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How Habitat Filtering Can Affect Taxonomic and Functional Composition of Aquatic Insect Communities in Small Amazonian Streams

G Nicacio[1], EJ Cunha[1], N Hamada[2], L Juen[1,3]

[1]Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Univ Federal do Pará, Belém, Pará, Brasil
[2]Programa de Pós-graduação em Entomologia, Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia – INPA, Manaus, AM, Brasil
[3]Instituto de Ciências Biológicas, Univ Federal do Pará, Belém, PA, Brasil

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Correspondence
G Nicacio, Pós-Graduação em Zoologia, Instituto de Ciências Biológicas, Univ Federal do Pará, Rua Augusto Correia, Bairro Guamá, Belém, Pará, Brasil; gilnicacio@gmail.com

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Abstract

Responses in taxonomic and functional composition of communities were analysed in small Amazonian streams at the small and large scale (habitat patches, river segment scale, and catchment scale). We hypothesised that similar responses in community structure to local environmental factors were a correlation between taxonomic and functional composition. To evaluate the response of taxonomic composition to environmental variables, redundancy analysis (RDA) and *RLQ* analysis were performed to investigate the response of community abundance (*L*) as a function of the environment (*R*) and traits (*Q*). The fourth-corner analysis was applied to summarize specific interactions between environmental variables and traits. Then, community taxonomic composition was associated with models at multiple scales of habitat (i.e. riparian/channel, substrates, and water variables). Likewise, the fourth-corner tests and *RLQ* axes showed associations between trait composition and environmental variables related to variables, such as riparian cover and channel morphology followed by variation in substrate size and composition. Unexpectedly, these results did not show specific associations between unique environmental variables and traits. At last, results showed that local conditions of stream habitat regulated community structure and functional composition of aquatic insects. Thus, these findings indicate that the local environmental filtering appears to be strongly associated with selected species traits adapted to occur in a range of habitat conditions. Despite the low number of analysed streams, these results provide important information for understanding the simultaneous variation in functional trait composition and community composition of aquatic insect assemblages.

Introduction

How stream habitats support different species compositions and how species coexist within and among communities are recurring issues in riverine ecology (Vinson & Hawkins 1998). To address these questions, niche-based approaches have extensively been applied to explain and predict species distributions based on spatiotemporal variation in environmental conditions (Poff 1997). Additionally, studies have emphasized the influence of ecological processes on functional and evolutionary patterns in riverine assemblages (Usseglio-Polatera *et al* 2000). Often, species distribution is related to differences in their life-history traits, the availability of resources, and ecological interactions, mainly considering the contribution of differences in species traits and their categories as a proxy for responses to environmental filters (Menezes *et al* 2010, Schmera *et al* 2015).

When predicting species distribution, a common method is to model the environmental influence on community structure, but applying only this approach often fails to support specific responses to ecosystem processes (Frainer *et al* 2014). Because aquatic ecosystems have complex ecological dynamics (e.g. connectivity, dendritic networks, and dispersal limitations), it can be evaluated at many spatial scales: regional contexts (whole basins and drainages), mesoscale habitats (riparian structure and pool-riffle sequences), and microhabitats (substrate composition) (Brown 2003, Swan & Brown 2011). Thus, studies have been proposed wherein species classified into groups with similar biological and ecological traits are expected to respond similarly along specific environmental gradients (Usseglio-Polatera *et al* 2000, Tomanova & Usseglio-Polatera 2007). Therefore, functional classification of stream insect communities (i.e. behaviour, physiology, and morphology) has contributed to define how assemblages respond to the environment and key aspects of the environment that influence species distribution at multiple spatial scales (Colzani *et al* 2013).

Relationships between functional traits and environmental factors is considered a good indicator for understanding human effects on stream insect communities (Townsend *et al* 1997, Díaz *et al* 2007). Considering particular groups, weak relationships between taxonomical identity and functional composition may support minor implications for ecosystem function when species loss is common in communities (Flynn *et al* 2009). According to theoretical references in the habitat templet, initially proposed by Southwood (1977), trait composition is affected by a set of environmental conditions that determine species traits in particular habitats and shape local species composition (Townsend & Hildrew 1994). If similar physical conditions tend to promote equivalent biological trait responses between communities, then taxonomic and functional composition should exhibit dependent responses along environmental gradients (Vinson & Hawkins 1998, Heino *et al* 2007). Regard to this, previous finds confirmed that patterns for functional redundancy (mostly conducted on plants and vertebrates) is linked to variation in species richness. Then, if there is high species richness with low categories of functional traits, the equivalence between communities tends to be high. In contrast, if species richness is high with variation in unique species in community composition, the functional equivalence in trait composition may be low (Fonseca & Ganade 2001, Hubbell 2005, Luck *et al* 2013).

These patterns are quite well understood for many aquatic systems in temperate zones, while few patterns related to aquatic insect assemblages in tropical streams are well known especially in species-rich communities (Tomanova & Usseglio-Polatera 2007, Reynaga & Santos 2013). For tropical streams, few studies have compared patterns in taxonomic and functional trait structure in response to anthropogenic degradation of ecosystem conditions (Reynaga & Santos 2013, Tupinambás *et al* 2014). Therefore, Amazonian streams are considered good models to address these issues. The region is known for high species-rich ecosystems with aquatic biodiversity bearing more niches, enabling habitat specialization and longer food chains than correspondent environments in temperate regions (Tomanova *et al* 2006, Albert *et al* 2011).

Responses of macroinvertebrate communities along environmental gradients at reach and catchment scales are expected to exhibit similar patterns for taxonomic and functional composition because they are strongly influenced by species richness that may control functional richness in the regional pools (Dolédec *et al* 2000, Mouchet *et al* 2010). Thus, it is expected that in high species-rich tropical streams, the taxonomic and functional trait composition produces contrary responses to habitat filtering, considering habitats with unique species and low functional redundancy (Dolédec *et al* 2000, Mouchet *et al* 2010). In view of this, the main goal of this study was to evaluate taxonomic and functional trait composition of aquatic insect assemblages in response to local inter-habitat variation of habitats among small streams. More importantly, we tested two hypotheses: (i) response of taxonomic and functional composition is redundant for environmental gradients in habitats at larger-scales (river segment scale, and catchment scale); (ii) functional composition in habitats from small scales (habitat patches) is influenced by specific environmental variables (i.e. links between specific variables and traits). To achieve this, we tested responses in taxonomic and functional composition of communities in streams from small- and large-scale (habitat patches, river segment scale, and catchment scale).

Materials and Methods

Study area

This study was performed at eight streams located at Floresta Nacional do Tapajós, an important protected area from the Tapajós River in the Amazon basin (Fig. 1). The area is covered by dense rain forest and located in the watershed of the Tapajós River, located in the south-west region of Pará State, Brazil. The forests are characterized as "*terra firme*," or upper-level forest (80%), and have a small floodplain area with several "igapó" (flooded forest) areas (20%). The climate of the region, according to the Köppen classification, is a tropical monsoon climate (Am) with a short dry season from June to September.

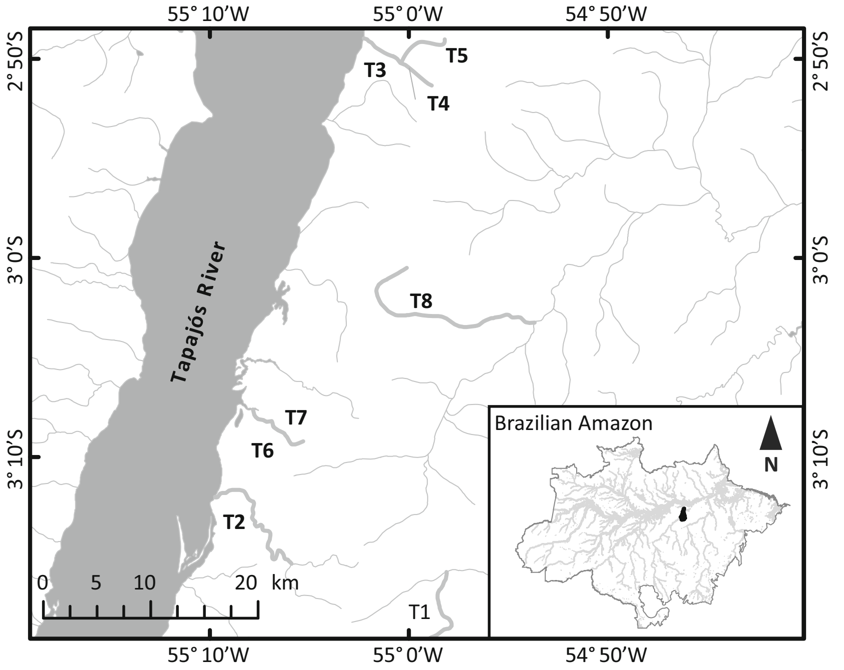

Fig. 1 Study area with eight stream sites at Floresta Nacional do Tapajós (Flona Tapajós), Santarém/Belterra, Pará State, Brazil

Field sampling and sample processing

Aquatic insects were collected in the habitats at headwaters in the streams. The environmental variables were measured at the same sampling time during the dry season in June 2015. Specimens were collected using a circular dip net (190 mm in diameter, 0.25 mm mesh size) during a survey of benthic macroinvertebrates. A screening was performed in each riffle and pool zone and collected 20 substrate subsamples from each stream as replicates. Benthic subsamples were collected systematically from all available in-stream habitats (e.g. cobble, wood debris, vegetated banks, submerged leaves, sand, and other fine sediment) by kicking the substrate into the circular dip net. The same effort sampling were performed for all streams covering 150 m of each stream site from the downstream end of the reach moving upstream following an approach currently applied to assess aquatic habitat in Amazonian streams (Juen *et al* 2016). Specimens were sorted in the field and stored in alcohol at the Zoological Collection at Universidade Federal do Pará, Belém, Brazil. Then, insects were identified at the genus level or assigned them to the lowest taxonomic level using keys available in the literature (Hamada *et al* 2019).

Environmental data

In each stream, samples were collected on a 150 m stretch, which was subdivided into 10 continuous sections, 15 m in length, resulting in 11 cross-sectional transects. Habitat variables included measurement of stream channel morphology, in-stream habitat, and riparian structure. Finally, to test the influence of inter-habitat variation on insect assemblages in further analysis, we considered groups of habitat variables representing a hierarchical organization of streams as subsystems at three spatial scales (i.e. reach the system, pool/-rifle system, and microhabitat system). We applied a selection process by removing variables from the environmental component; specifically, variables were removed if they (a) had values of zero for more than 90% of their data, (b) were highly correlated with other variables (Pearson correlations $r > 0.7$) or (c) were redundant with other variables.

The environmental component contained 12 variables grouped as riparian/channel variables: (1) canopy density mid-stream (%); (2) large woody debris (LWD) in and above the active channel (pieces/100 m); (3) thalweg mean depth (cm); and (4) mean ratio of wetted width to thalweg depth; substrate variables: (5) percentage of sand; (6) percentage of fine substrates (silt, clay, and muck); (7) percentage of roots (mostly *Euterpe oleracea* Mart., Arecaceae); and (8) percentage of wood and organic detritus; and water variables: (9) pH, (10) electrical conductivity (μS/cm), (11) temperature (°C), (12) dissolved oxygen (mg/L) (Table 1). The selected variables are based on ecological relevance and their past use in studies of aquatic insects in Amazonian streams (Couceiro *et al* 2012, Datry *et al* 2016, Juen *et al* 2016).

Functional trait composition

A trait categorical database were computed comprising six biological traits and 30 trait categories (Table S1, S2 in

Table 1 Descriptive statistics of environmental variables considered habitat models from eighth streams at Floresta Nacional do Tapajós, Pará State, Brazil

Variables	Codes	Min	Max	Mean	SD*	SE**
Riparian cover/channel morphology						
Mean % canopy density mid-stream	XCDENMID	63.904	98.262	92.296	11.594	4.099
Mean thalweg depth (cm)	XDEPTH_T	4.490	16.011	9.936	3.500	2.581
Mean wetted width / depth (m/m)	XWD_RAT	5.381	13.141	8.337	2.843	1.238
Large woody debris (pieces/100 m)	C1T_100	8.000	32.381	18.214	7.301	1.005
Substrate size and composition						
% sand (0.6–2 mm)	PCT_SA	20	58.095	39.844	12.248	4.330
% fine (silt/clay; < 0.6 mm)	PCT_FN	0	48.571	12.103	16.170	5.717
% wood or detritus	PCT_ORG	36.190	73.333	49.177	12.388	4.380
% thin roots	PCT_RT	11.250	33.333	20.972	8.050	2.846
Water variables						
Temperature (°C)	T	23.700	25.833	25.150	0.668	0.236
pH	pH	4.493	5.400	4.839	0.265	0.094
Electrical conductivity (μS cm^{-1})	Cond	12.133	20.633	17.546	3.195	1.130
Dissolved oxygen (mg L^{-1})	OD	4.133	8.533	6.590	1.628	0.576

*Standard deviation. **Standard error of the mean

Supplementary Material). Trait groups and their modalities for each taxa were computed from available studies considering the limited knowledge on functional traits available for Neotropical species (e.g. Cummins *et al* 2005, Tomanova *et al* 2006, Tomanova & Usseglio-Polatera 2007, Colzani *et al* 2013, de Castro *et al* 2017). In addition, the categorical matrix of species traits were compared with prior studies that evaluated relationships between biological attributes of aquatic insects linked with the environment from temperate streams (Cummins 1973, Finn & Poff 2005, Poff *et al* 2006, Merritt & Cummins 2007, Merritt *et al* 2008). Trait variables recognized for aquatic insects and their habitat included the following modalities: two trophic trait groups (i.e. "food" and "guilds"), respiration mode, two morphological adaptations (i.e. body shape and specific adaptations to flow) and mobility mode (see Table S2 in Supplementary Material).

Data analysis

Prior to ordination methods, Hellinger transformation was applied to the species abundance matrix (**L**: insect composition) to best fit the variation in community composition. To test our first hypothesis and evaluate environmental influence on taxonomic community composition, a distance-based redundancy analysis (dbRDA) was performed on the abundance matrix (based on the Bray–Curtis distance). We tested the null hypothesis (i.e. no relationship) using an ANOVA with 999 permutations. (Legendre & Anderson 1999).

To test our second and third hypotheses, *RLQ* analysis and the fourth-corner method were performed to evaluate patterns in community composition based simultaneously on the influence of environmental variables and functional trait composition (Dolédec *et al* 1996, Legendre *et al* 1997). Relationships were analysed among the matrices of environmental variables (R), abundance (L: 135 taxa), and traits (Q). *RLQ* is an extension of co-inertia analysis that searches simultaneously for linear combinations of variables in *Q* and linear combinations of variables in *R* while maximizing covariance and using abundance-weighting in the *L* matrix. For this step, the *R* and *Q* tables were first submitted to principal component analysis (PCA) (the *Q* table using the Hill and Smith ordination method for mixing quantitative variables and factors) and the *L* table submitted to correspondence analysis.

The fourth-corner method was performed to test specific environment–trait relationships (i.e. relationships between *Q* and *R*) with two suitable models (hereafter referred to as models 2 and 4 according to Dray *et al* (2014). The first model tests the hypothesis that species assemblages are dependent upon the environmental characteristics of the sites where they are found (i.e. environmental control over species assemblages). The second model tests that the distributions of the species among the sites, which are related to their preferences for site conditions, depend on the adaptations (traits) of the species (i.e. non-random species attributes). This step consists of bivariate tests to analyse associations between one trait and one environmental variable at a time. Permutation methods were applied using adjusted *p* values (Bonferroni procedure for multiple tests of significance) for multiple comparisons using a significant level of $\alpha = 0.05$. To visualize fourth-corner modelling results, standardized coefficients were applied for all environment–trait interaction correlations. We performed all statistical analyses with functions from the packages *vegan* (dbrda), *ade4* (rlq), and *mvabund* (fourth-corner modelling) in R version 3.3.0.

Results

Insect Diversity

A total of 5469 aquatic insects were collected (Coleoptera, Diptera, Ephemeroptera, Hemiptera, Lepidoptera, Megaloptera, Odonata, Plecoptera, and Trichoptera) and classified into 135 taxa and categorized them into six groups based on functional traits (see Tables S2 and S3 in Supplementary Material). An average of 74 genera and 685 individuals were collected per stream. Diptera and Coleoptera were the orders with the highest richness, with 48 and 19 genera, respectively. Ephemeroptera and Diptera were the most abundant orders, with 1564 and 1467 individuals, respectively (Fig. 2). Among the most common genera, the following 20 represented 67% of the total relative abundance: *Miroculis*, *Leptonema*, *Macrogynoplax*, *Farrodes*, *Anacroneuria*, *Campylocia*, *Gyretes*, *Macronema*, *Parapoynx*, *Riethia*, *Phaenopsectra*, *Limnophila*, *Hagenulopsis*, *Zonophora*, *Chimarra*, *Endotribelos*, *Macrostemum*, *Helicopsyche*, *Paratanytarsus*, and *Simulium* (see Tables S3 in Supplementary Material).

Relationships among Environmental Variables and Community Structure

Overall, our first hypothesis was corroborated by the response of community structure to the multiple scales of habitat characteristics. Results of distance-based redundancy analysis (dbRDA) indicated that the inter-habitat variation affected community composition of aquatic insect assemblages (and their abundances) (Table 2). All models indicating multiple scales of habitat, such as riparian/channel, substrate, and water variables influenced community composition and species distribution. The main predictors in each model were mean canopy density mid-stream (XCDENMID), mean wetted width (XWD_RAT) percentage of sand (PCT_SA), percentage of fine substrates (PCT_FN), temperature, and pH.

Summary of the Response of Community Structure to Environmental Variables and Trait Composition

Our results from *RLQ* and fourth-corner analysis corroborated the second and third hypothesis that assemblages are structured by environmental variables and traits for each group at multiple scales of habitat (Tables 3 and 4). For all models of habitat scale, the first two axes of *RLQ* analysis explained more than 60% of the total variance. Permutations tests on fourth-corner models (*pseudo-F* and *Pearson r* for one quantitative variable and one qualitative variable) showed that the overall functional trait composition was significantly correlated with the environmental variables (Table 3). However, we did not find support for our third hypothesis. No significant bivariate associations between specific traits and environmental variables were detected in the Fourth-corner test for specific environment–trait relationships (i.e. specific associations between a trait and an environmental variable).

The response of overall functional composition to environmental gradients can be summarized as a group of traits. Predator species (e.g. *Polyplectropus*, *Cernotina*,

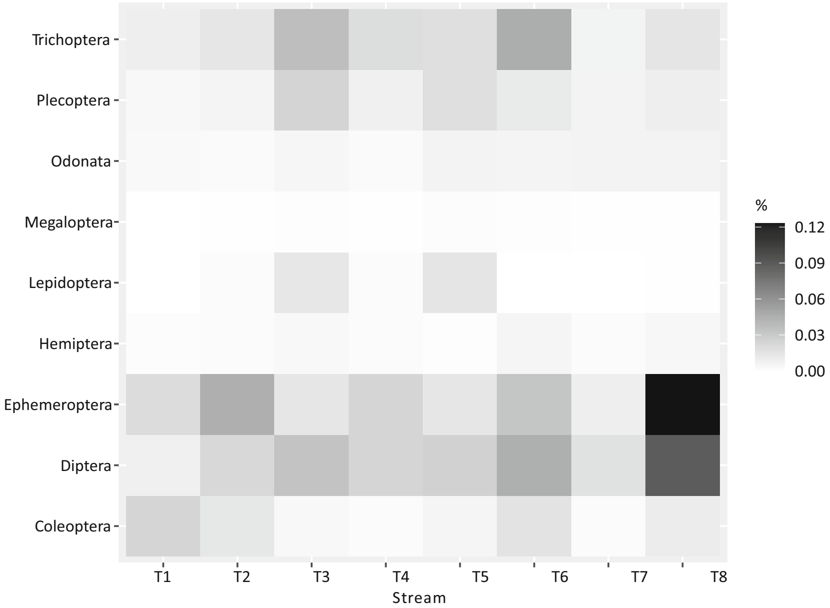

Fig. 2 The relative abundance for aquatic insect orders from eight streams at Floresta Nacional do Tapajós, Pará State, Brazil

Aeschnosoma, and most Dipteran predators) and collector-gatherers (e.g. *Americabaetis*, *Cryptonympha*, *Farrodes*, *Miroculis*, and *Waltzoyphius*) exhibited the higher interactions. The association for environment and traits for shredder species (e.g. *Anacaena* and *Hydrodessus*) and collector-filterers (e.g. *Chimarra*, *Leptonema*, *Macrostemum*, and *Simulium*) was weakly significant. For scraper species (e.g. *Askola*, *Hydrosmilodon*, and *Pheneps*), only water variables were weakly associated with traits. Moreover, piercer taxa (e.g. *Paratrephes*, *Tenagobia*) were weakly associated with all groups of environmental variables. Then, as expected, traits for the type of foods were correlated to feeding habits, such as macroinvertebrates (MaIn) and coarse (CPOM) and fine (FPOM) particulate matter.

Discussion

We found that the distribution of aquatic insect species in the streams evaluated was regulated by their association with environmental conditions dependent on species traits that occur at multiple habitat scales. Our results showed that the variation in functional traits and taxonomical community composition had the same response to environmental variables. As expected, patterns of functional and taxonomical composition represented a response to environmental gradients reflected by different aspects of macro- and microhabitat conditions. Moreover, trait response to inter-habitat variation highlighted the key response of feeding functional groups to the environment, which could be associated with traits mostly related to species interactions. This pattern corroborated the hypothesis that community composition and species traits exhibited strong relationships under local environmental conditions; also, it is regulated by species interactions that drive local assembly rules in insect communities.

When considering the contribution of variation in species traits and their categories in response to environmental filtering, the variation in functional community composition can be mostly summarized as associations of functional feeding groups (FFG) to habitat structure. Our results revealed some patterns in the studied taxa and could be summarized according to patterns in assemblage structure, such as species richness and abundance (Merritt *et al* 2008). First, shredders (e.g. *Miroculis*) were the most abundant feeding group found; this group is common in autotrophic/heterotrophic aquatic systems because these organisms are strongly linked to variation in the riparian zone (Cummins *et al* 2005, Poff *et al* 2006). Our results corroborated this fact, as we found environmental variability in the studied streams, including a high percentage of woody debris and vegetal substrates ranging from coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM). The second most abundant group was the collector-gatherer group (e.g. *Campylocia*, *Riethia*, *Hagenulopsis*, *Endotribelos*, and *Helicopsyche*). In natural communities, these taxa are associated with environments that have heterogeneous substrates, channel stability, and habitats composed of cobbles, boulders, large woody debris, and rooted

Table 2 Summary of results for distance-based redundancy analysis (dbRDA) using the Bray–Curtis distance computed to abundance matrix of aquatic insect assemblages from eight streams at Floresta Nacional do Tapajós, Pará State, Brazil

Variables*	F	R^2	p^{**}	dbRDA 1	dbRDA 2	Inertia
Riparian cover/channel morphology	1.497	–	0.045	0.310	0.162	0.665
XCDENMID	1.947	0.217	0.049	− 0.614	− 0.763	
C1T_100	0.940	0.105	0.481	0.741	0.588	
XDEPTH_T	1.233	0.138	0.257	− 0.566	− 0.325	
XWD_RAT	1.858	0.207	0.043	0.153	0.723	
Substrate size and composition	1.656	–	0.028	0.341	0.183	0.688
PCT_SA	1.675	0.177	0.065	− 0.425	− 0.706	
PCT_FN	2.213	0.233	0.011	0.800	− 0.265	
PCT_ORG	1.094	0.116	0.354	0.290	0.466	
PCT_RT	1.481	0.156	0.111	− 0.587	− 0.333	
Water variables	1.895	–	0.009	0.332	0.174	0.716
Temp	3.044	0.266	0.002	0.863	0.166	
pH	1.357	0.184	0.185	− 0.217	− 0.856	
Cond	1.110	0.150	0.345	0.990	0.082	
OD	1.180	0.116	0.298	0.127	0.218	

*Variable codes: *XCDENMID* mean % canopy density mid-stream, *XDEPTH_T* mean thalweg depth (cm), *XWD_RAT* mean wetted width / depth ($m.m^{-1}$), *C1T_100* large woody debris (pieces/100 m), *PCT_SA* % sand (0.6–2 mm), *PCT_FN* % fine (silt/clay; < 0.6 mm), *PCT_ORG* % wood or detritus, *PCT_RT* % thin roots, *PCT_RA* percent rapids, *PCT_RI* percent riffle, *PCT_GL* percent glide, *PCT_SLOW* percent glides + all pool types, *T* temperature (°C), pH, *Cond* electrical conductivity (μS cm^{-1}), *OD* dissolved oxygen (mg L^{-1}). **Significance level $\alpha = 0.05$

Table 3 Summary of *RLQ* analysis for the relationship between environmental variables (riparian, substrate, water) and traits computed to abundance matrix and traits of aquatic insect assemblages from eight streams at Floresta Nacional do Tapajós, Pará State, Brazil

	Riparian[1]		Substrate[2]		Water[3]	
	RLQ 1	*RLQ* 2	*RLQ* 1	*RLQ* 2	*RLQ* 1	*RLQ* 2
Correlation (*L*)	0.242	0.194	0.269	0.169	0.239	0.202
Projected inertia	87.167	10.021	69.674	24.882	58.961	32.229
Co-inertia axis (*R*)	0.990	0.135	0.727	0.668	0.901	− 0.218
Co-inertia axis (*Q*)	0.517	0.139	0.419	0.152	0.197	− 0.451
Total inertia	0.448		0.362		0.381	
Model 2*	*0.033*		0.075		*0.045*	
Model 4*	*0.038*		*0.016*		*0.054*	

[1] Riparian cover/channel morphology: mean % canopy density mid-stream, mean thalweg depth (cm), mean wetted width/depth (m m^{-1}), large woody debris (pieces/100 m); [2] substrate size and composition: % sand (0.6–2 mm), % fine (silt/clay; < 0.6 mm), % wood or detritus, % thin roots. [3] Water variables: temperature (°C), pH, electrical conductivity (µS cm^{-1}), dissolved oxygen (mg L^{-1}). *Permutation for models ($n = 999$) at the significance level $\alpha = 0.05$ (in italic)

vascular plants (Cummins *et al* 2005). Thus, we found a relationship between the presence of collector-gatherer taxa and the variation in woody debris and substrate size. Rooted vascular plants were frequently found in riparian zones of most streams, contributing to canopy cover and channel stability (e.g. *Euterpe oleracea* Mart., Arecaceae).

The functional feeding habit of a taxon is considered a good indicator that can be used to group taxa based on their functional traits, as we did in our study; this method revealed patterns previously known to describe community structure and stream habitats (Cummins *et al* 2005). When highlighting many trait states that co-occur and are tightly linked, the categories had strong phylogenetic or taxonomic affinities (Poff *et al* 2006). Shredders, collector-gatherers, and predators composed convergent assemblages, which were mostly associated with other traits, such as food resources, body form, specific adaptation to flow, mobility, and attachment to substrata. Considering pure environmental effects, *RLQ* analysis showed convergent trait assemblages (shredders and collector-gatherers) in streams with high dissolved oxygen concentrations. These assemblages often occur in shallow, high-flow habitats where individuals expend more energy to resist flow constraints (Tomanova *et al* 2006). In contrast, epi- and endobenthic burrowers (most of the predators and Diptera taxa) were found mainly in deep, low-flow stream reaches where habitats commonly have mineral substrata (e.g. sand and gravels) that are easier to penetrate (Moya *et al* 2007).

Table 4 Summary of fourth-corner analysis to evaluate the global significance of the traits-environment relationships based on the total inertia of the *RLQ* analysis. Tests for the links between *RLQ* axes and traits ("Q.axes") and environmental variables

Models	Axis	Variables*	*r*	Std.Obs	*p* value	*p* value adj*
Riparian cover/channel morphology	AxcQ1	XCDENMID	0.237	3.090	0.001	*0.008*
		C1T_100	− 0.245	− 3.219	0.001	*0.008*
		XDEPTH_T	0.181	2.383	0.001	*0.008*
		XWD_RAT	− 0.179	− 2.377	0.019	0.152
	AxcQ2	XCDENMID	0.056	0.611	0.717	1.000
		C1T_100	− 0.059	− 0.632	0.592	1.000
		XDEPTH_T	− 0.045	− 0.469	0.686	1.000
		XWD_RAT	0.108	1.119	0.303	1.000
Substrate size and composition	AxcQ1	PCT_SA	0.193	2.350	0.005	*0.040*
		PCT_FN	− 0.161	− 1.780	0.040	0.320
		PCT_ORG	− 0.120	− 1.481	0.151	1.000
		PCT_RT	0.204	2.345	0.003	*0.024*
	AxcQ2	PCT_SA	0.099	1.249	0.248	1.000
		PCT_FN	0.134	1.714	0.090	0.720
		PCT_ORG	− 0.100	− 1.236	0.249	1.000
		PCT_RT	− 0.046	− 0.555	0.586	1.000
Water variables	AxcQ1	T	0.215	2.294	0.001	*0.008*
		pH	− 0.013	− 0.163	0.902	1.000
		Cond	0.239	2.562	0.001	*0.008*
		OD	0.059	0.613	0.549	1.000
	AxcQ2	T	0.019	0.315	0.788	1.000
		pH	− 0.158	− 2.458	0.002	*0.016*
		Cond	− 0.058	− 0.827	0.467	1.000
		OD	0.133	1.952	0.031	0.248

*Variable codes: *XCDENMID* mean % canopy density mid-stream, *XDEPTH_T* mean thalweg depth (cm), *XWD_RAT* mean wetted width / depth (m.m^{-1}), *C1T_100* large woody debris (pieces/100 m), *PCT_SA* % sand (0.6–2 mm), *PCT_FN* % fine (silt/clay; < 0.6 mm), *PCT_ORG* % wood or detritus, *PCT_RT* % thin roots, *T* temperature (°C), pH, *Cond* electrical conductivity (µS cm^{-1}), *OD* dissolved oxygen (mg L^{-1}). **p* values adjusted using the Bonferroni correction (in italic)

In riverine landscapes, local habitat attributes act as the main filter, and the variables evaluated here related to stream channel morphology, riparian structure, substrate size, and large wood debris play considerable roles in species composition and traits of aquatic insect assemblages (Heino *et al* 2005, Juen *et al* 2016). At local-scale, environmental filtering may act to control assemblages by allowing the distribution of similar coexisting species, which should lead to high functional redundancy of traits and similar response to habitat structure by both functional and taxonomical composition (Mouchet *et al* 2010). At that point, our results are in line with previous studies, highlighting that local physical habitat variables that appear to be more highly related to functional composition than to patterns of the taxonomic structure because the environment should select attributes regardless of taxonomic variation (Poff & Ward 1990, Finn & Poff 2005). Trait variables have been shown to effectively describe community patterns because joint taxonomical composition often summarize biological interactions (e.g. predation and competition) at the small to large-scale (Jonsson *et al* 2001). Patterns in community structure should also be evaluated from different scales, to detect effects of environmental filters acting on traits related to dispersal and life history (e.g. locomotion modes, resistance forms, and dispersal) (Heino, 2005).

Although small streams within the same regional context are often physically and chemically similar, they can also differ markedly because of habitat heterogeneity (LeCraw & Mackereth 2010). Our sampling sites were naturally acidic streams with discrete gradients of other limnological variables. These conditions provide evidence that streams with lower pH values are accompanied by a number of other chemical changes, and the response of an organism is caused by various physiological and behavioural strategies (Lewis 2008). Moreover, we found that specific local conditions (physical habitat and water variables) are the mechanisms driving species diversity and abundance. Additionally, a similar set of conditions had a strong influence on the functional composition. This phenomenon may be caused by ecosystem processes that are relatively unaffected by species substitutions if the substituted species has similar traits (Dangles *et al* 2004).

The observed patterns in community composition and functional traits may be related to local conditions that are often found in Amazonian streams, including black acidic waters, low values of electrical conductivity, and high variation in substratum characteristics. Moreover, for most tropical stream communities, these in-stream conditions are considered key factors for explaining the variance in community structure and ecosystem function at different scales (Jacobsen *et al* 2008).

In summary, our trait-based approach showed that both functional and taxonomical composition are dependent on local conditions; in this way, the habitat conditions associated with species interactions shape most of the functional composition of the aquatic insects. At the local scale, environmental gradients can produce similar effects influencing both traits and taxonomic patterns in aquatic insect communities. Despite the low number of analysed streams, our analyses provide important information for understanding the simultaneous variation in functional trait composition and community composition found in Amazonian streams. In addition, the present study seems to support habitat templet models for the aquatic insect communities in Amazonian streams. Thus, we can highlight that variation in stream riparian/channel, substrate, and water variables primarily predict trait composition at the stream scale. Therefore, we recommend that future research would address these issues by applying quantitative measures of traits related to biotic interactions to account unique features of Neotropical aquatic diversity.

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Author's Contribution GN and LJ conceived the research. GN and EJC conducted the field sampling and analysed the data. NH contributed with laboratorial training and revised the taxonomic data. GN wrote the manuscript. All authors revised and approved the manuscript.

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