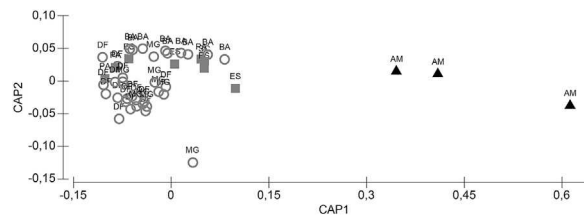
Fig. 3. Canonical analysis of principal coordinates, CAP, based on decomposition rates (total and microbial), primary productivity and growth rate of biofilms, and sporulation rates (log (x+1) transformation) from 45 stream sites located in Cerrado (grey open circles), Atlantic Forest (grey squares) and Amazonia (black triangles) biomes. States where the sites are located are given by the codes AM (Amazon), BA (Bahia), Minas Gerais (MG), DF (Distrito Federal), ES (Espírito Santo), RJ (Rio de Janeiro), PA (Paraná), Santa Catarina (SC).
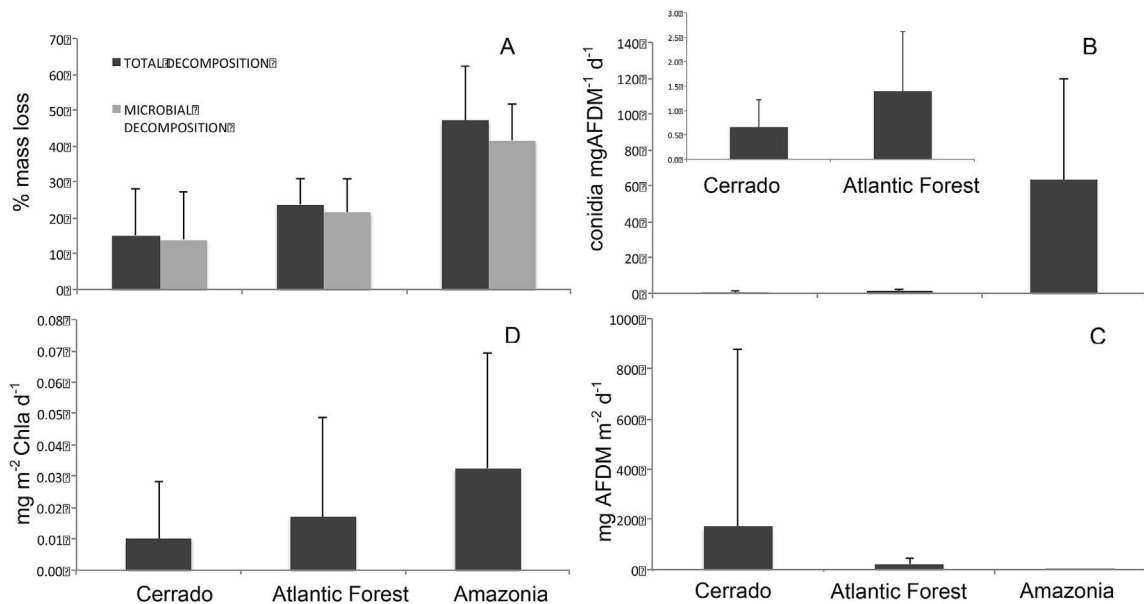

Fig. 4. Mean (and standard deviation) of functional variables for each biome (Cerrado, Atlantic Forest, Amazon): A) % of mass loss for total decomposition and microbial decomposition in 60 days of incubation; B) sporulation rates (number of conidia mg AFDM^{-1} day^{-1}; C) daily biofilm growth rate (mg of AFDM m^{-2} d-1); and D) chlorophyll a (mg m^{-2} d^{-1}) in biofilms.

(38 and 30%, respectively), while the Amazonian samples had a low similarity (12%). The most representative species (Table 3) in all biomes was *Flagellospora curvula* (68%, 60% and 100% of contribution to similarity within Cerrado, Atlantic rainforest and Amazon sites, respectively). Three species were only representative of Cerrado (*Colispora curvata, Anguillospora longissima* and *Helicus lungdunensis*) and two were only representative of the Atlantic rainforest (*Clavariopsis aquatica* and *Anguillospora crassa*).

The aquatic hyphomycete assemblages were globally different for the biomes (PERMANOVA: Pseudo-F: 2.173, p = 0.029, 999 perm). However, pairwise tests showed significant differences only between the Cerrado and Atlantic Forest sites (t = 1.745, p = 0.013, 999 perm) but not between Cerrado and Amazon sites (t = 1.264, p = 0.17, 892 perm) nor Atlantic Forest and Amazon sites (t = 1.091, p = 0.421, 93 perm). The CAP (Fig. 6) shows also the proximity between some sites of Cerrado and Atlantic Forest, and one Amazon site closer to the other biomes. Within the sites of Atlantic Forest and Cerrado, assemblages of the same state (in general geographically closer) are not necessarily more similar to each other than with samples of other states.

4. Discussion

Biomes are usually classified by macroclimate, phytophysiognomy, soils, and altitude (Walter, 1986), but do not incorporate aquatic environments in a meaningful way. Our data confirmed these differences with variables based on climate and stream characteristics. The mean annual air temperatures between 23 °C in Cerrado and 25 °C in Amazon are reflected in water temperatures measured during sampling (between 20 in Cerrado and 25 °C in Amazon) and are in agreement with the classical diagram of Whittaker (1975).

Table 2

Taxa contributing most to the within biome Bray-Curtis similarity (up to 90% cumulative contribution; SIMPER analyses) based on macroinvertebrate assemblage contributive % (presence/absence data).

Cerrado	Atlantic Forest	Amazon
	Aeshnidae (5%)	
Baetidae (2%)		
Calamoceratidae (2%)	Calamoceratidae (7%)	Calamoceratidae (3%)
Ceratopogonidade (4%)	Ceratopogonidade (4%)	Ceratopogonidade (12%)
Chironomidae (41%)	Chironomidae (15%)	Chironomidae (22%)
Elmidae (15%)	Elmidae (28%)	Elmidae (10%)
		Dytiscidae (2%)
	Gomphidae (1%)	
	Helicopsychidae (3%)	Helicopsychidae (5%)
Hydropsychidae (6%)	Hydropsychidae (3%)	Hydropsychidae (3%)
Leptoceridae (3%)	Leptoceridae (15%)	Leptoceridae (7%)
Leptohyphidae (1%)		Leptohyphidae (6%)
Leptophlebiidae (4%)	Leptophlebiidae (3%)	Leptophlebiidae (8%)
Libellulidae (1%)		
	Megapodagrionidae (3%)	
		Odontoceridae (5%)
Perlidae (5%)	Perlidae (3%)	
Polycentropodidae (1%)		
		Palaemonidae (9%)
Simuliidae (4%)		
Tipulidae (2%)		

Abiotic differences were reflected in the global patterns in processes and assemblages of the aquatic ecosystems. These findings are in accordance with the early study on functional ecosystem parameters of Minshall et al. (1983), in temperate North American streams, which found that although the gradual change proposed by the RCC was verified, there variations between biomes due to different regional climate, geomorphological and riparian conditions. Our results are also in accordance with the Stream Biome Gradient Concept (Dodds et al., 2015). This concept proposes that the same factors controlling terrestrial communities (temperature and precipitation) can be assumed to influence stream ecosystems because of their direct influence on hydrology, geomorphology and interactions with terrestrial vegetation.

However, the similarity patterns observed among biomes differed depending on the structural and functional components considered: no significant differences in parameters associated with biofilms (growth rate and primary production); significant differences among all biomes for total decomposition and sporulation rates and partial; and partial for invertebrate and fungi assemblages. These results partially confirm our hypothesis of aquatic differences among terrestrially defined biomes. Some authors have found different patterns between aquatic and terrestrial ecosystems among biomes, for example in litter decomposition, which may be due to the longitudinal character of rivers (not present in land), where water and nutrients move continually downstream (Gessner et al., 2010, García-Palacios et al., 2015). The fact that water travels in watercourses across large areas may contribute to explain these lower differences among aquatic ecosystems. In addition, the transitional character of the riparian vegetation between biomes may be at the same time a consequence and a contribute to the higher similarity in aquatic systems, dependent on terrestrial organic matter and energy inputs (Gonçalves et al., 2014; Rezende et al., 2016, Bambi et al., 2017). This is however an unexplored hypothesis in the literature.

The fact that total decomposition varied among all biomes may be related to the strong association of this aquatic process to the terrestrial systems as most organic material decomposed in streams is originated from the riparian vegetation (Rezende et al., 2016, Bambi et al., 2017). However, the invertebrate assemblages, that take part in the decomposition process, differed only between the Cerrado and the two rainforests but not among the later. This could indicate also a small contribution of invertebrates to the decomposition process of leaf litter in these tropical biomes, as proposed by other authors (Graça et al., 2015; Leite et al., 2016). Likewise, a study in the terrestrial environment of the Atlantic Forest biome found no relationship between invertebrate species richness and litter decomposition rates (Sobrinho et al., 2014). However, it could also be a response of litterfall patterns, and the adaptation of invertebrate assemblages to them (Leite et al., 2016). In fact, a recent study showed a greater and more similar litterfall in the Amazon and Atlantic Forest compared to the Cerrado, corresponding to the precipitation patterns (Tonin et al., 2017). In spite of this, the literature is not as consensual, as for terrestrial environments. White et al. (2013) found a relationship between precipitation and litterfall but not with decomposition rates. Another possibility is the influence of the parameter measured: a recent study showed that it is shredders biomass and not individuals' abundance that is positively correlated with decomposition (Aguiar et al., 2018). This aspect was not assessed here but should be further investigated in across-biome studies.

On the other hand, in our study microbial decomposition differed between the two rainforests (Amazon and Atlantic Forest), which might have compensated for the reduced contribution of invertebrates to decomposition. Nevertheless, no differences were found among biomes in the aquatic hyphomycete assemblages associated with the balsa wood and the most representative species was the same. Yet, sporulation rates of aquatic hyphomycete which are associated with microorganisms metabolism (Suberkropp and Chauvet, 2001; Medeiros et al., 2009; Graça et al., 2015) differed among biomes. This
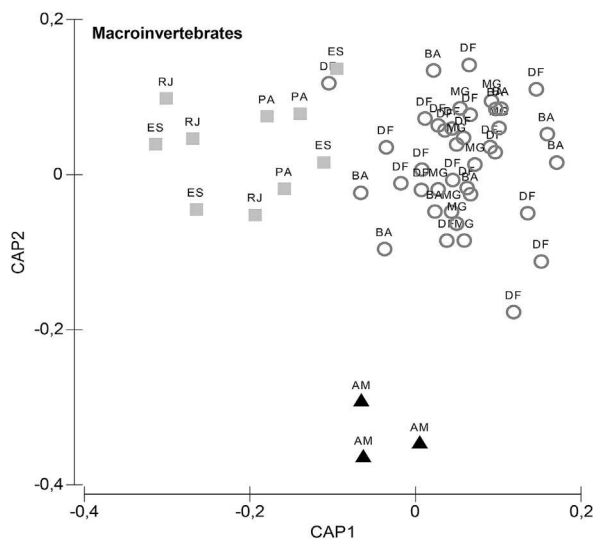
Fig. 5. Canonical analysis of principal coordinates, CAP, of macroinvertebrate assemblages (log (x+1) transformation) in 53 stream sites located in Cerrado (grey open circles), Atlantic Forest (grey squares) and Amazonia (black triangles) biomes. States where the sites are located are given by the codes AM (Amazon), BA (Bahia), Minas Gerais (MG), DF (Distrito Federal), ES (Espírito Santo), RJ (Rio de Janeiro), PA (Paraná), Santa Catarina (SC).

Table 3
Taxa contributing the most to the within biome Bray-Curtis similarity based on aquatic hyphomycetes assemblages (SIMPER analysis).

Cerrado	Atlantic Forest	Amazon
Flagellospora curvula (68%)	*Flagellospora curvula (60%)*	*Flagellospora curvula (100%)*
Lunulospora curvula (27%)	*Clavariopsis aquatica (35%)*	

may indicate that, more than the species it is the activity of fungi that mediates decomposition rates. This activity is known to be dependent on external factors associated to streams' characteristics such as nutrients, oxygen concentrations, temperature, pH, or alkalinity (Suberkropp, 2001; Abdel-Raheem & Shrearer 2002; Medeiros et al., 2009).

Microbial diversity is known to affect decomposition rates (Gessner et al., 2010). Here microbial decomposition contributed with 89% in Amazon, 91% in Atlantic Forest and 92% in Cerrado for total mass loss. This consistent answer in a large-scale study confirms the importance of microbial decomposition in these tropical systems, which is especially interesting since previous studies have been considered contradictory (Graça et al., 2015). In spite of the high proportion of microbial decomposition we observed a relative low diversity of aquatic hyphomycetes in our streams (maximum 12 species). This low diversity is normal in tropical systems, as acknowledge by Graça et al. (2016). For example, a survey in four Cerrado regions obtained 14 taxa (Schoenlein-Crusius, 2002) while a review by Fiuza et al. (2017) indicates the existence of a total of 21 hyphomycete taxa in Cerrado, 19 in Amazon and 53 in the Atlantic Forest, being this last the only biome where the number of fungi is much higher than ours (which could be due to the small number of sites analysed too). Anyway a possible explanation for the higher microbial rates could be existence of other aquatic fungi with a more important role in decomposition than initially thought, as observed in some studies in the tropics (Wong et al., 1998; Bärlocher et al., 2012; Graça et al., 2016).

Recently several authors agreed on the important contribution of algae to the food webs in tropical rivers (e.g., Davies et al., 2008; Neres-Lima et al., 2016; Brett et al., 2017). Our data indicate that algal concentration in the biofilms is similar across biomes but lower than in temperate systems. The values in Chla were comparable to those previously obtained for the Cerrado in pristine streams, as ours (Gücker et al., 2009) but 2−3 times lower than in temperate streams (e.g., Feio et al., 2010). This small algae growth could be due to light limitation and consequently in photosynthesis in channels shaded by the site riparian forests of all biomes three biomes. In fact, despite a more seasonal character of Cerrado streams (Tonin et al., 2017), with a higher input of leaves during the dry season, shading is still dominant, because most riparian trees are perennial (Ribeiro and Walter, 1998, Felfini and Silva Júnior 2005; Gonçalves et al., 2014; Bambi et al., 2017).

The type of substrate used for colonization, which is known to be important for fungal and bacterial diversity (Hellal et al., 2006) also could have created a confounding effect. In fact, the reduced roughness of the acetate substrates, compared to natural substrates, may have contributed to poorer establishment of biofilms (Murdock and Dodds, 2007). However, as values of Chla were lower than those obtained by Feio et al. (2010) with the same substrates in reference temperate streams, this cannot be the only reason. Our results could however be due to high variability in chlorophyll concentrations measured in all biomes, and not only in the Cerrado (as proposed by Dodds et al., 2015). In spite of being generally low, light intensities varies
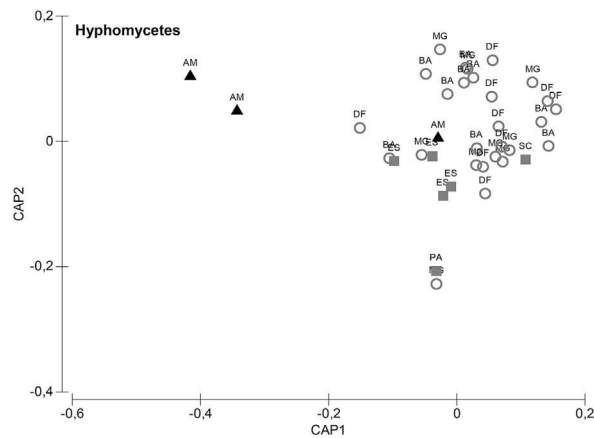
Fig. 6. Canonical analysis of principal coordinates, CAP, of aquatic hyphomycetes assemblages (log (x+1) transformation) in 36 stream sites located in Cerrado (grey open circles), Atlantic Forest (grey squares) and Amazon (black triangles) biomes. States where the sites are located are given by the codes AM (Amazon), BA (Bahia), Minas Gerais (MG), DF (Distrito Federal), ES (Espírito Santo), RJ (Rio de Janeiro), PA (Paraná), Santa Catarina (SC).

within a stream site leading to a high variability of results, as also found in temperate systems (Feio et al., 2010; Warren et al., 2017).

At the structural level, the two assemblages studied showed different patterns. For benthic invertebrates, the assemblages differed between the rainforests and the Cerrado. This pattern might be related to the hydrological patterns, which affect the aquatic invertebrates through drift and changes in water quality (Leigh, 2013; Callisto and Goulart, 2005), and that are more similar among rainforests whereas in the Cerrado flow variations are more extreme because of the longer and more extreme dry season. In addition, plant litter dynamics, theoretically a major food resource for aquatic invertebrates of small streams, is influenced mainly by precipitation, and therefore enhance differences between Cerrado and rainforests sites (Tonin et al., 2017). On the other hand, the aquatic hyphomycetes associated with the balsa wood did not change significantly among biomes. Yet, the absence of statistical difference might be due to the variability in species composition within biomes, as the total number of species found in the study was fourteen, but the average richness per site was only 1−5 species. In addition, the fungi colonization might have been slowed by the hardness of the substrate (wooden balsa) (Gonçalves et al., 2012). In that case we could have obtained different results after microbial succession was completed.

Finally, in this study had to use consistent methods to obtain comparable results across biomes; therefore we selected artificial substrates for biofilms colonization (acetate) and to measure decomposition (balsa wood). This is a recommended procedure for large-scale studies, because the typical substrates (leaf species for decomposition and stones or macrophytes for biofilms) vary naturally among regions, hindering scientifically rigorous comparisons impossible (Keuskamp et al., 2013). However, use of other substrates should be tested in the future to maximize the processes measured, reduce errors associated with low values and allow a quicker assessment of streams. In the case of biofilms, rougher substrates in which the biofilm could adhere and grow better could be advantageous. For experiments where time is a limiting condition, and at least to measure microbial decomposition, substrates that decompose faster, such as the cotton strips or tea bags could be a better alternative (Tiegs et al., 2013; Keuskamp et al., 2013).

Finally, a drawback of this study is the small number of sites in Amazon (3) and their geographic proximity. This has limited the variability of conditions included in the study for this biome and has possibly leaded to more unclear patterns (differences) between biomes. On the other hand, this biome has clear differences from the remaining and the stream sites selected have typical conditions of this biome. On the statistic point of view, the tests made based on permutations (and since the minimum number recommended was achieved always) should have minimized that problem (Anderson et al., 2008).

5. Conclusions

This study was innovative in joining functional and structural parameters of aquatic ecosystems across tropical biomes. This approach allowed a more integrative analysis of the aquatic ecosystems that would studies addressing a single aspect. That allowed four important conclusions: 1) Aquatic ecosystems differed across biomes, being also influenced by climatic variables, but the variation was not as pronounced as for terrestrial systems; 2) Functional and structural variables did not behave similarly among biomes, with decomposition rates and sporulation showing a greater difference among biomes than assemblage structure; 3) Invertebrate assemblages differed between the rainforests and Cerrado sites, but not between the two types of rainforest; 4) the processes measured were generally lower in Cerrado sites and higher in Amazon sites, but no clear pattern was found in aquatic assemblage richness because of high among-site variability in all three biomes.

Considering the potential use of these indicators in a national-wide ecological assessment, our results indicate the need to define different reference values for different biomes and possibly also within biomes for different stream types, depending

on the (functional/structural) variable used. Two further steps should include testing the effect of disturbance and temporal variability on each of these potential indicators. The reduced number of studies on tropical stream biofilms, specially related with the influence of light and on their potential as bioindicators, also show the necessity of investigating more patterns of variation at large and small scales (but see Burgos-Caraballo et al., 2014; Burns and Ryder, 2001; Neres-Lima et al., 2016). Finally, future studies should test the patterns evidenced here with sites from other areas of the three biomes and especially with more Amazon sites, which was the least represented biome.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00498.

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