

Contrasting associations between habitat conditions and stream aquatic biodiversity in a forest reserve and its surrounding area in the Eastern Amazon

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Abstract Streams of protected areas should be subjected to less environmental degradation than surrounding areas and consequently support greater aquatic biodiversity. To test this, 186 environmental and landscape variables were measured in 34 streams within the Caxiuanã National Forest (CNF) and its surrounding zone in the eastern Amazon. We expected that streams inside the CNF protected area would have more riparian forest cover and large woody debris (LWD) that increase instream habitat complexity and aquatic biodiversity. Several environmental variables differed between streams in the CNF and surrounding

zone; however, the major difference was greater LWD, leaf litter, and channel depth in CNF streams. Richness of fish, Chironomidae, EPT (Ephemeroptera + Plecoptera + Trichoptera), and all-groups combined were positively associated with LWD. Assemblage taxonomic composition was correlated with several variables, but most groups revealed no clear differentiation between the two areas. This lack of differentiation may be explained by relatively minor environmental impacts in areas surrounding the CNF given the region's small human population. The most notable impact to streams outside of the CNF was removal of LWD to facilitate boat passage. To conserve aquatic biodiversity, we recommend expansion of protected areas and adoption of policies governing land use in surrounding zones.

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Introduction

Rivers and streams provide important ecosystem services supporting human needs, such as fish production and nutrient cycling (MEA, 2005), and yet they are among the most severely impacted ecosystems worldwide (Malmqvist & Rundle, 2002). Small streams and associated riparian habitats are particularly vulnerable to a variety of human activities (Mensing et al., 1998), with negative consequences for global freshwater biodiversity (Dudgeon et al., 2006). Impacts are particularly severe in the tropics, which encompass the greatest proportion of the world's freshwater ecosystems (Vörösmarty et al., 2010) and biodiversity (Agostinho et al., 2005). For example, conversion of forest to oil palm plantations is impacting streams in the Amazon, particularly within the eastern region (Figueiredo et al., 2010). Associated deforestation, nutrient runoff, and sedimentation lead to changes in hydrology and water quality, which ultimately result in changes in habitat structure and biodiversity loss (Juen et al., 2016; Leal et al., 2016).

The Brazilian government established protected areas within the Amazon region as a strategy to mitigate human impacts on local ecosystems as well as global climate (Ferreira et al., 2014; Correia et al., 2016). Virtually all of these protected areas were designed for conservation of forest biodiversity and ecosystem services, with comparatively little consideration of the Amazon's aquatic biodiversity (Castello et al., 2013). These protected areas generally experience less environmental degradation than surrounding areas (Naughton-Treves et al., 2005; Soares-Filho et al., 2010). The eastern Amazon has a large indigenous population that exploits natural resources for subsistence (Silveira & Quaresma, 2013). People

living near rivers, known locally as “ribeirinhos”, depend on streams for transportation and fishing. Owing to new economic pressures, eastern Amazonian streams are increasingly subjected to human impacts, including deforestation, replacement of natural riparian vegetation with crops, pollution, and channel dredging for boat transportation (de Faria et al., 2017), all of which alter aquatic habitat and tend to reduce species richness (Malacarne et al., 2016; Leitão et al., 2018; Nicacio & Juen, 2018). An effective means for assessing ecosystem impacts is to compare areas affected by humans to reference locations where such pressures are absent or minimal (Leal et al., 2016; Martins et al., 2018), and these kinds of evaluations are lacking for aquatic systems in the Amazon.

The goal of the present study was to evaluate stream habitat and biota inside a protected area for comparison with streams in the surrounding area that has been impacted by human activities, including logging and subsistence farming (Monteiro-Júnior et al., 2016; de Faria et al., 2017; Nicacio & Juen, 2018). We hypothesized that streams inside the natural reserve have more riparian cover and woody debris that increases structural complexity of instream habitat. Since environmental features provide a template that determines the suitability of stream habitat to support aquatic biota (Poff & Ward, 1990; Casatti et al., 2006; Nessimian et al., 2008; Juen et al., 2016), greater aquatic biodiversity would be expected in streams within the protected area due to greater availability of ecological niches (Fahrig et al., 2011). Species richness, species relative abundance and assemblage composition are widely used indicators of ecosystem status; and we evaluated relationships between environmental factors and these aspects of fish and aquatic insect assemblages at a local scale (Hooper et al., 2005; Isbell et al., 2011). Lastly, we sought to identify habitat variables potentially useful for future environmental impact assessment and monitoring.

Materials and methods

Study area

Surveyed streams are located in the Caxiuanã National Forest (CNF) and surrounding areas, and local watersheds have similar climate, geology, topography and

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vegetation (Behling & da Costa, 2000; Peel et al., 2007). This forest reserve was established in 1961 (Federal Decree 239 of November 28, 1961) and is one of the largest protected areas in the eastern Amazon. The designation of “National Forest” allows sustainable exploitation of natural resources by local indigenous people (Federal Law no. 9985 of July 18, 2000). The reserve surrounds the lower Anapu River between the Tocantins and Xingu rivers, an area that encompasses the municipalities of Portel and Melgaço in northeastern Pará State, Brazil (Fig. 1). The climate is classified as tropical hot and humid Am type in the Köppen scheme (Peel et al., 2007), with a dry season from July to November and a rainy season between December and June (Oliveira et al., 2008).

The local economy is based on exploitation of natural resources, in particular timber that is processed to make wood products (Veríssimo et al., 2006). Several sawmills operate in the region, and an estimated 100,000 trees are harvested each year from the area surrounding the CNF (SFB & AMAZON, 2010). Local aquatic ecosystems are impacted by logging that typically involves clear-cutting and burning to clear land for agriculture (Moran, 2010), such as palm plantations and cattle ranching (Homma, 2012). The municipality of Portel in the Marajó Region is an important center for production of charcoal and crops such as cassava, banana, corn, and palm heart (Brasil, 2007).

Characteristics of rivers and streams in the CNF and surrounding area differ from most Amazonian streams, and this is largely due to the legacy of Caxiuanã Bay. This bay was formed from a natural impoundment of the Anapu River during the upper Holocene when changes in climate, sea level and tectonic activity restructured the basin’s geomorphology and hydrology (Behling & da Costa, 2000). The bay was subsequently filled with alluvium, and contemporary streams have low gradients, and slow current velocities (Behling & da Costa, 2000).

Data collection

We sampled 34 streams (see Table S1 for coordinates), ranging from 1st to 3rd order (Strahler, 1957), during the dry season (October–November 2012 and October 2013) to minimize seasonal effects on comparisons of stream habitats (Peck et al., 2006). Seventeen streams were located within the CNF, and 17 were in the

surrounding area to a distance of up to 60 km from the reserve border. Streams that were sampled in the area surrounding the CNF included local watersheds spanning a range of human impacts. A 150-m reach of each stream was surveyed, which was subdivided into 15-m longitudinal sections delineated by 11 cross-channel transects. Survey protocols followed Kaufmann et al. (1999) and Peck et al. (2006), and have been used previously for Amazon streams (e.g. de Faria et al., 2017; Benone et al., 2017; Ferreira et al., 2018).

Biological sampling

Fish assemblages were sampled using two circular 55-cm diameter sieve nets with 2-mm mesh. For each 15-m section, sampling effort was 18 min by each of two collectors according to the protocol used by Prudente et al. (2017) and Ferreira et al. (2018). Fish were euthanized with lethal doses of anesthetic (Eugenol) following the accepted protocol (Civil House, Federal Law no. 11.794 of October 8, 2008), then fixed in 10% formalin solution, and after 48 h transferred to 70% ethanol. Fish specimens were identified to the lowest feasible taxonomic level using identification keys in the literature (e.g. Albert, 2001; Reis et al., 2003; Van der Sleen & Albert, 2018) complemented by guidance from expert ichthyologists. Voucher specimens were deposited in the Ichthyological Collection of Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil.

Following the protocol used by de Faria et al. (2017) to survey aquatic insects, ten 15-m sections were divided in three 5-m subunits, of which only the first two were sampled. In each subunit, two samples of substrate were collected with dip nets (18-cm diameter and 250- μ m mesh) to obtain specimens of immature stages of Ephemeroptera, Plecoptera, Trichoptera and Chironomidae. Odonata adults were sampled using a hand-held sweep net (40-cm diameter, 65-cm deep, with a 90-cm aluminium handle) (Monteiro-Júnior et al., 2016). Specimens of Ephemeroptera, Trichoptera, Plecoptera and Chironomidae were sorted in the field and then fixed in 85% ethanol. In the laboratory, specimens were identified using published keys (e.g. Hamada & Couceiro, 2003; Pes et al., 2005; Domínguez et al., 2006; Salles & Lima, 2014). Chironomid specimens were dried and mounted onto slides with Hoyer’s solution according to the methodology proposed by Trivinho-Strixino

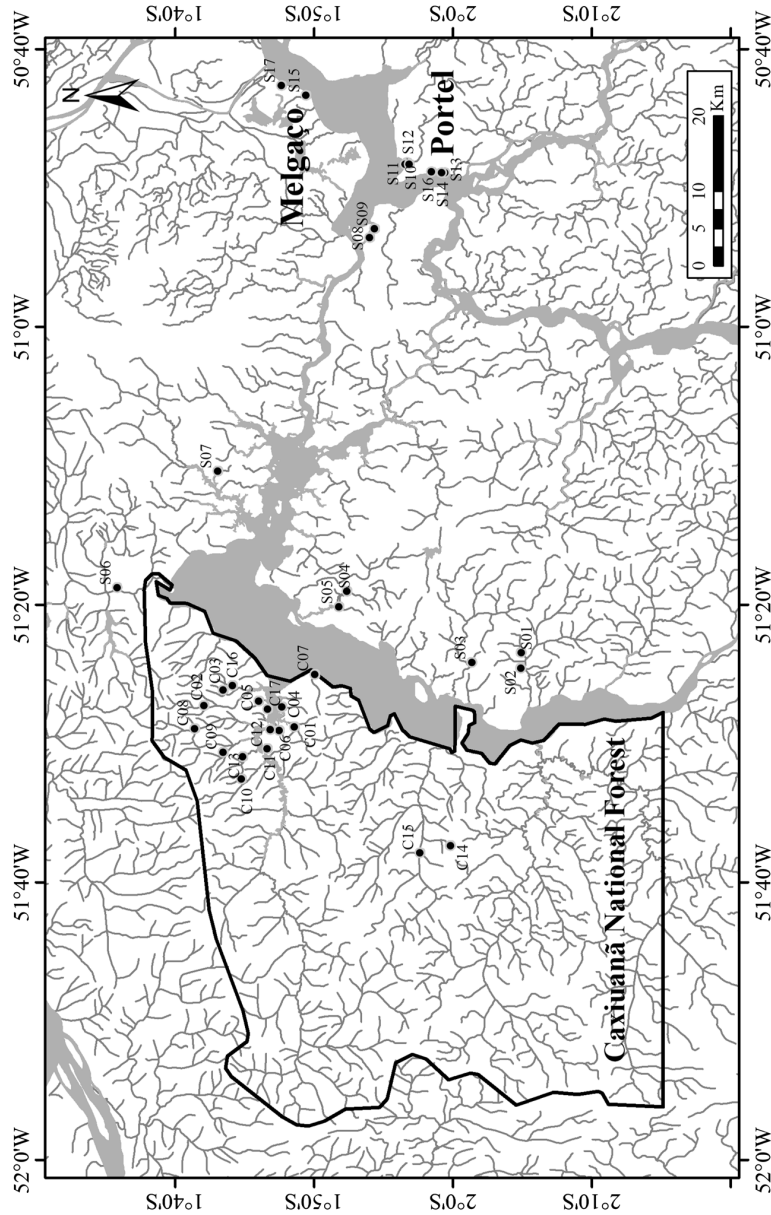


Fig. 1 Map showing locations of 34 streams sampled within the Caxiuaná National Forest and surrounding area, Pará, Brazil

(2014) and identified to either genus or species level with the use of taxonomic literature (Ferrington, 2008; Trivinho-Strixino, 2014). Odonata specimens were stored in paper envelopes for transport to the laboratory for identification using taxonomic keys (Lencioni, 2005; Garrison et al., 2006, 2010). Specimens were stored in the Zoological Collection of the Ecology and Conservation Laboratory at Universidade Federal do Pará, Belém, Brazil.

Stream habitat

Stream habitat measurements and observations followed the assessment protocol of the US Environmental Protection Agency (Kaufmann et al., 1999; Peck et al., 2006) and were performed at the same locations as the fish and aquatic insect surveys. Variables that represent habitat features, with emphasis on those most important for aquatic biota, were analysed following procedures described by Kaufmann et al. (1999) and Barbour et al. (1999).

Habitat measurements were made within all cross-channel transects and longitudinal sections in each of the 34 streams, and values are reported as averages and standard deviations for each stream (see Supplementary Material for a more complete description of habitat measurements). Some metrics were combined to form composite variables (see also Peck et al., 2006 and Kaufmann et al., 1999). 186 habitat measurements were obtained, among which 27 were related to channel morphology and hydraulics, 26 to substrate, 28 to cover for aquatic organisms, 60 to large woody debris (LWD), 16 to riparian vegetation, and 29 to human influences (see Supplementary Material Tables S2, S3 and S4). A sequence of steps was followed to reduce the number of variables for analysis. First, variables with repeated values in $\geq 80\%$ of samples (72 variables) were removed. After that, 12 variables with low variability across streams (i.e. coefficient of variation $< 10\%$) were removed. From the remaining set of variables, redundant variables were excluded among those with strong correlations (Spearman correlation tests > 0.7) (see Supplementary Material Table S2) (73 variables). A total of 29 variables remained, all of which are known to be relevant for the ecology of fish and aquatic insects in streams (Monteiro-Júnior et al., 2016; Prudente et al., 2017; Ferreira et al., 2018; Nicacio & Juen, 2018). Finally, a forward selection procedure

(Blanchet et al., 2008) was performed to reduce further the number of variables, selecting only those metrics that were significantly associated with local assemblages composition of each group. Prior to this analysis, we standardized the environmental metrics and log-transformed biological variables. After this step, 11 environmental variables remained for subsequent analyses.

The retained variables were channel morphology and hydraulics [mean thalweg depth and bankfull width], substrate [percentage of fine substrate, percentage of wood, and percentage of roots], large woody debris [LWD inside the channel—class 3 (medium to very large) and LWD above the channel—class 3 (medium to very large); explanation of combinations of wood diameter and length that define size classes appears in Kaufmann et al. (1999)], cover for aquatic organisms [mean overhanging vegetation cover and leaf litter cover], riparian vegetation [mean ground cover (< 0.5 m height)], and human influences [presence and proximity of human disturbances (for example, crops, pasture, trash and logging)]. LWD includes tree trunks with a minimum diameter ≥ 0.10 m and length ≥ 1.5 m occurring either inside the channel or near the channel margin where they can affect water flow and channel morphology. Additional details about environmental variable measurements can be found in Juen et al. (2016) and de Faria et al. (2017).

Data analysis

The selected set of environmental variables was used to compare habitat between CNF and surrounding streams. First, a principal components analysis (PCA) was performed to decompose environmental variables along orthogonal axes, or components, that identify gradients (Peres-Neto et al., 2003). To reduce effects of variables measured according to different units, all variables were standardized (mean equal to 0 with standard deviation equal to 1). We applied a permutational multivariate analysis of variance (PERMANOVA—Anderson, 2001) to the environmental variables to verify the level of differentiation between the habitat conditions of streams in CNF and habitat of streams in the surrounding area. These analyses were based on 9,999 permutations for the calculation of the significance value using the Monte Carlo test ($P < 0.05$), with the assumption of homogeneity of

dispersal being tested a priori by PERMDISP (Anderson, 2005).

For biological data, we first examined the potential influence of spatial autocorrelation on aquatic biodiversity using data for species richness and local assemblage composition. We calculated pairwise fluvial distances among surveyed sites using QGIS software (QGIS Development Team, 2017). We then obtained spatial filters using principal coordinates of neighbour matrices (PCNM—Dray et al., 2006) based on the fluvial distance matrix, selecting only those filters with Moran's $I > 1$ and $P < 0.05$. We ran multiple regression analysis and redundancy analysis (RDA) between the spatial filters with species richness and biological composition, respectively, for each taxonomic group. Whenever the biological data showed spatial autocorrelation, we extracted the residuals for further analysis (Borcard et al., 2011).

Generalized linear models with forward stepwise selection were used to analyse relationships of explanatory variables (11 quantitative habitat variables plus one categorical variable [treatment]) on species richness of fish, Chironomidae, Ephemeroptera, Plecoptera, and Trichoptera (EPT), and Odonata, considering each of these taxa separately, and then species richness of all four taxa combined. For composition data, we ran principal coordinates

analysis PCoA) on each major taxonomic group and selected the first two axes for analysis using GLMs.

All analyses were performed using the *vegan* (Oksanen et al., 2018), *packfor* (Dray et al., 2011), *PCNM* (Legendre et al., 2012), and *MASS* packages (Venables and Ripley, 2002) in R (R Core Team, 2014).

Results

When compared with its surrounding areas, streams in the CNF had higher percentage of wood substrate, amounts of large woody debris inside the stream channel and on the stream banks, greater leaf litter cover, higher proportions of fine sediments, and greater thalweg depth (Table 1, Fig. 2). There were significant environmental differences between streams in the CNF and the surrounding zone (PERMANOVA: pseudo- $F_{(1,33)} = 3.35$; $P < 0.01$). The variances were homogeneous among treatments (PERMDISP: $F_{(1,33)} = 1.44$; $P = 0.24$), indicating that treatments had similar levels of environmental heterogeneity.

Effect of stream habitat on aquatic biodiversity

A total of 194 aquatic species and 25,384 individuals were recorded, of which 136 species (11,941

Table 1 Variables used to assess stream habitat within the Caxiuanã National Forest and its surrounding zone and their PCA axis loadings (LWD is large woody debris)

Variables	Abbreviation	PCA 1	PCA 2
Thalweg depth (cm)	Thal	0.67	0.45
Bankfull width (m)	Bank	0.53	− 0.36
Fine sediment (%)	Fines	− 0.69	0.45
Wood (%)	Wood	0.69	0.00
Live trees or roots (%)	Roots	0.39	0.06
LWD inside the channel (pieces/reach)—class 3 (medium to very large)	LWDin	0.03	0.79
LWD above the channel (pieces/reach)—class 3 (medium to very large)	LWDab	− 0.32	0.71
Ground-layer vegetation cover (ground-layer woody cover + ground-layer herbaceous cover)	Ground	0.52	0.41
Overhanging vegetation cover	Veget	0.36	0.25
Leaf litter cover	Leaf	0.61	− 0.20
Total human impact (proximity-weighted sum)	Human	− 0.40	− 0.50
Eigenvalue		2.88	2.19
Explanation (%)		26.10	20.00
Cumulative explanation (%)		26.10	46.10

Variables in bold are > 0.6

Fig. 2 Biplot showing ordination of streams located inside and outside the Caxiuaná National Forest along the first two axes (gradients) derived from PCA of stream habitat variables. The percent total variation modelled by each axis is shown in parentheses; see Table 2 for variable codes and loadings

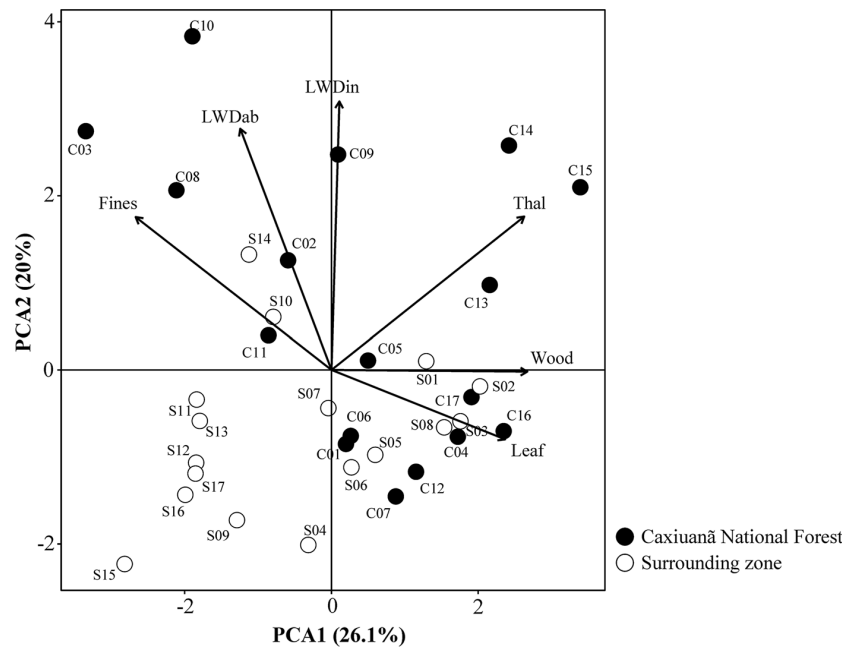


Table 2 Results of the GLM analysis with a forward selection procedure

Biological group	Variables	Estimate	SE	t-value	P value
Total richness	(Intercept)	0.000	0.023	0.000	1.000
	Bank	- 0.037	0.025	- 1.472	0.152
	Roots	0.071	0.025	2.802	< 0.01
	LWDab	0.088	0.025	3.544	< 0.01
Fish	(Intercept)	0.000	0.028	0.00	1.000
	Bank	- 0.056	0.032	- 1.76	0.089
	Fines	0.095	0.032	2.98	0.006
	LWDin	0.079	0.029	2.72	0.011
Chironomidae	(Intercept)	- 0.104	0.080	- 1.301	0.204
	Treatment	0.208	0.121	1.716	0.097
	Bank	0.127	0.056	2.250	0.032
	LWDin	- 0.221	0.063	- 3.490	< 0.01
EPT	(Intercept)	0.135	0.064	2.107	0.044
	LWDab	0.137	0.056	2.475	0.020
	Ground	0.137	0.056	2.475	0.020
	Leaf	0.137	0.056	2.475	0.020
Odonata	(Intercept)	1.772	0.063	28.003	< 0.01
	Roots	0.233	0.066	3.537	< 0.01
	LWDab	0.165	0.066	2.492	0.018
	Leaf	- 0.261	0.065	- 4.039	< 0.01
Surrounding zone	(Intercept)	0.213	0.116	1.830	0.077
	Treatment	- 0.425	0.165	- 2.575	0.015
	Bank	- 0.195	0.087	- 2.238	0.033
	Roots	0.128	0.087	1.468	0.153

Habitat variables and treatment were included as explanatory variables, while the response variables were the species richness for each biological group and total species richness. Variables in bold are significant at $P < 0.05$

SE standard error

individuals) were found in the CNF and 150 species (13,443 individuals) were found in the surrounding area. Surveys yielded 20,308 individual of 79 fishes, including 49 species (10,223 individuals) in the CNF and 61 species (10,085 individuals) in the surrounding area; 2,535 individual of 47 Chironomidae, including 38 species (929 individuals) in the CNF and 44 species (1,606 individuals) in the surrounding area; 2,261 individuals of 28 EPT species, including 23 species (695 individuals) in the CNF and 19 species (1,566 individuals) in the surrounding area; and 280 individuals of 44 Odonata, including 26 species (94 individuals) in the CNF and 26 species (186 individuals) in the surrounding area (See Supplementary Material Table S5).

Analysis of autocorrelation revealed significant associations with PCNM spatial filters for total species richness (adjusted $R^2 = 0.34$, $P = 0.01$), Chironomidae (adjusted $R^2 = 0.47$, $P = 0.001$), and Odonata (adjusted $R^2 = 0.26$, $P = 0.02$). However, since fish (adjusted $R^2 = 0.16$, $P = 0.09$) also showed a relatively high R^2 values (although nonsignificant), we used their residuals as well. EPT (adjusted $R^2 = -0.01$, $P = 0.49$) showed no signs of spatial autocorrelation, so we used the raw values for species richness for this group.

GLM results indicated that ‘Live trees or roots’ and ‘LWD above the channel—class 3 (medium to very large)’ were positively correlated with total species richness of fish and aquatic insects (adjusted $R^2 = 0.34$). For fish (adjusted $R^2 = 0.54$), species richness was positively correlated with ‘fine substrate’, ‘LWD inside the channel—class 3 (medium to very large)’, and ‘overhanging vegetation cover’. For Chironomidae (adjusted $R^2 = 0.38$), ‘bankfull width’, ‘LWD above the channel—class 3 (medium to very large)’, and ‘ground-layer vegetation cover’ were positively associated to species richness, and the ‘LWD inside the channel—class 3 (medium to very large)’ was negatively related to species richness. EPT species richness (adjusted $R^2 = 0.49$) had a positive correlation with ‘live trees or roots’, ‘LWD above the channel—class 3 (medium to very large)’, and negative correlation with ‘leaf litter cover’. For Odonata (adjusted $R^2 = 0.21$), ‘bankfull width’ and ‘surrounding zone’, and level of the categorical variable ‘treatment’ were negatively correlated with species richness (Table 2).

For assemblage composition data, all taxonomic groups revealed evidence of spatial autocorrelation (Fish: $F = 2.18$, $P < 0.05$; Chironomidae: $F = 1.45$, $P < 0.05$; EPT: $F = 1.91$, $P < 0.05$; Odonata: $F = 1.48$, $P = 0.01$), and thus, we used residuals in subsequent analyses. PCoA revealed that biological groups had different degrees of separation between the CNF and surrounding zone (Fig. 3), and we selected the first PCoA axis for each group to access the influence of environmental variables and treatment on assemblage composition.

Table 3 summarizes results from GLM analysis with scores on the first PCoA axis representing local assemblage composition. The first PCoA axis for fish (adjusted $R^2 = 0.76$) was positively associated with ‘overhanging vegetation cover’, ‘LWD inside the channel—class 3 (medium to very large)’ and ‘fine sediment’, and negatively associated with ‘surrounding zone’ level of the categorical variable ‘treatment’. For Chironomidae (adjusted $R^2 = 0.49$), the first PCoA axis was positively associated with ‘fine substrate’ and ‘live trees or roots’, and was negatively associated with ‘total human impact’ and ‘LWD above the channel—class 3 (medium to very large)’. For EPT (adjusted $R^2 = 0.56$), the first PCoA axis was negatively associated with ‘fine substrate’ and ‘LWD inside the channel—class 3 (medium to very large)’. The first PCoA axis for Odonata composition (adjusted $R^2 = 0.73$) was negatively associated with ‘fine substrate’, ‘live trees or roots’ and ‘LWD inside the channel—class 3 (medium to very large)’, whereas ‘bankfull width’ had a positive association.

Discussion

Stream habitat in the protected forest and surrounding area

We found significant habitat differences between streams located within CNF and those in the surrounding area with regard to substrate, channel morphology, and vegetation. The surrounding areas had shallower thalweg depth and smaller proportions of large woody debris, leaf litter and wood substrate, and fine sediments. Riparian forests are the source of LWD in streams (Sweeney & Newbold, 2014), and LWD was more prevalent in CNF streams. LWD influences hydrology, hydraulics and sediment

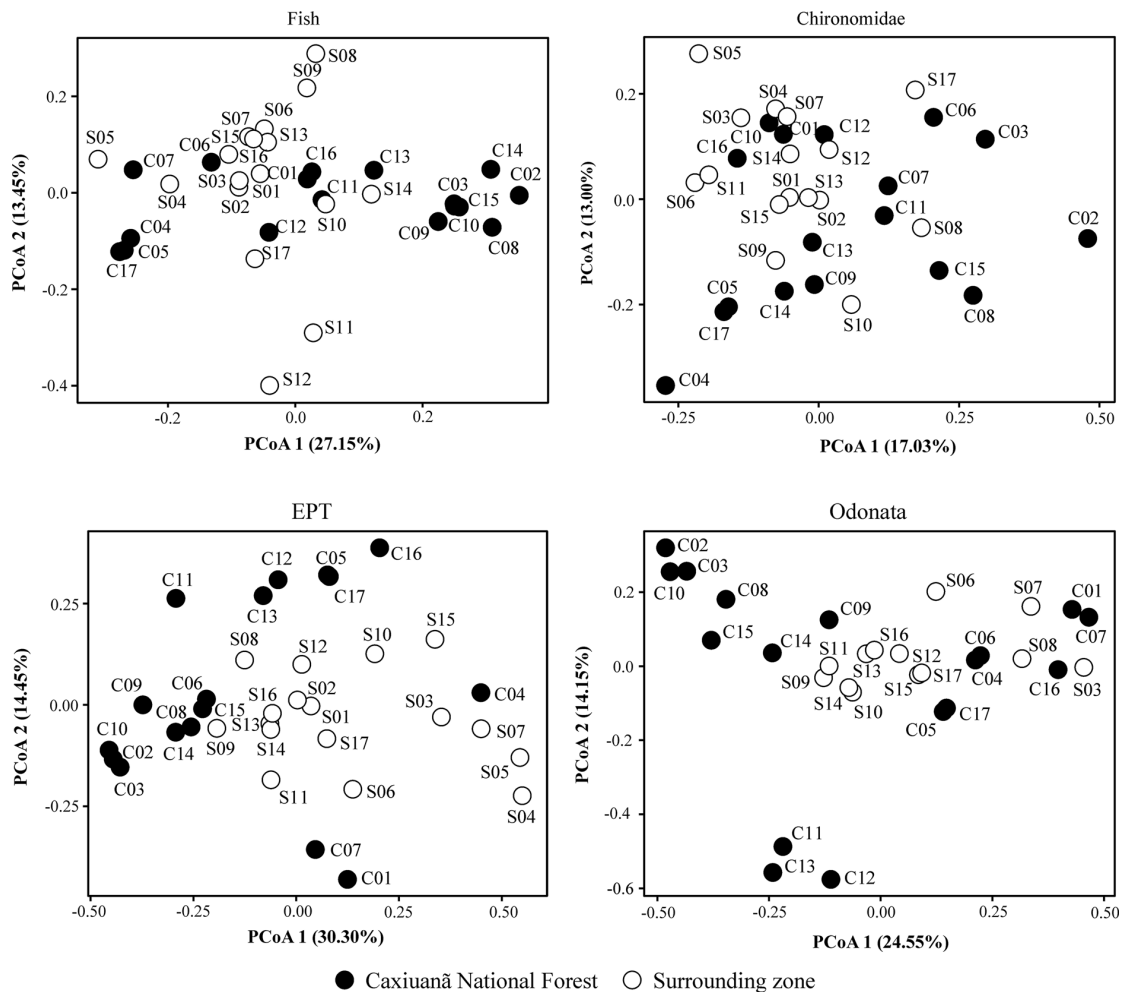


Fig. 3 PCoA ordination plots for taxonomic groups showing relationships of streams within and outside the CNF. The percent total variation modelled by each axis is shown in parentheses

dynamics (Gurnell et al., 2002), as well as development and stability of pools and backwaters (Daniels & Rhoads, 2003; Wallerstein & Thorne, 2004; Kaufmann & Faustini, 2012). Streams within the CNF tend to have slower water velocities than streams in the surrounding area (Monteiro-Júnior et al., 2016; de Faria et al., 2017), and this could have been associated with greater amounts of LWD. LWD increases not only structural complexity of instream habitat that affects biodiversity, but also retention of particulate organic matter that supports aquatic food webs (Díez et al., 2000; Krause et al., 2014).

We estimated LWD abundance both within stream channels and on stream banks, and both were higher inside the CNF. These streams lie within an area of floodplains drained by rivers used by the local population for boat transportation (Brasil, 2007). In the area surrounding the CNF, wood is removed from stream channels and banks to facilitate boat passage (Monteiro-Júnior et al., 2016). Removal of LWD from streams would alter dynamics involving particulate organic matter, invertebrate feeding and microbial processing of material affecting ecosystem respiration and nutrient cycling (Eggert et al., 2012).

Table 3 Results from GLM analysis

	Taxonomic group	Variable	Estimate	SE	<i>t</i> -value	<i>P</i> -value	
Habitat variables and category variable 'treatment' (CNF and surrounding zone) were included as explanatory variables, and the response variable is score on the first axis from PCoA indicating assemblage composition of taxonomic groups. Variables in bold are significant at $P < 0.05$ <i>SE</i> standard error	Fish	(Intercept)	0.041	0.024	1.729	0.096	
		Bank	− 0.031	0.018	− 1.690	0.103	
		Fines	0.077	0.022	3.503	< 0.01	
		LWDin	0.078	0.019	4.163	< 0.01	
		LWDab	− 0.032	0.021	− 1.499	0.146	
		Veget	0.085	0.017	5.070	< 0.01	
		Leaf	− 0.036	0.020	− 1.798	0.084	
	Chironomidae	(Intercept)	− 0.003	0.021	− 0.134	0.895	
		Fines	0.133	0.026	5.156	< 0.01	
		Roots	0.051	0.022	2.351	0.026	
		LWDab	− 0.056	0.027	− 2.091	0.046	
		Human	− 0.066	0.023	− 2.824	< 0.01	
		EPT	(Intercept)	0.000	0.031	0.000	1.000
			Fines	− 0.147	0.033	− 4.447	< 0.01
	Roots		− 0.055	0.032	− 1.699	0.100	
	LWDin		− 0.106	0.034	− 3.068	< 0.01	
	Human		0.065	0.034	1.919	0.065	
	Odonata		(Intercept)	0.022	0.027	0.835	0.412
		Bank	0.070	0.030	2.318	0.029	
		Fines	− 0.145	0.030	− 4.902	< 0.01	
Roots		− 0.080	0.028	− 2.850	< 0.01		
LWDin		− 0.107	0.028	− 3.788	< 0.01		
Ground		− 0.040	0.028	− 1.388	0.178		

Streams within the CNF have very low gradients and extensive floodplains (~ 100 m wide) (Benone et al., 2018) and continuously accumulate fine sediments (Behling & da Costa, 2000). These streams also receive large amounts of leaf litter and fine particulate organic matter (Montag & Barthem, 2006). This accumulation of organic matter from the riparian forest depends not only on forest productivity, but also on the capacity of the stream to retain allochthonous organic material, which in turn depends on both intrinsic properties of that material and physical features of the stream (Li & Dudgeon, 2011). For example, woody debris and leaf litter retention in CNF streams reduce flow velocity (Hoover et al., 2006) and create extensive backwaters (Behling & da Costa, 2000). CNF streams had greater water depth at the thalweg compared to streams outside the CNF. These deeper thalwegs are associated to reduced flows and lower shear stress near the bottom (Hoover et al., 2006), which leads to greater deposition of fine

particles that otherwise would be transported in suspension.

Aquatic biota in streams of the protected forest and surrounding area

Taxonomic richness of fish, Chironomidae, EPT and all groups combined was positively associated with LWD within and at the margins of streams, and both LWD and taxonomic richness were higher in streams inside the CNF. Our study is in agreement with previous surveys in the region (Juen et al., 2016; de Faria et al., 2017; Prudente et al., 2017), since we found moderate relationships between other environmental variable and species richness (i.e. < 60% explanation of variation). The moderate levels of explanation may be due to the dynamic nature of small streams in the Amazon, which are prone to effects of other variables not measured in our study associated

with disturbance regimes, reproduction/recruitment, dispersal, metacommunity dynamics, and others.

The positive association of medium to very large LWD inside the channel with aquatic species richness and composition reflects the dependence of aquatic species on submerged structures to provide cover from predators, nesting sites, and food resources (Wright & Flecker, 2004; Valente-Neto et al., 2015; Pilotto et al., 2016). LWD contributes not only to the quantity but also the quality of microhabitats available in streams (Braccia & Batzer, 2001), providing structural complexity that influences the spatial distribution of several taxa (Smith et al., 1993). Habitat structural complexity facilitates coexistence of species with different ecological requirements (Barreto, 1999), and has been shown to be positively associated with aquatic species richness in streams and rivers (Wright & Flecker, 2004; Willis et al., 2005).

The positive relationship between LWD and richness of aquatic insect taxa and fish species in the study area is consistent with findings from other studies (e.g. Watson & Hilman, 1997; Wright & Flecker, 2004; Schneider & Winemiller, 2008). This relationship involving fishes has been inferred to be due to the high abundance and diversity of aquatic insects that colonize woody debris and provide food for fishes, as well as the structural complexity of woody debris that provides shelter from predators (Wright & Flecker, 2004; Schneider & Winemiller, 2008).

CNF streams had higher percentages of fine sediment and this metric was positively correlated with fish species richness and assemblage composition. Deposition of fine sediments in streams results from both natural processes and human activities (Wood & Armitage, 1999) and influences stream hydrology, geomorphology and ecology (Berkman & Rabeni, 1987; Owens et al., 2005). Although deposition of fine sediments is generally recognized as negatively impacting aquatic ecosystems (e.g. Sutherland et al., 2012; Chapman et al., 2014), that apparently is not the case in the CNF streams where high abundance of particulate organic matter is associated with higher fish species richness.

Taxonomic richness and assemblage composition of Odonata, Chironomidae and EPT were most strongly associated with variables linked to substrate and other habitat features, with only chironomids showing a strong association with human impacts. This finding is consistent with other studies (e.g.

Heino, 2005; Rinella & Feminella, 2005; Entekin et al., 2007; Sueiro et al., 2011) that showed chironomid and EPT responses to changes in terrestrial detrital inputs and substrates, such as fine sediments and LWD. Some have proposed that such responses by benthic invertebrates reflect spatio-temporal variation in disturbances dynamics in riparian habitats (Wallace et al., 2001; Glaz et al., 2009; Hartwig et al., 2016).

Similar results for chironomid species richness and assemblage composition for streams inside and outside the CNF could be related to the dispersal abilities and environmental tolerance of this group (Franquet, 1999). Adult Odonata abundance in streams may be linked to conditions required for oviposition and larval development (Resende & De Marco, 2010; Monteiro-Júnior et al., 2015; Miguel et al., 2017; Oliveira-Junior et al., 2017). Riparian forest structure, canopy cover, and level of human impact were the principal environmental factors associated with Odonata assemblage composition.

Environmental impacts on aquatic biota appear to be low in this region of low human population density. Woody debris creates structurally complex habitat that promotes high aquatic biodiversity. Our findings suggest that the CNF remains relatively pristine and therefore provides a reference site for the assessment of stream habitat quality in the region. Reference sites are increasingly difficult to find, especially in developing tropical regions, such as the eastern Amazon, where environmental impacts are increasing rapidly. In addition, we emphasize the need to protect streams in the surrounding areas, both for sheltering an important proportion of the local aquatic biodiversity and because it represents a buffer area for the conservation unit. Given that the area surrounding the CNF remains sparsely populated and has not yet been severely deforested, it still has significant ecosystem services and conservation value. At present, the main impact to streams in areas surrounding the protected area seems to be the removal of LWD to improve boat navigation. However, population expansion, urbanization and exploitation of natural resources, especially logging, pose serious threats to aquatic diversity in the region. To conserve aquatic biodiversity, we recommend expansion of the CNF protected area and/or adoption of management policies, including land use restrictions, within its buffer zone. Such measures are urgent, because licensing for reduced-impact logging was recently approved for

nearly 200,000 ha within the CNF over the next 40 years (Ministry of Environment, Ordinance no. 467 of December 2014; Brazilian Forest Service, Ordinance no. 231 of December 2, 2016).

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