

Responses of aquatic food webs to the addition of structural complexity and basal resource diversity in degraded Neotropical streams

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Abstract The loss of riparian forests can disrupt the structure and function of lotic ecosystems through increased habitat homogenization and decreased resource diversity. We conducted a field experiment and manipulated structural complexity and basal resource diversity to determine their effect on multiple aspects of community and food-web structure of degraded tropical streams. In-stream manipulations included the addition of woody debris (WD) and the addition of wood and leaf packs (WLP). The addition of structural complexity to degraded streams promoted detritus retention and had a positive effect on stream taxonomic richness, abundance and biomass. At the conclusion of the experiment, abundance and richness in the WD-treated reaches increased by over 110% and 80%, respectively, while abundance and richness in the WLP-treated reaches increased by over 280% and 170% respectively. Wood debris and leaves were consumed only by few taxa. Detritivorous taxa were the most abundant trophic guild at the beginning and at the end of the experiment. Food webs in treated reaches were relatively more complex in terms of links and species at the conclusion of the experiment, with highest maximum food chain length in the WD treatments and highest number of trophic species, links, link density, predators and prey at the WLP treatment. Despite differences observed in diet-based food webs, there was little variation in isotopic niche space, likely due to the high degree of omnivory and trophic redundancy, which was attributed to the importance of fine detritus that supported a broad range of consumers. Even in these degraded streams, aquatic taxa responded to the addition of increased complexity suggesting that these efforts may be an effective first step to restoring the structure and function of these food webs.

Key words: habitat heterogeneity, Neotropics, stable isotope analysis, stream biota, stream restoration.

INTRODUCTION

The removal of riparian forests for agricultural practices is one of the most common and destructive impacts on stream ecosystem structure and function (Sweeney *et al.* 2004). Deforestation can cause headwater streams to shift from heterotrophic to autotrophic systems due to increased solar radiation into the water column, which boosts the abundance of primary producers such as algae and macrophytes (Ceneviva-Bastos & Casatti 2014). Forest loss also results in higher sediment inputs that, along with increased water temperature and evaporation, accelerate the siltation process (Barrela *et al.* 2000).

Inputs of allochthonous resources such as tree trunks, logs, branches and leaves are also absent in deforested streams (Sweeney *et al.* 2004; Carvalho & Uieda 2010; Ferreira *et al.* 2012; Sweeney & Newbold 2014). The concomitant action of these factors ultimately leads to in-stream habitat homogenization (Casatti *et al.* 2009), loss of functional diversity (Moore & Palmer 2005) and thus alteration of food-web structure, detritus dynamics, primary production and, consequently, ecosystem function (Nakano & Murakami 2001; Sweeney *et al.* 2004; Ceneviva-Bastos & Casatti 2014).

Structural complexity is an important determinant of species diversity and richness, and it influences the habitat selection of individual species (Huston 1994). Positive relationships between species richness and increased habitat complexity have been found in

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tropical and temperate regions, ranging from large to small spatial scales (Angermeier & Karr 1984; Willis *et al.* 2005; Arrington & Winemiller 2006; Schneider & Winemiller 2008; Montaña *et al.* 2015). Higher heterogeneity of physical structures provides more diverse substrates, resource availability, foraging opportunities and more diverse ways of exploiting environmental resources (Willis *et al.* 2005; Montaña *et al.* 2015). In aquatic ecosystems, the addition of woody debris and leaf litter can enhance structural complexity and provide microhabitats utilized by macroinvertebrates and fishes (Arrington & Winemiller 2006; Schneider & Winemiller 2008). Wood debris also provide a hard surface for colonization by algae, microorganisms and invertebrates, which are food resources for other invertebrates and fishes (Angermeier & Karr 1984; Arrington & Winemiller 2006; Schneider & Winemiller 2008).

Restoring structural complexity to streams that have experienced habitat homogenization may be an effective strategy to restore stream biodiversity, especially macroinvertebrate richness (Miller *et al.* 2010 (but see Palmer *et al.* 2010). Many stream restoration studies (predominately conducted in the United States, Europe, and Australia) evaluate the response of a small set of macroinvertebrate community attributes (usually richness and abundance or density) to enhanced heterogeneity (e.g. Miller *et al.* 2010; Palmer *et al.* 2010 and citations therein). The assessment of macroinvertebrate responses to enhanced heterogeneity can also be studied as a part of a long-term institutional or governmental restoration project (e.g. Scaely *et al.* 2007). Fish are rarely used as target species in restoration efforts of stream heterogeneity (but see Schneider & Winemiller 2008) and studies that include the responses of the entire stream community are even scarcer. Even though Neotropical streams have been subjected to habitat and biota homogenization caused by anthropogenic impacts (Casatti *et al.* 2009; Dala-Corte *et al.* 2016), absence of long-term restoration projects and biomonitoring programmes have resulted in little progress in our understanding of the response of biodiversity to restoration of in-stream heterogeneity in these degraded habitats.

The understanding of how tropical stream ecosystems are affected by land-use changes is of primary importance for their conservation (Boyero *et al.* 2009), but the lack of information regarding ecosystem structure and dynamics before anthropogenic impacts occurred is a major impediment (Power *et al.* 1996). For instance, the native forest cover of north-western São Paulo State, Brazil, is currently restricted to less than 4% of its original area and the region is regarded as the most degraded of the state (Nalon *et al.* 2008). The deforested streams embedded in this landscape have been highly impacted due

to heavy siltation and proliferation of grasses within the stream channel, which has led to habitat homogenization (Casatti *et al.* 2015). These impacts reduced the functional diversity of fishes (Casatti *et al.* 2015), while studies that investigate macroinvertebrate communities are very scarce (but see Marques *et al.* 2013; Ceneviva-Bastos & Casatti 2014).

Stream restoration projects should include a multitude of actions that target not only the recovery of in-stream structural heterogeneity but also channel morphology, bank stability and riparian forests (Palmer *et al.* 2010), which allow for self-sustaining stream function. However, several practical and logistical issues limit such restoration actions (e.g. high costs; see Rodrigues *et al.* 2011). More common management practices, such as fencing off the riparian area, would limit access to cattle thereby allowing the native riparian forest to re-establish. However, the effectiveness of these practices remains unknown as the re-establishment of riparian forest occurs slowly and long-term studies on these restoration efforts are absent. A more proactive approach to restoring the structural and functional diversity of degraded stream ecosystems would entail in-stream manipulations of resources used by aquatic taxa (e.g. microhabitats, food resources). Yet few studies have experimentally tested the response of in-stream fauna and trophic structure of degraded streams in agricultural landscapes after adding structural complexity (Lester *et al.* 2007). Hence, ecological processes affected by structural complexity additions, such as changes in detritus dynamics, trophic ecology, food-web complexity (in terms of links and species) and energy flows, remain unexplored.

We conducted a field experiment to investigate the response of in-stream biota and food webs of degraded streams to experimental manipulations of in-stream structural complexity and resource diversity and abundance. We used a multifaceted approach to examine: (i) whether the additions of wood and leaf packs influence detritus dynamics (specifically, if they promote detritus retention and if they are processed locally by the community), and (ii) the responses of community structure (i.e. richness, abundance, biomass) and food-web structure (i.e. trophic diversity and other food-web attributes) due to increased habitat and resource heterogeneity.

METHODS

Study area

We conducted the experiment in three physically degraded headwater streams (Stream 1: S20°59'25"S, W49°15'47"; Stream 2: S20°28'15", W49°24'45"; Stream 3: S20°26'21", W49°21'29") of north-western São Paulo State, southeast Brazil, a region that has been historically deforested for

agriculture and livestock grazing (Nalon *et al.* 2008; Gerhard & Verdade 2016). According to slope classification, the region is flat or smoothly rolling (Silva *et al.* 2007), and presents a high erosive potential for its unconsolidated sand and silt sedimentary origin (IPT 2000). The climate is hot tropical (Nimer 1989) with two marked seasons (rainy and dry, IPT (Instituto de Pesquisas Tecnológicas do Estado de São Paulo) 2000). The experiment was conducted from July to October 2012, a period corresponding to the annual dry season. During this period we expected minimum influences of seasonal variation, as water levels descend and habitats become more homogeneous in terms of water velocity and depth. The streams in our study were located in a landscape that shared similar environmental conditions. The sites selected were characterized by the predominance of silted, narrow and shallow runs (stream width ~ 3 m; depth ~ 0.3 m; water velocity ~ 0.2 m s⁻¹; discharge ~ 0.04 m³ s⁻¹), without riparian forest and with abundant grasses on their margins. The riparian areas were completely deforested, grasses dominated stream channels and land use was represented by pasture and sugar cane.

Experimental design, sample collections and preparation

Three treatments were established within three 5-m reaches of each stream: one reach remained unaltered (CTRL – control reach), another received a wood structure (WD – reach) assembled with logs and branches of native trees, and the last reach received a wood structure plus leaf packs (WLP – wood debris and leaf pack reach). The wood structures were assembled with a bundle of logs and branches with 1–10 cm diameter and approximately 1 m in length. The leaf packs were assembled using a bag (dimensions: 80 × 30 × 40 cm, mesh: 0.7 cm) with a mixture of leaves (C₃ plants) from native riparian forest vegetation. The wood bundle and the leaf packs were dried at 45°C for 36 h and weighed before installation into the streams. Treated reaches within each stream were at least 20 m from each other and treatments were ordered as CTRL, WD and WLP from upstream to downstream to avoid the possibility of the control treatment being colonized by drifting invertebrates from the other treatments.

Sampling was conducted in each reach before the experiment was set up (July 2012, the start of the dry season) and re-sampled 3 months afterwards (October 2012, the end of the dry season). We used stable isotope analysis to characterize diet, and because isotope ratios are sensitive to turnover following diet switches (Vander Zanden *et al.* 2015), our experiments were set for a period of 3 months to allow for enough time for tissue turnover by the macroinvertebrate community in case experimental resources were assimilated (a 75% invertebrate tissue turnover takes about 5–10 days *cf.* Ostrom *et al.* 1997). We also wanted to prevent confounding seasonal effects and ended our experiment after 3 months to avoid overlap with novel resources that may occur at the start of the rainy season. Fish muscle tissue turnover rates reported in the literature can be highly variable (Garcia *et al.* 2007), although incorporation of carbon from new resources has been reported to take less than

3 months in rapidly growing organisms (Hesslein *et al.* 1993; Zuanon *et al.* 2006; Vander Zanden *et al.* 2015).

Prior to in-stream biota samplings, the 5-m reaches were blocked upstream and downstream with 3-mm mesh block nets and overall disturbance within the reach was avoided. A combination of different sampling methods (each with its respective standardized effort) was used to represent the entire biota within each 5-m stream reach studied. Algae and macrophytes were collected by hand from stream substrate along the entire reach. Benthic invertebrates were sampled with a Surber net by washing, for 1 min, the substrate delimited by the sampler (positioned in the middle of the reach) and also along the 5-m reach with a D net (both with 250 µm mesh size), passed for 5 min. Finally, fish were sampled with a 0.3-cm mesh seine (1.0 × 2.0 m), passed along the entire reach, and with a 0.1-cm mesh sieves (0.8 m diameter), passed along the margins, until no fish were caught after five consecutive passes of each equipment. When the experiment concluded after 3 months, the sampling protocol was repeated as described above and the structures were removed from the stream and immediately placed on large trays to collect associated taxa. Specimens associated with the wood structure were sampled by scraping off the surface of the logs and branches with a soft brush and leaves from the leaf packs were washed in the laboratory over a 250-µm mesh sieve, where specimens were retained. Both wood and leaves were dried at 45°C for 36 h and re-weighed.

During each sampling event, we visually estimated the abundance of benthic macrophytes and macroalgae (% of reach occupancy) along the reach, and a sample of each primary producer morphotype was collected for further identification and for isotopic analysis of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$). Substrate samples were taken in the middle of each reach with a PVC (polyvinyl chloride) core sampler. The percentage of organic matter in the substrate (mostly composed of fine particulate organic matter, FPOM) was also estimated. Substrate samples were dried at 60°C for 36 h, weighed, combusted at 500°C for 6 h and weighed again to obtain substrate FPOM through the dried ash-free mass (g).

All samples were fixed in ethanol (70%), except for fish because the fixation process was reported to change their tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signals (Sweeting *et al.* 2004), which is less likely to occur with macroinvertebrates (Jardine *et al.* 2005; Syväranta *et al.* 2008). For fish, a small muscle sample from below the dorsal fin (and above the lateral line) was collected and frozen until isotopic processing (*sensu* Lopes *et al.* 2007). All taxa were identified to the lowest taxonomic level possible (species level in fish, and usually generic level in most macroinvertebrates and producers), and then weighed (wet weight) on a digital scale (Quimis SA 210).

Food web and isotopic analysis

We performed gut content analysis on 10 specimens of each consumer taxa identified (or all individuals when taxon abundance was lower than 10). Guts were removed through ventral incision, dissected and mounted on a slide (Ceneviva-Bastos & Casatti 2014). Food items were

identified to the lowest taxonomic resolution possible and each feeding interaction was assigned to a trophic link in the food webs (namely, the 'diet-based' food webs). As both diet and stable isotope data accounted for the different food-web approaches used in this study, we standardized terminology. We used 'food-web parameters' to describe diet-based food-web statistics, while we used 'community-wide metrics' to describe isotope-based food webs. We also used 'basal species' (i.e. species that have predators but not prey, *sensu* Cohen *et al.* 1990) for diet-based food webs and 'basal sources' (which represent the potential sources of energy for consumers) when referring to isotope-based food webs (Winemiller 2007).

Macroinvertebrates that had their guts removed were prepared and submitted for stable isotope analysis (so that gut contents would not influence the isotopic signal of the assimilated food sources; Jardine *et al.* 2005), along with fish muscle tissue and basal sources. All samples were dried at 60°C for 24–36 h, ground, weighed and packaged into an Ultra-Pure tin capsule and sent to the Isotope Ecology Laboratory at CENA-USP, Piracicaba, Brazil, for measurement of stable isotope ratios of carbon and nitrogen. A total of 365 samples were used for stable isotopes analysis (17 organic substrate (FPOM) samples, 43 basal resources (e.g. algae, macrophytes, wood and leaf packs), 124 fishes and 181 macroinvertebrates). With exception of the wood and leaf packs, the isotopic ratios of the main basal sources among reaches were averaged per each stream.

Statistical analysis

To evaluate whether the experimental structures promoted detritus retention, we compared the amount of substrate FPOM at each treatment before and after the experiment using a Mann–Whitney test, as the data were non-normal. To determine whether the experimental inputs (wood debris and leaves) decayed across time, we used a Mann–Whitney test to compare the weight of the experimental inputs before and after the experiment. We compared richness, abundance and biomass of invertebrates and fish in each treatment at before the start of the experiment and at the conclusion of the experiments using a Paired Wilcoxon test, as the data were non-normal. We used a SIMPER analysis to evaluate which taxa contributed the most to the differences among treatments, and calculated the percentage accumulation of trophic group abundance within each treatment.

Food webs obtained from gut content data were constructed based on binary predation matrices of predator–prey interactions (Cohen *et al.* 1990). Based on these matrices, a series of food-web parameters (from Pimm *et al.* 1991) were calculated: number of trophic species (S), number of links (L), link density (L/S), number of basal species (given by producers, detritus, fungus and terrestrial items), number of intermediate species (those that have both predators and prey), number of top species (those that have only prey and were not preyed upon), number of prey and predators, predator/prey ratio, maximum food chain length (given by the number of links of the longest path from food-web base to a top predator), minimum food chain length (shortest path) and connectance (C), given by

$C = 2L/S(S - 1)$. A Mann–Whitney test was applied to test for differences for each food-web parameter by comparing the parameters at the beginning and at the conclusion of the experiment for each treatment.

We used community-wide metrics (Layman *et al.* 2007) to compare food-web structure before and after treatments with the isotopic data. The metrics considered were $\delta^{15}\text{N}$ range (NR), a measure that represents the vertical structure within the food web, $\delta^{13}\text{C}$ range (CR), a measure of the diversity of basal sources used by the community (indicating niche diversification), total area (TA), a measure of the total amount of isotopic niche space occupied (i.e. the magnitude of food-web isotopic diversity), mean distance to centroid (CD), representing the average degree of food-web isotopic diversity, mean and standard deviation of nearest-neighbour distance (mean NND and SD NND), representing the degree of isotopic redundancy and the uniformity of isotopic niches distribution respectively (Layman *et al.* 2007). These metrics were calculated for the consumer food web (i.e. considering fish and macroinvertebrates together). Estimation of the community-wide metrics was calculated using the *SIAR* (Stable Isotope Analysis in R, Parnell *et al.* 2010) package in the R software version 3.0.2 (R Core Team 2013). Alternatively, we calculated the standard ellipse areas (SEA and SEAc, the last corrected by sample size), which are less sensitive to sample size than the TA metric, using the *SIBER* package in R (Jackson *et al.* 2011). A Mann–Whitney test was then conducted on the metrics to test for differences at the beginning and the end of the experiment for all treatments.

RESULTS

The experimental structures were colonized by algae, periphyton, aquatic invertebrates, crabs and armoured catfishes, and also promoted detritus retention (Appendix S1). At the conclusion of the experiment, the amount of FPOM was significantly higher at the WLP treatments ($\text{WLP}_{\text{before}} = 0.10 \pm 0.03$; $\text{WLP}_{\text{after}} = 0.20 \pm 0.07$; $P = 0.045$). Wood debris and leaf packs exhibited evidence of decay as both inputs weighed significantly less at the conclusion of the experiment ($P = 0.045$ for all treatments) (mean \pm SD of wood debris weight (g): $\text{WD}_{\text{before}} = 4481 \pm 115$; $\text{WD}_{\text{after}} = 2380 \pm 208$; $\text{WLP}_{\text{before}} = 4947 \pm 100$; $\text{WLP}_{\text{after}} = 3134 \pm 764$; leaf pack weight (g): $\text{WLP}_{\text{before}} = 475 \pm 44$; $\text{WLP}_{\text{after}} = 82 \pm 49$).

Thirteen producers and 154 consumer taxa represented by 73 064 individuals were collected across all streams and sampling periods (specimens used for gut content analysis = 6409 individuals) (Appendix S2). At the conclusion of the experiment, taxonomic richness was higher than at the beginning across all treatments, but only marginally higher in the CTRL treatment ($P = 0.05$). Taxonomic richness increased with the addition of structural complexity and resource diversity and was significantly higher for both the WD ($P = 0.045$) and WLP ($P = 0.045$) treatments at the conclusion of the experiment. Both

abundance and biomass were higher for all treatments, including the CTRL, at the conclusion of the experiment (Table 1). The CTRL treatment exhibited the smallest increase in abundance (about an 80% increase) and biomass (about a 10% increase) at the conclusion of the experiment, compared to the WD treatment in abundance (over 110% increase) and biomass (about an 80% increase), and the WLP treatment in abundance (over a 280% increase) and biomass (a 170% increase) (Appendix S2).

In the treated reaches we observed a shift in the trophic guild of consumers with an increase in the proportion of omnivorous, herbivorous and detritivorous/herbivorous taxa (Fig. 1). The SIMPER analysis

Table 1. Results of the paired Wilcoxon test comparing taxa richness (number of taxa), abundance (number of individuals) and biomass (g) at each treatment before and after the experiment

	Before Median	After Median	W	Z	P-values
Richness					
CTRL	1	1	533	1.89	0.05
WD	1	1	867	2.54	0.01
WLP	1	1	925	3.57	0.003
Abundance					
CTRL	1	3	5098	5.38	0.001
WD	1	5	5858	6.55	0.001
WLP	2	6.5	7380	7.23	0.001
Biomass					
CTRL	0.0006	0.004	4397	4.23	0.003
WD	0.0005	0.011	4995	5.79	0.002
WLP	0.0011	0.025	6307	6.52	0.006

CTRL, control reach; WD, wood debris reach; WLP, wood debris + leaf pack reach.

revealed that in the CTRL reaches, the consumers that contributed the most to the differences at the end of the experiment were micro-caddisflies, baetid mayflies, blackflies and two non-biting midges (Table 2). The baetid mayflies and blackflies decreased in abundance at the conclusion of the experiment (by 63% and 53%, respectively), while the micro-caddisflies and two non-biting midges exhibited the opposite pattern (Table 2). In the WD reaches, the consumers that contributed the most to differences at the end of the experiment were the micro-caddisflies, baetid mayflies, two non-biting midges and ram-horn snails (Table 2). The top five consumers (with the exception of *Americabaetis* mayflies, which decreased in abundance) increased in their abundance by at least 1.5-fold (Tanypodinae, midges) and as high as 125-fold (*Oxyethira* micro-caddisflies; Table 2). Finally, in the WLP reaches, caddisflies, micro-caddisflies, midges, mayflies and ostracods contributed the most to the differences through their increased abundance at the end of the experiment (Table 2).

The top five taxa contributing the most to differences at the conclusion of the experiment in the CTRL and WD treatments were similar in their trophic diversity and contained four detritivores and an invertivore (the predatory non-biting midge, Tanypodinae (Table 2)). In the WLP, an over 100-fold increase in the abundance of the omnivorous caddisfly (*Smicridea*) contributed the most to the differences at the conclusion of the experiment (Table 2). The top five taxa that differed at the end of the experiment in the WLP all exhibited an increase in total abundance (Table 2).

Most food-web parameters were higher at the conclusion of the experiment (Table 3). The number of links and link density was significantly higher

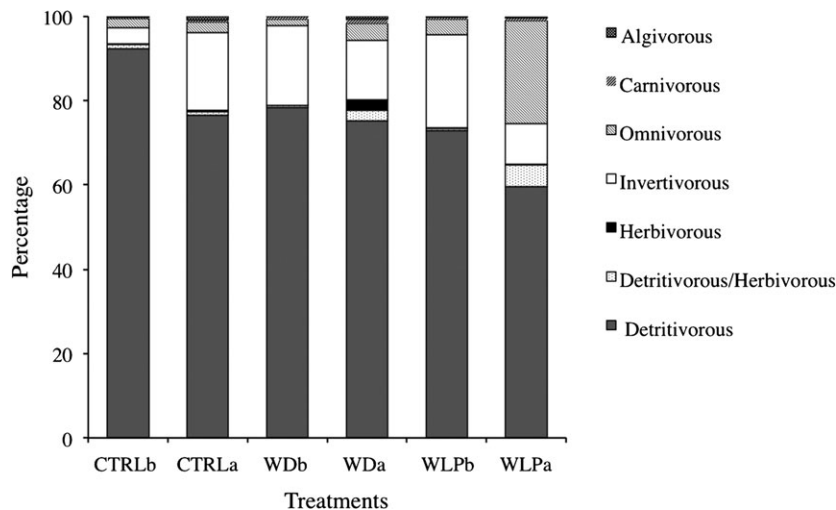


Fig. 1. Percentage of trophic groups within each treatment. a, after the experiment; b, before the experiment; CTRL, control; WD, wood debris; WLP, wood debris + leaf packs.

($P = 0.045$) at the WD and WLP treatments at the conclusion of the experiment. The maximum food chain length and the number of trophic levels increased ($P = 0.045$) in the WD treatment, although this pattern was not observed for the WLP treatment. The number of basal resources and top species (i.e. trophic species that were not preyed upon), number of predators and prey and overall number of trophic

species were significantly higher only in the WLP treatment (Table 3).

Substrate FPOM $\delta^{13}\text{C}$ did not exhibit much variation across treatments and the FPOM $\delta^{15}\text{N}$ value was slightly lower at the end of the experiment (Appendix S3). Algae and macrophyte isotope ratios varied across treatments both before and after the experiment (Appendix S3). Experimental wood

Table 2. Results of the SIMPER analysis with the five taxa that contributed the most for the differences between periods at the control, wood debris and wood debris + leaf pack treatments

Treatments and taxa	Trophic group	Abundance		Percent of contribution
		Before	After	
Control				
<i>Oxyethira</i>	Detritivorous	21	751	25.02
<i>Americabaetis</i>	Detritivorous	458	165	10.05
<i>Simulium</i>	Detritivorous	237	4	7.986
Tanypodinae	Invertivorous	244	428	6.329
Chironominae	Detritivorous	140	324	6.318
Wood debris				
<i>Oxyethira</i>	Detritivorous	7	881	25.38
Chironominae	Detritivorous	160	595	12.64
<i>Americabaetis</i>	Detritivorous	602	290	9.053
<i>Biomphalaria</i>	Detritivorous	9	255	7.136
Tanypodinae	Invertivorous	253	414	4.667
Wood debris + leaf pack				
<i>Smicridea</i>	Omnivorous	21	2273	29.37
<i>Oxyethira</i>	Detritivorous	53	1162	14.5
Chironominae	Detritivorous	486	1306	10.73
Traverhyphes	Detritivorous	24	524	6.538
Ostracoda	Detritivorous	11	422	5.366

Table 3. Food-web parameters (mean \pm SD) obtained for food webs of the three treatments (CTRL, control; WD, wood debris; WLP, wood debris + leaf packs) before and after the experiment

Food-web parameter	CTRL		WD		WLP	
	Before	After	Before	After	Before	After
Number of trophic species	82 \pm 27	98 \pm 10	86 \pm 12	109 \pm 16	84 \pm 15	114 \pm 4
Number of links	181 \pm 85	240 \pm 36	191 \pm 46	294 \pm 65	194 \pm 62	323 \pm 42
Link density	2.11 \pm 0.43	2.44 \pm 0.13	2.19 \pm 0.26	2.67 \pm 0.24	2.27 \pm 0.39	2.83 \pm 0.27
Number of basal species	10 \pm 2	11 \pm 2	10 \pm 3	13 \pm 2	10 \pm 1	15 \pm 2
Number of intermediate species	40 \pm 22	51 \pm 2	41 \pm 5	50 \pm 13	40 \pm 8	53 \pm 8
Number of top species	32 \pm 6	36 \pm 9	35 \pm 9	47 \pm 11	34 \pm 7	45 \pm 3
Number of prey	50 \pm 23	62 \pm 2	51 \pm 3	63 \pm 14	50 \pm 8	68 \pm 7
Number of predators	72 \pm 26	87 \pm 10	76 \pm 14	96 \pm 15	74 \pm 14	99 \pm 5
Prey/predator ratio	0.67 \pm 0.10	0.72 \pm 0.09	0.68 \pm 0.09	0.65 \pm 0.10	0.68 \pm 0.02	0.69 \pm 0.04
Maximum food chain length	3.0 \pm 0.0	3.7 \pm 0.6	3.0 \pm 0.0	4.7 \pm 0.6	3.3 \pm 0.6	5.3 \pm 1.5
Minimum food chain length	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0	1.0 \pm 0.0
Connectance	0.050 \pm 0.005	0.051 \pm 0.03	0.052 \pm 0.003	0.049 \pm 0.005	0.052 \pm 0.001	0.052 \pm 0.002
Number of trophic levels	3.0 \pm 0.0	3.7 \pm 0.6	3.0 \pm 0.0	4.7 \pm 0.6	3.3 \pm 0.6	5.3 \pm 1.5

A bolded value indicates there was a significant difference ($P < 0.05$) between food-web parameters before the experiment and after the experiment.

debris and leaves from the leaf packs had similar carbon and nitrogen isotopic ratios (Appendix S3). Grass from adjacent pasture had enriched carbon ratios ($\delta^{13}\text{C} = -12.23$). There was high overlap in the dispersion of consumers in the isotopic niche space across streams (Appendix S4). The total area, an indicator of isotopic niche space, showed a slight increase in the WLP treatment (Fig. 2), although overall differences among treatments in TA, SEA and SEAc values were not significant (Appendix S5, $P > 0.05$ for all metrics). Overall, consumer taxa exhibited little variation in their $\delta^{15}\text{N}$ signature across streams and treatments, and food-web vertical structure (NR) was not significantly different at the conclusion of the experiment (Fig. 2). Consumers had

$\delta^{13}\text{C}$ values that ranged between -35‰ and -17‰ before the experiment and between -32‰ and -18‰ at the conclusion of the experiment, resulting in a decrease in CR values at all treatments, although differences were only significant for the WD treatment ($P = 0.049$) (Fig. 2). Overall, the isotopic food-web structure did not change at the conclusion of the experiment, regardless of experimental inputs (i.e. wood debris or leaves).

DISCUSSION

The addition of habitat and resource heterogeneity to degraded streams promoted detritus retention and

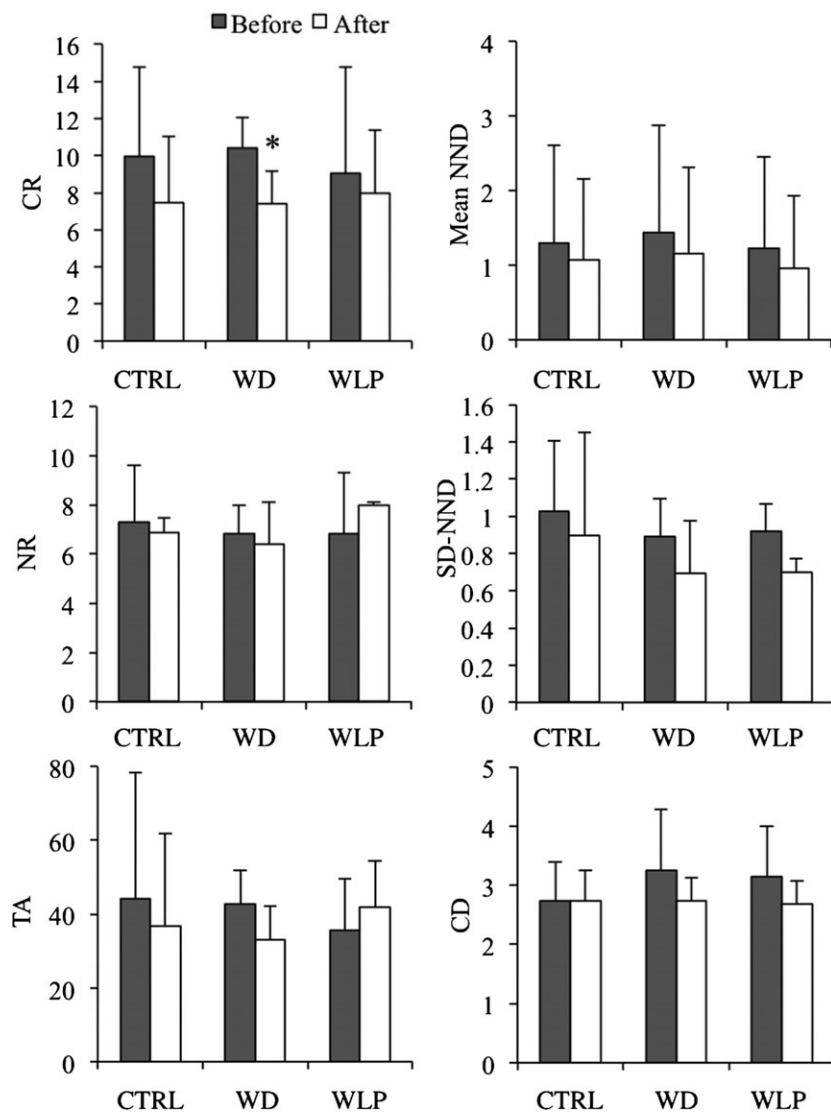


Fig. 2. Community-wide metrics of food-web structure calculated for the three treatments: control, wood and wood + leaf pack, before and after the experiment. CD, mean distance to centroid; CR, carbon range; NND, nearest-neighbour distance; NR, nitrogen range; SDNND, standard deviation of nearest-neighbour distance; TA, total area. See Methods for an explanation of these metrics. Significant differences ($P < 0.05$) between metrics are marked with an asterisk (*).

had a positive effect on stream consumer richness, abundance and biomass. Food webs of treated reaches were relatively more complex (in terms of links and species) at the conclusion of the experiment, with highest maximum food chain length in the WD treatment and highest number of trophic species, links and link density at the WLP treatment. The wood and leaf additions enhanced resource abundance, which in turn can support more diverse food webs (Polis & Strong 1996). Wood structures in aquatic systems have been used as a surrogate for habitat complexity (Arrington & Winemiller 2006; Lester *et al.* 2007) as they contribute to the physical in-stream variation and promote detritus accumulation (Lepori *et al.* 2005; Flores *et al.* 2011), consequently increasing in-stream biodiversity (Lester *et al.* 2007). The experimental inputs were likely utilized as a food resource by consumers as both wood debris and leaf packs decreased in mass at the end of the experiment. Litter breakdown can be relatively fast in tropical streams (with litterbags weighing 25% of initial leaf mass in only 90 days, *cf.* Malacarne *et al.* 2016). Along with macroinvertebrate consumers, microbial activity likely also contributed to the decrease in leaf litter at the conclusion of the experiment. However, we are unable to define which group had the greater effect on the subsequent leaf litter decrease.

After the addition of wood structures, a variety of taxa that were not present in the initial surveys colonized the experimental structures at these stream reaches. For instance, the dobsonflies (Family Corydalidae), which are known to occur mostly in riffles of forested streams (Ceneviva-Bastos *et al.* 2012), only occurred at the end of the experiment. Wood-eating beetle larvae (Family Elmidae) increased in abundance, and periphyton-feeding armoured catfishes (*Hypostomus ancistroides* and *H. nigromaculatus*; Family Loricariidae) fell from the wood debris when they were being removed (M. Ceneviva-Bastos, pers. obs., 2014). The abundance of the omnivorous caddis *Smicridea* and the micro-caddis *Oxyethira* was higher at the treatments as well, which suggests that many taxa used the debris and leaf packs as food and shelter.

Consumer abundance and biomass increased across all treatments at the end of the experiment. Although the distribution of aquatic insects in general is spatially discrete, passive downstream dispersal by drift can move 1–2% of benthic fauna (Waters 1972). While macroinvertebrates can actively move throughout stream systems, drift is more common than active upstream dispersal (Bilton *et al.* 2001), which often occurs via flight (Bilton *et al.* 2001; Mazzucco *et al.* 2015). Thus, while we cannot disregard the possibility that individuals moved throughout the treatments within the streams, little is known about

actual macroinvertebrate adult dispersal (Bohonak & Jenkins 2003) and no information is available for the taxa in our study, thus further discussion on macroinvertebrate movement would be speculative. Regardless, the magnitude of increased taxa abundance for the WLP treatment is evidence that increased heterogeneity with wood and leaves supported more individuals at the conclusion of the experiment as compared to the CTRL treatment.

At large spatial scales, harsh or variable environmental conditions impose strong environmental filters on the regional species pool, resulting in co-occurring taxa to exhibit high functional redundancy (Schalk *et al.* 2015, 2017). Anthropogenic impacts can cause communities to disassemble in predictable ways, which is often explained by the traits of the species (Lindo *et al.* 2012). Impacted stream communities are characterized by the presence of generalist and opportunistic species, which are tolerant to habitat loss or degradation (Lake *et al.* 2007). Indeed, most of the taxa collected across the streams in this study are widespread and known to endure living in physically degraded aquatic habitats (Ceneviva-Bastos & Casatti 2014). Streams within our study system are within the most impacted region of São Paulo State and it is possible that sensitive species are scarce and the regional species pool is compromised. Lack of success of stream restoration efforts on aquatic communities is widespread (Palmer *et al.* 2010) and the lack of source populations in surrounding areas (0–5 km distance), and in turn, the ability for colonization, is regarded as one of the major causes for unsuccessful improvement of the benthic communities (Sundermann *et al.* 2011). If community attributes (richness, abundance and biomass) are considered, as in most restoration studies, we were able to improve the aquatic communities of the treated streams with the addition of wood debris and leaf packs. However, restoring the ‘quality’ of communities (e.g. restoring sensitive species; Sundermann *et al.* 2011) in a historically impacted region, for which there is practically no record of sensitive species or a proper species pool, could be a difficult task. In fact, we did not observe a significant increase in the number of trophic guilds in the degraded streams, as the vast majority of consumers were classified as detritivorous or omnivorous.

Several studies in tropical streams have found that food webs are often detritus based (Mantel *et al.* 2004; Motta & Uieda 2005; Ceneviva-Bastos *et al.* 2012; Ceneviva-Bastos & Casatti 2014) and that fine detritus (i.e. FPOM) is one of the most important food resources for stream invertebrates (Dudgeon *et al.* 2010) and even for top predatory fishes (Ferreira *et al.* 2012; Ceneviva-Bastos & Casatti 2014). Indeed, the minimum food chain length observed

was one for all treatments, meaning that even the top predators fed on the food-web basal resources and exhibited a high degree of omnivory. Maximum food chain length and number of trophic levels were higher in the WD treatments, while the number of trophic species, basal and top species, prey and predators was higher at the WLP treatments. Increased species richness and trophic complexity were reported to occur in macrophyte-rich habitats, with high habitat complexity (Motta & Uieda 2005). In our study, complexity was likely promoted by the experimental structures, which were used as habitat and food by different organisms (directly and indirectly by promoting detritus retention). In a similar vein, the number of links and link density were significantly higher at both WD and WLP treatments, which is indicative that interconnectivity increased in food webs from the treated reaches at the conclusion of the experiment. Increased number of trophic species, however, does not imply that the number of possible connections will increase exponentially in practice, especially when density-dependent foraging and high detritivory are in place. Accordingly, connectance was relatively low for all food webs when compared with other studies (Uieda & Motta 2007; Hernandez & Sukhdeo 2008), with values similar to other degraded streams in the region (Ceneviva-Bastos & Casatti 2014).

Despite differences observed in diet-based food webs, overall differences in the community-wide metrics of trophic structure were not significant. The use of these metrics has been criticized (Hoeinghaus & Zeug 2008) when isotopic signature of the basal sources is not considered because $\delta^{13}\text{C}$ values might be influenced by physiochemical and other environmental characteristics across systems. In our study, however, the use of these metrics appear appropriate, as the main basal source consumed (FPOM) did not vary across streams.

Isotopic ratios of FPOM were relatively enriched across all pasture streams (dominated by C_4 grasses) and did not appear to change much among samples, indicating adjacent pastures as its most likely origin. Garzon-Garcia *et al.* (2017) found that C_3 litter was the main carbon source exported to streams of pasture-dominated basins of Australia, although headwaters in the region were relatively forested and the study was conducted in a much larger spatial scale (catchment) than this study (headwaters, local scale). Delong and Thorp (2006) found that the contribution of the algal fraction of transported organic matter for most primary consumers in the Mississippi River was more important than that of detritus, despite the carbon ratios of algae were more depleted than that of fine detritus. Although we did not separate the possible components of FPOM (for instance, fine detritus samples contained a small fraction of

diatoms), diatoms and other microalgae (as *Chlosterium* and *Cosmarium*) were scarcely found in gut contents, so it is unlikely that they could be the main source (within the organic detritus) assimilated by consumers.

We also did not observe significant $\delta^{13}\text{C}$ isotopic variation in substrate FPOM among the treatments. If the consumers in these streams fed mainly on FPOM, both before and after the experiment, then it is likely that their carbon signature would not change significantly with experimental inputs from each treatment, regardless of the diversification of basal sources promoted by the wood and leaf packs. For example, the $\delta^{13}\text{C}$ signature of shrimp (which fed on the leaves and other resources as macroinvertebrates) was more depleted at the treated reaches after the experiment. However, as they were top species (i.e. were not preyed upon) in most food webs this resource assimilation would not be reflected in the entire food web. Conversely, the $\delta^{13}\text{C}$ of baetid mayflies, blackflies, non-biting midges, micro-caddis and snails, for example, changed very little and remained relatively $\delta^{13}\text{C}$ -enriched after the experiment. The abundant detritivorous taxa (especially in the treated reaches) that colonized the debris were the main food resources for several predators, thus resulting in decreased carbon range at the conclusion of the experiment.

At the community level, the range in nitrogen isotope values did not significantly increase with increased habitat or resource heterogeneity, although $\delta^{15}\text{N}$ was slightly higher at the WLP treatments by the end of the experiment. According to the productivity (Briand & Cohen 1987) and productive space (Schoener 1989) hypotheses, higher resource availability can support longer food chains; longer food chains can, in turn, contain more trophic levels and thus a higher degree of trophic diversity (Layman *et al.* 2007). Diet-based maximum food chain length was higher at both WD and WLP treatments (although significantly higher only at the former). A heterogeneous habitat patch that contains high FPOM availability, for instance, could attract detritivorous species and their predators, promoting food-web complexity. On the other hand, if most species feed on the most abundant resource (i.e. FPOM) and predators feed on the most abundant prey, it is reasonable that the degree of trophic diversity estimated with stable isotopes would not change considerably. Similarly, despite the increased taxonomic richness in the experimental treatments of this study, trophic redundancy also increased and consumers were more even in their trophic niches, probably because species in these degraded streams tend to be functionally redundant. In deforested watersheds, large inputs of organic matter and sediment from adjacent land into the streams are common (Sweeney

& Newbold 2014), and the enriched carbon signal of FPOM observed is evidence that the adjacent pasture is the likely source.

These results indicate that increasing structural heterogeneity with wood debris and leaf packs in degraded streams can promote species richness, abundance and biomass. To illustrate the relevance of such results, only 2 of 78 stream restoration studies observed a significant increase in macroinvertebrate richness with experimentally increased structural heterogeneity (Palmer *et al.* 2010). Although it is fundamentally important to fully restore riparian forests, this process can take decades, while the subsequent natural addition of wood debris to these repatriated habitats can take centuries (Parkyn *et al.* 2003). As our results indicate, management practices of in-stream addition of wood debris and leaf packs can enhance the in-stream diversity that is normally provided by the forest, resulting in a faster recovery of fish and macroinvertebrate richness, abundance and biomass. The experimental additions also promoted overall food-web complexity, with more trophic species linked by more trophic interactions and longer food chains, characterized by high omnivory, which are food-web features that can be related to stability. Our results showed that even in these degraded streams, embedded in a highly deforested watershed and far from potential colonization sources, the aquatic communities responded to increased complexity, which is suggestive that a simple first-stage restoration action of adding wood debris and leaf packs has the potential to promote overall community diversity and complexity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. General overview of the three stream reaches (Stream 1 = S1, Stream 2 = S2 and Stream 3 = S3) sampled before the experiment (left panel) and 3 months after the experiment (middle and right panels).

Appendix S2. List of primary producers (qualitative data) and consumer taxa (quantitative data) sampled in the three stream treatments before and after the experiment.

Appendix S3. Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the main basal sources collected at the three streams (namely S1, S2 and S3), across the three treatments, before (B) and after (A) the experiment.

Appendix S4. Bi-plots of carbon and nitrogen values of macroinvertebrates, fish and basal sources collected at the three treatments (CTRL = control; WD = wood debris; WLP = wood debris + leaf packs) of each stream (S1, S2 and S3) before (white markers) and after (dark markers) the experiment.

Appendix S5. Isotopic niche metrics represented by standard ellipses area for communities sampled in the three treatments before and after the experiment.