Hydrobiologia (2015) 762:239–251
DOI 10.1007/s10750-015-2353-7

PRIMARY RESEARCH PAPER

Influence of an exotic grass on benthic macroinvertebrate communities in a tropical rural landscape

Daniel G. Fonseca · Marcel O. Tanaka

Received: 23 April 2015 / Revised: 26 May 2015 / Accepted: 31 May 2015 / Published online: 12 June 2015

Abstract Riparian deforestation in rural areas has led to changes in bankside vegetation communities that may have unexpected effects on stream ecosystems. In particular, plants such as grasses can colonize the streambed from adjacent terrestrial habitats, thus altering the physical structure of the streambed and potential influencing macroinvertebrate communities. Here we evaluated if the presence of patches of grasses (*Urochloa* sp.) on the streambed influenced the structure and composition of macroinvertebrate communities in deforested rural streams. We sampled patches with and without grasses in three low-order streams, in the wet and dry seasons. We recorded higher abundances of macroinvertebrates in patches with grasses in the wet season when compared with bare patches. We also found significant differences in taxonomic and functional feeding group composition between patch types, due to higher overall abundances in patches with grasses, probably due to more food and shelter there. These influences were stronger in the wet season, when in-stream grasses may have provided greater refugia from flood disturbance that occur with increased frequency and intensity. Therefore, although deforestation of rural streams can simplify streambed habitats, in-stream grasses such as *Urochloa* sp. provide resources that contribute for the maintenance of macroinvertebrate communities.

Keywords Rural streams · Land use · Disturbance · Functional feeding groups · Distribution · Riparian zone

Handling editor: Verónica Jacinta Lopes Ferreira

Electronic supplementary material The online version of this article (doi:10.1007/s10750-015-2353-7) contains supplementary material, which is available to authorized users.

D. G. Fonseca (✉)
Programa de Pós-Graduação em Ecologia e Recursos Naturais (PPGERN), Universidade Federal de São Carlos, Rodovia Washington Luiz Km 235,
Caixa Postal 676, São Carlos, SP CEP 13565-905, Brazil
e-mail: danielfonsecabio@gmail.com

D. G. Fonseca · M. O. Tanaka
Departamento de Ciências Ambientais (DCAm), Centro de Ciências Biológicas e da Saúde, Universidade Federal de São Carlos, Rodovia Washington Luiz Km 235,
Caixa Postal 676, São Carlos, SP CEP 13565-905, Brazil

Introduction

Headwater streams are strongly influenced by catchment use, and the consequences of land use changes has increasingly attracted the attention of ecologists in the last 20 years (Allan, 2004; Melles et al., 2012; Heino, 2013). Numerous studies have evaluated the impacts of converting riparian vegetation into areas of urban, pasture, and agricultural use, on the physical and biologic processes of the adjacent streams (Gregory et al., 1991; Roth et al., 1996; Allan, 2004; Nessimian et al., 2008; Miserendino et al., 2011).

Deforestation of riparian areas can result in impacts on aquatic communities (Menninger & Palmer, 2007; Minaya et al., 2013), mainly by changing flow and sediment deposition patterns, and reducing the availability and quality of habitats and food resources (Karr & Schlosser, 1978; Vannote et al., 1980; Sweeney, 1993; Thompson & Townsend, 2004; Shields et al., 2010). In addition, deforestation of the riparian forests increases the input of solar radiation on the channel (Fletcher et al., 2000), and common responses to open stream canopies include increases in algal productivity (England & Rosemond, 2004) and development of grasses on the banks and beds of these systems (Quinn et al., 1997; Bunn et al., 1997, 1998; Clapcott & Bunn, 2003; Casatti et al., 2009).

Colonization and development of grasses can occur both along stream bank margins (Menninger & Palmer, 2007; Casatti et al., 2009) and within the stream channel, where they grow as macrophytes (Bunn et al., 1998; Fernandes et al., 2013). Grasses rooted on stream banks can reduce margin erosion (Davies-Colley, 1997) and contribute with allochthonous resources and habitats for both macroinvertebrates (Menninger & Palmer, 2007) and fish (Casatti et al., 2009). On the other hand, grasses that grow as dominant macrophytes in the stream channel can reduce the water quality by reducing the availability of dissolved oxygen (Bunn et al., 1997) and affect channel morphology and hydrology, reducing the effective channel capacity by sediment accumulation (Davies-Colley, 1997; Bunn et al., 1998). Biological effects of exotic grasses on the streambed include dominance of the stream channel in macrophyte-poor streams or stream reaches (*Urochloa arrecta*: Fernandes et al., 2013; Michelan et al., 2013), homogenization of macroinvertebrate communities (*Glyceria maxima*: Clarke et al., 2004), increased local macroinvertebrate abundances (*U. mutica*: Douglas & O'Connor, 2003), possible negative effects on fish due to changes in habitat structure, water quality, and food web structure (Pusey & Arthington, 2003), low contribution of basal resources to detrital food webs, although breakdown of these plants may occur through physical or microbial action (Clapcott & Bunn, 2003; but see Menninger & Palmer, 2007).

Degraded ecosystems are generally characterized by habitat structural simplification (Loke et al., 2015), influencing species distributions and biotic interactions, with deleterious consequences for ecosystem functioning and food web stability (Burdon et al., 2013). In degraded pasture streams, the effects of habitat simplification and higher disturbances due to higher frequency and magnitude of floods may influence the stability and diversity of the aquatic communities (Allan, 2004; Dolédec et al., 2006; Shields et al., 2010; Burdon et al., 2013). These effects can be attenuated by increased structural complexity, which can provide a wider range of resources (e.g., shelter, food, microhabitats) (Townsend, 1989; Loke et al., 2015), increasing faunal diversity through higher niche availability, thereby reducing interspecific competition (Chesson, 2000), and indirectly reducing community variability (Brown, 2003). In degraded pasture streams, invading grasses can increase habitat structural complexity and resource availability, reducing the effects of flood disturbances and increasing community resistance due to the presence of the physical structure provided by the plants. Although ecological stability has a multidimensional nature (Pimm, 1984; Grimm & Wissel, 1997; Donohue et al., 2013), we expected that the presence of these physical structures would maintain the macroinvertebrate communities throughout flood events by reducing the chances of the organisms being dislodged. Therefore, these effects would be related to resistance, e.g., the extent of change in community structure caused by disturbances (Pimm, 1984). Understanding the effects of habitat structure on anthropogenic impacts is important to evaluate biodiversity patterns and processes in simplified systems (Loke et al., 2015).

In Brazil, streams in pasture and agriculture-dominated watersheds are mostly deforested, so that grasses of the genus *Urochloa* such as *U. arrecta* are increasingly common in streambeds and wetlands (Pott et al., 2011; Fernandes et al., 2013). In this study, we evaluated whether patches of an exotic grass (*Urochloa* sp.) on the streambed of tropical deforested pasture low-order streams influenced the structure, resistance, taxonomic composition, and functional organization of local benthic macroinvertebrate communities, when compared with bare patches (areas without exotic grasses), in the dry and wet seasons. We tested the following hypotheses: (1) macroinvertebrate communities in patches with grasses would be more diverse and abundant than those in bare patches; (2) these differences would influence taxonomic and functional composition of these communities, (3) macroinvertebrate community structure and composition would change less (i.e., be more resistant) in patches with grasses than in bare patches when subjected to hydrological disturbances since grasses would provide shelter for the macroinvertebrates.

Materials and methods

Study area

This study was carried out in three low-order streams (Matinha, Cana Dobrada, Jacutinga) that drain into the lower Jacaré-Guaçu river, within the Tietê River watershed, Central São Paulo State, SE Brazil (Table 1). The Jacaré-Guaçu watershed is strongly affected by human activities, with land use dominated by orange and sugarcane cultures, pastures, and reforested areas (CETESB, 2007). The climate of the region is characterized by cold and dry winters and hot and wet summers, with precipitation concentrated between October and March. During the studied period, total precipitation was 209 mm in the dry season (July 2010) and 1118 mm in the wet season (February 2010), whereas mean monthly temperatures varied between 18.05 and 25.21°C.

The streams were located in pasture areas and presented low cover of trees throughout their extension, with varying characteristics of degraded streams including simplified streambed, eroded banks, and sedimentation. The streambed of all streams was predominantly covered with sandy sediments, with patches of *Urochloa* sp. of varying sizes (0.5–5.0 m^2), sometimes with the presence of water primroses (*Ludwigia* sp.). Although the presence of other macrophyte species could increase patch habitat complexity when compared to *Urochloa* patches, this additional complexity was not considered in this study because we only wanted to compare macroinvertebrate communities in bare patches versus macrophyte (mainly *Urochloa*) patches. The stream reaches sampled were formed predominantly by runs, with very few pools and slow water velocities (Table 1), presenting low mesohabitat heterogeneity. Matinha was slightly different from the other two streams sampled, since the channel was not well delimited and the stream spread over a small wetland dominated by southern cattail (*Typha domingensis*), with very low water current velocity and wider wetted width (Table 1). Although the streams had different characteristics, we were interested in within-stream differences, not among-stream differences; therefore, if community composition differed among streams, it was not relevant to the hypothesis being tested.

Sampling design

To evaluate if the presence of macrophyte patches (mainly *Urochloa* sp.) influenced the structure, resistance, taxonomic composition, and functional

Table 1 Geographical locations of studied streams and physical and chemical variables measured in the wet (July 2010) and dry (February 2010) seasons

Streams	Matinha		Cana Dobrada		Jacutinga	
Seasons	Wet	Dry	Wet	Dry	Wet	Dry
Latitude	−21.7397879		−21.78148599		−21.77753193	
Longitude	−48.83888152		−48.78103838		−48.68040464	
Order	1st		2nd		2nd	
Current (m/s)	<0.1	<0.1	0.43 ± 0.16	0.28	0.55 ± 0.05	0.25 ± 0.17
Depth (m)	0.34 ± 0.04	0.26 ± 0.11	0.47 ± 0.91	0.31 ± 0.19	0.28 ± 0.12	0.23 ± 6.95
Width (m)	7.71 ± 0.34	6.93 ± 0.10	3.39 ± 1.12	2.65 ± 0.66	2.23 ± 0.63	1.52 ± 0.36
EC (μS/cm)	104.66 ± 0.51	103.07 ± 13.42	103.8 ± 0.41	80 ± 0.57	47.75 ± 1.25	45 ± 1.00
TDS (mg/l)	60 ± 0.50	77 ± 9.86	70 ± 0.50	53 ± 0.50	30 ± 0.90	33 ± 0.98
DO (mg/l)	3.12 ± 0.13	3.73 ± 0.23	5.18 ± 2.68	5.19 ± 0.13	5.64 ± 0.49	5.18
pH	6.69 ± 0.10	6.88 ± 0.23	7.10 ± 0.05	7.28 ± 0.04	6.63 ± 0.03	6.53 ± 0.12

EC, TDS, and DO correspond, respectively to electric conductivity, total dissolved solids, and dissolved oxygen concentrations. Values are mean ± SD organization of benthic macroinvertebrate communities, we sampled patches with and without grasses within each stream, hereafter referred to as grass patches and bare patches, respectively. In each stream, a 100-m reach was marked and three points were randomly established. Then, we marked the nearest patch of grasses to the sorted point, as well as the nearest patch of bare substrate. All patches sampled within a stream presented similar morphological and hydrologic characteristics. Within each patch, a Surber sampler with an area of 0.09 m^2 and mesh size of 250 μm was positioned in the center of the patch, and macroinvertebrates were collected and fixed with formalin 10%. In the laboratory, macroinvertebrates were identified to family level, and further classified to functional feeding groups following Merritt & Cummins, (1996) and Cummins et al., (2005).

To evaluate temporal variation in macroinvertebrate communities in grass and bare patches, sampling was carried out both in the wet (February 2010) and dry (July 2010) seasons.

Data analysis

To evaluate whether the presence of *Urochloa* sp. on the streambed influenced the distribution and resistance of the community, we calculated the following variables: rarefied taxa richness (Sanders, 1968; Hurlbert, 1971), unbiased Shannon diversity index (Chao & Shen, 2003), Gini–Simpson diversity index, total abundance, and abundance of dominant taxa (>3.0% of relative abundance per season). Abundances represent the number of macroinvertebrates per sample (i.e., 0.09 m^2). We used both the Shannon and Gini–Simpson diversity indices because they weight differently rare and dominant taxa (Jost, 2006).

We used a linear-mixed effects modeling approach (LME) with analysis of variance (ANOVA) to test our hypotheses, with Streams as a fixed effect (3 levels: Cana Dobrada, Jacutinga, and Matinha), Grasses as a fixed effect (2 levels: grass vs. bare patches), and Patches nested within Streams as a random effect (3 levels); the resultant model follows a partial nested design without replicates within patches, so no effects related to patches could be analyzed (Quinn & Keough, 2002):

$$Y_{ijk} = \mu + S_i + P(S)_{j(i)} + G_k + GS_{ik} + GP(S)_{jk(i)} + w$$

where S is the effect of Streams, $P(S)$ is the effect of patches within streams, G is the effect of Grasses, and w is the error. The construction of the F-tests is described in Table S1 (supplementary material), where appropriate denominators for each line of the ANOVA were determined according to their expected mean squares following Underwood (1997). Streams were considered a fixed effect because the number of streams sampled was very low to test a more general hypothesis on rural streams. We carried out separate analyses for each season to evaluate if distinct patterns were found between seasons. Abundance data were transformed to (ln + 1) to obtain homoscedasticity. These analyses were carried out with Systat 13.1 software.

To test if the composition of macroinvertebrate communities was influenced by the presence of grasses, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) model similar to the ANOVA model described above, with the same construction of the tests (Anderson, 2001). Abundance data were transformed to (ln + 1) to balance the contribution of rare and dominant taxa, and we constructed a similarity matrix using the Bray–Curtis similarity index (Clarke, 1993). To identify which taxa were responsible for the observed differences between grass and bare patches, we used a similarity percentage breakdown (SIMPER) analysis, following Clarke (1993). The PERMANOVA model was fitted using the software PRIMER/PERMANOVA 6.0 (Anderson et al., 2008).

To evaluate if grasses influenced macroinvertebrate functional organization, we compared the abundance of functional feeding groups (predators, collector-gatherers, filtering-collectors, scrapers, and shredders) between grass and bare patches with the same ANOVA model described above. We also tested if the composition of functional feeding groups was influenced by the presence of grasses, using the same PERMANOVA model described above.

Results

A total of 5034 individuals were sampled in the wet season, and 4358 in the dry season. In both periods, the dominant taxa were Chironomidae (33.9 and 77.9% in the wet and dry seasons, respectively), Simuliidae

(48.6 and 4.8%), Oligochaeta (8.1 and 5.5%), and Elmidae (1.0 and 3.3%). Other taxa that represented more than 1% of the individuals sampled included Sphaeriidae and Nematoda in the wet season, and Hydropsychidae in the dry season (Table 2).

The presence of *Urochloa* sp. influenced benthic macroinvertebrate community descriptors. Total abundance was significantly higher in patches with grasses during the wet season, but did not significantly differ between patches in the dry season (Table 3; Fig. 1). Taxon richness did not significantly differ between seasons or patch types (Table 3; Fig. 1). Diversity indicators differed between patches, with significantly lower diversity in bare patches during the dry season (Table 3), both for the Shannon (Fig. 1c) and Gini–Simpson (Fig. 1d) diversity.

The effects of *Urochloa* sp. on the dominant taxa were varied (Table 3). Chironomidae presented high abundances in the dry season both in patches with (159.4 ± 1.43, mean ± SE) or without grasses (82.6 ± 1.43), but in the wet season bare patches had significantly lower abundances (11.2 ± 1.44)

Table 2 Relative abundance (in percentage) of taxa and total abundance of functional feeding groups of macroinvertebrate communities sampled in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons

Wet season	Grass	Bare	Dry season	Grass	Bare
Taxonomic composition					
Simuliidae	52.57	14.07	Chironomidae	74.73	85.32
Chironomidae	33.47	37.45	Oligochaeta	4.44	7.91
Oligochaeta	7.17	16.35	Simuliidae	6.74	0.23
Sphaeriidae	1.24	4.37	Elmidae	4.63	0.15
Nematoda	0.67	9.13	Hydropsychidae	2.73	
Elmidae	0.58	4.94	Ceratopogonidae	0.36	2.28
Thiaridae		9.13	Empididae	1.02	0.23
Libellulidae	0.95	0.38	Gomphidae	0.26	1.75
Ceratopogonidae	0.80	0.57	Libellulidae	0.89	0.30
Polycentropodidae	0.55	2.09	Baetidae	0.92	0.08
Hydropsychidae	0.55		Sphaeriidae	0.59	0.61
Baetidae	0.44	0.19	Culicidae	0.72	
Empididae	0.24	0.19	Coenagrionidae	0.59	0.08
Hydrophilidae	0.20	0.38	Polycentropodidae	0.39	0.46
Gomphidae	0.16	0.38	Naucoridae	0.26	
Physidae	0.11		Perlidae	0.23	
Coenagrionidae	0.07	0.19	Hydroptilidae	0.13	
Calopterygidae	0.07		Pyralidae	0.10	0.08
Naucoridae	0.04		Thiaridae		0.30
Hydrobiidae	0.02	0.19	Leptohyphidae	0.10	
Hirudinea	0.02		Calopterygidae	0.07	
Planorbidae	0.02		Hirudinea	0.03	0.08
Caenidae	0.02		Caenidae	0.03	
Belostomatidae	0.02		Chrysomelidae	0.03	
			Stratiomyidae		0.08
			Staphylinidae		0.08
Functional composition					
Collector–gatherers	1758	338		2355	1118
Filtering–collectors	2476	108		340	17
Predators	267	31		340	175
Scrapers	7	49		4	4
Shredders				4	1

Table 3 Linear-mixed effects ANOVA results comparing descriptors of macroinvertebrate communities and density of dominant taxa in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons

Community descriptors		Total abundance		Taxon richness		Shannon diversity index (H')		Gini–Simpson index (1–D)	
Source of variation	df	MS	F	MS	F	MS	F	MS	F
Wet season									
Stream: S	2	4.743	75.230**	1.706	8.250*	0.508	7.664*	0.093	12.290**
	6	0.063		0.207		0.066		0.008	
Patch(Stream): $P(S)$	1	21.962	30.790**	0.339	4.946	0.001	0.046	0.018	1.691
Grasses: G									
$G \times S$	2	1.152	1.615	0.087	1.264	0.129	4.876	0.016	1.503
$G \times P(S)$	6	0.713		0.069		0.026		0.011	
Dry season									
Stream: S	2	0.788	1.596	0.590	0.280	0.010	0.036	0.001	0.015
Patch(Stream):$P(S)$	6	0.493		2.109		0.267		0.079	
Grasses: G	1	3.069	3.423	3.630	5.234	0.495	13.570*	0.086	8.564*
$G \times S$	2	2.365	2.638	1.399	2.018	0.103	2.836	0.033	3.277
$G \times P(S)$	6	0.897		0.694		0.036		0.010	

Dominant taxa		Chironomidae		Simuliidae		Oligochaeta		Elmidae	
Source of variation	df	MS	F	MS	F	MS	F	MS	F
Wet season									
Stream: S	2	2.488	5.404*	30.373	14.980**	3.385	5.541*	2.453	3.440
Patch(Stream): $P(S)$	6	0.460		2.028		0.611		0.713	
Grasses: G	1	27.781	32.180**	16.285	49.070**	3.928	3.442	0.118	0.071
$G \times S$	2	0.401	0.465	4.164	12.550**	4.983	4.366	0.047	0.028
$G \times P(S)$	6	0.863		0.332		1.141		1.648	
Dry season									
Stream: S	2	0.803	0.821	3.621	1.497	5.273	9.434*	4.377	6.142*
Patch(Stream): $P(S)$	6	0.978		2.419		0.559		0.713	
Grasses: G	1	1.944	2.387	7.258	5.827	1.303	1.947	8.690	19.570**
$G \times S$	2	2.929	3.597	1.860	1.493	0.686	1.024	2.422	5.453*
$G \times P(S)$	6	0.814		1.246		0.669		0.444	

* $P < 0.05$; ** $P < 0.01$

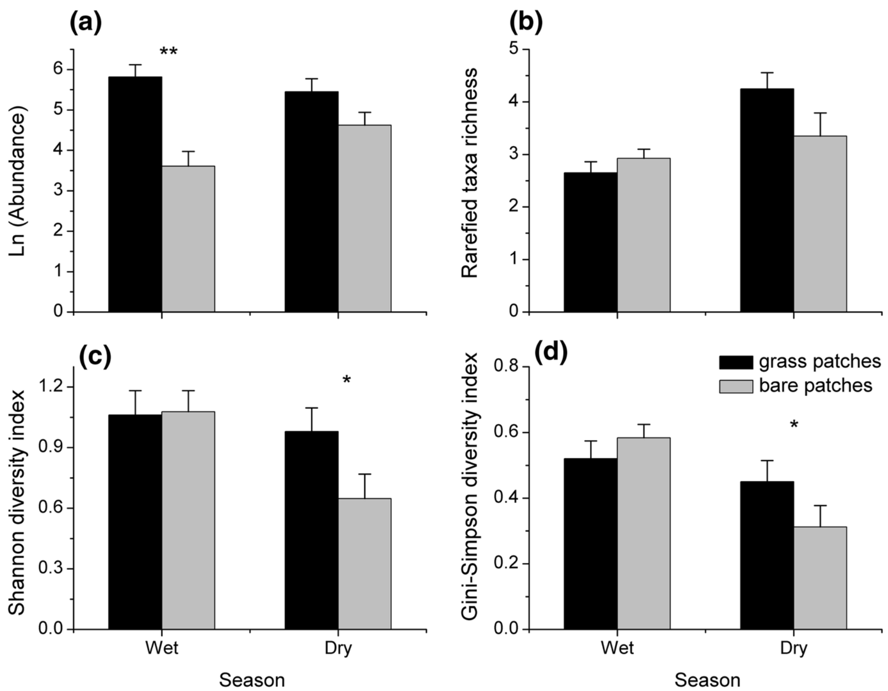

Fig. 1 Descriptors of macroinvertebrate communities in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons: **a** total abundance; **b** rarefied taxa richness (24); **c** unbiased Shannon diversity index; **d** Gini–Simpson diversity index. Values are means + SE. $^{*}P < 0.05$; $^{**}P < 0.01$

than grass patches (134.7 ± 1.28). Abundances of Simuliidae depended on the stream studied (Table 3), since this taxon was not found in Matinha; abundances were higher in patches with grasses (18.9 ± 2.58) than in bare patches (2.8 ± 1.66) in the wet season, and the same trend was found in the dry season ($P = 0.052$, Table 3; grass patches: 45 ± 1.95, bare patches: 1.3 ± 1.12). Abundances of Oligochaeta were not significantly affected by patch type (Table 3). Finally, Elmidae presented similar abundances between patches in the wet season, but in the dry season abundances were significantly higher in patches with grasses (4.7 ± 1.69) than in bare patches (1.2 ± 1.11); this taxon was not found in Matinha, resulting in a significant interaction in this season ($P = 0.045$, Table 3).

The composition of macroinvertebrate communities was influenced by patch type in both seasons (Table 4; Fig. 2a). Large differences in taxon composition between patches were recorded in the wet season, with a mean dissimilarity of 61.5%, except for Jacutinga where mean dissimilarity was 46.5%, resulting in a significant interaction between patch type and streams (Fig. 2a). SIMPER analysis indicated that the differences were due to higher abundances of all taxa in patches with grasses, with the exception of Thiaridae, which was absent in these patches. In the dry season, mean dissimilarity between grass and bare patches was 53.0% (Fig. 2a). SIMPER analyses indicated that most taxa presented higher abundances in patches with grasses in this season, except for Gomphidae and Ceratopogonidae, which occurred in higher abundances in bare substrate patches.

Functional feeding groups

A total of 26 taxa were identified in dry season, 11 of these were predators, 7 collector–gatherers, 5 filtering–collectors, 2 scrapers and 2 shredders. In the wet season, a total of 25 taxa were identified, 11 of these were predators, 6 collector–gatherers, 4 filtering–collectors, and 4 scrapers (Table 2).

The effect of grasses was different for each functional feeding group. The abundance of filtering–collectors was consistently higher in patches with grasses in relation to bare patches in both seasons (Table 5; Fig. 3a). Collector–gatherers occurred in high abundances in both season, with similar values for both patches in the dry season, but significantly lower abundances in bare patches during the wet season (Table 5; Fig. 3b). A similar pattern was found

Table 4 Mixed-model PERMANOVA results comparing the taxonomic and functional feeding groups (FFG) composition of macroinvertebrates communities in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons

Source of variation	df	Taxonomic composition			FFG composition		
		MS	*F*	*P*	MS	*F*	*P*
Wet season							
Stream: *S*	2	4982	6.319	0.003	2308	15.940	0.004
Patch(Stream): *P(S)*	6	788			144		
Grasses: *G*	1	5860	8.380	0.003	4904	22.070	0.001
$G \times S$	2	2386	3.413	0.014	565	2.550	0.094
$G \times P(S)$	6	699			222		
Dry season							
Stream: *S*	2	3506	5.764	0.003	627	3.040	0.021
Patch(Stream): *P(S)*	6	608			206		
Grasses: *G*	1	3907	4.632	0.016	964	3.690	0.058
$G \times S$	2	1476	1.750	0.122	496	1.900	0.191
$G \times P(S)$	6	843			261		

for predator abundances (Table 5; Fig. 3c). Scrapers occurred in very low densities except in Cana Dobrada, with higher abundances in bare patches during the wet season, resulting in significant interaction between patch type and streams (Table 5; Fig. 3d). Shredders were not found in the wet season and occurred in very low abundances in the dry season, so that no significant effects were found for this functional group.

As a result of these differences in abundance, the composition of macroinvertebrate functional feeding groups was influenced by the presence of grasses and season (Table 4). Community composition differed between grass and bare patches in the wet season (Fig. 2b). SIMPER analysis indicated an average dissimilarity of 41.3% between patches with and without grasses in the wet season due to greater abundance of filtering-collectors, collector-gatherers, and predators in patches with grasses, and more scrapers in bare patches. No significant differences between community types were found in the dry season (Table 4).

Discussion

The results of this study indicate that the presence of patches with grasses influence the composition and functional organization of macroinvertebrate communities in tropical rural streams. In the wet season, when the streambed is subject to large and frequent disturbances by floods, the presence of grasses increases the macroinvertebrate community resistance through more shelter and feeding sites, increasing structural habitat features. When disturbances are rare (dry season), the increase of structural habitat features and the increased niche availability provided by patches of grasses allow higher evenness in community structure resulting in higher diversity, when compared with control areas (bare patches).

The higher abundances recorded in patches with grasses in the wet season suggest that the additional structural habitat provided by these plants play an important role as a shelter against disturbances. Our study was carried out in largely deforested streams, located in pasture-dominated rural areas. These changes in land use frequently result in increased frequency and magnitude of floods after strong rains, scouring and simplifying the streambed and disturbing the macroinvertebrate communities (Allan, 2004; Sweeney et al., 2004; Dolédec et al., 2006). Although we do not have data on stream hydrology, the cumulative precipitation in the study area along the ten previous days before sampling in the wet season was about 175 mm, whereas no precipitation was observed in the dry season (data from National Institute of Meteorology). Previous studies found positive relationships between structural habitat features and benthic invertebrates (Brown, 2003; Rennie & Jackson, 2005) and between structural habitat features and protection from flooding (Taniguchi et al., 2003). In deforested stream reaches, grass

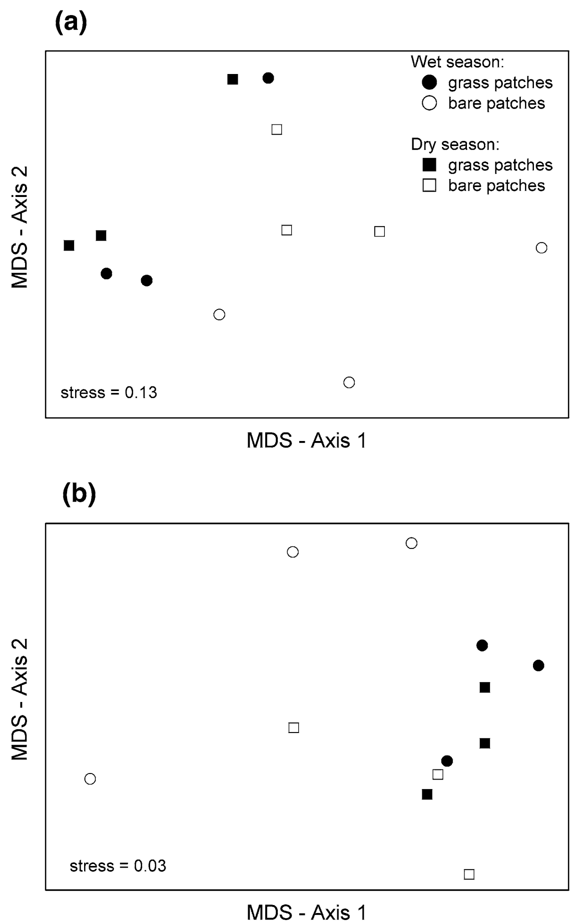

Fig. 2 Centroids of MDS results comparing **a** taxonomic, and **b** functional feeding groups composition of macroinvertebrate communities found in grass (*filled symbols*) and bare patches (*empty symbols*) in three rural streams in central São Paulo State, in the wet (*circles*) and dry (*squares*) seasons. The stress values are also indicated

patches may have a similar role, so that high abundances of most taxa are maintained, increasing macroinvertebrate community resistance to flood disturbances. Thus, streambed areas with grass patches may have positive effects on tropical pasture streams, avoiding the simplification of these systems by providing shelter during heavy rains, since the habitat provided by these plants is more stable than the sediment of bare patches.

Although higher abundances were recorded in the wet season, higher diversity in patches with grasses was recorded only in the dry season. In the wet season, when disturbances caused by floods occur in high frequency and magnitude, only resistant taxa with good dispersal and colonization abilities persist (McCabe & Gotelli, 2000; Allan, 2004), a pattern found in other streams located in pasture-dominated microbasins (Hepp et al., 2010). Higher sedimentation during the wet season can result in smothering of plant parts, reducing the effects of the added complexity provided by the grasses. The effects of increasing sediment deposition on macroinvertebrate community structure and composition are well documented, reducing mainly the abundances of sediment-sensitive taxa (Burdon et al., 2013). Thus, disturbances may override the positive effects of structural habitat features on the community diversity. On the other hand, less resistant taxa can increase their abundances in the dry season due to the higher habitat complexity provided by patches with grasses, where more food, shelter, and other resources can be found, increasing diversity values when compared with bare patches. Since no differences in taxon richness were found between patches, lower diversity found in bare patches should be due to the higher dominance of some taxa.

The capacity of in-stream grasses to provide shelter and food accumulation sites influenced the functional feeding composition in both seasons. The reduction in habitat availability and increased flooding events, resulting from the removal of riparian vegetation (Allan, 2004; Miserendino & Masi, 2010), make in-stream grasses one of the few stable substrates for filtering-collectors. The barriers formed by leaves and roots favor the deposition of organic material mainly in wet season, which is positively related to the abundance of collector-gatherers (Clapcott & Bunn, 2003; Thompson & Townsend, 2004; Miserendino & Masi, 2010). Predators also showed higher density in patches with grasses in the wet season, and this may be due to prey availability, since most taxa were more abundant in these patches. Encounter rates between predators and prey may have increased during floods due to the concentration of macroinvertebrates in this refuge from hydrodynamic disturbance (Thomson et al., 2002).

Scrapers occurred in very low densities and in the wet season were consistently more abundant in bare patches. Scrapers track small-scale variation in algal abundance (Heino et al., 2004), being negatively related both to organic material standing stocks and to shading due to their negative effects on development and accumulation of periphyton (Dudgeon, 1989). In-stream grasses can favor the accumulation

Table 5 Linear-mixed effects ANOVA results comparing the presence of functional feeding groups in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons

Source of variation	df	Filtering–collectors		Collector–gatherers		Predators		Scrapers	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*
Wet season									
Stream: *S*	2	4.170	19.300**	0.199	2.670	0.093	1.710	1.240	36.930**
Patch(Stream): *P(S)*	6	0.216		0.075		0.054		0.034	
Grasses: *G*	1	3.780	43.500**	3.640	21.420**	3.619	35.770**	0.208	6.720*
$G \times S$	2	0.139	1.600	0.155	0.910	0.069	0.684	0.270	8.720*
$G \times P(S)$	6	0.087		0.170		0.101		0.031	
Dry season									
Stream: *S*	2	0.927	2.480	0.128	1.270	0.147	2.260	0.015	0.375
Patch(Stream): *P(S)*	6	0.374		0.101		0.065		0.040	
Grasses: *G*	1	2.750	9.320*	0.511	3.170	0.387	2.850	0.000	0.000
$G \times S$	2	0.031	0.105	0.495	3.070	0.263	1.940	0.106	2.630
$G \times P(S)$	6	0.295		0.161		0.136		0.040	

* $P < 0.05$; ** $P < 0.01$

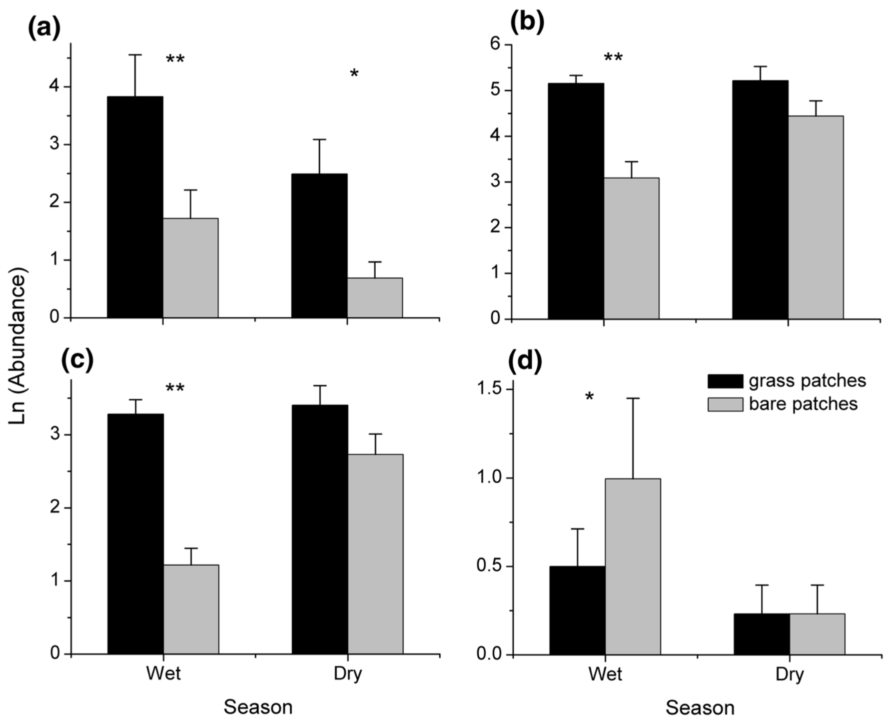

Fig. 3 Abundances (means + SE) of functional feeding groups of macroinvertebrate communities in grass and bare patches of rural streams, central São Paulo State, in the wet and dry seasons: **a** filtering–collectors; **b** collector–gatherers; **c** predators; **d** scrapers. *$P < 0.05$; **$P < 0.01$

of organic material (mainly in the wet season) and shading, possibly inhibiting colonization and permanence of scrapers. Shredders were present in low abundances and were the only functional feeding group that was not associated with grasses. Low diversity and abundance of shredders has previously been observed in tropical streams (Rueda-Delgado et al., 2006), both forested and deforested (Li & Dudgeon, 2009). Furthermore, Clapcott & Bunn (2003) found that shredder abundance correlated poorly with grasses. Anyway, our results suggest that patches with grasses can provide shelter to the macroinvertebrates, and also feeding sites, allowing the maintenance, at least to some degree, of functional processes within pasture streams, even though these processes are assured by a high density of few tolerant taxa.

We conclude that *Urochloa* sp. grasses may invade streambeds and influence macroinvertebrate communities in the deforested, pasture streams studied. Several aspects of community structure and composition were influenced, mainly differential abundance of distinct functional groups, and increased diversity during dry season periods. However, values of diversity observed in grass patches were much lower than in forest streams without grasses in a nearby region (Corbi & Trivinho-Strixino, 2006); the number of taxa found in forest streams varied between 18 and 23, whereas in our study values varied between 5 and 12 in grass patches, and the Shannon diversity index varied between 1.6 and 1.8 in forest streams, and between 0.7 and 1.3 in grass patches in pasture streams. These results indicate that the communities in pasture streams, even in the presence of grasses, are very degraded when compared to forest, reference streams for the region, and thus in-stream grasses do not mitigate biodiversity losses in pasture streams. Also, the effects of stream deforestation are largely negative on stream characteristics, and grasses can lead to large changes in channel morphology and hydrology, because these plants act as sediment traps, especially in rural streams (Davies-Colley, 1997; Bunn et al., 1998). Sediment deposition, channel narrowing, flood disturbances, stream bank erosion, and riparian deforestation can have profound effects on pristine stream macroinvertebrate communities, on natural patterns of distribution (Vannote et al., 1980) and functional organization of these communities, leading to significant changes in ecosystem functions (Clapcott & Bunn, 2003). The effects of in-stream grasses can contribute to stream macroinvertebrate diversity and resistance, but also contribute to changes on streambed morphology and channel structure, maintaining disturbed conditions for these communities, possibly resulting in degraded communities (Davies-Colley, 1997). Therefore, the added complexity may have positive effects for macroinvertebrate communities, but the presence of these grasses can make restoration actions more difficult. Including physical structures could potentially benefit macroinvertebrate communities in the same way of these grasses by increasing habitat complexity, but we are not aware of any studies evaluating this hypothesis. Deforested streams invaded by grasses that thrive in aquatic systems are becoming increasingly common worldwide, and more studies are necessary to understand their effects on lotic systems.

Acknowledgments We thank Rogério A. Libório, Fábio T. T. Hanashiro, Francisco V. Neto, Gustavo R. Mazão, and Melissa O. Segura for help during fieldwork and sorting of samples in the laboratory, the Instituto Nacional de Meteorologia (INMET) for providing meteorological data, Andrea L. T. de Souza for help in statistical analyses. D.G.F. received a scholarship from Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP, Proc. no 2008/07970-7), M. O. T. acknowledges grants from Conselho Nacional de Desenvolvimento Cientifico e Tecnológico (CNPq, Proc. nos. 552554/2007-3, 302890/2007-6, 308630/2010-6). We also thank the anonymous reviewers who greatly contributed to increase the quality of this manuscript.

References

Allan, J. D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257–284.

Anderson, M. J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Anderson, M. J., R. N. Gorley & K. R. Clarke, 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth.

Brown, B. L., 2003. Spatial heterogeneity reduces temporal variability in stream insect communities. Ecology Letters 6: 316–325.

Burdon, F. J., A. R. McIntosh & J. S. Harding, 2013. Habitat loss drives threshold response of benthic invertebrate communities to deposited sediment in agricultural streams. Ecological Applications 23: 1036–1047.

Bunn, S. E., P. M. Davies & D. M. Kellaway, 1997. Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. Marine Freshwater Research 48: 173–179.

Bunn, S. E., P. M. Davies, D. M. Kellaway & I. P. Prosser, 1998. Influence of invasive macrophytes on channel morphology and hydrology in an open tropical lowland stream, and potential control by riparian shading. Freshwater Biology 39: 171–178.

Casatti, L., C. P. Ferreira & F. R. Carvalho, 2009. Grass-dominated stream sites exhibit low fish species diversity and dominance by guppies: an assessment of two tropical pasture river basins. Hydrobiologia 632: 273–283.

CETESB, 2007. Relatório da qualidade de águas interiores do Estado de São Paulo – São Paulo. Companhia de Tecnologia de Saneamento Ambiental. 2v. 327.

Chao, A. & T. J. Shen, 2003. Nonparametric estimation of Shannon's index of diversity when there are unseen species

in sample. Environmental and Ecological Statistics 10: 429–443.
Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology, Evolution, and Systematics 31: 343–366.
Clapcott, J. E. & S. E. Bunn, 2003. Can C_4 plants contribute to aquatic food webs of subtropical streams? Freshwater Biology 48: 1105–1116.
Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.
Clarke, A., P. S. Lake & D. J. O'Dowd, 2004. Ecological impacts on aquatic macroinvertebrates following upland stream invasion by a ponded pasture grass (*Glyceria maxima*) in southern Australia. Marine and Freshwater Research 55: 709–713.
Corbi, J. J. & S. Trivinho-Strixino, 2006. Influence of taxonomic resolution of stream macroinvertebrate communities on the evaluation of different land uses. Acta Limnologica Brasiliensia 18: 469–475.
Cummins, K. W., R. W. Merritt & P. C. N. Andrade, 2005. The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. Studies in Neotropical Fauna and the Environment 40: 69–89.
Davies-Colley, R. J., 1997. Stream channels are narrower in pasture than in forest. New Zealand Journal of Marine and Freshwater Research 31: 599–608.
Dolédec, S., N. Phillips, M. Scarsbrook, R. H. Riley & C. R. Townsend, 2006. Comparison of structural and functional approaches to determining land use effects on grassland stream invertebrate communities. Journal of the North American Benthological Society 25: 44–66.
Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. Mcnally, M. Viana, K. Healy, M. Lurgi, N. E. O'Connor & M. C. Emmerson, 2013. On the dimensionality of ecological stability. Ecology Letters 16: 421–429.
Douglas, M. M. & R. A. O'Connor, 2003. Effects of the exotic macrophyte, para grass (*Urochloa mutica*), on benthic and epiphytic macroinvertebrates of a tropical floodplain. Freshwater Biology 48: 962–971.
Dudgeon, D., 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. Hydrobiologia 179: 183–194.
England, L. E. & A. D. Rosemond, 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshwater Biology 49: 721–734.
Fernandes, L. F. G., M. C. Teixeira & S. M. Thomaz, 2013. Diversity and biomass of native macrophytes are negatively related to dominance of an invasive Poaceae in Brazilian sub-tropical streams. Acta Limnologica Brasiliensia 25: 202–209.
Fletcher, D. E., S. D. Wilkins, J. V. McArthur & G. K. Meffe, 2000. Influence of riparian alteration on canopy coverage and macrophyte abundance in Southeastern USA blackwater. Ecological Engineering 15: 67–78.
Gregory, S. V., F. J. Swanson, A. McKee & K. W. Cummins, 1991. An ecosystem perspective of riparian zones. BioScience 41: 540–551.
Grimm, V. & C. Wissel, 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109: 323–334.
Heino, J., 2013. The importance of metacommunity ecology for environmental assessment research in the freshwater realm. Biological Reviews 88: 166–178.
Heino, J., P. Louhi & T. Muotka, 2004. Identifying the scales of variability in stream macroinvertebrate abundance, functional composition and assemblage structure. Freshwater Biology 49: 1230–1239.
Hepp, L. U., S. V. Milesi, C. Biasi & R. M. Restello, 2010. Effects of agricultural and urban impacts on macroinvertebrates assemblages in streams (Rio Grande do Sul, Brazil). Zoologia 27: 106–113.
Hurlbert, S. H., 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52: 577–586.
Jost, L., 2006. Entropy and diversity. Oikos 113: 363–375.
Karr, J. R. & I. J. Schlosser, 1978. Water resources and land-water interface. Science 201: 229–234.
Li, A. O. Y. & D. Dudgeon, 2009. Shredders: species richness, abundance, and role in litter breakdown in tropical Hong Kong streams. Journal of the North American Benthological Society 28: 167–180.
Loke, L. H. L., R. J. Ladle, T. J. Bouma & P. A. Todd, 2015. Creating complex habitats for restoration and reconciliation. Ecological Engineering 77: 307–313.
McCabe, D. J. & N. J. Gotelli, 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. Oecologia 124: 270–279.
Melles, S. J., N. E. Jones & B. Schmidt, 2012. Review of theoretical developments in stream ecology and their influence on stream classification and conservation planning. Freshwater Biology 57: 415–434.
Menninger, H. L. & M. A. Palmer, 2007. Herbs and grasses as allochthonous resource in open-canopy headwater streams. Freshwater Biology 52: 1689–1699.
Merritt, R. W. & K. W. Cummins, 1996. An introduction to the aquatic insects of North America, 3rd ed. Kendall/Hunt, Dubuque.
Michelan, T. S., S. M. Thomaz & L. M. Bini, 2013. Native macrophyte density and richness affect the invasiveness of a tropical Poaceae species. PloS One 8: e60004.
Minaya, V., M. E. McClain, O. Moog, F. Omengo & G. A. Singer, 2013. Scale-dependent effects of rural activities on benthic macroinvertebrates and physic-chemical characteristics in headwater streams of the Mara River, Kenya. Ecological Indicators 32: 116–122.
Miserendino, M. L. & C. I. Masi, 2010. The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. Ecological Indicators 10: 311–319.
Miserendino, M. L., R. Casaux, M. Archangelsky, C. Y. Di Prinzio, C. Brand & A. M. Kutschker, 2011. Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. Science of the Total Environment 409: 612–624.
Nessimian, J. L., E. M. Venticinque, J. Zuanon, P. Marco Jr, M. Gordo, L. Fidelis, J. D. Batista & L. Juen, 2008. Land use, habitat integrity, and aquatic insect assemblages in Central Amazonian streams. Hydrobiologia 614: 117–131.
Pimm, S. L., 1984. The complexity and stability of ecosystems. Nature 307: 321–326.
Pott, V. J., A. Pott, L. C. P. Lima, S. N. Moreira & A. M. K. Oliveira, 2011. Aquatic macrophyte diversity of the

Pantanal wetland and upper basin. Brazilian Journal of Biology 71: 255–263.
Pusey, B. J. & A. H. Arthington, 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. Marine and Freshwater Research 54: 1–16.
Quinn, G. P. & M. J. Keough, 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge.
Quinn, J. M., A. B. Cooper, R. J. Davies-Colley, J. C. Rutherford & R. B. Williamson, 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand Journal of Marine and Freshwater Research 31: 579–597.
Rennie, M. D. & L. J. Jackson, 2005. The influence of habitat complexity on littoral invertebrate distributions: patterns differ in shallow prairie lakes with and without fish. Canadian Journal of Fisheries and Aquatic Sciences 62: 2088–2099.
Roth, N. E., J. D. Allan & D. L. Erickson, 1996. Landscape influence on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141–156.
Rueda-Delgado, G., K. M. Wantzen & M. B. Tolosa, 2006. Leaf-litter decomposition in an Amazonian floodplain stream: effects of seasonal hydrological changes. Journal of the North American Benthological Society 25: 233–249.
Sanders, H. L., 1968. Marine benthic diversity: a comparative study. American Naturalist 102: 243–282.
Shields Jr, F. D., R. E. Lizotte Jr, S. S. Knight, C. M. Cooper & D. Wilconx, 2010. The stream channel incision syndrome and water quality. Ecological Engineering 36: 78–90.
Sweeney, B. W., 1993. Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. Proceedings of the Academy of Natural Sciences of Philadelphia 144: 291–340.
Sweeney, B. W., T. L. Bott, J. K. Jackson, L. A. Kaplan, J. D. Newbold, L. J. Standley, W. C. Hession & R. J. Horwitz, 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proceedings of the national Academy of Sciences of the United States of America 101: 14132–14137.
Taniguchi, H., S. Nakano & M. Tokeshi, 2003. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. Freshwater Biology 48: 718–728.
Thompson, R. M. & C. R. Townsend, 2004. Land-use influences on New Zealand stream communities: effects on species composition, functional organization, and food-web structure. New Zealand Journal of Marine and Freshwater Research 38: 595–608.
Thomson, J. R., P. S. Lake & B. J. Downes, 2002. The effect of hydrological disturbance on the impact of benthic invertebrate predator. Ecology 83: 628–642.
Townsend, C. R., 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8: 36–50.
Underwood, A. J., 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge University Press, Cambridge.
Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.