Ecological Indicators 72 (2017) 365–373

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Partitioning taxonomic diversity of aquatic insect assemblages and functional feeding groups in neotropical savanna headwater streams

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ARTICLE INFO

Article history:
Received 5 February 2016
Received in revised form 19 August 2016
Accepted 24 August 2016

Keywords:
Beta diversity
EPT assemblages
Functional feeding groups
Brazilian cerrado

ABSTRACT

Biological diversity can be divided into: alpha (α, local), beta (β, difference in assemblage composition among locals), and gamma (γ, total diversity). We assessed the partitioning of taxonomic diversity of Ephemeroptera, Plecoptera and Trichoptera (EPT) and of functional feeding groups (FFG) in neotropical savanna (southeastern Brazilian cerrado) streams. To do so, we considered three diversity components: stream site (α), among stream sites (β_1), and among hydrologic units (β_2). We also evaluated the association of EPT genera composition with heterogeneity in land use, instream physical habitat structure, and instream water quality variables. The percentage of EPT taxonomic α diversity (20.7%) was smaller than the β_1 and β_2 diversity percentages (53.1% and 26.2%, respectively). The percentage of EPT FFG collector-gatherer α diversity (26.5%) was smaller than that of β_1 diversity (55.8%) and higher than the β_2 (17.7%) diversity. The collector-gatherer FFG was predominant and had the greatest β diversity percentage among stream sites (β_1, 55.8%). Our findings support the need for implementing regional scale conservation strategies in the cerrado biome, which has been degraded by anthropogenic activities.

1. Introduction

Whittaker (1960) first proposed the concepts of alpha (α), beta (β), and gamma (γ) diversities. In general terms, alpha diversity corresponds to local diversity, beta diversity corresponds to difference in assemblage composition among locals, and gamma diversity corresponds to total regional diversity. In the additive partitioning of species diversity, α diversity is typically expressed as the mean number of taxa observed at any given scale (Lande, 1996; Veech et al., 2002; Anderson et al., 2011). β diversity is the difference in the α diversities between two scales in the spatial hierarchy, and γ diversity represents the sum of the α diversity and all involved β diversities within a given region (Jost et al., 2010). Knowing how the taxa of a regional pool are distributed among multiple scales is an important issue in ecology (Jankowski et al., 2009; Heino et al., 2015a). Therefore, evaluating the pattern of diversity distribution through additive partitioning is important when determining scales of major interest for conserving and rehabilitating aquatic ecosystems (Diniz-Filho et al., 2009; Molozzi et al., 2013). Determining the scale where most biological variability occurs helps managers and conservationists focus their efforts and resources where they are most likely to have the greatest effect.

Recent studies focusing on the additive partitioning of species diversity have sought to understand the distribution patterns of assemblages at several spatial scales (Frissell et al., 1986; Rietkerk et al., 2002; Jost et al., 2010; Ligeiro et al., 2010; Ávila et al., 2011). Such studies are needed because ecological processes and distribution patterns vary with the scale of spatial observation, which can range from centimeters to kilometers (Allan and Castillo, 2007). In addition, enhancing the understanding of spatial differences in

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http://dx.doi.org/10.1016/j.ecolind.2016.08.042
1470-160X/

organism interactions with their habitats and the processing of food resources facilitates the refinement of biomonitoring programs. For example, Boyero (2003) showed that assemblages of Ephemeroptera, Plecoptera and Trichoptera (EPT) varied substantially among habitats, streams and basins. So, biotic indices and ranges of measures must be analyzed and calibrated at different scales to adjust for such geographic differences if one wishes to increase the sensitivity of those indices (Stoddard et al., 2008a). Similarly, several authors have shown that habitat heterogeneity, which supports biological diversity in aquatic ecosystems, is organized in a spatial hierarchy (Cortes et al., 2010; Ligeiro et al., 2010; Ávila et al., 2011; Hepp et al., 2012). Determining how biological traits and ecological processes vary with spatial scale aids managers and conservationists in refining biological metrics and indices and in separating natural variability from anthropogenic disturbances.

In lotic ecosystems, local scales show heterogeneity in assemblage structure and abiotic conditions (Ligeiro et al., 2010; Macedo et al., 2014; Heino et al., 2015a). Taxonomic surveys, the evaluation of functional feeding groups (FFGs), and studies of the heterogeneity and distribution of assemblage characteristics among discrete sites are all important for elucidating how taxonomic diversity and biological traits are distributed in ecosystems (Boyero, 2003). In particular, including functional aspects of biological assemblages is important for making more comprehensive assessments of ecological condition than are possible with taxonomic assessments alone. Although FFGs are essential for understanding many processes in aquatic ecosystems, studies of the distribution of the taxonomic composition of functional feeding groups (e.g., predators, shredders, collectors, and scrapers) across spatial scales are lacking for tropical regions (Boyero, 2005). Each of these groups relies on specific food resources, which are in turn influenced by different habitat characteristics. For instance, collector-gatherers feed on fine particulate organic matter (FPOM), and are more common in fine substrates and still waters, whereas collector-filterers position themselves on substrates exposed to flowing water, from which they sieve FPOM that is suspended in the water (Cummins et al., 2005; Merritt et al., 2008). Thus, differences in resources and habitat characteristics (Boyero, 2003) are likely to produce differences in the proportions of various functional feeding groups. Studies dealing only with assemblage taxa richness miss important variations in the functional composition of those assemblages (Marzin et al., 2012; Leitão et al., 2016).

The EPT are generally sensitive to changes in aquatic environments (Bonada et al., 2006; Stoddard et al., 2008a). Because of their sensitivity to anthropogenic disturbances, the EPT are among the most commonly used ecological indicators in large-scale (regional and national) biological assessments (e.g. Stoddard et al., 2008a; Moya et al., 2011; Chen et al., 2014). Therefore, it is useful to evaluate how geographic scale and functional feeding groups (FFGs) affect EPT diversity.

In this study we evaluated how the taxonomic composition of whole EPT assemblages and of individual FFG are distributed among spatial scales, using a hierarchical series of three diversity components in neotropical savanna streams: stream site (α), among stream sites ($\beta 1$), and among hydrologic units ($\beta 2$). We evaluated two hypotheses: (i) β diversity is not evenly distributed among spatial scales. Environmental variables at the local scale (e.g., substrate type, current velocity, width and water depth) greatly influence biological communities (Ligeiro et al., 2010; Hepp et al., 2012) and for this reason we expected that taxonomic composition and FFG would show greater variability among sites than among hydrologic units. (ii) Taxonomic diversity distribution follows distinct patterns among the different FFG. Considering that food resources and habitat availability vary at different scales (Boyero, 2003), we expected that individual FFG would display distinct α and β diversities and that the partition pattern of whole EPT assemblages would be defined by the partition of the most abundant FFG.

2. Material and methods

2.1. Study area and site selection

We sampled 160 wadeable stream sites (stream orders ranging from 1 to 3 on 1:100,000 scale maps) (Strahler, 1957) belonging to the Araguari, São Francisco, Rio Grande, and Paranaíba River Basins in the states of Minas Gerais, São Paulo, and Goiás, southeastern Brazil (Fig. 1). The hydrologic units (Seaber et al., 1987) were defined as the contributing drainage areas within 35 km upstream of each of four major hydropower reservoirs (Nova Ponte, Três Marias, Volta Grande, São Simão). The sites are all located in the neotropical savanna, which has a humid tropical and seasonal climate with approximately 1600 mm mean annual rainfall (Brasil, 1992). Regional climate is characterized by a dry season from May–September, with monthly precipitation between 10 and 55 mm, and a rainy season between October-April, with monthly precipitation between 100 and 300 mm. The neotropical savanna, which is one of the most threatened biomes worldwide, is a priority hotspot for biodiversity conservation (Myers et al., 2000). Since the 1950s, agriculture and pasture have progressively replaced natural areas (Diniz-Filho et al., 2009), resulting in clearing of more than half of the original ~2 million km^2 forested area (Klink and Machado, 2005; Wantzen et al., 2006). We selected sampling sites by using a randomized, spatially balanced, systematic sample design adapted from one the U.S. Environmental Protection Agency developed for its National Rivers and Streams Assessment (Olsen and Peck, 2008). Each year (2009–2012) during the dry season, we sampled 40 wadeable stream sites in one of the four regions for a total of 160 sites.

2.2. Catchment land use and land cover

We classified land use and cover within the catchment upstream of each site by interpreting a combination of high-resolution satellite images (0.6–5.0 m spatial resolution, Google Earth data: Google 2010) and Landsat multispectral satellite images (R4G3B2 false color band combination). This method is very accurate because the high-resolution satellite images better distinguish the shape of units, while multispectral images better distinguish vegetation leaf structure (e.g., more- or less-dense canopy and biomass concentration) (Macedo et al., 2014). We identified four natural vegetation cover types (woodland savanna, grassy-woody savanna, parkland savanna, and wetland palm swamps) and four land uses (pasture, agriculture, *Eucalyptus* forest, and urban areas) in the 160 catchments.

2.3. Site physical habitat structure and water quality

We characterized physical habitat structure and water quality at each sampling site with standardized field methods (Kaufmann et al., 1999; Peck et al., 2006); this included multiple metrics of channel morphology, riparian structure, flow type, substrate type, and instream habitat cover (Kaufmann et al., 1999, 2008). Metrics were selected from a master list (see Table 1) by removing redundant metrics through use of correlation analysis and principal component analysis (PCA; Ferreira et al., 2014). To assess water quality, we measured temperature (°C), electrical conductivity (μS cm^{-1}), pH, turbidity (NTU), and total dissolved solids (mg L^{-1}) in situ with a multi- probe (YSI, 650 MDS, model 6920). Total nitrogen (mg L^{-1}) and dissolved oxygen concentrations (mg L^{-1}) were

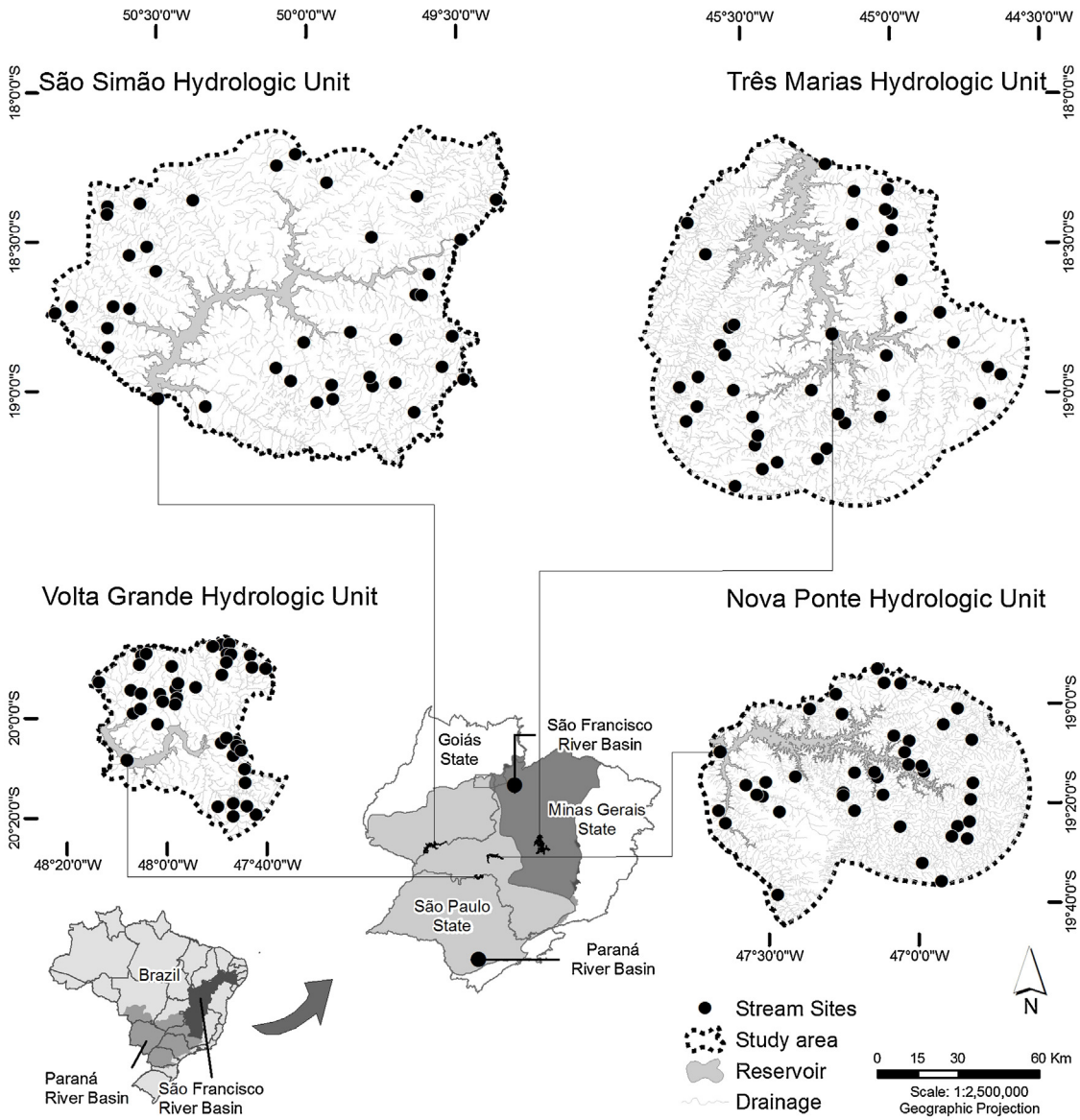

Fig. 1. Locations of wadeable stream sites (n = 160) in four hydrologic units in the neotropical savanna, Minas Gerais, southeastern Brazil.

determined from preserved water samples in the lab following Standard Methods (APHA, 2005).

2.4. Benthic macroinvertebrate sampling and functional feeding group classification

We sampled aquatic insects at all 160 sites with a D-framed kick net (30 cm aperture, 500 μm mesh, and 0.09 m^2 area) for a total of 1 m^2 per site. Sampling was performed at 11 equidistant transects via a systematic zigzag pattern throughout each site (minimum of 150 m), as described in Hughes and Peck (2008). Insect samples were fixed in 4% formalin then returned to the Benthos Ecology Laboratory of the Federal University of Minas Gerais, Brazil. In the laboratory, samples were rinsed on a 500 μm mesh sieve, then sorted EPT specimens were identified to genus-level with a stereo microscope (80×) using published keys (Wiggins, 1996; Pes et al., 2005; Salles, 2006; Merritt et al., 2008; Mugnai et al., 2010). The EPT FFG classifications were assigned to each taxa using published descriptions (Merritt et al., 2008; Oliveira and Nessimian, 2010; Shimano et al., 2012; Brasil et al., 2014). Scrapers feed on periphyton; shredders feed on leaves; collector-gatherers feed on fine particulate organic matter from stream bottoms; filterers feed on fine particulate organic matter in the water column; and predators eat live invertebrates.

2.5. Data analysis

We used additive partitioning to assess EPT genera and FFG diversities (Lande, 1996; Crist et al., 2003; Jost et al., 2010; Hepp and Melo, 2013). All data were assessed within a hierarchical scheme defined by each stream site (α), among stream sites (β1), among hydrologic units (β2), and total study area, where $\gamma = \alpha + \beta1 + \beta2$ (Fig. 2). We compared the observed diversity of each component with the expected diversity, as defined with the random individual-based (Type I) model of Crist et al. (2003). The additive partitioning randomizes macroinvertebrate individuals among the smallest sampling units, thereby removing any taxonomic or FFG aggregation that may exist among individuals on the analyzed scales (Crist et al., 2003; Ligeiro et al., 2010). We assessed the significance of our results by comparing the percents of diversity components from the observed values with the percents obtained from 999 randomizations. A high proportion of the data gen-

Table 1
Candidate physical habitat structure and water quality variables (from Ferreira et al., 2014).

Variables group and name	Variable code
Channel morphology	
Mean depth of cross-section (cm)	xdepth_s
Mean wetted width (m)	xwidth
Mean bankfull width (m)	xbkf_w
Mean residual depth (cm)	rp100
Channel water surface slope—reach mean (%)	xslope
Channel sinuosity ($m\,m^{-1}$)	Sinu
Bed substrate	
Mean embeddedness of channel and margin (%)	xembed
Standard deviation of embeddedness in channel + margin (%)	vembed
Log_{10} (Relative bed stability) Kaufmann et al(2008)	lrbs[a]
Substrate—log_{10}(geometric mean diameter mm)	lsub_dmm[a]
Substrate% cobbles (diameter 64–250 mm)	pct_cb
Riparian	
Mean mid-channel canopy density (%)	xcdenmid
Standard deviation – mid-channel canopy density (%)	vcdenmid
Riparian vegetation canopy + mid + ground cover (%)	xcmg
Flow type	
Glide (% of reach)	pct_gl
Pools – all types (% of reach)	pct_pool
Slow water habitat (% glide + pool)	pct_slow
Shelter	
Coarse litter (%)	pct_bf
Large wood debris in bankfull channel (number/m^2 – all size classes)	c1w_msq
Brush and small debris (areal proportion)	xfc_brs
Undercut banks (areal proportion)	xfc_ucb
Anthropogenic fish cover (areal proportion)	xfc_ant
Water quality	
Dissolved oxygen ($mg\,L^{-1}$)	DO
Negative log hydrogen ion concentration	pH
Turbidity (NTU)	Turbidity
Total nitrogen ($mg\,L^{-1}$)	N-total
Electrical conductivity ($\mu S\,cm^{-1}$)	Cond.
Total dissolved solids ($mg\,L^{-1}$)	TDS
Temperature of water	T°C

[a] lrbs and lsub_dmm (Kaufmann et al., 2008).

erated at random with values higher than the observed values ($Prop_{exp > obs} > 0.975$) indicates that the observed values were significantly less than those expected at random. In contrast, low proportions ($Prop_{exp > obs} < 0.025$) indicates that the observed values were significantly greater than those expected at random. Randomizations were performed with Partition v 3.0 software (Veech and Crist, 2009).

The stream site and catchment environmental metrics (Table 1) were subjected to PCA to select those that had the highest correlation with PCA principal component 1. We selected metrics within each metric group (see Table 2) that contributed most to the dispersion of the data in the multivariate space of a principal component analysis (PCA). The 1st axis of each PCA (PCA 1) represents the clearest univariate gradient formed by the habitat metrics in each group (Ferreira et al., 2014). For example, PCA 1 for the channel-morphology metric group in the hydrologic units represents mean cross-section depth (cm) and mean residual depth (cm) (Table 2). We compared the selected metrics among the four hydrologic units via one-way ANOVA. Then, we subjected the selected metrics to a nested ANOVA by using the stream sites and the hydrologic units as random factors. We transformed the data (log x + 1) to fulfill the variance homogeneity assumption for the nested ANOVA.

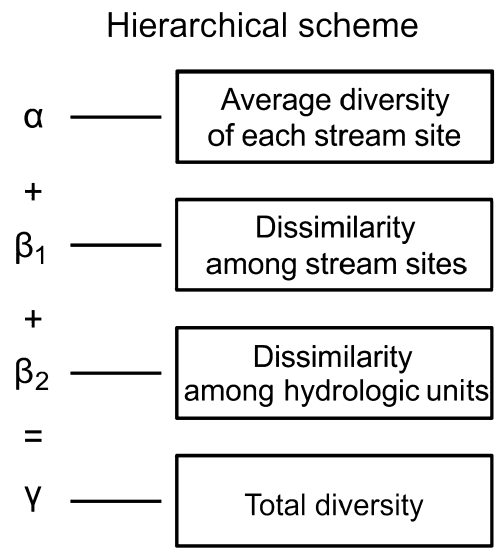

Fig. 2. Schematic of diversity partitioning at different hierarchical levels.

3. Results

3.1. EPT assemblage composition and functional feeding groups

We collected 45,481 EPT specimens distributed among 80 genera in the 160 stream sites sampled (Fig. 3a). The greatest abundance was found in Três Marias (14,943 individuals), and the lowest was found in Nova Ponte (5463 individuals). The most abundant FFG was collector-gatherers (47%) and the lowest was predators (3.3%).

3.2. Physical habitat, land use, and cover

Site-specific channel morphology, riparian cover, flow types, instream habitat cover, and water quality were all significantly different among hydrologic units (one-way ANOVA: $p < 0.05$, Table 2), but dissolved oxygen and percent cobble were not. Significant differences were observed among the four hydrologic units for all land use and land cover types except percent woodland savanna ($F_{(3,156)} = 1.3$, $p > 0.05$) and percent urban area ($F_{(3,156)} = 1.3$, $p > 0.05$). Três Marias had the greatest proportion of pasture (40.7%), whereas Nova Ponte, Volta Grande and São Simão had large proportions of agriculture (46.6%, 70.4% and 68.1%, respectively, Table 2). The nested ANOVA indicated that variation in environmental metrics was almost always greater among hydrologic units than among sites (Table 2).

The sites showed good water quality values by Brazilian water quality standards (Brasil, 2005; Tables 2 and 3), but the hydrologic units differed in electrical conductivity ($F_{(3,156)} = 18.5$, $p < 0.001$) and total dissolved solids ($F_{(3,156)} = 12.2$, $p < 0.001$). The highest mean conductivity value ($76.1 \pm 92.3\ \mu S.cm^{-1}$) was observed in Três Marias, and the lowest ($43.6 \pm 29.3\ \mu S.cm^{-1}$) in Volta Grande. The highest mean value of total dissolved solids ($41.1 \pm 33.5\ mgL^{-1}$) also occurred in Três Marias, and the lowest ($15.2 \pm 11.8\ mgL^{-1}$) occurred in Nova Ponte (Table 2).

3.3. Additive partitioning of taxonomic composition of EPT assemblages and individual FFG categories

The percentage of observed mean stream site (α) diversity (20.7%) for EPT taxonomic composition was lower than that observed among stream sites (β_1) and among hydrologic units (β_2) (53.1 and 26.2%, respectively). The expected α taxonomic diver-

Table 2
Physical habitat structure and water quality variables (mean, standard deviation) selected by PCA plus land use metrics that explain EPT distributions in the Neotropical Savanna.

Variable groups and names	Comparison of hydrologic units							nested ANOVA (Random factors)			
	Variable code	Nova Ponte	Três Marias	Volta Grande	São Simão	ANOVA		Stream sites		Hydrologic units	
						F-value	*p-value*	F-value	*p-value*	F-value	*p-value*
Site											
Channel morphology											
Mean depth of cross-section (cm)	xdepth_s	20.6 (10.4)	27.8 (11.68)	26.8 (11.37)	25.2 (11.86)	3.76	0.01*	1.07	0.38	3.82	0.01*
Mean residual depth (cm)	rp100	10.3 (5.6)	23.7 (12.8)	17.5 (6.1)	17.0 (8.6)	14.16	<0.001*	0.82	0.75	13.53	<0.001*
Bed substrate											
Substrate% cobbles (diameter 64–250 mm)	pct_cb	7.9 (10.5)	8.8 (12.9)	10.3 (12.5)	8.1 (9.9)	0.26	0.85	1.35	0.11	0.27	0.84
Riparian											
Standard deviation: mid-channel canopy density (%)	vcdenmid	13.4 (10.50)	14.2 (8.59)	13.9 (9.1)	13.6 (9.4)	2.88	0.03*	1.08	0.35	2.95	0.03*
Flow type											
Pools – all types (% of reach)	pct_pool	14.6 (18.3)	31.1 (30.8)	5.0 (12.4)	4.4 (12.9)	19.38	<0.001*	0.98	0.50	19.32	<0.001*
Shelter											
Anthropogenic fish cover (%)	xfc_ant	3.3 (9.0)	6.7 (11.8)	1.7 (4.8)	7.9 (19.8)	3.62	0.01*	1.07	0.37	3.68	0.01*
Water quality											
Dissolved oxygen (mg L^{-1})	DO	7.5 (1.16)	7.7 (2.9)	8.4 (3.2)	7.6 (1.7)	0.41	0.74	0.93	0.59	0.39	0.75
Total dissolved solids (mg L^{-1})	TDS	15.2 (11.8)	41.1 (33.5)	19.8 (23.9)	38.6 (31.5)	12.20	<0.001*	0.75	0.84	11.46	<0.001*
Catchment											
Woodland savanna (%)	wood_sav	15.3 (8.0)	16.0 (13.0)	12.1 (5.8)	13.6 (6.5)	1.28	0.19	0.82	0.75	0.90	0.44
Park land savanna (%)	park_sav	9.6 (23.7)	17.7 (18.9)	0.00 (0.00)	0.8 (2.3)	24.99	<0.001*	1.43	0.07	50.51	<0.001*
Grassy-woody savanna (%)	gras_sav	11.0 (14.8)	10.3 (9.0)	1.36 (1.47)	1.5 (2.9)	19.78	<0.001*	1.05	0.4	23.30	<0.001*
Wetland palm swamps (%)	palm_sav	0.6 (1.3)	1.4 (3.2)	0.4 (1.1)	2.4 (2.6)	12.34	<0.001*	0.91	0.61	12.18	<0.001*
Pasture (%)	pasture	16.6 (18.3)	40.7 (18.2)	11.6 (10.7)	10.6 (14.6)	29.25	<0.001*	0.92	0.59	20.68	<0.001*
Agriculture (%)	agriculture	46.6 (29.7)	3.0 (4.1)	70.4 (15.8)	68.1 (20.4)	105.28	<0.001*	1.19	0.22	116.99	<0.001*
Eucalyptus forest (%)	eucalyptus	0.00 (0.00)	8.9 (11.1)	0.2 (1.3)	0.7 (1.4)	30.83	<0.001*	1.10	0.34	32.03	<0.001*
Urban (%)	urban	0.5 (2.6)	2.1 (11.0)	3.9 (12.1)	2.3 (13.4)	2.23	0.55	2.84	<0.001*	6.33	<0.001*

* Significant difference.

Table 3
Mean and standard deviation of water quality variables and one-way ANOVA of the differences among the four hydrologic units.

Hydrologic unit	Water quality variables				
	pH	Turbidity (NTU)	Electrical conductivity (μS cm^{-1})	Temperature (°C)	Total Nitrogen (mg L^{-1})
Nova Ponte	6.89 (0.46)	7.6 (10.5)	23.3 (17.7)	20.3 (1.8)	0.05 (0.01)
Três Marias	7.7 (0.5)	8.2 (14.5)	76.1 (92.3)	17.3 (1.8)	0.24 (0.98)
Volta Grande	7.1 (1.8)	5.8 (4.7)	43.6 (29.3)	20.6 (1.4)	0.11 (0.03)
São Simão	6.8 (0.5)	6.9 (4.2)	68.7 (51.2)	19.7 (3.6)	0.10 (0.03)
ANOVA, $F_{(3,156)}$–value	2.09	0.82	18.52	3.88	1.72
p–value	0.10	0.48	<0.001	0.01	0.16

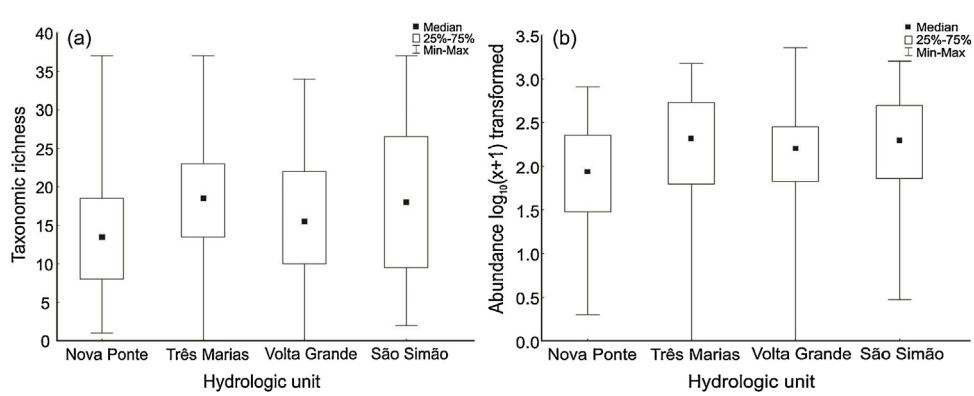

Fig. 3. Distribution of (a) richness and (b) abundance of EPT genera in hydrologic units in the neotropical savanna, Minas Gerais, southeastern Brazil.

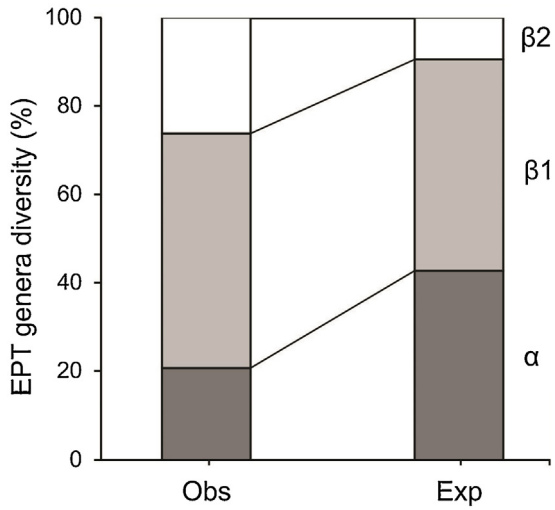

Fig. 4. Additive partitioning of EPT observed and expected taxonomic composition in wadeable stream sites (α; $Prop_{exp > obs}$: >0.999), among stream sites (β_1; $Prop_{exp < obs}$: <0.001), and among hydrologic units (β_2; $Prop_{exp < obs}$: <0.001) in the neotropical savanna, Minas Gerais, southeastern Brazil.

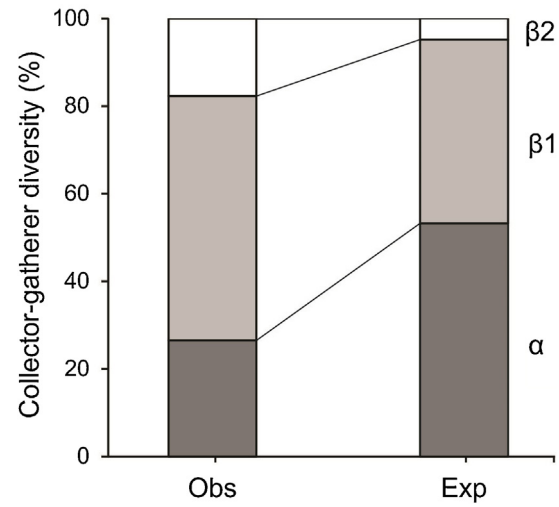

Fig. 5. Additive partitioning of observed and expected EPT functional feeding group composition for collector-gatherers in wadeable stream sites (α; $Prop_{exp > obs}$: > 0.999), among stream sites (β_1; $Prop_{exp < obs}$: <0.001), and among hydrologic units (β_2; $Prop_{exp < obs}$: <0.001) in the neotropical savanna, Minas Gerais, southeastern Brazil.

sity percentage (42.7%) was slightly less than that for expected β_1 diversity (47.8%) and greater than that for expected β_2 (9.4%) diversity. The observed β_1 taxonomic diversity percentage (53.1%) was slightly greater than that expected at random (47.8%) (Fig. 4). In contrast, the observed β_2 taxonomic diversity percentage was nearly three times greater than the expected value (9.4%).

Separate functional analysis of the α and β diversity was possible only for the collector-gatherer FFG. Abundances of all other FFG were too low. Therefore, individuals from the remaining FFG were pooled to facilitate further diversity partitioning. The observed α diversity percentage for the collector-gatherer FFG (26.5%) was less than the observed β_1 diversity (55.8%) and greater than the observed β_2 diversity (17.7%), whereas the expected percentage of α diversity (53.25%) was greater than the expected percentage for β_1 and β_2 diversities (41.96% and 4.83%, respectively). The observed percentage of β_1 diversity for the collector-gatherer FFG was greater (55.8%) than that expected at random and greater than that for the observed β_2 collector-gatherer diversity (20.7%) (Fig. 5). The same pattern was observed for the combined FFG (predators + shredders + filterers + scrapers) in which the observed percentage of β_1 diversity was slightly greater (55.6%) than that expected at random (50.5%) and greater than for the observed β_2 diversity (17.7%) (Fig. 6).

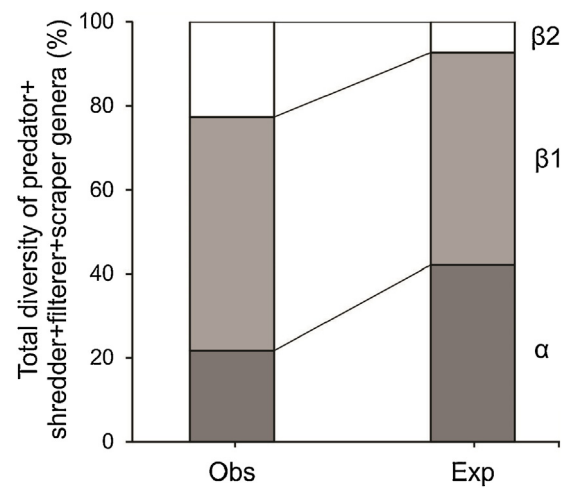

Fig. 6. Additive partitioning of observed and expected of EPT functional feeding group composition for predators + shredders + filterers + scrapers in stream sites (α; $Prop_{exp > obs}$: > 0.999), among stream sites (β_1; $Prop_{exp < obs}$: >0.001), and among hydrologic units (β_2; $Prop_{exp < obs}$: <0.001) in the neotropical savanna, Minas Gerais, southeastern Brazil.

4. Discussion

In our investigation of the distribution patterns of the α and β diversities of EPT taxonomic composition, the largest β diversity was observed among stream sites (β_1) and not among hydrological units (β_2) or within sites (α). Both β diversities were much higher than the α diversity, indicating that each stream site represented only a small part of the total (γ) diversity. In addition, the environmental metrics usually varied more among hydrologic units than among sites (see nested ANOVA, Table 2). Thus, the β diversity was not evenly distributed throughout the spatial scales, which supported our first hypothesis.

As observed in previous studies (Ferreira et al., 2014; Macedo et al., 2014), our results indicate that the taxonomic and functional composition of EPT assemblages in neotropical savanna streams is determined by local (stream physical habitat structure and water quality) and catchment (land use, land cover) factors. Heino et al. (2015a) studied the relationship between β diversity and habitat heterogeneity and proposed two models. (i) Assemblage compositions are scale-dependent, and β diversity varies positively with habitat heterogeneity based on the observation that organisms disperse at all spatial scales. (ii) The relationship between β diversity and habitat heterogeneity may be affected by the dispersal ability of the organisms. According to those authors, evaluations of β diversity at multiple spatial scales are required for clear observations of the relationship between β diversity and habitat scale. We did not evaluate the dispersal ability of organisms, but EPT individuals have relatively low dispersion capacity along stream channels (Greenwood et al., 2001; Petersen et al., 2004; Yaegashi et al., 2014). However, we observed that β diversity was more strongly associated with habitat heterogeneity among sites than among hydrologic units. Additionally, our study corroborates the statements of Heino et al. (2015a) regarding habitat heterogeneity, because we observed significant differences in physical habitat among the hydrologic units and in land use and cover of site catchments (Table 2). Hepp and Melo (2013) also highlighted the

importance of stream site heterogeneity. According to them, when there is only a spatial effect, the trend in assemblage composition is similar in different stream sites of the same river because of insect dispersion characteristics (especially for EPT). In an earlier study conducted in the Nova Ponte and Três Marias hydrologic units, Ferreira et al. (2014) observed the importance of site-scale physical habitat on the distribution of EPT richness and concluded that channel morphology (width and depth), riparian structure, substrate composition, and water quality were important for structuring macroinvertebrate richness in neotropical savanna streams. This study corroborates those results because we also showed that the among-site scale (β_1) was most important for the distribution of EPT genera and for biological variation. Similarly, Ligeiro et al. (2010) investigated the distribution patterns of diversity in neotropical savanna streams and emphasized the importance of the stream site scale for β diversity, as did Hepp et al. (2012).

We observed similar EPT genera richness among hydrologic units; however, slightly fewer sites in the Três Marias hydrologic unit had low richness of EPT genera compared with the other hydrologic units. This probably occurred because the land use in most Três Marias catchments is pasture and small farms versus row-crop agriculture (Ferreira et al., 2014). On the other hand, land use in most Nova Ponte, Volta Grande and São Simão catchments is primarily row-crop agriculture (soy, coffee, corn, and sugar cane), which generally disturbs streams to a greater degree than pasture (Ligeiro et al., 2013). Agricultural practices tend to increase the introduction of sediments, nutrients and biocides, which tend to reduce instream insect richness, especially EPT (Hepp and Santos, 2009), which are sensitive to anthropogenic disturbance (e.g., Stoddard et al., 2008b). The low EPT abundances observed in the Nova Ponte hydrologic unit also may have resulted from higher mean annual precipitation in 2009, compared with 2010 in Três Marias, 2011 in Volta Grande, and 2012 in São Simão (1939 mm vs 958 mm, 968 mm and 1155 mm, respectively; ANA, 2014). The Nova Ponte hydrologic unit also had greater long term annual precipitation than the others (1657 mm vs 1449 mm, 1591 mm, 1589 mm for Três Marias, Volta Grande and São Simão, respectively; Hijmans et al., 2005). That greater precipitation may have produced greater natural environmental disturbance (flushing flows in headwaters) and greater runoff of agricultural pollutants, affecting the abundance and richness of EPT assemblages. Macedo et al. (2014) showed that decreased benthos richness was associated with increased rainfall in the Nova Ponte and Três Marias hydrologic units. Lastly, the similarity in EPT genera richness among hydrologic units is likely due to the fact that all four units occurred in the neotropical savanna, an ecoregion with broadly similar climate, potential natural vegetation, and land surface form that has persisted for a very long time (Myers et al., 2000; Wantzen et al., 2006; Brasil et al., 2014). Such a region tends to support generally similar aquatic biota (Omernik, 1987; Whittier et al., 1988; Stoddard et al., 2008a; Pinto et al., 2009).

Our data revealed that the collector-gatherers drove the patterns of diversity partitioning of the EPT assemblage. The collector-gatherer FFG exhibited greater EPT richness and genera abundance compared with the other FFG, which supported our second hypothesis. Our study revealed low shredder abundance in the neotropical savanna, which supports reports of shredder scarcity in tropical regions (Wantzen and Wagner, 2006; Boyero et al., 2011; Rezende et al., 2016). However, the abundance and importance of shredders may differ among biomes because of differing availabilities of leaf litter as food and for providing physical habitat structure (Ferreira et al., 2015).

Another important factor regarding the FFG that we did not consider is the food plasticity of macroinvertebrates, which could contribute to a greater proportion of collector-gatherers in our sites. It is usually accepted that macroinvertebrates exhibit plasticity in their feeding habits (Tomanova et al., 2006; Carvalho and Graça, 2007). Our specimens were classified according to the literature (Merritt et al., 2008; Oliveira and Nessimian, 2010; Shimano et al., 2012; Brasil et al., 2014). However, a rigorous assessment of their gut contents would be required for a more precise EPT FFG classification. Ferreira et al. (2015) evaluated the gut contents of *Phylloicus* larvae, which are typically considered shredders, in the Nova Ponte and Três Marias hydrologic units. They noted that the larvae exhibited collector-gatherer behavior in Nova Ponte based on the predominance of fine particulate organic matter (particles <50 μm) in their digestive tracts. Thus, Ferreira et al. (2015) concluded that *Phylloicus* larvae could change their feeding strategies depending on food availability and habitat type, which are affected by land use, human population density, and the geomorphic characteristics within each hydrologic unit.

The four hydrologic units differed in several environmental variables (Table 2). For example, Três Marias has experienced replacement of its natural areas with pasture, whereas agriculture has replaced natural vegetation in the other hydrologic units, with greater intensities in the São Simão and Volta Grande hydrologic units. Because of such anthropogenic activities, the neotropical savanna has reduced habitat heterogeneity, which has affected the composition and distribution of benthic macroinvertebrate assemblages (Ferreira et al., 2014; Macedo et al., 2014, 2016). Such changes help explain the differences in EPT taxonomic composition among the stream sites as well as their habitat heterogeneity, resulting in greatest β diversity among stream sites. Hepp and Santos, (2009) observed decreased EPT richness in *Araucaria* rain forest sites over an urban and agriculture gradient. Sensolo et al. (2012) studied Atlantic rain forest streams and observed that substantial changes in the composition of Chironomidae (Diptera) genera were influenced by changes in catchment land use and cover. Ligeiro et al. (2013) also studied neotropical savanna streams and observed that increased human pressures resulted in decreased EPT richness and abundance.

We observed the greatest variability in β diversity among stream sites, although there were also substantial differences among hydrologic units. This suggests that the regional effects on the biota were indirect and that the invertebrate taxa were directly affected by local physical habitat structure and water quality. In our study, only the percentage of urban area showed significant variability at both the stream site and hydrologic unit scales, indicating the direct effects on sites of urban point sources of pollution and land use. As an example of these local and regional influences, Macedo et al. (2014) evaluated the influence of the geophysical landscape, land use and cover, and site physical habitat structure on macroinvertebrate richness. They concluded that site physical habitat structure determined benthic assemblage composition either independently or in combination with a gradient of anthropogenic pressures. Moreno et al. (2010) studied streams in another hydrologic unit in the São Francisco River Basin and evaluated the factors determining the structure and distribution of benthic invertebrate assemblages. They determined that the main structuring factors were degree of habitat conservation around the sites, nutrient concentration, and substrate size. Heino et al. (2015b) investigated the relationship between ecological factors and the β diversity of aquatic insect meta-communities within and among catchments. They reported that environmental metrics explained insect β diversity better than spatial metrics in aquatic ecosystems, although they might be weak predictors.

5. Conclusions and recommendations

We identified the scales of major importance for biodiversity in neotropical savanna streams through use of additive partitioning to analyze EPT genera diversity and FFG. Our findings should

help focus sampling efforts for future biodiversity surveys and local and regional bioassessments. Our results also can facilitate decision-making aimed at the recovery and conservation of watersheds by underlining the primary factors and spatial scales for mitigating disturbance and maintaining aquatic life in neotropical savanna streams. Taxonomic and functional biodiversity is inextricably linked to the preservation of the essential functions of ecosystems and preservation of biodiversity is currently an urgent concern of environmental policy (Di Battista et al., 2016). We highlight the need for further studies evaluating the relationship among β diversity at multiple spatial scales and the incorporation of meta-community studies to assess the dispersal ability of benthic organisms and the relationships between organism traits and their habitats. Additional studies of FFG partitions also are necessary because individual partitioning of groups other than collector-gatherers was not possible because of low numbers and because ecological function is a critically important component of ecological condition. Finally, we recommend further gut content evaluations of macroinvertebrates to obtain more accurate FFG classification. Such studies are needed because classifications based only on the literature and mouthparts may incorporate substantial errors when regional differences in available food and habitats are considered.

We stress the importance of studying river basin condition at multiple scales. Such approaches help us understand ecological patterns and processes with greater certainty, which can lead to more scientifically rigorous and rational conservation and management of water resources. Our results indicate that multiple scale approaches would greatly benefit effective design and evaluation of measures aimed at conserving biodiversity and the habitats that foster it. Such measures might include: (1) Identifying small streams to include preserves, conservation areas, and protected areas because they support high levels of biological variability (beta diversity) and represent over 80% of the stream length in drainage basins. (2) Maintaining and restoring natural riparian zone vegetation cover and complexity to buffer streams from land use disturbances and provide alternative food and energy sources to streams. (3) Focusing financial investments into riparian zone recovery programs. (4) Developing public policies and biomonitoring programs focused on conservation and assessment of water resources such as those resulting from the U.S. Clean Water Act and National Rivers and Streams Assessment, the European Union Water Framework Directive, and the Australian Sustainable Rivers Audit.

Acknowledgements

We thank the Fundação de Amparo à Pesquisa do Estado de Minas Gerais/FAPEMIG/CAPES/Programa Mineiro de Pós-Doutorado—PMPD II/ProcessoCRA-BPD-00494-13, Peixe-Vivo Program of Companhia Energética de Minas Gerais, Pesquisa & Desenvolvimento/Agência Nacional de Energia Elétrica/Companhia Energética de Minas Gerais-P&D ANEEL/CEMIG (GT-487), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Fulbright-Brasil for financial support; Carlos Bernardo Mascarenhas Alves for logistical support; and colleagues from the Federal University of Minas Gerais Benthic Ecology Laboratory, Federal Center of Technological Education of Minas Gerais, Federal University of Lavras, and Pontifical Catholic University of Minas Gerais for help with field collections. MC was awarded research productivity CNPq (no. 303380/2015-2), research project CNPq (no. 446155/2014-4), and Minas Gerais research grant FAPEMIG PPM-IX – 00525-15. LUH received financial support from CNPq (no. 471572/2012-8). We thank Dan McGarvey for his review of an earlier draft of this manuscript, which was also reviewed by the U.S.EPA National Health and Environmental Effects Research Laboratory's Western Ecology Division and approved for publication. Approval does not signify that the contents reflect the views of the USEPA, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

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