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ORIGINAL ARTICLE

Does environmental disturbance also influence within-stream beta diversity of macroinvertebrate assemblages in tropical streams?

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ABSTRACT

Riparian deforestation is a major threat to the ecological integrity of streams and aquatic biodiversity, influencing microhabitat availability and susceptibility to disturbances. Here we tested if riparian deforestation of tropical streams influenced beta diversity of macroinvertebrate assemblages, by comparing indices that weighted differentially rare and dominant taxa, and testing if nestedness in community composition increased in deforested streams. Within-stream beta diversity was higher in deforested than forested streams, mainly due to taxon loss and higher dominance. In disturbed streams, higher sedimentation in pool mesohabitats resulted in larger differences in community composition, whereas mesohabitats in forested streams were more stable.

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KEYWORDS mesohabitats; sedimentation; nestedness; turnover; biomonitoring

Introduction

Streams and rivers are among the most endangered ecosystems of the world, especially in tropical regions, where the conversion of large forested areas for planting and pasture continues unabated (Boyero et al. 2009). These changes at the watershed scale often include riparian deforestation, one of the most important threats to the conservation of stream biodiversity (Naiman & Décamps 1997; Sweeney et al. 2004). Deforested streams can exhibit lower habitat diversity with narrower and simpler channels, less wood and litter, fewer obstructions, higher proportions of run and glide mesohabitats, and less variability in active channel width (Jackson et al. 2015). Furthermore, riparian deforestation may increase rates of runoff to streams, as well as flash floods of higher amplitude and shorter duration (Dudgeon et al. 2006) that result in bank instability and increased inputs of inorganic sediment (Pusey & Arthington 2003; Sánchez-Arguëllo et al. 2010). Macroinvertebrate communities represent an important fraction of stream biodiversity and their assemblage composition and richness exhibit a strong correlation with environmental change at reach levels (Strayer 2006). For example, increases in sediment loading and deposition by anthropogenic disturbance can bury macroinvertebrates and their habitats and cause the loss of species in streams (Connolly & Pearson 2007).

Measures of local species richness (alpha diversity, α) and regional diversities (gamma diversity, γ) are well documented for many taxonomic groups and have provided enormous amounts of information on the effects of human-driven disturbance on local stream communities (Maloney 2011; Hawkins et al. 2015). However, they do not estimate the differentiation of community composition among locations (beta diversity, β), an important contribution to regional diversity which allows testing of hypotheses of processes shaping variation in biotic communities (Maloney et al. 2011; Tonkin et al. 2016). Differentiation in community composition can be decomposed into two components: turnover of species between sites and richness differences where species-poor assemblages are simply nested subsets of richer assemblages (Wright & Reeves 1992; Baselga 2010). These two components of beta diversity can be analyzed separately, for example, to explore how they vary along environmental gradients or disturbance (Podani et al. 2013; Legendre 2014). Gutiérrez-Cánovas et al. (2013) found that along natural gradients beta diversity patterns of macroinvertebrate assemblages among streams reflected mainly species turnover, whereas along

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anthropogenic gradients of disturbance nestedness was the main component.

Beta diversity can be estimated as the mean dissimilarity among sites, and species abundances can contribute to differences in community composition (Koleff et al. 2003). Jost (2007) showed that the similarity indices that take into account species abundances are monotonic transformations of the original formulation of beta diversity (Whittaker 1960), so that differentiation can be analyzed in relation to relative weights of rare or common species given by the parameter q. Although some studies considered similarity measures such as the Bray-Curtis index to study beta diversity patterns both among (Mykrä et al. 2011) and within (Costa & Melo 2008) streams, we are not aware of any study that systematically varied the weight given to species relative abundances to evaluate beta diversity patterns.

Environmental gradients can result in heterogeneity at different spatial scales, resulting in variation both among and within streams. For example, Tonkin et al. (2016) found high turnover and beta diversity among streams in the Niger Delta region of Nigeria, whereas Heino et al. (2015), using a worldwide database on different insect groups, found that ecological factors was weakly related to variation among and within stream metacommunities. On the other hand, Hawkins et al. (2015) analyzed a large database of disturbed and reference streams in Finland and the USA, and found higher beta diversity of macroinvertebrate communities (at genus level) among disturbed streams, suggesting a strong influence of environmental filtering, although other mechanisms such as among-taxa differences in stress tolerance could also be important. Johnson and Angeler (2014) found that beta diversities of fish and macroinvertebrates decreased in streams with higher total phosphorus concentrations, whereas primary producers were not affected.

Fewer studies analyzed within-stream beta diversity, even though streams are heterogeneous in relation to environmental conditions and resource availability (Heino et al. 2004). Physical variation within stream reaches are caused by longitudinal alternation of riffle, run, and pool mesohabitats that are clearly delimited by different combinations of flow, depth and substrate types (Angermeier & Schlosser 1989; Passy & Blanchet 2007). This heterogeneity results in high variability of biological community composition within streams (Heino et al. 2004; Costa & Melo 2008). For example, Armitage and Cannan (1998) identified a number of mesohabitat types characterized by particular macroinvertebrate assemblages, whereas Silva et al. (2014)

found that differences in mesohabitat distribution influenced stream macroinvertebrate composition and within-stream beta diversity patterns. In tropical Peninsular Malaysia, Al-Shami et al. (2013) associated decreased within-stream beta diversity of macroinvertebrate communities with low water pH. Thus, the possibility of human-driven habitat alteration influencing patterns of beta diversity both among and within streams needs to be further investigated, particularly those in the Neotropics. In this study, we analyzed whether environmental disturbances related to riparian deforesting influenced patterns of beta diversity of macroinvertebrate assemblages within tropical streams. Although forested streams can present higher withinstream diversity of mesohabitats, deforested streams are more subject to hydrological disturbances that result in higher sediment delivery and loss of refugia (Stanley et al. 2010). The following hypotheses were then evaluated, hypothesis 1 (H1): within-stream beta diversity is higher in deforested streams due to variation resulting from higher disturbance frequency or magnitude, but patterns in beta diversity are influenced by the relative abundance of component taxa (e.g. rare and dominant taxa influence differently within-stream macroinvertebrate composition); hypothesis 2 (H2): within-stream beta diversity in deforested streams are more related to the nestedness component than forested streams due to the effects of disturbances.

Materials and methods

Study area

This study was carried out in Analândia municipality in four low-order streams belonging to the Alto Corumbataí basin, a sub-basin of the Corumbataí River located in the midwest region of São Paulo State, SE Brazil, at the coordinates 22°04'46"-22° 41'28" S, 47°26'23"-47°56'15" W (Valente & Vettorazzi 2005). Land use in the Alto Corumbataí region is mainly pasture and sugarcane plantations, with remaining native vegetation characterized by seasonal semideciduous forests, deciduous forests, riparian forests, swamp forests, and savannas (Cerrado) (Valente & Vettorazzi 2005). We sampled two streams with forested riparian zones located in rural landscapes (F1 = 22°06'14" S, 47°42'15" W and $F2 = 22^{\circ}06'14''$ S, $47^{\circ}42'11''$ W), representing reference streams and two streams without forested riparian zones located in areas near to urban development $(D1 = 22^{\circ}07'25'' \text{ S} - 47^{\circ}40'07'' \text{ W} \text{ and } D2 = 22^{\circ}07'32''$ S - 47°39'30" W). All streambeds are composed mostly of boulders, cobbles and gravel substrates,

allowing us to sample riffle and pool mesohabitats even in streams without forested riparian zones. According to the Köppen classification, the climate in the region is subtropical (Cwb), with dry winters and wet summers. The average air temperature in the warmest month (January) is higher than 22°C and in the coldest month (July) is higher than 17°C (Garcia et al. 2006). Sampling was carried out during the wet season, between October and November 2009, to evaluate responses to hydrological disturbances.

Sampling of macroinvertebrates

Macroinvertebrates were sampled along an experiment on leaf litter breakdown using litterbags with leaves from a standard species. Although it is a selective method, we considered that microhabitat differences within each sampled mesohabitat could contribute to differences in macroinvertebrate community structure and composition, and sampling different microhabitats by chance could increase artificially differences between mesohabitats. On the other hand, using a standard resource to obtain the macroinvertebrates would sample the available taxa within the species pool of each mesohabitat, as well as drifting organisms. Therefore, although we expected fewer differences among macroinvertebrate communities by a selective method (litterbag), any difference detected in community dissimilarities would reflect the local species pool with less error.

In each stream, we selected four reaches at least 50 m from each other, each containing one riffle and one pool. For macroinvertebrate sampling, within each mesohabitat, we placed four litter bags (15×40 cm bags, with 10-mm mesh size), containing 6 g of dry leaves of Magnolia ovata St. Hil. (Magnoliaceae), a common species in the region whose leaves are a high quality food resource for stream macroinvertebrates (Janke & Trivinho-Strixino 2007). The green leaves were collected and air-dried before constructing the litter bags. After seven, 14, 21 and 28 days, one litter bag was retrieved from each mesohabitat in each reach of each stream for a total of 128 samples (two mesohabitats \times four reaches \times four streams \times four sampling dates). Each litter bag was stored within plastic bags filled with 4% formalin solution and transported to the laboratory. During each sampling day, we also measured water temperature, electric conductivity (EC), pH, dissolved oxygen concentrations (DO) and total dissolved solids with a multiprobe YSI 556 (Yellow Springs Instruments Inc., Yellow Springs, OH, USA) for each mesohabitat (n = 4). Stream water velocities were determined with a flowmeter, whereas stream width and depth were measured using a measuring tape; those measurements were carried out before assembling the experiment.

In the laboratory, the contents of each bag was washed into a 250 µm mesh sieve; macroinvertebrates were separated from the remaining leaf material and preserved in 70% ethanol and then identified to family level. We used this level of identification to determine if beta diversity patterns in deforested streams would also be detected at coarse resolution levels; any difference found would also reflect patterns at species level (Gutiérrez-Cánovas et al. 2013). Monitoring of stream water quality using macroinvertebrate communities is time-consuming, and studies at genus or family levels have been used in different countries (Buss et al. 2015). Heino and Soininen (2007) found that relatively similar amounts of variation were explained by environmental and spatial variables on macroinvertebrate assemblage structure at genus or family levels, and that the same key environmental variables were selected. In Brazil, several studies on stream monitoring found similar results using both taxonomic levels (e.g. Corbi & Trivinho-Strixino 2006; Baptista et al. 2007), and land-use differences using family level resolution were also detected (Suga & Tanaka 2013; Moraes et al. 2014; Tanaka et al. 2016). Therefore, biomonitoring studies could be benefited if differences in beta diversity could be found at the family level resolution.

Data analysis

We estimated beta diversity of macroinvertebrate assemblages separately for each reach. We calculated the compositional similarity of macroinvertebrates between pool and riffle mesohabitats and estimated beta diversity using the complement of each index (ranging between zero and one). Compositional similarity was quantified by Sørensen, Horn and Morisita-Horn indices, as these indices are monotonic transformations of beta diversity parameterized by q order that determine the sensibility to rare or common species (Jost 2007). Indices parameterized by q < 1 favor rare species (e.g. Sørensen index, q = 0), whereas indexes parameterized by q > 1 favor common species (Morisita–Horn index, q = 2) (Keylock 2005; Jost 2007). The critical point that weighs all species by their frequency, without favoring either common or rare species, occurs when q = 1 (Horn index) (Jost 2007).

We analyzed beta diversities with repeated measures analysis of variance (RM-ANOVA), using Stream as a fixed factor between objects and Time as a fixed factor within objects, since the same mesohabitat was sampled along the four sampling dates. To control problems of temporal autocorrelation, the *F*-values

, ,		,		,				
	F1		F2		D1		D2	
Variable	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle
Temperature (°C)	21.1 (0.6)	21.1 (0.6)	21.2 (0.3)	21.2 (0.3)	23.2 (1.2)	23.1 (1.2)	24.2 (1.6)	24.2 (1.6)
Conductivity (µs cm ⁻¹)	0.028 (0.002)	0.028 (0.002)	0.024 (0.001)	0.024 (0.001)	0.034 (0.004)	0.035 (0.002)	0.033 (0.002)	0.033 (0.003)
рН	7.4 (0.06)	7.3 (0.04)	7.3 (0.06)	7.3 (0.04)	6.9 (0.04)	6.9 (0.17)	6.9 (0.10)	6.9 (0.24)
Dissolved oxygen (mg l ⁻¹)	8.7 (0.9)	9.1 (1.0)	8.6 (0.7)	8.9 (0.7)	8.1 (0.8)	8.3 (0.6)	8.1 (0.6)	8.3 (0.7)
Total dissolved solids (g l ⁻¹)	0.018 (0.002)	0.018 (0.002)	0.015 (0.001)	0.015 (0.001)	0.022 (0.003)	0.023 (0.001)	0.022 (0.002)	0.022 (0.001)
Water velocity (m s)	0.03 (0.06)	0.88 (0.27)	0.02 (0.03)	0.73 (0.15	0.15 (0.13)	0.99 (0.27)	0.16 (0.09)	0.74 (0.20)
Width (m)*	1.17 (0.32)	0.68 (0.21)	1.64 (0.44)	0.98 (0.12)	1.83 (0.33)	1.55 (0.44)	1.78 (0.38)	2.08 (0.38)
Depth (m)*	0.22 (0.08)	0.10 (0.02)	0.17 (0.04)	0.08 (0.02)	0.26 (0.08)	0.20 (0.02)	0.24 (0.07)	0.14 (0.02)

Table 1. Mean values and SD (in parentheses) of physical and chemical characteristics for each mesohabitat types (n = 16) of each forested (F1 and F2) and deforested (D1 and D2) stream in Analândia, SE Brazil.

n = 4 for each mesohabitat types of each forested and deforested stream.

were adjusted following the procedures of Greenhouse–Geiser and Huynh–Feldt (Winer et al. 1971). The univariate model used was:

$$Yijk = \mu + A_i + B_{j(i)} + C_k + AC_{ik} + CB_{kj(i)} + error$$
(1)

where A_i is the effect of Streams, $B_i(i)$ are the reaches nested within streams and Ck is the effect of Time (factor within objects). We evaluated the effect of time for colonization, because along the process of leaf pack colonization macroinvertebrate communities can change (Tanaka et al. 2006; Reid et al. 2013). We used this partly nested design because there were not enough replicates to directly test stream type (i.e. forested vs. deforested); therefore, we used reaches within streams as replicates for the analyses following Quinn and Keough (2002), so that the four streams were levels within the factor Streams. When the effect of Streams was significant, but no interaction with Time was recorded, we used orthogonal contrasts (Winer et al. 1971), to test the following hypotheses within the main hypothesis 1 (H1): (1) there are differences in beta diversity between forested and deforested streams; (2) there are differences in beta diversity between the two forested streams; (3) there are differences in beta diversity between the two deforested streams. Multivariate patterns were visualized using nonmetric multidimensional scaling (MDS) based on the similarity matrix calculated for each index. To test hypothesis 2 (H2), we partitioned the beta diversity calculated using Sørensen's index into the additive components of turnover and nestedness following Baselga (2010). We calculated multiple-site dissimilarities for each stream in R (R Development Core Team 2014) using the function betapart (Baselga & Orme 2012).

Results

Although streams used in this study had different levels of human influence, physicochemical characteristics of

the stream water varied little among them (Table 1). A total of 56,071 macroinvertebrates were identified to family, distributed in 30 taxa (Table 2), with slightly more taxa recorded in the forested (F1 = 24, F2 = 19) than in deforested streams (D1 = 18, D2 = 17). Estimates of beta diversity using Sørensen's index (which favors rare taxa) resulted in significant stream effects (Table 3, Figure 1), with higher within-stream beta diversity of macroinvertebrate in streams without forested riparian zones when compared to forested streams (orthogonal contrast: $F_{1,12} = 13.94$, p = 0.003). These differences were consistent along the study, with no significant effects of time (Table 3). Within each stream type, no differences in beta diversity were observed (between forested streams - orthogonal contrast: $F_{1,12} = 0.817$, p = 0.384 and between deforested streams - orthogonal contrast: $F_{1,12} = 0.085$, p = 0.776). These results can be observed in the MDS analysis, where samples of pools and riffles from streams without forested riparian zones are more separated than those from forested streams, indicating higher within-stream dissimilarity in macroinvertebrate assemblage composition in the former (Figure 2).

When we included abundance data on beta diversity estimates, the results depended on the weight given to dominant taxa. Estimates of beta diversity that balanced the contribution of rare and dominant taxa using the Horn index did not differ between streams (Table 3), and was constant along the studied period (Figure 1). However, when more weight was given to dominant taxa using the Morisita-Horn index, we found significant effects of Stream and Time along the experiment (Table 3, Figure 1). Deforested streams presented higher beta diversity than forested ones (orthogonal contrast: $F_{1,12} = 7.26$, p = 0.010), whereas no differences were found between streams of the same type (orthogonal contrast: between forested streams: $F_{1,12} = 3.776$, p = 0.070; between deforested streams, $F_{1,12} = 2.692$, p = 0.126). Higher dissimilarities were thus found between mesohabitats in deforested streams than in forested ones (Figure 2). In addition, beta

Table 2.	Relative abundances (%) of macroinvertebrate taxa in pools and riffles of forested (F1 and F2) and deforested (D1 and	d D2)
streams	n Analândia, SE Brazil.	

Taxon Pool Riffle Pool Riffle Pool Riffle Pool Riffle Tridoptaria - - - - 0.33 6.02 0.45 15.26 Philopotamidae - - - - 0.04 - - Glossoomanidae - - - 0.42 0.09 - - Glossoomanidae 0.26 0.10 0.30 0.16 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - <th></th> <th></th> <th>F1</th> <th>F</th> <th colspan="2">F2</th> <th>1</th> <th colspan="2">D2</th>			F1	F	F2		1	D2	
Tridoptera victorspychidae 0.33 5.76 0.12 6.07 0.35 6.02 0.45 15.26 Philopotamidae 0.04 Glossosomatidae 0.05 0.06 Odontoceridae 0.26 0.10 0.30 0.16 Polycentropodidae 0.03 0.01 Polycentropodidae 0.03 0.01 Polycentropodidae 0.03 0.01 Polycentropodidae 0.08 0.01 0.07 0.28 0.44 0.03 0.00 0.61 Tipulidae 0.02 0.48 0.12 0.57 0.28 0.83 0.10 0.40 Psychodidae 0.01	Taxon	Pool	Riffle	Pool	Riffle	Pool	Riffle	Pool	Riffle
Hydropsychidae 0.33 5.76 0.12 6.07 0.35 6.02 0.45 15.26 Philopotamidae 0.06 0.06 Odontoceridae 0.42 0.09 Calamoceratidae 0.03 0.01 Polycentropodidae 0.03 0.01 Polycentropodidae 0.03 0.01 Diptera	Trichoptera								
Philopotamidae - - - - 0.04 - - Glossosomatidae - - - 0.06 - 0.06 Odontoceridae 0.26 0.10 0.30 0.16 - - - - Hydrobiosidae 0.03 - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Hydropsychidae	0.33	5.76	0.12	6.07	0.35	6.02	0.45	15.26
Glossosomatidae - - - - 0.06 - 0.06 Odontoceridae 0.26 0.10 0.30 0.16 - - - - Hydrobiosidae 0.03 - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Philopotamidae	—	—	—	—	—	0.04		
Odontoceridae - - - 0.42 0.09 - - Calamoceratidae 0.26 0.10 0.30 0.16 - - - - Hydrobiosidae 0.03 - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - <td>Glossosomatidae</td> <td>_</td> <td>—</td> <td>_</td> <td>—</td> <td>_</td> <td>0.06</td> <td></td> <td>0.06</td>	Glossosomatidae	_	—	_	—	_	0.06		0.06
Calamoceratidae 0.26 0.10 0.30 0.16	Odontoceridae	_	—	_	—	0.42	0.09		
Hydrobiosidae 0.17 0.04 P Polycentropodidae 0.03 0.01	Calamoceratidae	0.26	0.10	0.30	0.16	_			
Polycentropodidae 0.03 0.01 </td <td>Hydrobiosidae</td> <td>—</td> <td>0.17</td> <td>—</td> <td>0.04</td> <td>—</td> <td>—</td> <td></td> <td></td>	Hydrobiosidae	—	0.17	—	0.04	—	—		
Hydroptilidae - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Polycentropodidae	0.03	—	0.01	—	_			
Diptera Chironomidae 88.15 52.24 80.04 51.26 84.72 34.76 94.02 40.48 Ceratopogonidae 0.08 0.10 0.17 0.23 0.14 0.03 0.30 0.61 Tipulidae 0.02 0.03 0.01 0.06 0.01 0.05 0.06 Psychodidae - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Hydroptilidae	_	0.01	_	_	_		_	
Chironomidae 88.15 52.24 80.04 51.26 84.72 34.76 94.02 40.48 Ceratopogonidae 0.08 0.10 0.17 0.23 0.14 0.03 0.61 Tipulidae 0.02 0.03 0.01 0.06 — 0.01 0.05 0.06 Empididae 0.20 0.48 0.12 0.57 0.28 0.83 0.10 0.40 Psychodidae - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Diptera								
Ceratopogonidae 0.08 0.10 0.17 0.23 0.14 0.03 0.30 0.61 Tipulidae 0.02 0.03 0.01 0.06 0.01 0.05 0.06 Empididae 0.20 0.48 0.12 0.57 0.28 0.83 0.10 0.40 Psychodidae 0.01	Chironomidae	88.15	52.24	80.04	51.26	84.72	34.76	94.02	40.48
Tipulidae 0.02 0.03 0.01 0.06 0.01 0.05 0.06 Empididae 0.20 0.48 0.12 0.57 0.28 0.83 0.10 0.40 Psychodidae 0.01	Ceratopogonidae	0.08	0.10	0.17	0.23	0.14	0.03	0.30	0.61
Empididae 0.20 0.48 0.12 0.57 0.28 0.83 0.10 0.40 Psychodidae - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -<	Tipulidae	0.02	0.03	0.01	0.06	_	0.01	0.05	0.06
Psychodidae - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - <	Empididae	0.20	0.48	0.12	0.57	0.28	0.83	0.10	0.40
Simulidae 2.23 23.18 0.51 13.64 1.54 36.18 0.30 29.40 Coleoptera	Psychodidae	_	0.01	_	_	_		_	
Coleoptera Elmidae 5.42 7.78 8.06 16.23 5.65 9.29 0.80 3.84 Dytiscidae 0.08 0.01 0.02 0.54 - 0.01 - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - - -<	Simuliidae	2.23	23.18	0.51	13.64	1.54	36.18	0.30	29.40
Elmidae 5.42 7.78 8.06 16.23 5.65 9.29 0.80 3.84 Dytiscidae 0.08 0.01 0.02 0.54 0.01 Noteridae 0.01 0.00 0.02 0.02 0.02 0.02 0.03 0.02 0.03 0.02 0.03 0.02 0.03 0.02 0.007 0.02 0.02 0.02 0.02 0.02 0.01 0.02 0.02 0.01	Coleoptera								
Dytiscidae 0.08 0.01 0.02 0.54 0.01 Noteridae 0.01 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.0	Elmidae	5.42	7.78	8.06	16.23	5.65	9.29	0.80	3.84
Noteridae 0.01	Dytiscidae	0.08	0.01	0.02	0.54	_	0.01	_	
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Gripopterygidae 0.70 4.78 0.36 2.55 0.35 0.79 0.25 0.38 Perlidae - 0.05 - 0.06 - 0.19 - 0.02 Odonata - - 0.06 - 0.19 - 0.02 Odonata - - 0.07 0.27 0.08 - - 0.10 0.02 Coenagrionidae 0.03 0.01 0.02 - 0.21 - 0.10 - Libellulidae - - - - 0.07 - 0.02 Ephemeroptera - - - - 1.88 2.38 0.15 0.19 Caenidae - - - - - - - - - - - - - - - - - - - - - - - - - - - -	Plecoptera								
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Libellulidae 0.07 0.02 Ephemeroptera 1.88 2.38 0.15 0.19 Baetidae	Coenagrionidae	0.03	0.01	0.02	—	0.21		0.10	_
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Baetidae 0.02 0.03 1.88 2.38 0.15 0.19 Caenidae	Ephemeroptera								
Caenidae	Baetidae	0.02	0.03	_	—	1.88	2.38	0.15	0.19
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Megaloptera OUS OUS <th< td=""><td>Leptophlebiidae</td><td>0.09</td><td>0.83</td><td>0.01</td><td>0.03</td><td>_</td><td></td><td></td><td></td></th<>	Leptophlebiidae	0.09	0.83	0.01	0.03	_			
Corydalidae - 0.02 - 0.02 - - 0.06 Oligochaeta 1.47 3.43 9.90 8.09 3.98 9.13 3.29 9.16	Megaloptera								
Oligochaeta 1.47 3.43 9.90 8.09 3.98 9.13 3.29 9.16	Corydalidae	_	0.02	_	0.02	_			0.06
	Oligochaeta	1.47	3.43	9.90	8.09	3.98	9.13	3.29	9.16

Table 3. Repeated-measures ANOVA comparing the effects of stream and time on the similarity indexes analyzed.

		Søre	Sørensen		Horn		Morisita–Horn	
Source of variation	df	MS	F	MS	F	MS	F	
Between subjects	Between subjects							
Stream	3	0.121	4.96*	0.057	2.39	0.272	4.58*	
Error 1	12	0.024		0.024		0.059		
Within subjects								
Time	3	0.023	0.96	0.021	1.56	0.171	6.07**	
Time $ imes$ Stream	9	0.045	1.87	0.017	1.27	0.042	1.49	
Error 2	36	0.024		0.014		0.028		

*p < 0.05; **p < 0.005

diversity was higher in the beginning of the experiment, but with similar patterns between stream types (Figure 1).

As expected (H2), the partitioning of beta diversity using presence-absence data indicated that the nestedness component was higher in deforested streams (D1 = 53%, D2 = 39%), than in streams with forested riparian zones (F1 = 21%, F2 = 28%), where the turnover component was higher.

Discussion

This study showed that riparian deforestation can reduce within-stream similarity of macroinvertebrate assemblages, mainly by taxon loss and alteration of dominant taxa. Within-stream beta diversity estimated by both Sørensen and Morisita-Horn indices were higher in deforested streams, indicating differential effects of riparian deforestation and stream habitat alterations on macroinvertebrate assemblage structure, and these patterns did not change along the leaf litter colonization trajectories. In particular, riparian deforestation causes channel narrowing (Sweeney et al. 2004), affects hydrology and discharge regimes (Pringle & Benstead 2001), increases rates of runoff and sediment delivery (Allan 2004; Dudgeon et al. 2006) and degrades stream habitats (Iwata et al. 2003). These events result in streambed patches that experience different amounts or types of disturbance or remain undisturbed (Matthaei et al. 1999). Along the



Figure 1. Complementary form of Sørensen, Horn, and Morisita–Horn indices of stream macroinvertebrate samples obtained in riffle and pool mesohabitats of deforested and forested streams.

studied period, pools in deforested streams were visually more unstable mainly after flood events, changing their physical structure due to sediment accumulation, so that the litter bags were covered with sediment during these events, whereas riffles remained more stable. Erosion, transport and accumulation of sediments within streams often is associated with habitat modifications, which can have detrimental effects on stream communities (Sánchez-Argüello et al. 2010). For example, Hogg and Norris (1991) found that fine sediment deposition following peak flows events was the major cause of low macroinvertebrate numbers and



Figure 2. MDS ordination using Sørensen, Horn, and Morisita– Horn indices (RD = riffles/deforested, PD = pools/deforested; RF = riffles/forested, PF = pools/forested).

species richness in pools. Also, Harrison et al. (2007) found that fine sediment deposition resulted in lower abundances and diversity in macroinvertebrate assemblages. Increases of fine sediment in streams generally modify substrate suitability for some taxa, increasing drift due to substrate instability, impairing respiration due to low oxygen concentrations in fine sediment accumulation and feeding due to a reduction in the energetic value of periphyton and prey density (Wood & Armitage 1997; Buendia et al. 2013). In our study, fine sediment accumulation and sedimentation of the litter bags in pools within deforested streams contributed to a higher differentiation of macroinvertebrate assemblage composition between riffle and pool mesohabitats, resulting in higher beta diversities.

Other studies also examined patterns of beta diversity in relation to anthropogenic disturbance. For example, Hawkins et al. (2015) found higher macroinvertebrate beta diversity in temperate disturbed streams when compared to reference streams. Fugère et al. (2016) compared forested and agricultural streams in tropical Africa and found higher macroinvertebrate beta diversity across the agricultural landscape than inside the forest. Al-Shami et al. (2013) examined the effects of environmental factors and geographical variables on beta diversity of macroinvertebrate assemblages within tropical streams in Peninsular Malaysia, finding lower values of beta diversity with low water pH. However, there is still a gap of knowledge on how anthropogenic degradation affects the beta diversity of stream macroinvertebrate communities in Neotropical streams (Al-Shami et al. 2013).

In this study, changes in beta diversity using distinct indices indicated different processes in the responses to anthropogenic disturbances. Higher beta diversity within deforested streams was influenced by different rare and dominant taxa of macroinvertebrate, supporting H1. When considering only taxon identity with the Sørensen index, the effects of pool sedimentation was related to the loss of taxa, resulting in impoverished communities, where the remaining taxa constitute a fraction of the taxa originally present, increasing differences between habitats. When including abundance information, only the Morisita-Horn index was significant, whereas the Horn index, which balances contribution of rare and dominant taxa, did not differ among the studied streams. Significant results with the Morisita-Horn index showed that the contribution of dominant taxa was also important along the experimental study, and the MDS showed that pool communities converged to similar macroinvertebrate assemblages, whereas riffle communities were largely different, mainly among riffles from deforested streams (Figure 2). This indicates that highdensity taxa characterized the studied pools, resulting in higher similarity, even though pools in deforested streams presented lower taxon richness. Higher differentiation among riffle communities in deforested streams could be due to the dominance of different taxa in each riffle (e.g. Heino & Soininen 2010), since a high similarity in taxon composition was found using the Sørensen index. This dominance could be due to smaller effects of high-flow events, where only a few opportunistic taxa can thrive; in fact, lower disturbance can increase local dominance by distinct taxa (Lake 2000; Tonkin et al. 2013).

Natural and anthropogenic disturbances can influence the processes resulting in variation among macroinvertebrate assemblages. Within-stream beta diversity in deforested streams was more related to the nestedness component than forested streams due to the effects of disturbances (e.g. Baselga 2010), whereas forested streams presented higher components of turnover, indicating that differences between mesohabitats were more related to specific assemblages colonizing each mesohabitat (e.g. Beisel et al. 1998; Silva et al. 2014). These results are in accordance with Gutiérrez-Cánovas et al. (2013), who evaluated beta diversity of macroinvertebrates among streams subject to different types of stressors; they found higher turnover among streams along natural environmental gradients, but higher nestedness among streams subject to anthropogenic stress gradients. Therefore, both among- and within-stream differentiation among invertebrate assemblages can respond to anthropogenic disturbances, mainly due to an impoverishment of faunal communities.

Our results suggest that changes at the watershed scale and deforestation of the riparian zones potentially influence the natural dynamics of stream mesohabitats and heterogeneity. Higher within-stream beta diversity of macroinvertebrate assemblages in deforested streams was related with higher physical instability and sedimentation of pools, and could be an indicator of habitat loss and reduced taxon richness at the stream scale. The usage of beta estimators of different orders was a complementary approach for the interpretation of beta diversity and to understand factors contributing to heterogeneity in forested and deforested streams, indicating changes both due to a reduced number of taxa and changes in dominance patterns among mesohabitats. This approach was robust enough to detect differences even using a selective method of sampling (litter bags) and coarse identification level (family). Therefore, the results of our study support the conclusions of Hawkins et al. (2015) on impacted and reference temperate streams (but see Passy & Blanchet 2007; Johnson & Angeler 2014), suggesting that changing the focus from alpha diversity (commonly used in monitoring studies, but always subject to reference streams for interpretation) to beta diversity can potentially identify changes of differentiation diversity within the same stream, and thus degradation of the whole stream ecosystem. Our results emphasize the need to better understand how different mesohabitats and their associated biological assemblages within streams respond to anthropogenic change, particularly in tropical regions.

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