

Influence of discharge patterns on temporal variation of macroinvertebrate communities in forested and deforested streams in a tropical agricultural landscape

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Received: 5 October 2016 / Revised: 8 March 2017 / Accepted: 10 March 2017 / Published online: 17 March 2017
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Abstract Deforestation of riparian forests can directly influence stream macroinvertebrate communities, through changes in resource availability, habitat quality, and hydrological alterations. Here we evaluated whether mean discharge and discharge coefficient of variation (CV), estimated over a 15-month study, influenced forested and deforested stream macroinvertebrate communities. Higher diversity and mean discharge were recorded in deforested streams, and community composition was strongly related to mean discharge. Streams formed a gradient of both mean discharges and discharge CV, which both influenced patterns of diversity. Discharge CV negatively influenced diversity in a nonlinear model, whereas both mean discharge and discharge CV influenced differentiation of macroinvertebrate communities among five sampling occasions. Similarity among sampling times within each stream estimated by the Morisita–Horn index decreased with increasing mean discharge, whereas response to CV was quadratic, with higher similarity at intermediate values and lower similarity

at more extreme values. These results suggest that stability of stream macroinvertebrate communities display different responses to mean discharge and discharge CV, and that hydrological alterations can interact with land use changes to determine community dynamics at local scales.

Keywords Stability · Riparian forests · Disturbance · Rural landscapes

Introduction

Land use changes for agriculture has large impacts on rural landscapes, with a strong influence on stream ecosystem functioning and water quality and quantity (Allan, 2004; Clapcott et al., 2012; Piggott et al., 2015). Streams in watersheds dominated by agricultural use are subject to changes in biogeochemistry, habitat simplification, increased pollution, canopy opening, and hydrological alterations (Quinn et al., 1997; Allan, 2004; Recha et al., 2012; Woodward et al., 2012; Cooper et al., 2013). Most effects are due to reductions in forest cover along catchments, or direct deforestation of riparian zones (Sweeney et al., 2004; Iñiguez-Armijos et al., 2014). Riparian forests have strong effects on stream ecosystems, as they are the interface between terrestrial and aquatic systems, buffering streams due to increased infiltration rates, sediment retention, increasing shade, and providing

Handling editor: Verónica Jacinta Lopes Ferreira

Electronic supplementary material The online version of this article (doi:10.1007/s10750-017-3163-x) contains supplementary material, which is available to authorized users.

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allochthonous food and shelter resources (Benstead & Pringle, 2004; Sweeney et al., 2004; Lorion & Kennedy, 2009; Coe et al., 2011; Deegan et al., 2011; de Souza et al., 2013; Fernandes et al., 2014; Bleich et al., 2015). Therefore, deforestation for agricultural activities results in direct and indirect physical, chemical, and biological effects on streams (Gregory et al., 1991; Miserendino et al., 2011).

These effects may result from changes at both the catchment and riparian scales, since different stressors can have effects at different scales on stream ecosystem functioning and aquatic biological communities (Roth et al., 1996; Feld, 2013; Ligeiro et al., 2013; Tanaka et al., 2016). The prediction of biological responses to these stressors, however, is complex, because the organisms, and thus assemblages, can present linear or nonlinear responses to gradients of anthropogenic disturbance (Norris & Thoms, 1999; Villeneuve et al., 2015). For example, benthic macroinvertebrate communities have long been used as bioindicators of stream condition and environmental impacts (Bonada et al., 2006; Buss et al., 2015), and present a large diversity of traits that facilitate tolerance to aspects such as pollution and altered environmental conditions, and to cope with differential resource availability (Statzner & Bêche, 2010; Lange et al., 2014).

Responses of macroinvertebrates to deforestation are complex and include responses to increased nutrient and pollutant concentrations, reduced dissolved oxygen concentrations, habitat simplification, increased temperatures and primary production, and hydrological alterations (Sponseller et al., 2001; Couceiro et al., 2007; Matthaei et al., 2010; Clapcott et al., 2012; Masese et al., 2014). Streams are dynamic systems, and discharge patterns and flow regimes can directly influence macroinvertebrate communities, either by creating hydrological heterogeneity in flow regimes (Hart & Finelli, 1999; Tickner et al., 2000; Lorion & Kennedy, 2009), or to disturbances caused by high flows (Resh et al., 1988; Townsend et al., 1997). Variation in streamflow regimes on macroinvertebrate communities has been studied by several authors using hydrological indices, including Clausen & Biggs (1997), who verified effects of both average flow conditions and variability (i.e., flood frequency) on biological indices, and Booker et al. (2015), who analyzed a national database of streams in New Zealand and detected influence of gradients in both

low-flow and high-flow magnitude on taxon richness and biotic indices. On the other hand, Townsend et al. (1997) observed that both discharge variation (e.g., coefficient of variation, variance, and flood frequency) and bed movement measures correlated significantly with macroinvertebrate composition, but only the latter measures influenced taxon richness.

The effects of hydrological disturbances on macroinvertebrate diversity can be intensified in deforested watersheds due to effects such as higher sediment delivery and loss of refugia when compared to forested catchments (Stanley et al., 2010). Although these interactions can be common, few studies have evaluated effects of hydrological disturbances between forested and deforested streams, mainly in tropical regions, since hydrological patterns can differ between catchments with distinct land uses. For example, Guzha et al. (2015) compared a pasture-dominated catchment to a primary forested catchment in the Amazon, with higher mean streamflow in the pasture catchment, mainly due to the contribution of peak discharges related to rainstorm events which were propagated faster, resulting in greater event water contribution in the pasture catchment than the forested one.

Understanding the effects of hydrological disturbances on stream biological communities is essential to evaluate climate change effects on lotic ecosystems. In fact, increasing tropical precipitation extremes as expected by climate change models may influence streamflow dynamics, and small tropical streams can become flashier (reviewed in Taniwaki et al., 2016). The effects of these hydrological changes may interact with other stressors such as land use changes, related to agriculture and urbanization intensification, and the effects of such interactions are still poorly known (Carlson et al., 2014; Taniwaki et al., 2016).

Studies evaluating differences of ecological communities to environmental gradients cover mainly spatial variation, with fewer studies evaluating ecological responses to temporal variability across the same sites (Booker et al., 2015). For example, Hawkins et al. (2015) recorded higher beta diversity among disturbed streams than among reference streams, relating this difference to environmental variables associated with disturbances such as pH, total dissolved solids, and total nitrogen concentrations. Reference streams were more similar than would be expected by chance, whereas degraded

streams were more dissimilar than expected. Strong heterogeneity effects on the stability of macroinvertebrate communities were observed by Mykrä et al. (2011) when comparing variation among years in boreal streams, relating these differences to higher availability of refuges against disturbances and food resources in more heterogeneous streams. Therefore, environmental filtering due to increased heterogeneity or due to differential effects of stressors on common versus rare taxa could contribute to higher beta diversity in disturbed streams.

In this study, we evaluated if deforestation of the riparian zones influenced macroinvertebrate community structure and composition in an agricultural landscape in SE Brazil. We sampled forested and deforested streams five times over a period of 15 months to evaluate whether communities were more stable in forested streams, or if taxon turnover was higher in deforested streams. We expected that deforested streams would experience higher variance in discharge patterns, thus influencing community patterns due to higher hydrological disturbance. Since macroinvertebrate community structure can be related to land use patterns rather than local patterns in the region (Tanaka et al., 2016), we also evaluated if patterns recorded were related to a gradient in discharge patterns rather than to a categorical distinction between forested and deforested streams.

Materials and methods

Study area

This study was carried out in low-order streams that drained into the lower Jacaré-Guaçu River watershed, which is part of the Tietê–Jacaré Water Resources Management Unit (UGRHI–13), central region of São Paulo state. The Jacaré-Guaçu River watershed occupies an area of 4108 km² and presents a drainage density of 0.88 km km⁻² (DNAEE/EESC, 1980). The headwaters are about 1040 m asl; the river then flows 148 km until Ibitinga Reservoir, in the Tietê River, at 400 m asl (Instituto de Pesquisas Tecnológicas, 2000). Land use in the UGRHI-13 is mainly agriculture, pasture, and forestry, with only 11.3% of remaining native vegetation (Tundisi et al., 2008). The climate in the lower Jacaré-Guaçu River watershed is tropical wet and dry (Aw) according to Köppen's

classification, with monthly temperatures varying between 19.3 and 25.4°C, and mean annual rainfall of 1260 mm; the dry season extends from April to September (Miranda et al., 2012).

A total of six streams were sampled, three that presented forested riparian zones, Água Quente (21°42'58.70"S, 48°50'2.88"W; riparian forest width = 13.7 m), Macaúba (21°42'18.06"S, 48°44'40.09"W; riparian forest width = 38.3 m), and Queixada (21°43'15.40"S, 48°50'40.37"W; riparian forest width = 16.0 m), and three with deforested riparian zones (riparian forest width = 0.0 m), Cana Dobrada (21°46'56.60"S, 48°46'50.49"W), Jacutinga (21°46'38.47"S, 48°40'46.67"W), and Matinha (21°44'23.24"S, 48°50'19.97"W) (Table 1). All streams studied were first-order streams, with the exception of Jacutinga, a second-order stream. All streams considered were dominated by sandy substrate (>75% of the streambed) and deposited plant debris (>56% of the streambed). Land use in the watersheds was mainly for rural activities (sugarcane and orange plantations, pasture, and farm urban infrastructure). The main cultivar was sugarcane, which varied between 28.1% (Matinha, which also presented most urban infrastructure) and 86.7% (Macaúba), whereas native vegetation cover varied between 4.4% (Matinha) and 20.9% (Queixada) (detailed data on land use/cover for all streams can be found in Tanaka et al., 2015).

Sampling was carried out in 2 years: 2008 in early June (1–8 days without rain before sampling, total of 0.0–0.4 mm cumulative rainfall in the week before sampling; data from Brazilian National Institute of Meteorology), August (7–22 days without rain, 0.0 cumulative rainfall), and early November (0 days without rain, 20.0 mm cumulative rainfall); 2009 in June (0–2 days without rain, 0.4–8.4 mm cumulative rainfall), and August (3 days without rain, 27.0 mm cumulative rainfall). 2009 was atypical because there was no dry season at all, with total rainfall of 1646 mm, whereas in 2008 total rainfall was 1204 mm in São Carlos district, a nearby station (Brazilian National Institute of Meteorology).

Sampling

In each stream, a 100 m reach was marked, and the following variables were obtained on each sampling date with a handheld YSI 556 multiprobe system: pH, dissolved oxygen concentrations (DO), total dissolved solids (TDS), and electrical conductivity (EC,

Table 1 Mean \pm SE values of physical and chemical characteristics of forested and deforested streams studied along five sampling times

Variable	Forested	Deforested	$F_{1,18}$
pH	5.90 \pm 0.163	6.67 \pm 0.163	16.3**
Total dissolved solids (mg l ⁻¹)	17.3 \pm 5.19	35.4 \pm 8.27	2.9 ^{ns}
Dissolved oxygen (mg l ⁻¹)	6.20 \pm 0.693	6.12 \pm 0.528	0.0 ^{ns}
Electrical conductivity (μ S cm ⁻¹)	27.4 \pm 7.31	60.5 \pm 11.32	5.0*
Stream width (m)	0.84 \pm 0.117	1.55 \pm 0.245	5.1*
Stream depth (cm)	7.91 \pm 0.846	13.95 \pm 1.334	12.1**
Discharge (m ³ s ⁻¹)	0.008 \pm 0.0017	0.036 \pm 0.0075	11.0**
Discharge CV ^a	0.67 \pm 0.121	0.35 \pm 0.060	

Data were previously ln-transformed for analyses, and back-transformed values are shown here. No interaction between stream condition and sampling dates were recorded, so only results of *F*-tests for stream condition are indicated

^{ns} $P > 0.05$; * $P < 0.05$; ** $P < 0.01$

^a Differences not significant according to a *t* test ($t = 2.369$, $df = 4$, $P = 0.077$)

standardized at 25°C). Discharge during each sampling date was determined at the downstream end of the reach, by first measuring mean water velocities with a flowmeter (precision = 0.1 m s⁻¹) positioned at 60% of maximum depth (Gordon et al., 2004). Cross-sectional area of the water was then determined by measuring stream channel width, and later measuring stream depth at ten equidistant points along the stream wetted width; discharge was estimated with the velocity-area method (Gordon et al., 2004), using the equation $Q = AV$, where Q is the discharge (m³ s⁻¹), A is the cross-sectional area (m²) estimated by mean depth \times total stream width, and V is the average velocity (m s⁻¹). Macroinvertebrates were sampled with a Surber sampler (area = 0.09 m², mesh = 250 μ m), with three random samples from each reach. In the laboratory, each sample was examined on a transilluminated white tray, and macroinvertebrates were picked by hand. Insects were identified to family, and other taxa to higher levels. Although this level of taxonomic resolution can underestimate true diversities, studies in the region indicate that patterns typically recorded at the genus level are also recorded at the family level (Corbi & Trivinho-Strixino, 2006; Suriano et al., 2011).

Data analysis

In June 2008 we could not sample Matinha; in August 2008 one sample was lost from Cana Dobrada and Queixada, whereas in November 2009 one sample was

lost from Água Quente and Jacutinga, resulting in 83 samples. Therefore, we considered each stream and sampling date as a replicate, using the mean values for each stream ($n = 29$). Means were calculated for ln-transformed densities to obtain normality, and back-transformed for the statistical analyses; values were rounded to the nearest integer to calculate diversity and overlap indices (see below). Stream physical and chemical characteristics, and macroinvertebrate community descriptors, were analyzed with a two-way ANOVA, with fixed effects (stream condition vs sampling dates), and streams as replicates. Community composition was evaluated by two steps. First, we carried out a PERMANOVA with two fixed factors (stream condition vs sampling dates); the resemblance matrix was calculated with ln-transformed density values using the Bray–Curtis index to balance the contribution of rare and dominant species (Clarke, 1993); analyses were carried out in Primer/Permanova 6.0. To evaluate the effects of environmental variables on community composition, we carried out a Canonical Correspondence Analysis (CCA) on ln-transformed density values. To avoid multicollinearity, independent variables were previously analyzed with Pearson's correlation coefficient, and the following variables were selected: pH, DO, EC, and discharge. The remaining variables were significantly correlated ($P < 0.001$) to the selected variables: TDS and EC ($r = 0.811$), stream depth and discharge ($r = 0.733$), stream width and EC ($r = 0.618$). The complete CCA model was evaluated with a Monte Carlo permutation

Table 2 Mean \pm SE values of macroinvertebrate community descriptors of forested and deforested streams studied along five sampling times

Variable	Forested	Deforested	$F_{1,19}$
Density (ind 0.09 m ⁻²)	103.9 \pm 26.05	188.0 \pm 56.10	1.5 ^{ns}
Taxon richness	11.3 \pm 1.25	14.6 \pm 2.09	2.3 ^{ns}
Rarefied taxon richness	3.85 \pm 0.25	4.80 \pm 0.50	3.7 ^{ns}
Shannon diversity index (H')	0.92 \pm 0.08	1.24 \pm 0.13	5.6*
Pielou evenness index (J')	0.39 \pm 0.03	0.48 \pm 0.03	5.1*
Simpson dominance index (D)	0.59 \pm 0.04	0.45 \pm 0.05	7.3*

No interaction between stream condition and sampling times were recorded, so only results of F -tests for stream condition are indicated

^{ns} $P > 0.05$, * $P < 0.05$

test under reduced model (999 permutations), and we carried out a stepwise analysis to evaluate which independent variables were significantly related to community composition (200 permutations) following Legendre & Legendre (2012). Analyses were carried out in R (R Development Core Team, 2014), using the “vegan” package (Oksanen et al., 2013).

Since only stream discharge was significantly related to community composition (see “Results” section), we evaluated if changes in community composition among sampling dates would be related to this variable. Differences in community composition were estimated for each stream following the framework proposed by Chao et al. (2008) and Jost et al. (2011), by calculating multiple-assemblage overlap measures C_{qN} (similarity indices): the Sørensen index ($q = 0$), the Horn index ($q = 1$), and the Morisita–Horn index ($q = 2$). $n = 5$ for all streams, except for Matinha where $n = 4$. We used the “SpadeR” package to estimate all indices (Chao et al., 2015). We related all indices to estimated stream discharge means and coefficients of variation using linear or quadratic functions. All univariate analyses were carried out using Systat 13.0 software. Significance levels used were $P < 0.05$.

Results

Physical and chemical characteristics of the studied streams varied consistently along the studied period (Table 1), with no significant interactions between Stream condition and Sampling dates ($P > 0.50$ for all tests). Similar values were recorded for TDS and DO

in forested and deforested streams, whereas higher values of pH, EC, stream width, stream depth, and discharge were recorded in deforested streams (Table 1). In fact, EC values were 2.2 times higher and discharge was 4.5 times higher in deforested streams than in forested ones. No variation in TDS, EC, stream width, stream depth, and discharge was recorded along the studied period, and only higher values of DO concentrations were recorded in June 2009, and lower values of pH in August 2009. Finally, we compared the coefficient of variation of discharges calculated among sampling dates for each stream, but there were no significant differences (Table 1); however, a trend for lower variation in deforested streams was observed ($t = 2.37$, $df = 4$, $P = 0.077$); discharge CV varied between 0.25 and 0.91.

A total of 19,004 specimens distributed across 46 taxa were recorded (Online Appendix). Three taxa constituted almost 80% of the total fauna: Chironomidae (45.5%), Oligochaeta (18.9%), and Simuliidae (15.5%). Densities in forested and deforested streams did not differ significantly (Table 2), and densities were higher in June 2009 (318.4 ± 91.86 , mean \pm SE) than in the other sampling dates (99.1 ± 23.71) (Tukey HSD test). Taxon richness and rarefied taxon richness (estimated for 22 individuals) did not differ between stream condition types (Table 2), but higher taxon richness was observed in June 2009. However, this pattern could be due to higher densities recorded, since no differences among sampling times were detected for rarefied taxon richness. All diversity indicators were significantly higher in deforested streams, with no significant variation along sampling dates (Table 2). Also, no

significant differences of community differentiation (mean dissimilarity among sampling dates) were observed between forested and deforested streams (t test, $P > 0.15$ for all cases), either for the Sørensen (total range 0.18–0.41), Horn (0.01–0.22), or Morisita–Horn (0.02–0.26) indices.

PERMANOVA analysis confirmed that temporal differences were similar for both stream types (interaction stream condition \times sampling time: $F_{4,19} = 0.67$, $P = 0.880$). However, both main effects were significant, sampling time ($F_{4,19} = 1.96$, $P = 0.016$) and Stream condition ($F_{1,19} = 2.90$, $P = 0.022$). The first two axes of the CCA were responsible for 74.2% of the variation explained by the full model, with a significant relationship between community composition and independent variables ($F_{4,24} = 1.63$, $P = 0.026$). The first axis explained 51.3% of this variation, and was mainly related to discharge and pH (Fig. 1). Thus, a separation between samples of streams in relation to stream discharge was observed along the first axis, with samples from two deforested streams (Cana Dobrada and Jacutinga) presenting positive scores, whereas all samples from forested streams plus Matinha (a deforested stream), presented negative scores (Fig. 1). The second axis explained 22.9% of the model variation, and was positively related to EC and negatively related to DO

concentrations, separating samples from one forested stream with higher DO concentrations from the other forested streams and Matinha, where lower DO concentrations and higher EC were observed (Fig. 1). However, the stepwise analysis indicated that only discharge was significantly related to community composition ($P = 0.004$), with less influence from the other variables.

To evaluate the effects of discharge in the studied communities, we related diversity and community differentiation estimated for each stream to observed mean discharge and coefficient of variation (discharge CV) among sampling dates. There were no significant linear relationships between taxon richness, Shannon diversity, and Simpson dominance indices and mean discharges. However, exponential relationships between Shannon and Simpson indices in relation to discharge CV were observed, with decreasing diversity and increasing dominance with higher variation in discharge (Fig. 2).

Community differentiation depended on the weight given to taxon abundances, since no significant relationship was observed for Sørensen and Horn indices (Fig. 3). However, a significant negative linear relationship between the Morisita–Horn index and mean discharge was recorded, with decreasing similarity of communities when mean discharge is

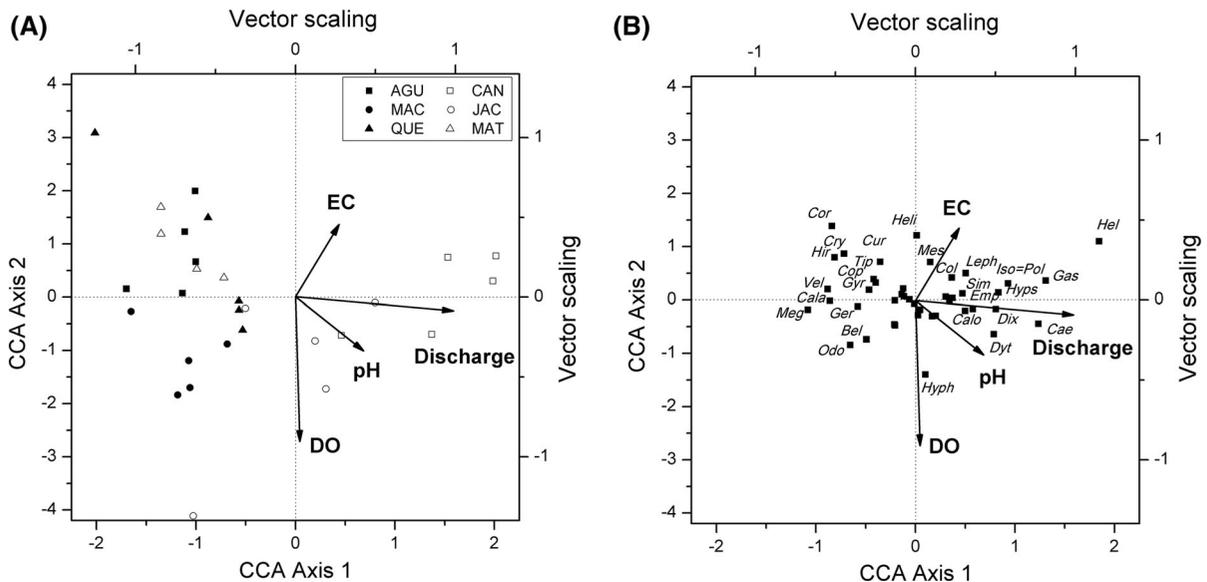


Fig. 1 Results of CCA ordination showing biplots of (A) sites in relation to independent variables (*solid symbols* forested streams, *open symbols* deforested streams), and (B) taxa in

relation to independent variables. *Symbols* as in Table 2; taxa near the origin are not indicated for clarity

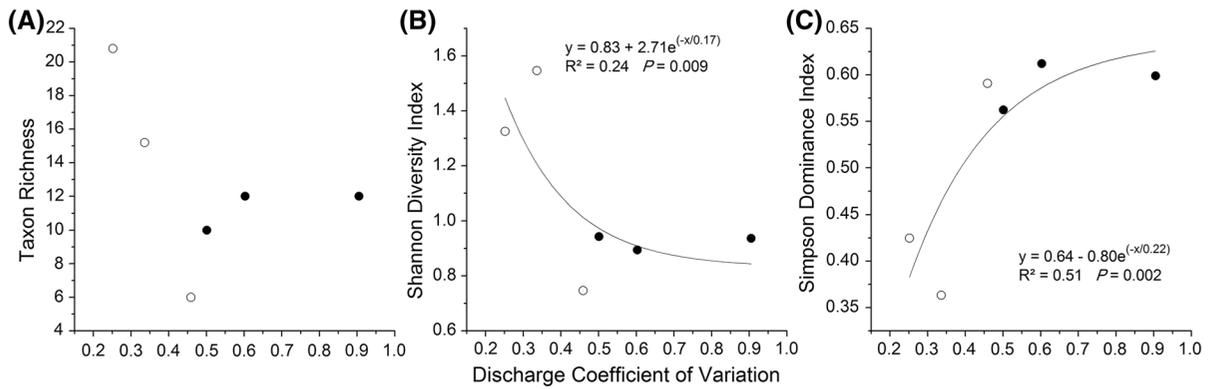


Fig. 2 Relationship between mean diversity indicators (taxon richness, Shannon–Wiener diversity index, Simpson dominance index) and discharge coefficient of variation estimated for forested (*solid symbols*) and deforested (*open symbols*) streams along five sampling dates

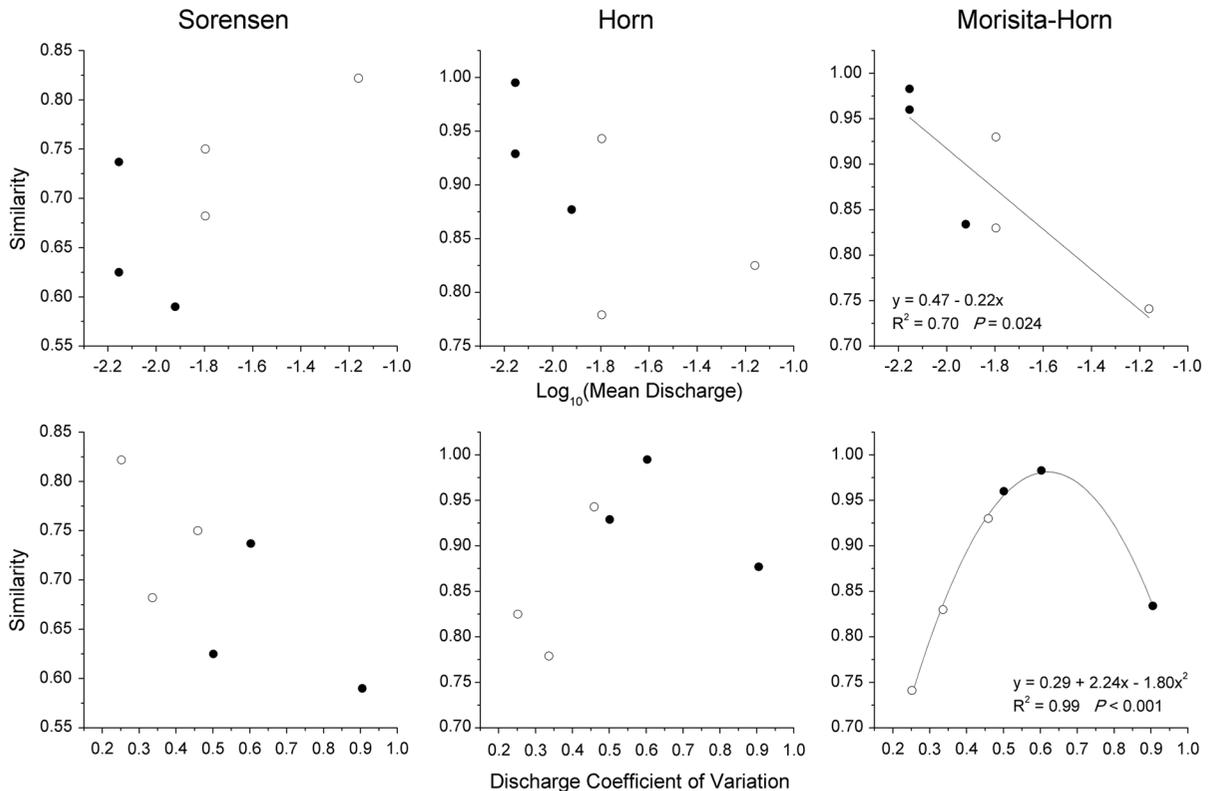


Fig. 3 Relationship between mean similarities (Sørensen, Horn, Morisita–Horn indices) of macroinvertebrate communities estimated for forested (*solid symbols*) and deforested (*open symbols*) streams along five sampling dates, and mean discharge (*upper panels*) and discharge coefficient of variation (*lower panels*)

increasing (Fig. 3). Finally, a quadratic relationship between the Morisita–Horn index and discharge CV was observed, with increasing similarity of

communities with increasing variation in discharge, but decreased similarity at very high (0.90) discharge CV (Fig. 3).

Discussion

Forested and deforested streams displayed no temporal variation in physical and chemical characteristics, although differences between stream conditions were recorded. Deforested streams that displayed higher values in EC and pH, were both wider and deeper, and discharge was higher than in forested streams. An opposite pattern in channel structure was found in pasture streams (narrower) versus forested streams (wider) in New Zealand (Davies-Colley, 1997) and the USA (Sweeney et al., 2004), due to encroachment of the channel margins by grasses in deforested streams. However, studies in Amazon streams found that pasture streams were generally wider and deeper than forested streams, with higher EC and pH values as observed in our study, although mean discharges did not differ (Neill et al., 2006; Deegan et al., 2011). Therefore, changes in channel structure due to deforestation can be variable, depending on factors such as colonization by grasses that influence sediment deposition patterns.

Despite these differences in water quality and channel structure, similar values of taxon richness were recorded between stream types, and only evenness significantly differed between stream types, with higher dominance in forested streams, although this relationship was related to discharge variation (Fig. 3). Similarly, no differences in macroinvertebrate richness were observed by Moraes et al. (2014) when comparing streams with different riparian forest widths in south Brazil, although differences in composition were detected. Our study showed that variation in macroinvertebrate community composition among streams in a tropical rural landscape is related to changes in relative abundances, and not changes in macroinvertebrate richness, in response to discharge variation. Also, these responses form a gradient in relation to discharge variation, even though the presence of riparian forests represented a categorical variable.

Discharge variation displayed a weaker relationship with macroinvertebrate species richness and trait distribution than bed movement measurements in streams in New Zealand; also, bed movement measurements were not correlated with discharge variation variables such as discharge CV, discharge variance, and flood frequency, suggesting that these different types of variables describe distinct aspects of disturbance, and that they may be correlated only when sites had similar particle size distributions

(Townsend et al., 1997). Regarding the relationship between discharge variation and relative abundances, Mykrä et al. (2011) did not find a relationship between community stability (measured as among-year similarity based on Bray–Curtis dissimilarity) and flow variability (estimated as Euclidian distances among years based on stream depth and current velocity). However, effects of habitat heterogeneity on stability were reported, and the authors related these results to the availability of both food resources and refuges against disturbances. Our studied streams displayed low habitat heterogeneity, with sandy streambeds and a few larger particles within the studied reaches, indicating that discharge CV could be an adequate variable to describe effects of disturbance on benthic communities, independently of habitat heterogeneity.

Hydrological variables can influence community composition and dynamics. For example, in a study on New Zealand streams, macroinvertebrate community changes were related to both time since a high-flow event (enough to result in bed movement) and to mean flow in the previous 60 days, so that a larger proportion of individuals and taxa assigned to rapid flow categories were observed initially, but were replaced by low-flow categories as the streams returned to normal flows (Greenwood et al., 2016). However, since the indices used in their study were weighted by abundance, it was not possible to determine if changes were due to taxon replacement or differences in abundance of generalist taxa. When comparing streams, dominance of slow flow categories of invertebrates was reported at sites with increased flow stability and a higher proportion of agricultural land use.

Contrary to our expectations, no significant differences in mean CV discharge were observed between stream types; although mean values were almost two times higher in forested streams, only a trend for these differences was observed ($P = 0.077$). The only significant relationship between overlap measures and discharge patterns was recorded using the Morisita–Horn index, which is more sensitive to dominant taxa (Jost et al., 2011). Therefore, compositional similarity decreased with increasing discharges, but displayed a hump-shaped relationship with discharge CV, whereas dominance increased exponentially with discharge CV. Mean discharge and flow regimes directly influence community composition, with higher similarity of macroinvertebrate communities in low discharge, and increasing

differentiation with increasing discharge, due to increased disturbances (e.g., Doyle et al., 2005). High flows and other elements of hydrological variation may influence invertebrate distribution and biotic indices, although land use/cover and catchment characteristics reduce their influence, suggesting an interaction of different predictor variables on invertebrate communities (Booker et al., 2015). In fact, although we recorded effects of land use on diversity estimators, these effects were primarily related to dominance by few taxa along a gradient in discharge CV.

Nonlinear responses by macroinvertebrate communities are expected when organisms have thresholds to particular stress effects, such as the frequency or magnitude of high flows (Allan, 2004). The quadratic relationship between the Morisita–Horn index and discharge CV suggests that intermediate values result in more stable communities, whereas both low and high discharge CV values result in community changes over time, although with distinct patterns. At low discharge CV values, high diversity and evenness were observed, and many taxa were absent in some samples, or occurred with high abundances in other samples (e.g., Simuliidae, Empididae, Hydropsychidae, Baetidae, among others), resulting in high differentiation among sampling times. On the other hand, at high discharge CV values, less taxa were observed, and patchy occurrence of some taxa resulted in higher differentiation, with large variation of dominant taxa among samples. The dominant taxa (Chironomidae and Oligochaeta) strongly influenced patterns in all communities studied, with higher differentiation when the abundances of these taxa differed among sampling times, and higher similarity when the abundances of these taxa varied less among sampling times.

Although strong relationships between beta diversity and both natural and anthropogenic stressors were reported (e.g., Gutiérrez-Cánovas et al., 2013), recent studies suggest that stream macroinvertebrate metacommunities have weak relationships with ecological factors, possibly due to their dynamic response to disturbances (Heino et al., 2015). For example, Campbell et al. (2015) verified that flow regime influenced metacommunity structuring, and that both stability and disturbance can contribute to spatial structure in metacommunities, since metacommunities which presented a period of stability just before sampling or after a long period of instability were

structured by spatial processes, whereas those of intermediate flow stability were structured by environmental factors. Understanding how hydrological processes structure macroinvertebrate communities, both among and within metacommunities, and recognizing that larger scales of temporal variation are necessary to determine the stability or range of natural variation of stream communities (e.g., Milner et al., 2016), will contribute to a better understanding of these dynamic communities.

The present study found that hydrological variation can strongly influence the stability and structure of stream macroinvertebrate communities, and that this effect can override water chemistry differences such as dissolved oxygen concentrations and electric conductivity. Although the patterns observed here were obtained at coarse taxonomic levels and few streams, the strong relationships suggest that community stability can be influenced by hydrological variation, so that discharge patterns can be an effective variable to evaluate effects of stressors such as land use/cover change on macroinvertebrate communities. In a nearby region, Libório & Tanaka (2016) found that in deforested streams higher sedimentation on pool habitats increased beta diversity due to higher taxon loss and dominance, whereas in forested streams macroinvertebrate communities were more stable but with lower beta diversity. Therefore, interactions between land use/cover changes and discharge patterns can strongly influence macroinvertebrate community structure, and hydrological variation can be an interesting parameter to include in tropical stream monitoring.

Acknowledgements We thank Sindicato Rural de Ibitinga and all the landowners for the support, L. A. Joaquim, D. G. Fonseca, R. A. Libório, F. T. T. Hanashiro, C. M. Suga, J. F. Fernandes, L. O. I. de Souza (*in memoriam*), and A. Kiyuna for help in the field and lab, A. L. T. de Souza for help in the field and throughout the project, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, procs. 552554/2007-3, 302890/2007-6, 308630/2010-6) for financial support, and two anonymous reviewers whose comments contributed to improve the manuscript.

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