



UNIVERSIDADE FEDERAL DO PARÁ
MUSEU PARAENSE EMÍLIO GOELDI
PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA



TESE DE DOUTORADO

**Determinantes da estrutura de comunidades de insetos aquáticos em riachos na
Amazônia: o papel do habitat e da escala espacial**

Gilberto Nicacio Batista

BELÉM

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Tese apresentada ao Programa de Pós-Graduação em
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Linha de pesquisa: Ecologia animal.

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SUPLENTES

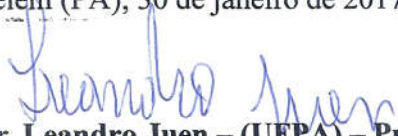
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ATA DE DEFESA DE DOUTORADO EM ZOOLOGIA APRESENTADA E DEFENDIDA PELO M. Sc. GILBERTO NICÁCIO BATISTA.

No dia 30 janeiro de 2017, às 08:00h, no auditório Paulo Mendes, localizado no Instituto de Ciências Biológicas da Universidade Federal do Pará, foi apresentada e defendida a tese do aluno de doutorado **GILBERTO NICÁCIO BATISTA**, intitulada: "**Determinantes da estrutura de comunidades de insetos aquáticos em ecossistemas naturais na Amazônia: o papel do habitat e escala espacial**". A comissão Examinadora, organizada obedecendo ao disposto nas Resoluções do Conselho Superior de Ensino e Pós-Graduação, foi constituída pelos professores: Dr. Leandro Juen – (UFPA), presidente (sem direito a voto) e pelos membros: Dr. Rogério Rosa da Silva (UFPA), Dr. Bruno Spacek Godoy (UFPA) e Dr. Raphael Ligeiro Barroso Santos (UFPA). Após haver o aluno apresentado os resultados de sua Tese, obedecendo ao prazo regimental, foi dada a palavra aos examinadores para arguição, tendo o candidato respondido adequadamente as perguntas formuladas. Logo após, reuniu-se a Comissão Examinadora para proceder ao julgamento, considerando o aluno Aprovado (Aprovado/Reprovado). Assim sendo, a Comissão Examinadora decidiu Recomendar (Recomendar/Não recomendar) o grau de Doutor em Zoologia a **GILBERTO NICÁCIO BATISTA**. Nada mais havendo a tratar, o Presidente da Banca Examinadora deu por encerrado os trabalhos e foi lavrada a presente ata que vai devidamente assinada pelo Presidente e examinadores.

Belém (PA), 30 de janeiro de 2017.


Dr. Leandro Juen – (UFPA) – Presidente


Dr. Rogério Rosa da Silva – (UFPA) – Titular


Dr. Bruno Spacek Godoy – (UFPA) – Titular


Dr. Raphael Ligeiro Barroso Santos – (UFPA) – Titular

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1 **RESUMO GERAL**

2 Os ecossistemas aquáticos são ambientes altamente complexos, pois os seus componentes
3 bióticos e abióticos são dependentes da variação na estrutura física e das características
4 limnológicas, que em geral, são fatores que atuam de forma específica em diferentes
5 escalas espaciais e temporais. Assim, considerando essa complexidade dos habitats
6 encontrados em ecossistemas lóticos amazônicos esta tese tem como objetivo geral
7 avaliar quais são os fatores determinantes dos padrões de distribuição das comunidades de
8 insetos aquáticos em riachos e suas relações com a variação ambiental desses
9 ecossistemas e os efeitos da escala geográfica (variação espacial). Para responder a este
10 objetivo a tese foi dividida em quatro capítulos. No primeiro através de uma análise
11 cienciométrica foi realizada uma avaliação em escala mundial do uso de insetos da família
12 Chironomidae (Diptera) em ecossistemas aquáticos e suas respostas como bioindicadores
13 nesses ambientes. Encontramos que as principais questões apresentadas nos estudos
14 foram relacionadas aos impactos antrópicos causados pelas atividades humanas sobre os
15 ecossistemas aquáticos e as dificuldades taxonômicas sobre a utilização das espécies em
16 biomonitoramentos. No segundo foram analisados os padrões de distribuição e
17 diversidade de comunidades de Chironomidae, sob as predições da Teoria de
18 Metacomunidades, para avaliar as relações das assembleias com a variação da escala
19 espacial e do ambiente. Como principais resultados, encontramos que as assembleias são
20 afetadas principalmente por componentes da estrutura física do habitat e parcialmente
21 limitadas pela dispersão entre os riachos quando consideradas em larga escala na região
22 hidrográfica. No terceiro capítulo, foi avaliada a composição de traços morfológicos e
23 funcionais das comunidades de insetos aquáticos (Coleoptera, Diptera, Ephemeroptera,
24 Hemiptera, Lepidoptera, Megaloptera, Odonata, Plecoptera, Trichoptera) e as suas
25 respostas à variação na estrutura do habitat consideradas sob as premissas da Teoria de

26 *Habitat Templet*. Assim, encontramos como resultados deste capítulo, relações entre a
27 distribuição dos traços morfológicos e funcionais com as variáveis da estrutura do habitat
28 e a características limnológicas dos riachos. No quarto capítulo foram avaliados os efeitos
29 da variação espacial e ambiental sobre a similaridade de composição das comunidades de
30 insetos das ordens Ephemeroptera, Plecoptera e Trichoptera em riachos de duas regiões
31 hidrográficas distintas. Neste último capítulo, encontramos diferenças na composição das
32 comunidades como resultado da distância geográfica e das características ambientais
33 locais de cada região. Demonstramos como a estrutura do habitat dos riachos pode afetar
34 as comunidades de insetos aquáticos em diferentes contextos de escala geográfica.
35 Também, as características dos habitats foram importantes para a seleção de atributos
36 ecológicos e funcionais das comunidades de insetos aquáticos. Com isso, a partir dos
37 resultados encontrados, concluímos que as variáveis que compõem a estrutura física dos
38 riachos são fatores determinantes na estruturação das comunidades de insetos aquáticos
39 em escalas geográficas em contextos regionais e locais específicos. Além disso, foi
40 destacada a importância dos fatores locais (proporção da vegetação ripária/composição
41 dos substratos/características limnológicas) em relação a composição de características
42 morfológicas e funcionais das assembleias, enquanto que os fatores regionais (distância
43 geográfica/limitação de dispersão) foram os componentes determinantes da similaridade
44 da estrutura das comunidades.

Palavras-chave: Inseto aquático; Amazônia; diversidade de espécies; Ecologia de rios.

1 **ABSTRACT**

2 Aquatic ecosystems are highly complex environments, mainly due to interactions
3 between their abiotic and biotic components; they are dependent on variation in physical
4 structure and limnological characteristics, which in general, are factors that specifically
5 act on different spatial and temporal scales. Therefore, considering this complexity in
6 structuring stream habitats, particularly in Amazonian lotic ecosystems, this doctoral
7 thesis aims to evaluate which are the determining factors to structure aquatic insect
8 communities and their distribution according to environmental variation and geographical
9 distances. To meet this goal the thesis is divided into four chapters. In the first, a
10 systematic revision was carried out with a global assessment about the use of insects
11 (Chironomidae: Diptera) in monitoring aquatic ecosystems and their responses as
12 bioindicators. We found that the main issues presented in the studies were related to
13 anthropogenic impacts on aquatic ecosystems and the taxonomic difficulties on the use
14 of species identification to biomonitoring. The second shows analysis of distribution
15 patterns and diversity of Chironomidae communities, under predictions of
16 Metacommunity models, to evaluate the relations of the assemblages with the spatial
17 scale and the environment. The main results showed that the assemblages were mainly
18 affected by components of the physical habitat structure and partly the communities were
19 limited by dispersal among the streams when considered at large scale in the region
20 studied. The third showed analysis of functional composition on the communities of
21 aquatic insects (Coleoptera, Diptera, Ephemeroptera, Hemiptera, Lepidoptera,
22 Megaloptera, Odonata, Plecoptera, Trichoptera) and their responses to variation in habitat
23 structure considered under the assumptions of the Habitat Templet. Overall, we found
24 relationships between the distribution of morphological and functional traits with the
25 physical habitat variables. The fourth chapter evaluates the effect of spatial distance on

26 the community similarity of Ephemeroptera, Trichoptera, Plecoptera communities in two
27 regions of Eastern Amazon. In this final chapter, we find differences in the composition
28 of communities expressed as species replacement because of the geographical distance
29 and local environmental characteristics of each region. Finally, the studies developed in
30 this thesis summarized how the structure of the habitat of streams can affect the aquatic
31 insect communities and variation in the riparian structure and physical habitat, can cause
32 variation in taxonomical composition and functional attributes. In summary, from these
33 findings, we conclude that the physical habitat variables are determining factors in
34 structuring aquatic insect communities. In addition, it is highlighted the importance of
35 local factors (riparian vegetation structure/composition of substrates/limnological
36 characteristics) as explanatory variables for taxonomical and functional composition. In
37 addition, the regional factors (geographical distance / dispersal limitation) are essential
38 components to affect similarity and structure of the communities.

Keywords: Aquatic insect; Amazon; species diversity; River Ecology.

1 INTRODUÇÃO GERAL

2 *Teorias ecológicas e a distribuição das espécies*

3 De acordo com a Teoria Neutra Unificada de Biodiversidade e Biogeografia
4 proposta por Hubbell, a dispersão é considerada o principal fator controlador das
5 comunidades ecológicas (Alonso *et al.*, 2006). De acordo com essa teoria, cada indivíduo,
6 de qualquer espécie em uma comunidade, é idêntico funcionalmente com relação à
7 probabilidade de ter descendentes, morrer, migrar e especiar (Hubbell 2005). O único
8 fator limitante seria a capacidade de dispersão das espécies. Segundo Ricklefs (2008), as
9 populações possuem uma estrutura geográfica definida por barreiras de dispersão, no qual
10 resultaria na interrupção do fluxo gênico, no isolamento pela distância e na diferenciação
11 genética local e ecotípica. Além disso, as comunidades podem ser influenciadas por
12 processos regionais de especiação alopátrica e dispersão geográfica (Ricklefs, 1987).
13 Nesse caso, uma vez que as comunidades locais são submetidas a eventos de especiação,
14 na escala regional haveriam barreiras geográficas somadas à relativa capacidade de
15 dispersão entre os organismos. Dessa forma, pressupõe-se que existe uma diminuição da
16 similaridade de espécies entre comunidades à medida que estas se distanciam
17 geograficamente, em função da dispersão espacialmente limitada (Rosindell *et al.* 2011).

18 Processos neutros e relacionados ao nicho podem atuar e determinar diversos
19 níveis de interações que podem ocorrer em diferentes comunidades em escalas locais e
20 regionais. Essas interações criam um fluxo dinâmico de indivíduos de diferentes espécies
21 entre as comunidades (Thompson & Townsend, 2006). Nesse caso, tais relações podem
22 ser abordadas num contexto de metacomunidades, as quais consistem num conjunto de
23 múltiplas comunidades locais de espécies que potencialmente interagem entre si e são
24 conectadas pela dispersão de algumas delas (Leibold *et al.*, 2004). O funcionamento das
25 metacomunidades é abordado sob quatro perspectivas: a) *patch-dynamics*, baseado no

26 modelo de *trade-off* entre competição e colonização, o qual assume que manchas de
27 habitats são idênticas e a diversidade de espécies nesses locais é limitada devido à baixa
28 dispersão (Leibold *et al.*, 2004, Hubert *et al.*, 2015); b) *species-sorting*, modelo no qual
29 os locais são vistos como heterogêneos e os resultados das interações locais entre as
30 espécies são dependentes de fatores abióticos (Urban *et al.* 2004); c) *mass effects*, modelo
31 que considera a existência de diferentes manchas com diferentes condições, onde a
32 dispersão é o fator determinante na dinâmica local (Mouquet & Loreau, 2002); iv) *neutral*
33 *processes*, assume que todas as espécies são similares (Hubbell, 2001).

34 Um caso especial, sob a perspectiva de metacomunidades, são comunidades de
35 espécies que vivem em ambientes lóticos, as quais revelam diversas particularidades que
36 as diferenciam da maioria dos sistemas na maioria dos estudos (e.g. lagos, fragmentos
37 florestais, solo) (Logue *et al.*, 2011). Nos sistemas lóticos, a dispersão da maioria dos
38 organismos é frequentemente orientada na direção do fluxo de água (e.g. macrófitas,
39 macroinvertebrados, peixes e salamandras). No entanto, outros padrões de dispersão,
40 também podem ser observados em diferentes grupos, por exemplo, larvas de insetos
41 aquáticos são dispersas, a princípio, seguindo o fluxo da corrente de água, porém, os
42 adultos podem se dispersar via terrestre em diferentes direções, como por exemplo, por
43 terra no sentido contrário ao fluxo de água (Brown *et al.*, 2011). Nesse contexto, é
44 possível observar que os processos determinantes da estrutura das comunidades e a
45 composição das metacomunidades de ambientes lóticos são dependentes da interação
46 entre os fatores locais (condições abióticas e interações entre as espécies) e os regionais
47 (dispersão e extinção) (Jacobson & Peres-Neto, 2010).

48 *Considerações sobre a biota em ecossistemas lóticos*

49 Riachos de cabeceira são considerados a menor unidade da paisagem de uma bacia
50 hidrográfica e são comumente conhecidos como sistemas lóticos de primeira ordem entre

51 os ecossistemas aquáticos (Allan and Castillo 2007). Os que drenam áreas florestais
52 naturais possuem fortes interações e dependência das características dos ambientes
53 terrestres adjacentes (Frissell et al. 1986; Ramírez et al. 2008). Esses sistemas, em geral,
54 são localizados em áreas com densa cobertura vegetal e estão sob um regime de reduzida
55 entrada de luz e de grande quantidade de matéria orgânica vegetal alóctone. Dessa forma,
56 esta é a principal fonte de energia disponível para os organismos aquáticos, pois os riachos
57 são ambientes com baixa produtividade primária (Roth et al. 1996; Allan and Castillo
58 2007). Além disso, o funcionamento desses ecossistemas complexos depende
59 primariamente das diversas interações entre os seus componentes bióticos e abióticos
60 (Wantzen et al. 2008). Dessa forma, os organismos aquáticos destacam-se como os
61 principais responsáveis da manutenção do fluxo de energia nesses ecossistemas, uma vez
62 que processam grande quantidade de matéria autóctone e alóctone, permitindo a ciclagem
63 de nutrientes por toda a bacia hidrográfica (Allan 2004; Davies et al. 2008).

64 A variação na estrutura física dos riachos e na composição das matas ciliares tem
65 sido apontada como fator essencial para o funcionamento dos riachos de cabeceira e
66 principalmente como os fatores controladores da diversidade da biota aquática (Cummins
67 1988; Clarke et al. 2008; Silva et al. 2016). Por serem os maiores componentes das bacias
68 hidrográficas, em proporção, os riachos são os principais contribuintes de elementos da
69 biota, matéria orgânica e minerais nas redes de drenagem (Maloney et al. 2008). Assim,
70 estudos que contribuam para a conservação desses ambientes é uma necessidade atual e
71 urgente para garantir o funcionamento ecossistêmico das bacias hidrográficas e a
72 manutenção da biodiversidade local e regional, frente ao efeito do crescimento da
73 conversão de florestas para uso do solo, principalmente nas regiões de florestas tropicais
74 como as da Bacia Amazônica (Fearnside 2006).

75 Em vista disso, a pesquisa sobre a diversidade das comunidades aquáticas além de
76 elucidar os padrões de distribuição das espécies nesses ecossistemas, também deve
77 compreender como funcionam os principais processos abióticos que ocorrem nestes
78 ambientes (Tonkin et al. 2014). Assim, a tarefa de descrever como os padrões de
79 distribuição dos organismos aquáticos são resultados das interações das comunidades
80 com os fatores da estrutura do hábitat e das características da bacia hidrográfica, também
81 deve considerar as interações locais entre as espécies, eventos climáticos e as limitações
82 à dispersão (Altermatt et al. 2013a). Além disso, nesses estudos as dinâmicas desses
83 processos precisam ser consideradas em suas diferentes escalas geográficas, uma vez que
84 seus efeitos sumarizam a variação ambiental em escalas locais, regionais e continentais
85 (eventos históricos) (Boyero and Bailey 2001; Duraes et al. 2016).

86 Entre os diversos grupos que compõem a biota aquática, os invertebrados são os
87 organismos mais abundantes e diversos, apresentando um papel ecológico central nos
88 ambientes lóticos (Malmqvist 2002). Eles apresentam uma série de adaptações para a
89 sobrevivência nesses ecossistemas que refletem em seus hábitos de forrageio, os quais
90 são específicos para muitos grupos e podem ser organizados em diferentes grupos tróficos
91 (Wallace et al. 1997). Assim, raspadores são grupos consumidores de algas das
92 superfícies dos substratos, rochas e detritos vegetais; fragmentadores consomem as folhas
93 e a matéria vegetal vindas da serapilheira já em decomposição pela ação da microbiota;
94 predadores consomem outros animais; e os coletores que alimentam-se das partículas
95 orgânicas em suspensão na água (Cummins 1973). Entre esses grupos funcionais, estão
96 os macroinvertebrados que incluem insetos, crustáceos, moluscos e diversos outros
97 táxons comumente organizados em suas características funcionais baseados na
98 similaridade de forrageio (Mihuc 1997; Ramírez et al. 1998).

99 Nas últimas décadas, estudos sobre a ecologia de riachos têm incluído os
100 invertebrados aquáticos como o principal componente da biota em modelos de
101 distribuição de espécies e testes das principais teorias sobre a ecologia de comunidades e
102 do funcionamento dos ecossistemas lóticos (Wilson 1987; Eyre et al. 2005; Prather et al.
103 2013). Em geral, os principais estudos sobre essa biota discutiram as suas respostas às
104 variação ambiental e utilizaram abordagens de diversidade linear (diversidade alfa local)
105 nesses ecossistemas, a qual ainda tem sido bastante comum em estudos sobre a dinâmica
106 de matéria, ecologia funcional e a ciclagem de nutrientes (Altermatt 2013b). Porém, esta
107 abordagem linear (diversidade alfa) na maioria dos estudos foram motivos de intensos
108 debates em relação à generalização desses resultados para outros ambientes lóticos
109 (Vinson and Hawkins 1998; Allan 2004). Conseqüentemente, as novas discussões sobre
110 as comunidades aquáticas estão voltadas para explicar a variação na distribuição das
111 espécies não apenas dentro mas, principalmente entre bacias de drenagem, considerando
112 a variação na composição das comunidades como uma resposta à variação ambiental
113 regional (Vinson and Hawkins 1998; Allan 2004; Maloney et al. 2008). Uma vez que, as
114 bacias de drenagem são redes interdependentes, com habitats complexos, estas devem ser
115 analisadas considerando os gradientes ambientais de cada região, os quais são apontados
116 como componentes importantes relacionados a variação na diversidade biológica nesses
117 ecossistemas (Maloney et al. 2008; Brown et al. 2011).

118 *Comunidades aquáticas e traços biológicos*

119 Em geral, os estudos de Ecologia de Comunidades visam esclarecer os processos
120 responsáveis pelos padrões de diversidade, abundância e composição das assembleias de
121 espécies, bem como, descrever os processos que determinam estes padrões. Além disso,
122 visa entender como funcionam as dinâmicas de coocorrência de espécies (i.e., a
123 persistência de um determinado conjunto de espécies em uma área específica), que

124 interagem em maior ou menor intensidade, em uma escala local (Lawton 1999; Vellend
125 2010). Como definição, as comunidades ecológicas são um conjunto de espécies que
126 coocorrem no tempo e no espaço, e que, potencialmente, interagem umas com as outras.
127 Dessa forma, a distribuição das espécies nas comunidades seria o resultado de processos
128 ecológicos atuais, de eventos do passado e de processos evolutivos contínuos (Mcpeck &
129 Miller, 1996). Além disso, os ecossistemas aquáticos têm dinâmicas ecológicas
130 complexas (por exemplo, interações bióticas e abióticas) e devem ser considerados em
131 muitas escalas espaciais variando de contextos regionais (bacias e drenagens), habitats
132 (sequências de piscinas e fluxos rápidos) e micro-habitat (composição de substratos)
133 (Brown 2003; Swan and Brown 2011). Portanto, para compreender os efeitos da distância
134 geográfica sobre a distribuição de espécies, deve-se procurar responder as mudanças
135 funcionais das comunidades incluindo os seus traços biológicos e ecológicos ao longo de
136 gradientes ambientais (Usseglio-Polatera et al. 2000; Tomanova and Usseglio-Polatera
137 2007; Hubbel 2005).

138 Uma vez que o objetivo central da pesquisa em biodiversidade é interpretar os
139 processos que atuam na coexistência de espécies em diferentes escalas espaciais e
140 temporais (Kneitel and Chase, 2004), uma forma de entender o papel desses processos
141 que atuam na organização das comunidades seria desintegrando os seus principais
142 componentes bióticos e abióticos (Meynard et al. 2013). Por exemplo, a elucidação de
143 fatores relacionados aos efeitos de filtros ambientais, limitação à dispersão e eventos
144 históricos, contribuem para abordagens robustas, mais gerais e preditivas, principalmente
145 permitindo uma ligação entre a ecologia de comunidades e de ecossistemas (Mcgill et al.,
146 2006). Assim, a inclusão dos traços biológicos das espécies para relacioná-los às
147 restrições ambientais em que elas são afetadas, potencializa o entendimento da
148 distribuição e função da biota em múltiplas escalas (Dolédec et al. 1996). Abordagens

149 como estas, aumentam a habilidade para predição dos resultados das interações entre as
150 espécies, assim como as consequências desses resultados para os ecossistemas e para os
151 processos evolutivos (Fountain-Jones et al. 2015).

152 A inclusão da investigação sobre o potencial preditivo do uso de traços de espécies
153 na ecologia de comunidades para definir as comunidades biológicas (abordagens
154 baseadas em traço) tem sido cada vez mais destacadas na literatura científica nas últimas
155 décadas (Laliberté and Legendre 2010). Entre os modelos mais utilizados na integração
156 do conhecimento entre as características biológicas das espécies na ecologia de
157 comunidades, destaca-se aqueles preditos na *Teoria de habitat Templet*, a qual propõe
158 que as principais estratégias ecológicas das espécies são características evoluídas em
159 resposta a um "*Habitat Templet*" (Southwood 1977). Nesse modelo, as características do
160 habitat teriam condições específicas que restringiria e favoreceria caracteres biológicos
161 específicos dos indivíduos (Townsend and Hildrew 1994). Desde então, a aplicação
162 dessas premissas foram as principais perspectivas utilizadas em centenas de trabalhos em
163 diferentes áreas do conhecimento da Ecologia de Comunidades, principalmente em
164 estudos de comunidades aquáticas (Poff et al. 2006; Menezes et al. 2010).

165 Nestas abordagens, a importância do nicho foi amplamente aplicada para explicar
166 e prever as distribuições das espécies de acordo com as principais características do
167 ambiente (Poff 1997; Auerbach e Poff 2011). Além disso, os estudos focaram em
168 descrever os papéis de padrões evolutivos e funcionais e seus efeitos sobre os processos
169 ecológicos responsáveis pela coexistência das espécies nas comunidades (Townsend e
170 Hildrew 1994; Usseglio-Polatera et al. 2000). Dessa forma, a coexistência de espécies foi
171 muitas vezes relacionada com as diferenças em seus traços e histórias de vida,
172 disponibilidade de recursos e outras interações ecológicas, principalmente considerando
173 a contribuição da variação desses traços nas espécies e suas "síndromes" como um *proxy*

174 para respostas aos filtros ambientais (Poff e Ward 1990; Townsend e Hildrew 1994;
175 Southwood, 1997; Poff et al, 2006).

176 *Considerações sobre as comunidades de Insetos Aquáticos*

177 Entre os componentes da biota aquática, destacam-se as comunidades de insetos
178 aquáticos, que é constituída por grupos com uma diversidade alta de caracteres
179 morfológicos, fisiológicos e comportamentais (atributos). São organismos de relevante
180 importância ecossistêmica, pois apresentam uma grande diversidade funcional e
181 taxonômica, sendo essenciais para a manutenção da estrutura trófica dos sistemas
182 aquáticos, pois apresentam fortes relações com as características ambientais (Ramírez and
183 Pringle 1998). Embora a riqueza e a diversidade das espécies de insetos aquáticos (há
184 uma enorme quantidade de espécies ainda não descritas – déficit lineliano) possam
185 representar dificuldades para os estudos, outras características do grupo podem ser
186 extremamente úteis para a detecção de perturbações e variações nos ecossistemas
187 aquáticos (Waite et al. 2004; Tomanova et al. 2006; Simaika and Samways 2008). A
188 diminuição da riqueza de espécies, bem como, alterações drásticas nas relações de
189 dominância entre as espécies, também a presença ou ausência de certos táxons, podem
190 ser indicadores do estado geral de integridade de ambientes aquáticos (Barbosa et al.
191 2001; Moya et al. 2007; Cardoso et al. 2013).

192 Além do exposto acima, os insetos aquáticos constituem um grupo com
193 distribuição cosmopolita, abundante e diversificado que são associados a diversas
194 mudanças relacionadas ao habitat e suas comunidades variam de acordo com a distância
195 geográfica (escalas locais e regionais) (Heino, 2009). Também são considerados bons
196 indicadores das condições locais e mudanças temporais. Assim, essas características
197 destacam sua importância funcional para os ecossistemas de água doce, principalmente
198 aquelas relacionadas aos diversos hábitos e grupos tróficos (Cummins 1973). Além da

199 estrutura das comunidades, os traços das espécies de insetos aquáticos têm sido utilizados
200 para prever respostas de interações bióticas (e.g. predadores) como também variação na
201 estrutura das condições do habitat (Usseglio-Polatera et al. 2000).

202 Assim, estudos sobre a ecologia de comunidades utilizando grupos de insetos
203 aquáticos, traços funcionais e características de seus habitats mostram-se de grande
204 importância e um bom modelo para elucidar questões relacionadas ao nicho. Além disso,
205 a distribuição e a organização das comunidades em diferentes escalas podem permitir a
206 inferência dos efeitos de processos neutros na distribuição desses insetos em comunidades
207 locais e regionais. Contudo, para as áreas naturais na Região Amazônica, essas
208 abordagens acima citadas são pobremente conhecidas e lacunas ainda existem sobre o
209 papel das condições bióticas e abióticas na estruturação das comunidades de insetos,
210 utilizando abordagens sobre os vários componentes da estrutura das comunidades (e.g.
211 variação na composição de espécies, estrutura funcional e espacial).

212 Considerando o exposto acima e a complexidade dos habitats encontrados em
213 ecossistemas lóticos amazônicos, esta tese tem como objetivo geral avaliar quais são os
214 fatores determinantes dos padrões de distribuição de comunidades de insetos aquáticos e
215 suas relações com a variação ambiental e a escala geográfica. Para responder a estas
216 questões esta tese está dividida em quatro capítulos, os quais são apresentados em formato
217 de artigos científicos, manuscritos submetidos e manuscritos para submissão em
218 periódicos científicos.

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CAPÍTULO I

Chironomids as indicators in freshwater ecosystems: an assessment of the literature

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* Capítulo publicado no periódico *Insect Diversity and Conservation*



MINOR REVIEW

Chironomids as indicators in freshwater ecosystems: an assessment of the literature

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Abstract. 1. Freshwater assessment studies have been used changes on individuals and populations of Chironomidae assemblages as bioindicators to assay aquatic ecosystems changes and environmental quality. To assess the contribution of the studies with this family to response aquatic environmental changes, we carried out a scientometric analysis of the papers published from 1992 to 2012.

2. We imported papers from ISI Web of Knowledge database (Thomson Reuters) in November 2013. A total of 2967 papers were evaluated and we carried out descriptive analysis to assay the main trends on Chironomidae research in freshwater assessments.

3. The main ideas and approaches in these studies were related to the impact of human influence on aquatic ecosystems and the status of conservation of this environments, as well as to limitations and difficulties in the applications of the assessments.

4. In view of our results, we suggest some ideas to contribute to the conservation of aquatic ecosystems, mainly in threatened environments in southern Hemisphere countries. However, Chironomidae identification for assessing aquatic environments, as well as the limitations of suitable tools and metrics, which still are strong issues that need more attention to make more robust approaches to assay aquatic ecosystems.

Key words. Literature review, Chironomidae, bioindicators, conservation.

Introduction

Despite the extraordinary importance for humans and biodiversity, freshwater ecosystems are among the most threatened environments worldwide. Inland waters are being subjected to abnormal levels of impacts from human transformation of aquatic habitats, and around the world, many rivers, lakes, wetlands, reservoirs, and ponds have been imperilled more intensively in recent decades (Malmqvist & Rundle, 2002; Dudgeon *et al.*, 2006). Many studies have demonstrated growing frequencies of extinctions in freshwater species due to high levels of human disturbance. This scenario is enigmatic, occurring mainly in aquatic environments in poorly studied regions, such as the countries in the southern hemisphere, where

the most of world's freshwater environments and biodiversity are concentrated (Strayer & Dudgeon, 2010; Vörösmarty *et al.*, 2010).

Habitat destruction, pollution, and climate changes due to anthropogenic impacts are the main causes of loss of biodiversity, mainly in streams and rivers. Although these threats are increasing, the effects of these disturbances regarding the impacts of many pollutants on freshwater biodiversity are still poorly understood. Inland waters constitute the environments that received less conservation efforts in recent decades compared to terrestrial habitats (Abell, 2002; Abell *et al.*, 2011; Carpenter *et al.*, 2011). There is a considerable global destruction of inland-water ecosystems in all regions, such as the neotropics, where urban and agricultural demands for water have increased, despite the lack of planned projects for conservation (Allan, 2004; Chin, 2006; Sensolo *et al.*, 2012). Land use commonly causes changes in river hydrology and water quality and usually results in habitat alterations due to

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wastewater effluent, deforestation, overgrazing, and forestry plantations. Such impacts may reflect an increase of forest disturbances due to reduced interception of rainfall and transpiration rates, thus affecting even the terrestrial ecosystems (Gergel *et al.*, 2002; Chadwick *et al.*, 2006).

Freshwater invertebrate fauna plays key ecological roles in the maintenance of aquatic ecosystem services, mainly in secondary production and energy flow dynamics (Cummins, 1973; Ramírez *et al.*, 1998). Among these organisms, aquatic insects are the most important, because they are the major proportion of functional feeding groups helping in ecosystem dynamics; but nonetheless they still are the most threatened (Tomanova *et al.*, 2006; Strayer, 2013). Furthermore, they have a noteworthy importance to freshwater monitoring, protection, and conservation due to their sensitivity to respond to unfavourable changes in environmental conditions (Barbosa *et al.*, 2001; Nedeau *et al.*, 2003). Hence, aquatic insects have been employed in many studies and methods to assess freshwater health. Many freshwater biomonitoring programmes have used changes in individuals, populations, and communities of aquatic insects to assay ecosystem changes and environmental quality. These approaches have been used exhaustively on insect orders and families as indicators of pollution, habitat modifications, and natural changes of water quality (Roy *et al.*, 2003; Camargo *et al.*, 2004; Beketov *et al.*, 2009; Molozzi *et al.*, 2012; Chang *et al.*, 2014).

Among aquatic insects, the dipteran family Chironomidae, commonly referred to as non-biting midges, is the most abundant and species-diverse insect group found in freshwater ecosystems (Ashe *et al.*, 1987; Cranston, 1995; Ferrington, 2008). Chironomidae is a very speciose group and members can be found in a variety of habitats. This family has a range of sensitive species as well as several species groups with tolerances to environmental gradients, ranging from undisturbed to human-impacted ecosystems (Heino & Paasivirta, 2008; Tang *et al.*, 2009; Roque *et al.*, 2010). Chironomids make up the most widespread insect family, and they have received attention by researchers worldwide due to their outstanding abilities as biological indicators of environmental conditions (Pinder, 1986). Ecological studies about these insects started focusing on the use of chironomid larvae as bioindicators. Many studies on chironomids as indicators have been performed using larvae for lake trophic typology (Lindgaard, 1995). These studies demonstrated the importance of chironomids as required bioindicators for use in several European and North American countries in the final decades of the 20th century. The robustness of chironomid responses to changes in the aquatic environment could enable their use to monitor many rivers, lakes, and ponds (Rosenberg, 1992). Recently, researchers have been using approaches of chironomids as bioindicators for freshwater environmental impact assessments, ecosystem health, toxicity tests, palaeoenvironmental studies, and climate change (Resh & Rosenberg, 2008; Eggermont & Heiri, 2012).

Although there are considerable amounts of research and information about chironomids as bioindicators for aquatic environments worldwide, the studies about these insects and their environment are still scarce (Ferrington, 2008). The knowledge regarding the impacts of many human disturbances on freshwater ecosystems and chironomids still contains gaps; there are few data for some developing regions, mainly in the tropics, which are areas that may be particularly at risk for species extinction in the near future due to human influence and climate changes (Abell *et al.*, 2008; Contador *et al.*, 2012). The suitability of appropriate bioindicators may also be useful for assessing the impacts of human disturbance, application of ecological thresholds to conservation prioritisation (areas with value for biodiversity), monitoring of ecosystem disturbances, and environmental management (quality of the assessment or monitoring) (Heino *et al.*, 2003; Huggett, 2005; Thieme *et al.*, 2007; Abell *et al.*, 2011). In view of this, we provide a comprehensive review of the literature on Chironomidae as bioindicators to assess freshwater environmental changes regarding the principal approaches to analyse the most threats to freshwater conservation and aquatic insects at global and continental scales. The goal of this review is to highlight research areas and describe the studies performed in the past 20 years. We also aim to determine whether there are differences across regions and countries regarding research of human impact on the ecology of these organisms, as expressed in the literature.

Methods

This systematic review is based mainly on published articles in international journals. Reference data sets were imported from the ISI Web of Knowledge (Thomson Reuters) database by combing keywords. All papers containing “Chironomidae”, “Chironomid*”, or “non-bit midge*” in their titles and abstracts from 1992 to 2012 were imported into Reference Manager software (professional edition, version 12). Papers were imported in .ris format in November 2013, and 2967 papers were evaluated.

Papers were refined by selection of abstracts discussing the use of Chironomidae for assessment of freshwater ecosystems. The main keywords and their derivatives recognised as important for the screening process were as follows: water assessment, water pollutants, water pollution, organic matter, bioassay, heavy metal, acid, water quality, water indicator, water monitoring, aquatic indicator, aquatic monitoring, water index, water ecological assessment, ecological condition, aquatic integrity, biotic integrity, ecological status, ecosystem health, biotic index, aquatic conservation, stream indicator, wetland indicator, lake indicator, palaeoecology, palaeolimnology, palaeoecological, and palaeolimnological. Abstracts of the retrieved papers were examined and literature out of scope (e.g. papers that did not deal with Chironomidae as

indicators and assessment of aquatic ecosystems; Systematics; Reviews; Book Reviews) was removed, yielding 558 articles. If papers dealt with Chironomidae and other organisms, they were also included. The screening followed these criteria and was applied to select only relevant papers of Chironomidae as indicators in freshwater assessments. After selection and assessments, papers deemed important for our purposes were retrieved for analyses (see supporting information).

We calculated simple descriptive statistics to assess trends and approaches in the literature (e.g., most frequent journals, environments, continents, countries, anthropogenic factors, etc.) and global trends in the environments studied. In addition, we performed a linear regression to assess trends in the number of publications over time.

Results

In which journals papers were published

Overall, the papers were published in 171 different journals; this amount is considerably large with respect to our goal. Among them, the Journal of Paleolimnology; Hydrobiologia; Environmental Toxicology and Chemistry; Freshwater Biology; the Journal of the North American

Benthological Society; Environmental Monitoring and Assessment; Archiv für Hydrobiologie; Environmental Pollution; the Journal of Freshwater Ecology; Palaeogeography, Palaeoclimatology, Palaeoecology; Quaternary Science Reviews; Ecological Indicators; Archives of Environmental Contamination and Toxicology; Canadian Journal of Fisheries and Aquatic Sciences; and Annales de Limnologie-International Journal of Limnology contain the most published papers (Fig. 1). The Journal of Paleolimnology was the journal with the most papers (8.29%), followed by Hydrobiologia (7.96%), Environmental Toxicology and Chemistry (5.14%), Freshwater Biology (3.98%), and the Journal of the North American Benthological Society (3.98%). These tendencies may be because they are the main periodicals with scopes specific to publishing research on aquatic ecosystems (Fig. 1).

Research trends

There was a trend involving the number of papers about Chironomidae as bioindicators per year; an increase of overall studies published involving this family occurred over time. The amount of papers increased significantly in the past 20 years ($R^2=0.82$; $P < 0.001$). The highest percentages of papers were published on North American and European continents, mainly in Canada, the United

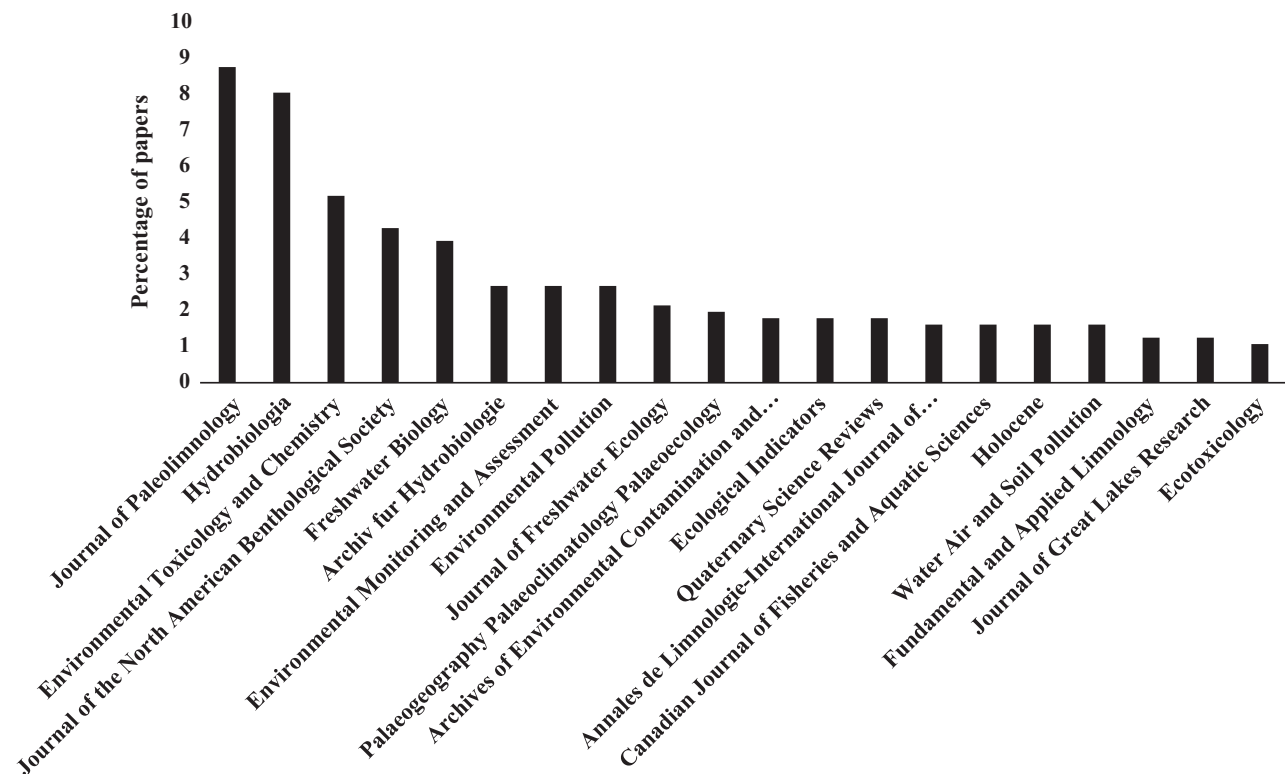


Fig. 1. The top 20 periodicals, which published papers on Chironomidae in bioassessment.

States, Finland, and the United Kingdom (in decreasing order). South America and Oceania produced the most papers published in the southern hemisphere, with Brazil and Australia being the main countries of publication (Figs 2 and 3).

Most publications were related to Chironomidae employed as a taxon for assessment of aquatic ecosystems (55.73%). Macroinvertebrates, although not representative of any taxa, comprise the other group of papers that aims to assess indicators of stream quality (44.26%). This group is represented by many invertebrate taxa, such as all the aquatic insects (e.g. Ephemeroptera, Odonata, Plecoptera, and Trichoptera), crustaceans, snails, and oligochaetes; in all of these studies, Chironomidae were cited as the most abundant and diverse. Thus, these studies have arisen some important issues of including chironomid data within the assessments of the aquatic environments evaluated, mainly on its ecological importance and applied significance (Fig. 4a).

At the global scale, the percentage of publications related to the Chironomidae and macroinvertebrates included studies that performed assessments using immature insects (98.38%) and occasionally pupae- and adult-stage ones. Chironomid species, species groups, and genera made up the most frequent taxonomical resolution at overall the papers, but it was not significantly different from the family level, which comprised the next most-cited group used in the assessments. In addition, chironomids were used as bioindicators of environmental perturbations for studies ranging from species assemblage (62.90%), following populations (28.13%), to organism level (8.96%) (Fig. 4b, c and d).

Riverine environments are the most represented in the literature, as 42.65% of all of the articles focussed on assessment of these environments, in which rivers and streams were the aquatic systems with high associated levels of human disturbances. Lakes represented a high

percentage of the research (33.15%), with a considerable amount of palaeolimnological studies. Fewer studies involved ponds, reservoirs, and wetlands (Fig. 5a).

The sources and effects of the most stressors on freshwater environments assessed in the literature can be summarised with the high percentages of studies on heavy metals, wastewater, pesticides, nutrients, agricultural systems, and acidification, mainly as results of anthropogenic influences. Similar to traditional biomonitoring, of the approaches currently employed in freshwater ecosystems, diversity indices that used chironomids to monitor the ecological status of these environments were the most used techniques (34.58%). In addition, chironomid species assemblages in palaeolimnological biomonitoring comprise the second group of approaches in the literature. Multivariate approaches, multimetric approaches, biotic indices (16.84%), and toxicity studies were other approaches (15.23%) that often used chironomids for assessment techniques. Molecular, morphometric, and genetic techniques were applied less in the studies (Fig. 5b).

Discussion

By assessing the literature for Chironomidae, the most abundant and diverse aquatic insect family, we were able to highlight some trends and biases on the research with this group during the past 20 years. Papers were mostly published in the main periodicals with specific scopes encompassing research about freshwater ecosystems. Nevertheless, a remarkable amount of papers was also published in journals with broad scopes and audiences, which indicates a current awareness to publish results on freshwater assessments. Chironomidae have been important components of biomonitoring programmes worldwide, and they have played a key role in the development of many biological indicators in many countries (e.g. Moya

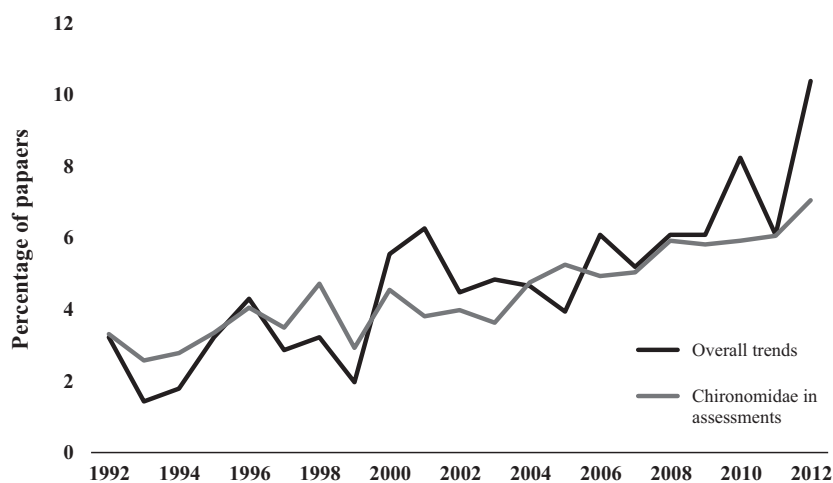


Fig. 2. Trends in number of overall papers about Chironomidae published and papers dealing with Chironomidae in bioassessments published per year.

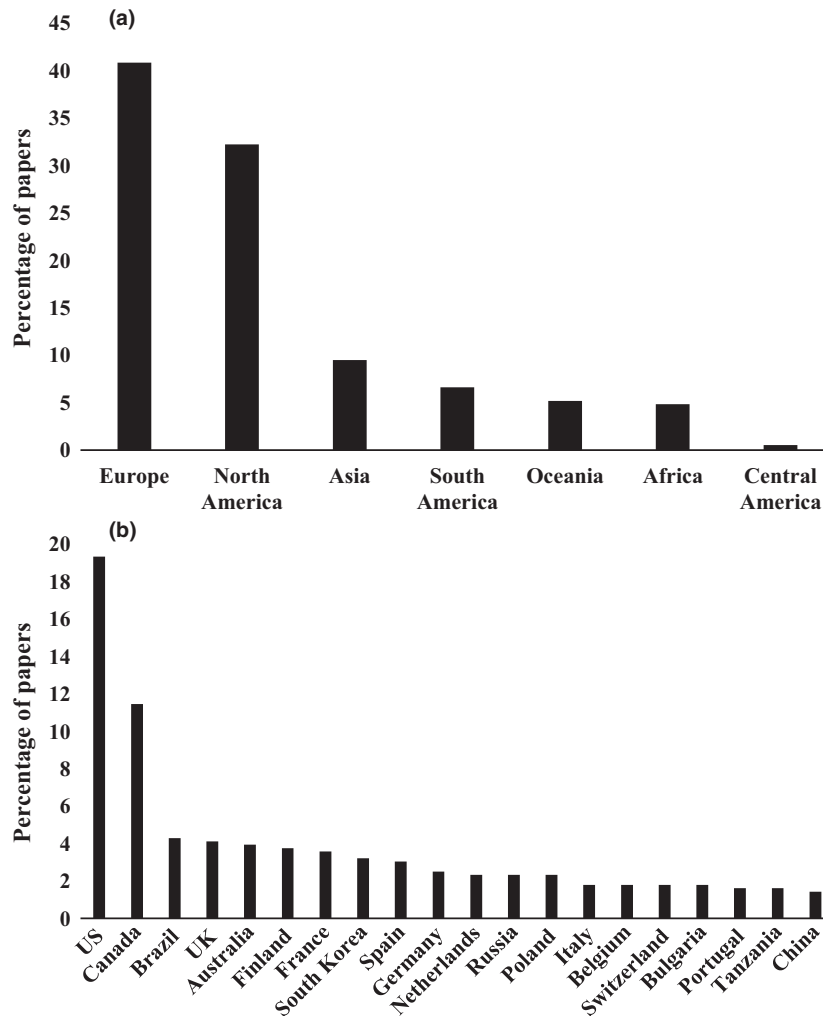


Fig. 3. Percentage of papers about Chironomidae in bioassessment: (a) per continent, (b) per countries.

et al., 2007; Couceiro *et al.*, 2012; Lencioni *et al.*, 2012; Lunde & Resh, 2012; Verdonshot *et al.*, 2012). Because of this, researchers may have published their results in a variety of periodicals worldwide.

Nevertheless, the amount of the publications also has some bias, since the ISI Web of Knowledge does not contain papers that are not indexed in its database. Many studies regarding Chironomidae as bioindicators performed at local or even regional scales are only published in journals that belong to regional databases, such as in South America (SciELO Database). As a result, many papers were not imported in our review, which could increase the global number of periodicals and papers published.

In this sense, now we can answer the following question: Which are the main trends on assessment studies using chironomids in freshwater ecosystems? The amount of papers with Chironomidae used as bioindicators shows that there is a tendency for the numbers to increase per

year, and, by analysing the overall publications regarding Chironomidae, we can see the same tendency. Research about Chironomidae has followed the modern history of biomonitoring early in the 20th century in Europe (Rosenberg, 1992). Most of the published papers from 1992 to 2012 assessed freshwaters on this continent; Europe exhibited the highest percentage of publications related to biomonitoring with Chironomidae. North American countries also have high instances of published papers on Chironomidae for assessments. Comparisons of the publications on European and North American continents do not generate large differences between biomonitoring results; in both regions, invertebrate fauna and bioindicators are substantially well documented. In addition, there are programmes developed for monitoring freshwater environments with effective agencies that apply many of policies for biomonitoring, which provide support for conservation (Li *et al.*, 2010; Cardoso *et al.*, 2011; New & Samways, 2014). The southern hemisphere,

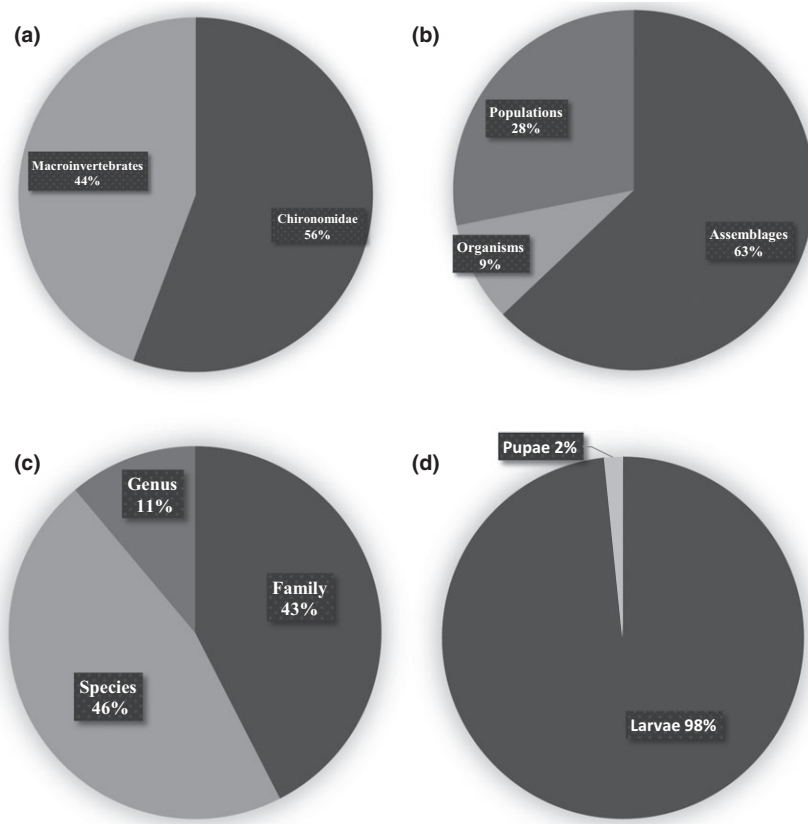


Fig. 4. Features and indicators mostly used in published papers on Chironomidae in bioassessment: (a) aquatic assemblage assessed, (b) level of organisation, (c) taxonomical resolution, (d) life stage.

South America, Oceania, and Africa have the lowest percentages of publications. These results indicate that there are still some gaps in monitoring the aquatic ecosystems in these regions. As a result, this also suggests weak efforts to monitor the aquatic environments in these regions and warrants an urgent request for conservation priorities, since in these regions exist the most endangered tropical forests and freshwater ecosystems, such as the Amazon (Couceiro *et al.*, 2006; Castello *et al.*, 2013).

Although the lower percentage of studies comes from countries of Africa, Oceania, and South America, some of the countries have a significant amount of papers published. Brazil and Australia are the countries with the most overall publications. In these countries, research has been developing in recent years, but many aquatic environments still lack study. Overall, in South America, the research on the ecology of aquatic insects occurs mainly on the southern portion of the continent (Contador *et al.*, 2012). Freshwater environments in the Andean and Amazon regions still lack studies of biomonitoring and conservation, mainly with the Chironomidae (Thieme *et al.*, 2007). It is also important to emphasise that this scenario is in urgent need of comprehensive taxonomic works to make species available for their use in biomonitoring. A conservation impediment for chironomid fauna in South

America and Africa may be related to their underrepresented documentation compared to North American and European fauna [e.g. Canada, the United States, United Kingdom, and Finland (in decreasing order)] (Ferrington, 2008).

Most assessments published were about disturbances related to heavy metals, wastewater, and pesticides. These impacts are related to land use development on the watershed and are increasing due to urban and agricultural expansion. These threats are some of the main problems for conservation because, overall, they lead to complete ecosystem loss and, in many environments, species and population extinction (Nedeau *et al.*, 2003; Maloney *et al.*, 2008; Wahl *et al.*, 2013). Although fewer studies assess environments affected by deforestation and climate changes, these are current threats to aquatic biodiversity, which have caused many habitat losses and require further attention (Bojsen & Jacobsen, 2003; Couceiro *et al.*, 2006; Rawi *et al.*, 2013).

For biomonitoring environmental stressors at the organismal level, studies on Chironomidae assemblages comprised the largest group of papers, according to the amount of studies. This family offers a high species richness compared with any other group of freshwater macroinvertebrates. This advantage has allowed researchers to

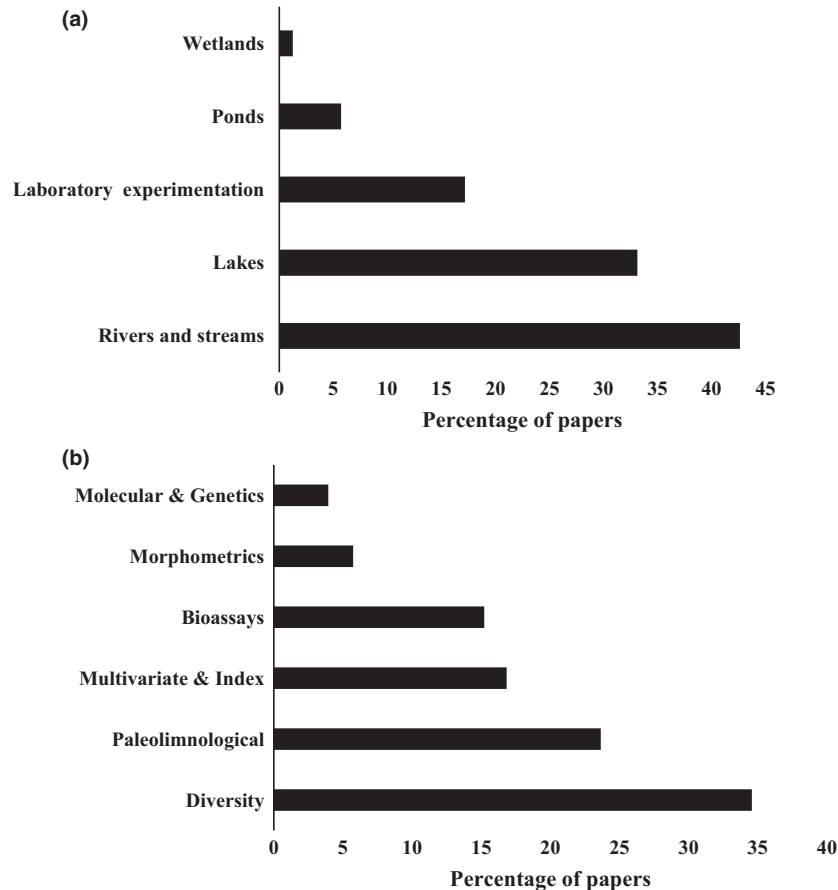


Fig. 5. Percentage of papers per: (a) aquatic environment where studies were performed, (b) most frequent analyses and approaches carried out on freshwater assessments with chironomids.

assess a wide spectrum of responses to variation in the aquatic environments. Typically, chironomid diversity and abundance of species at assemblages show specific requirements in their habitats, which, when modified, can indicate an environmental change. The Chironomidae assemblage level has been a suitable tool for measuring organic pollution in streams, measuring water quality using biotic indices, and classifying lake types (Thorne & Williams, 1997; Ruse, 2010; Lunde & Resh, 2012).

Populations of chironomid species comprise the other major group of papers in this review, and this organisation level is related to considerable amounts of studies on toxicity tests in laboratory experiments. Many of these papers involved approaches at the population and organismal levels aiming to measure effects of toxicants on mortality, growth, and/or behaviour of single and multiple species (Azevedo-Pereira *et al.*, 2010; Tassou & Schulz, 2013). Chironomids exhibit many features that make them suitable for toxicity tests, such as noticeable life stages, short life cycles, and suitability for bioassay purposes. Bioassays and toxicity tests are outstanding tools for the assessment of populations in response to environmental stress at the biochemical and physiological

levels; the insects (e.g. *Chironomus riparius* and *C. tentans*) accumulate aquatic contaminants, and they can be applied as sentinels to warn of adverse effects (Watts & Pascoe, 2000; Azevedo-Pereira *et al.*, 2012). In addition, laboratory experimentations employing morphometric, molecular, and genetics can be used in biomonitoring, as these analyses can help assess environmental stressors in Chironomidae populations and organisms. Although these approaches are useful tools, they were less represented in papers (Servia *et al.*, 2004; Sharley *et al.*, 2004; Carew *et al.*, 2013).

For palaeolimnological assessments, Journal of Paleolimnology was the most important journal and chironomid-based palaeoecological studies were the second major group of papers. These studies provided robust inferences about past changes in freshwater ecosystems, where chironomids have been applied as useful tools for performing reconstructions of a range of environments and have increasingly attracted attention over the past two decades (Walker *et al.*, 1991; Brooks, 2006). These environmental changes included lake eutrophication, climatic change, and past changes in lake water salinity, where Chironomidae larval head capsules often occur in high abundances

in sediments and remain for thousands of years in sediment (Walker *et al.*, 1995; Eggermont *et al.*, 2006). These features highlight the use of this family in several studies worldwide when compared to other living aquatic insects groups used for recent biomonitoring (e.g. EPT, Odonata) (Hofmann, 1988; van Hardenbroek *et al.*, 2011). In addition, continuous records of Chironomidae in palaeolimnological studies have allowed inferences on global-scale climate warming as well as limnological changes occurred at the end of the last glaciation (Walker & Cwynar, 2006; Axford *et al.*, 2009; Holmes *et al.*, 2011).

In summary, there are still main difficulties in assessment studies on establishing ecological thresholds in Chironomidae species assemblages in the southern regions as the lack of well-catalogued fauna and recognised taxonomic experts, which comprise much better documentation that allow description of the most species and quick recognition of many (Stribling *et al.*, 2008; Greffard *et al.*, 2011). Moreover, a wide community sympathy for conservation endeavours for aquatic insects, especially dipteran species is needed to describe the ecological understanding of the variety of threats to insects and their impacts on species, habitats, and communities. Hence, they could be available for most biomonitoring and conservation purposes.

Although chironomids are an important group for the assessment of ecosystem health, they are avoided from many assessment studies, but nonetheless that could lead to erroneous results in the aquatic environment assessment processes and, thus, to the wrong ecosystem evaluation (Raunio *et al.*, 2011). A major debate concerning the use of macroinvertebrates in rapid environmental assessment is the level of taxonomic resolution required (Resh, 1994). Family and species were the most frequently used levels of identification for Chironomidae in papers that examined the effects of disturbances on freshwater benthic macroinvertebrates; half of both lotic and lentic studies used this level. Although the species is the appropriate taxonomic level for most biomonitoring work, the level of identification ultimately will depend on the goals and objectives of the study and the resources available for it (Bonada *et al.*, 2006).

Conclusion

Chironomidae insects could play important roles in aquatic ecosystem biomonitoring and conservation due to their ecological diversity, ubiquitous occurrence, and critical position in food webs. In addition, they can be surrogates for many groups in some aquatic ecosystems. Thus, Chironomidae may successfully improve a variety of biomonitoring approaches. Regarding this assessment of the literature, we propose some efforts and improvements for approaches to overcome some conservation impediments and gaps in aquatic ecosystem studies using Chironomidae as bioindicators and as a useful group for insect conservation initiatives.

Focussing on taxonomical research improvements to description and identification of chironomid species

The main difficulties of working with Chironomidae insects are due to their small larval size and taxonomic problems worldwide. Traditional taxonomical methods for identification and description of species can be improved with new approaches, such as molecular genetics tools. These allow researchers to determine suitable information required for the selection of indicator species responses to impacts and ecosystem changes. The employment of these techniques will complement the expansion of rapid biomonitoring programmes through the ability for accurate species identification. These will help identify endangered status of chironomid species and freshwater ecosystems and determine priorities for legislation and conservation initiatives.

Increase the amount of research on under-represented freshwater ecosystems, such as those in Africa and South America

In the southern hemisphere, the studies with Chironomidae in these two neglected areas are still sparse compared to Europe and North America, as evident from the literature. Furthermore, with respect to conservation resources, initiatives are currently most limiting, and knowledge regarding aquatic ecosystems is still poor. Although these regions are reported to contain many hotspots of biodiversity, South America and Africa still experience increasing aquatic and terrestrial habitat destruction. Thus, advances in research on Chironomidae for biomonitoring aquatic ecosystems in these regions of the world would help assess the ecological thresholds (i.e., the point at which there is an abrupt change in an ecosystem quality) and the extent of human impacts on freshwater environments. This could lead to application of suitable conservation initiatives for protection of aquatic biodiversity in those regions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/icad.12123:

Table S1. Reference data set imported from ISI Web of Knowledge in November 2013 with the papers evaluated.

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CAPÍTULO II

Broad-scale patterns of physical habitat structuring chironomid metacommunities in
Amazonian floodplain streams

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1 **Broad-scale patterns of physical habitat structuring chironomid metacommunities**
2 **in Amazonian floodplain streams**

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26 **Abstract**

27 We studied the diversity and abundance of Chironomidae assemblages according to the
28 metacommunity framework, aiming to disentangle dispersal-driven processes at local and
29 regional scales. We investigated how species composition, total abundance, species
30 density, and species richness are affected by variation in habitat factors and differences
31 in distance measures explain metacommunity diversity in Brazilian Amazonian
32 floodplain streams. Our hypothesis was based on how metacommunity measures of
33 species are spatially structured by means of eigenfunctions in spatial analysis (Moran's
34 eigenvector maps), constrained ordination analysis and variation partitioning methods.
35 We found remarkable environmental (i.e., species sorting) and high spatial effects (i.e.,
36 dispersal limitation, mass effects) on the metacommunity structure. The main
37 environmental factors in habitat variation were substrate organic detritus and mean
38 thalweg depth. Only broad-scale spatial factors were significant to represent regional
39 patterns in metacommunity structure, suggesting that dispersal processes are important in
40 determining Chironomidae assemblages. Our results support that without dispersal
41 limitation, species sorting and mass effects are the main perspectives for structuring
42 chironomid metacommunities in forested habitat at Amazonian floodplain streams.

43

44 **Keywords:** Aquatic insects; species sorting; mass effects; flood pulse; non-biting midges.

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51 **Introduction**

52 Synergistic effects of environmental factors and spatial processes are the main
53 drivers for patterns of species composition in natural metacommunities. Dispersal-driven
54 processes at local and regional scales can create diversity gradients that may lead
55 biological assemblages to among-community similarity in habitats governed by
56 environmental disturbances (Urban, 2004; Brown, 2007). Thus, spatially structured
57 communities are dependent on the autocorrelation in assemblage composition, which
58 usually is a result of the combination of local (environmental filtering) and regional
59 (dispersal limitation) processes (Altermatt et al., 2011; Altermatt & Holyoak, 2012). The
60 metacommunity framework has provided insightful views and approaches to study the
61 assemblage dynamics and patterns of species diversity and distribution at different scales.
62 Its mechanisms are mainly focused on the interactions among local communities, which
63 are inherently linked by action of dispersal and spatial structure governing assemblages
64 at multiscale extents (Leibold et al., 2004; Swan & Brown, 2011).

65 In the last years, studies evaluating local and regional patterns of community
66 structure have greatly contributed to our knowledge about metacommunity processes.
67 Thus, ecologists are focusing on the empirical application of these approaches mainly in
68 niche-assembly metacommunity models, which assume environmental effects as one of
69 the most important assemblage drivers, also highlighting the role of spatial and dispersal
70 contribution in species distribution (Moritz et al., 2013). For this, empirical
71 metacommunity studies usually apply four perspectives (*species sorting*, *patch dynamics*,
72 *mass effects* and *neutral*) that describe local and regional assemblage distribution
73 regarding local forces and species characteristics (Logue et al., 2011). Then, they
74 provided general approaches to understand the relative role of space controlling biotic

75 and abiotic factors (i.e. environmental factors, biotic interactions and traits) (Davies et
76 al., 2009; Logue et al., 2011).

77 In riverine metacommunities, environment and dispersal have strong relative
78 importance to rule isolated assemblages, such as headwater streams with less connections
79 than high order streams; a minimum of dispersal upstream occurs against the down land
80 water flow (Finn & Poff, 2005). As expected, *species sorting* effects are high when
81 compared to habitats with lower dispersal dynamics. On the other hand, connected
82 streams have a high rate of dispersal because dendritic connections lead high mass effects
83 dynamics and neutral processes (Brown & Swan, 2010). Stream metacommunity studies
84 have recognised that *species sorting* is the main driver in shaping metacommunity
85 structures, although the dispersal processes are emphasised with increasing spatial scale
86 (Heino et al., 2015a, 2015b). Therefore, there is an increased need of new approaches to
87 increase the power of explanation of large scale metacommunity processes and describe
88 processes such as directional spatial influences on environmental data reflecting on
89 species assemblages (Dray et al., 2006, 2012).

90 The inclusion of a spatial perspective in models to study fine to large scale effects
91 (dispersal, neutral models) represented a pronounced contribution to explain patterns in
92 community ecology at different extents (Blanchet et al., 2008a, 2011). Although these
93 methods are increasingly applied, it is still unclear how space can generate ecological
94 structures. However, this is an important issue, since spatial processes often mask patterns
95 of particular interest in studies, such as the relative environmental contribution to indicate
96 the role of disturbances and changes in species extinction and strategies of life (He et al.,
97 2005; Legendre & Gauthier, 2014; Blundo et al., 2015). Thus, consideration of context
98 (local and regional) in community ecology should lead to apply spatial factors as either a
99 predictors (explanatory variables) or a covariables (response variables whose effects can

100 be controlled) for explaining patterns in many natural communities (Clarke et al., 2006;
101 Lindo & Winchester, 2009; Bonada et al., 2012).

102 While the influences of habitat heterogeneity jointed to spatial processes on
103 shaping composition and metacommunity structure are known for many terrestrial and
104 aquatic ecosystems, empirical studies on riverine metacommunities still lack adequate
105 application of the spatial perspective jointed an overall stream habitat characterization
106 (Altermatt, 2013). Studies applying a spatial perspective to understand environmental and
107 dispersal processes in the stream networks of Amazonian floodplains are scarce.
108 However, this region has a high diversity of habitat types and/or vegetation units, which
109 are expected to profoundly influence the habitat and spatial structure of communities
110 (Junk et al., 2012). For these stream networks, we can expect that metacommunities be
111 shaped by the joint influence of habitat and spatial factors accordingly to the scale applied.
112 Then, incorporating spatial models in metacommunity diversity it is expected that large
113 differences in species richness from headwater stream to large riverine communities.
114 Because local conditions (environmental filtering) lead to responses by measures of
115 community diversity that are dependent on the identity of the local species, functional
116 and phylogenetic diversity (Brown, 2007; Poff et al., 2010). In contrast, abundance is
117 expected to be high when extreme environmental conditions are dominant for well-
118 adapted species (VanDerWal et al., 2009; Dunbar et al., 2010). Although spatial processes
119 have recently become very popular in stream community ecology, they are still poorly
120 explored for invertebrate benthic distribution, usually due to variation in substrate type
121 and availability, which is often very heterogeneous due to large-scale influences (Dunbar
122 et al., 2010; Heino et al., 2015c; Leps et al., 2015). Furthermore, little is known about the
123 influence of dispersal and spatial processes effects on assemblages in Amazonian
124 floodplain systems, although some studies highlighted local and regional influence on

125 aquatic insects, the processes regulating biodiversity in these systems are not still well
126 understood (Landeiro et al., 2011, 2012).

127 In this study, we aimed to identify environmental effects, measured as different
128 physical habitat explanatory variables, and spatial structure among Chironomidae
129 metacommunities using distance between communities and diversity measures.
130 Additionally, we tested hypothesis based on flood homogenization in the absence of
131 barriers separating assemblages in the stream network, also allowing more dispersal
132 dynamics to maintain source-sink migrations. Thus, we hypothesised that flooding has
133 different effects on the two bays in the watershed (Caxiuanã and Portel Bay), representing
134 different environmental conditions for stream chironomid fauna and constraining
135 assemblage distribution. We believe that hydrological regime plays key factor driving
136 ecological functioning and biodiversity patterns in Amazonian floodplain systems. Then,
137 we considered effects of dendritic on network structure and dispersal effects to: (1)
138 describe the distribution, structure and composition of Chironomidae larvae assemblages
139 in floodplain streams, (2) analyse the environmental contribution along the stream
140 network gradient and (3) relate the most relevant metacommunity processes to
141 Chironomidae larvae assemblages in streams. As expected, many studies stressed *species*
142 *sorting* as the main metacommunity drivers for aquatic insects, but also reported the
143 influence of habitat variability and spatial distribution on structuring Chironomidae
144 assemblages (Puntí et al., 2009; Finn & Poff, 2011; Tejerina & Malizia, 2012; Petsch et
145 al., 2015). As expected for Chironomidae assemblages, we expect that diversity patterns
146 mainly respond to the local environmental conditions along the stream network gradient,
147 (Ferrington, 2008). Considering that the floodplain dynamics affects stream habitats, we
148 expected local and regional differences in species composition. Thus, considering *species*
149 *sorting* the most important driver for Chironomidae distribution, we aimed to answer to

150 following questions: (1) Do species composition dependent on environmental variation?
151 (2) Which metacommunity processes are driving assemblage patterns?

152 **Material and methods**

153 *Study area*

154 The study was performed at 33 sites in pristine and near-pristine forested streams
155 located at the watershed catchment between Caxiuanã and Portel Bay (Fig. 1). We
156 collected biological data and measured environmental factors only in the dry season from
157 October to November of 2012 and 2013. The area is covered by dense rain forest and
158 located in floodplains next to Marajó Inland estuary at the north central region of Pará
159 State, Brazil. The forests are characterised by "*terra firme*", or upper level forest (80%)
160 and a small floodplain are with several "*igapó*" (flooded forest) areas (20%). The climate
161 of the region, according to the Köppen classification, is tropical monsoon climate "*Am*"
162 with a short dry season (Oliveira et al., 2008). Caxiuanã Bay is an inland bay within the
163 catchment of Anapu River, about 40 km long and 8–15 km wide. The area experiences a
164 daily tidal influence; the range between low and high tides is approximately 17–21 cm
165 (Hida et al., 1997). Forests in this region are characterised as freshwater backup tidal
166 "*várzea*" which are flooded twice daily by fresh water backed up from tides (Behling &
167 Costa, 2000). The watershed comes from Caxiuanã and flows about 400 km via Portel
168 Bay and Melgaço, Pará River, flowing out into the Atlantic Ocean (Rossetti et al., 2008).

169 *Field sampling and sample processing*

170 Chironomids were collected using a circular net (mesh size = 250 μ m) covering
171 150 m of each stream site. We performed screening at each riffle and pool zones with 20
172 substrate subsamples at each stream as replicate of sites. Chironomidae specimens were
173 sorted in the field and preserved in 85% alcohol. Larvae specimens were desiccated and
174 mounted on slides with Hoyer's solution according to the methodology proposed by

175 Trivinho-Strixino (2014). We identified the Chironomidae larvae at genus and species
176 level when possible using available literature considering the limited knowledge available
177 for Neotropical fauna (Ferrington, 2008; Trivinho-Strixino, 2014). The specimens and
178 slides were stored in the Zoological Collection at Universidade Federal do Pará, Belém,
179 Brazil.

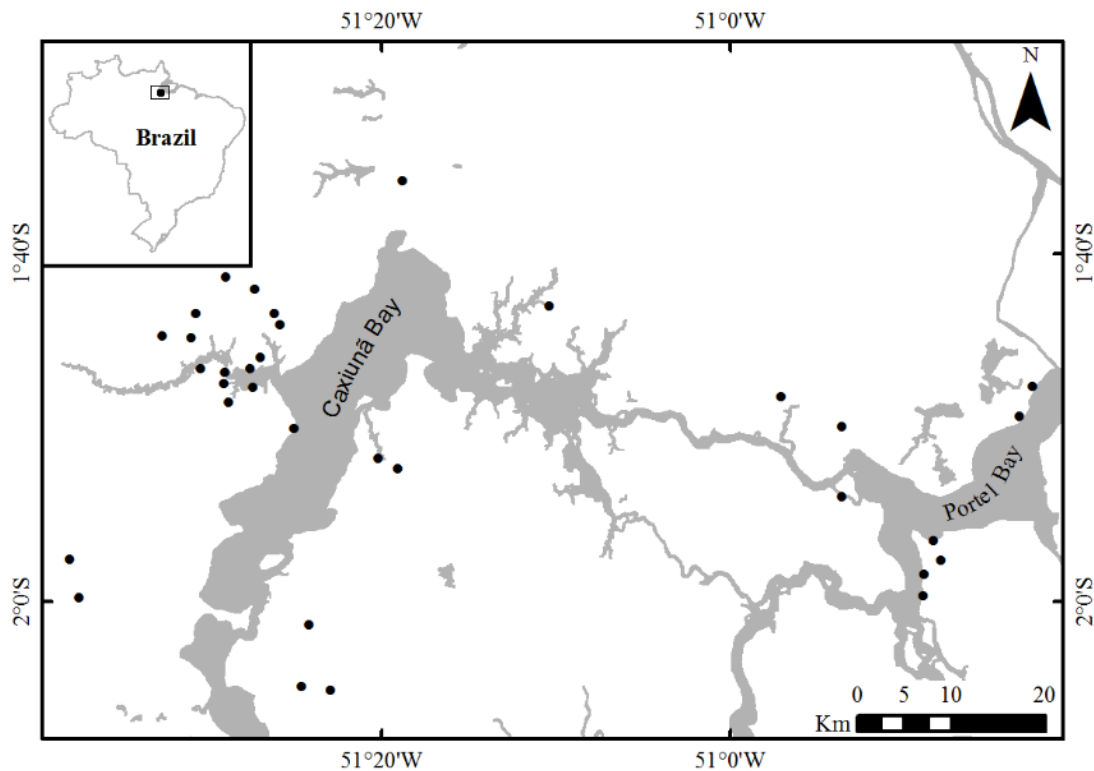


Fig. 1 Map of the study area showing the stream locations of sampled sites at Caxiuanã Bay and Portel Bay, Pará, Brazil.

180

181 *Environmental data*

182 For each site, we sampled stream physical habitat and constructed a dataset to use
183 as constraint environmental variables (**E**) influencing assemblage structure of
184 chironomids. From the water, we measured dissolved oxygen, conductivity, pH and
185 temperature. We measured physical characteristics and features of the habitats following
186 Peck et al. (2006). For each stream, a 150 m long site was subdivided into ten continuous
187 sections, 15 m long, with 11 cross-sectional transects. Measurements were made at
188 varying levels of resolution across sections and transects, but the response variables were

189 all analysed as stream site summaries (e.g., means, percentages or maxima). Habitat
 190 structure variables included measures of stream channel morphology (e.g., slope,
 191 sinuosity, depth, wetted and bankfull width, incision, bank angle), in stream habitat
 192 features (substrate size, flow types, presence of wood in the channel), riparian structure
 193 (e.g., canopy cover, vegetation type) and human alterations in the channel and riparian
 194 zones (e.g., presence of buildings, pasture, crops, roads, trash). Subsequently, physical
 195 habitat metrics were derived from the dataset and calculated according to Kaufmann et
 196 al. (1999). Finally, from the habitat variables dataset, only a smaller set for further
 197 analysis was selected, based on ecological relevance and their past use in studies on
 198 community diversity of aquatic insects in Amazonian river systems (e. g. Couceiro et al.,
 199 2011, 2012; Datry et al., 2016). The selection process consisted of removing variables
 200 from the environmental component, which (a) had more than 90% of zero values, (b)
 201 were highly correlated with other variables (Pearson correlations $r > 0.7$) and (c)
 202 represented more information that is redundant as other variables. That selection aimed
 203 to avoid artificial inflation on fitting multivariate models. Finally, our environmental
 204 component (**E**) was selected as 8 instream habitat variables (Table 1; Table S1 in
 205 Appendix I).

206 **Table 1.** Environmental variables measured in the 33 streams considered in this study from Caxiuanã Bay
 207 and Portel Bay, Pará, Brazil.

Name	Code	Min	Max	Average	SD
<i>Physical habitat metric variables</i>					
Coarse Litter - Leaf-litter Banks (%)	pct_bf	0.124	9.814	4.691	3.142
Substrate organic detritus (%)	pct_om	2.733	13.043	10.687	2.899
Mean bank angle (degree)	xbka	15.909	40.682	24.628	6.024
Water surface gradient over reach (%)	xslope	0	20.667	4.798	4.298
Mean canopy density mid-stream (%)	xcdenmid	86.497	99.332	95.183	3.335
Class 1 - very small to very large (pieces/m ²)	lwd_c1w	4.000	80.667	28.588	19.372
Mean wetted width (m)	xwidth	1.873	13.000	4.851	2.620
Mean thalweg depth (cm)	xdepth	24.833	81.160	48.191	15.149

208 *Spatial variables*
 209

210 To test our hypothesis about the role of spatial-related processes structuring the
 211 metacommunities, we used the spatial component (**S**) constructed from Moran's

212 Eigenvector Maps (MEMs) framework (Dray et al., 2006) based on sites coordinates,
213 created by a connection diagram according to Gabriel graph criteria (Legendre &
214 Legendre, 2012). The selected spatial eigenvectors were used as spatial explanatory
215 variables and covariables in our constrained analyses and correlations with environmental
216 variables. The spatial eigenvectors associated with high eigenvalues (e.g., the first
217 eigenvectors) represent a set of broad-scale patterns of relationships among sampling
218 sites, whereas those associated with low eigenvalues represent fine-scale patterns in data.
219 Spatial eigenvectors represent spatial structures generated by the spatial arrangement of
220 sampling sites. They are useful to explain metacommunity processes and can be
221 interpreted to represent spatial structures found in autocorrelation of environmental and
222 biotic processes, for instance, colonisation and dispersal (Griffith & Peres-Neto, 2006;
223 Dray et al., 2012).

224 *Statistical analysis*

225 To summarize environmental patterns, we performed Principal Components
226 Analysis (PCA) on environmental variables (**E**) calculated on the correlation matrix. We
227 used a priori classification of sites in order to define stream types and summarize natural
228 variability between small and large streams (see Table S1 in Appendix I). Prior to
229 analyses, the variables were transformed (centered and divided by their standard
230 deviation) to meet normality criteria. To see local patterns in community structures
231 among streams, we applied correlation tests on alpha diversity (e.g. species number, total
232 individuals, Shannon index; see Table S3 in Appendix I) with environmental variables.
233 Previously multivariate data analysis with species abundance matrix (**Y**: Chironomidae
234 composition), we applied Hellinger transformation (Legendre & Gallagher, 2001). We
235 investigated beta diversity from changes in composition and in relative abundance of
236 chironomids and patterns in environmental heterogeneity among streams using the

237 PERMDISP (group centroids) approach proposed by Anderson (2006) and Anderson et
238 al. (2006). To estimate chironomid beta diversity, we calculated centroid groups defined
239 a priori (Caxiuanã Bay and Portel Bay streams) through Principal Coordinate Analysis
240 (PCoA) based on Hellinger distance. We tested the null hypothesis that there are no
241 differences in within-Bay region, using a permutation test with 999 runs.

242 To test our hypothesis of environmental gradient contribution for Chironomidae
243 species distribution among stream site, we performed redundancy analysis (RDA) to
244 summarize the relationships among Chironomidae species and physical habitat variables.
245 Additionally we applied variation partitioning by Partial Redundancy Analysis (pRDA)
246 to the species matrix (Y), environmental variables (E) and MEMs predictors (S) (Borcard
247 et al., 1992). Variation partitioning was applied to summarise the relative importance of
248 (E) and (S) in explaining community structure and relate the most relevant
249 metacommunity processes to Chironomidae species. The final spatial and environmental
250 predictor variables were selected by fitting RDA models with a forward selection
251 procedure with a double stop criterion. First we carried out selection using a cut-off level
252 of $\alpha = 0.05$ and the procedure stopped when the adjusted R^2 accumulated by the variables
253 selected exceeded the adjusted R^2 of all the explanatory variables in the model. (Blanchet
254 et al., 2008b). Variation partitioning was based on partial Redundancy Analysis (pRDA),
255 calculated with the adjusted R^2 for each fraction, according to Peres-Neto et al. (2006).

256 Finally, to test which scale represent the diversity distribution, environmental
257 patterns and physical habitat effects on Chironomidae distribution, we applied
258 correlations tests between the site scores (from Redundancy Analysis) with the spatial
259 variables (MEMs), in order to express the absence or presence of spatial influence on
260 community data in particular scale group. Then, it is expected that the portion of variance
261 without spatial structure have the same R^2 values (measuring the amount of community

262 variation explained by each scale) uniformly distributed in the scalogram (Dray et al.,
263 2012).. We then performed a permutation procedure (with 999 runs) to test if the
264 maximum observed R^2 was significantly larger than values obtained in the absence of
265 spatial pattern. We used the packages *ade4*, *packfor*, *spacemakeR*, *spdep*, and *vegan* in R
266 version 3.3.0 (R Core Team, 2016) for all statistical analyses.

267 **Results**

268 We identified 2,535 Chironomidae larvae belonging to 41 taxa (Table S2, S3, S4
269 in Appendix I). The subfamily Chironominae was the most abundant and represented by
270 three tribes (Chironomini: 28; Tanytarsini: 5; Pseudochironomini: 1. Tanypodinae was
271 represented by 4 tribes (Pentaneurini: 6, Coelotanypodini: 2 taxa, Procladiini: 1 and
272 Macropelopiini: 1). We found only two Orthocladiinae taxa (Corynoneurini: 1,
273 Orthocladiini: 1). Of all taxa, Chironominae had the most diverse and abundant genera,
274 such as *Stenochironomus* with the highest relative abundance (11%). *Ablabesmyia* (8%)
275 within the subfamily Tanypodinae was the second abundant genera. The subfamily
276 Orthocladiinae was found in low numbers, with less than 3% for its taxa.

277 Our results highlight significant differences among assemblage compositions at
278 Caxiuanã and Portel Bay; also, we found significant variation in beta diversity among
279 stream sites in the Caxiuanã catchment as expressed by the dissimilarity measures (Table
280 2). We found that local Chironomidae diversity was negatively correlated with the depth
281 variation among streams. Overall, the Chironomidae alpha and beta diversity were not
282 related to the water variables. In addition, when we assessed the environmental factors
283 represented by physical habitat metrics, they were grouped, except for canopy as
284 explained by Principal Components Analysis among the bays (Fig. 2).

285 Considering only the water variables, they did not show a clear distinction of
286 between the regions and it was not found any relation to Chironomidae assemblages.

287 Moreover, in terms of physical habitat, the same analysis explained more than 50% of the
 288 total variation observed among the stream habitat structure. In this analysis, it still
 289 revealed a high correlation among most physical habitat variables, except for canopy
 290 density, which showed high values at Portel Bay streams (Fig. 2).

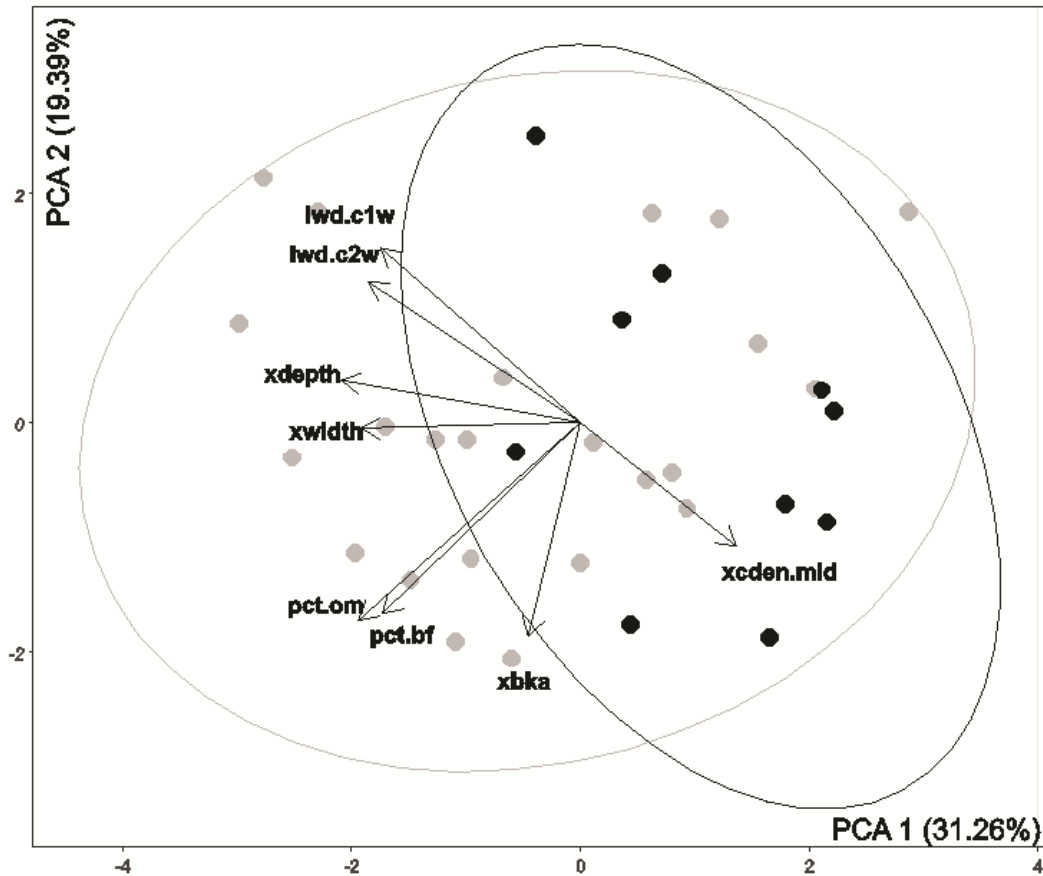


Fig. 2 Results of Principal Components Analysis for physical habitat variables. Grey circles indicate sites at Caxiuanã Bay and black circles sites at Portel Bay.

291

Table 2. Relationships between alpha diversity metrics and environmental variables.

	pct.bf	pct.om	xbka	xwidth	xdepth	lwd.c1w	lwd.c2w	xcden.mid
S	0.018	0.220	0.077	-0.150	-0.390	-0.320	-0.330	0.089
N	0.002	0.120	-0.074	-0.120	-0.480	-0.290	-0.260	0.150
H	0.088	0.160	-0.016	-0.070	-0.390	-0.230	-0.270	-0.020

293 * Pearson correlation test, significant levels of the correlations in bold ($p < 0.05$).

294 The PERMDISP results showed differences between bays for physical habitat
 295 heterogeneity and Chironomidae composition. Hellinger distance applied for species
 296 composition revealed among assemblages and highlighted that streams at Caxiuanã Bay

297 have high community dissimilarity than those at Portel Bay. In addition, for sites
 298 dissimilarity, we found variation in environmental heterogeneity of stream habitats at
 299 Caxiuanã and Portel region (Table 3).

300 **Table 3.** Results of tests for homogeneity of multivariate dispersions (PERMDISP) between Caxiuanã and
 301 Portel bays using average distance to centroid based on the following distance indices: Euclidean for
 302 environmental variables (**E**); Hellinger indices for Chironomidae dataset (**Y**).

Distance	Caxiuanã Bay	Portel Bay	F	p-value
<i>Euclidean</i>	0.188	0.267	6.845	0.017
<i>Hellinger</i>	0.426	0.358	5.382	0.014

303 The most important physical habitat variables considered were *pct_om* (substrate
 304 organic detritus), *xdepth* (mean thalweg depth). They represented a gradient in the
 305 Principal Components Analysis that shows high values of substrate organic detritus in
 306 large streams and conversely high values for mean thalweg depth (Table 4, Figs. 2, 3).
 307 The forward selection results retained three spatial variables as final explanatory factors
 308 for patterns in Chironomidae assemblages, which were used in variation partitioning
 309 (Table 5). The spatial variables retained were only those for Moran's Eigenvector Maps,
 310 representing broad scale patterns. The MEMs were divided in eight groups and used to
 311 plot the spatial patterns with ordination scores performed for the Chironomidae
 312 abundance table (**Y**), its constrained response by habitat variables (**E**) and its residual
 313 fraction when environmental dependence was removed (**R**).

315 We observed environmental influence in Chironomidae distribution by
 316 Redundancy analysis, regarding physical habitat variables with the presence of spatial
 317 dependence (Fig. 3, 4). When we separately considered the Chironomidae response to
 318 physical habitat in partial Redundancy analysis, the results showed remarkable
 319 contribution ($R^2 = 0.317$; $p = 0.002$), with the elevation, mean thalweg depth and substrate
 320 organic detritus presenting the higher correlation to the first two axes. Besides,
 321 considering only the full variance-partitioning model, with the environmental and spatial

322 factors prior selected, the results presented low fraction (14%) of the Chironomidae
 323 composition variation. Then, when we observed patterns separately, the pure spatial broad
 324 scale component (5%) lesser explained the variation in community composition,
 325 compared to the environmental component (7%) (Table 6).

326 **Table 4.** Forward selection results for spatial variables selected for variation partitioning model.

Variables	R ²	R ² Cum	AdjR ² Cum	F	p
MEM1	0.060	0.060	0.030	1.981	0.005
MEM3	0.050	0.110	0.050	1.675	0.021
MEM5	0.047	0.157	0.070	1.615	0.041

327

328 **Table 5.** Redundancy analysis results for
 329 physical habitat variables.

	RDA1	RDA2
pct.bf	0.507	0.241
pct.om	0.892	0.284
xbka	0.341	0.214
xwidth	0.279	0.110
xdepth	0.457	-0.536
lwd.c1w	0.149	0.043
lwd.c2w	0.058	-0.268
xcden.mid	0.168	0.040
Eigenvalues	3.304	2.856
<i>% Explanation</i>	31.73	
<i>Total inertia</i>	0.507	
<i>Constraneid</i>	0.161	
<i>F</i>	1.394	
<i>p-value</i>	0.004	

330

331 **Table 6.** Relative importance of environmental (env) and spatial variables (spa) for explaining the
 332 Chironomid composition.

Fractions	df	R ²	Adj R ²	testable	p value
Shared fractions					
<i>env + shared + spa</i>	11	0.435	0.138	true	0.002
<i>env + shared</i>	8	0.317	0.090	true	0.026
<i>spa + shared</i>	3	0.156	0.007	true	0.001
Pure fractions					
<i>Pure env</i>	2	-	0.070	true	0.009
<i>Pure spa</i>	8	-	0.050	true	0.039
Residual			0.861	false	

333

334

335

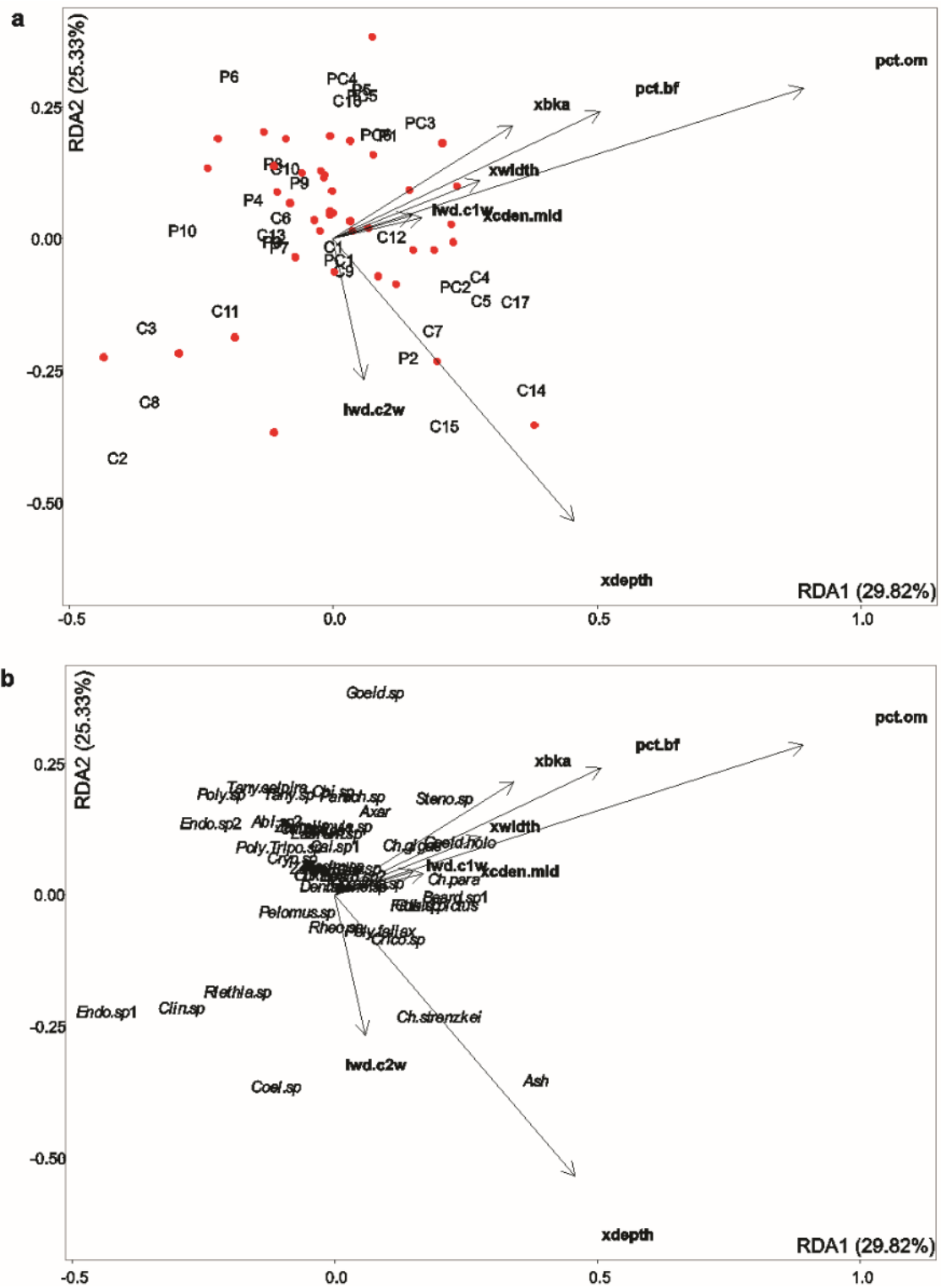


Fig. 3 Redundancy Analysis for Chironomidae species constrained by habitat variables. (a) results for site scores and species distribution among sites; (b) results showing species names.

336

337

The correlations applied to see spatial patterns in Chironomidae composition

338

constrained by environment showed significant broad scale influences shaping the

339 metacommunity structure (Figs. 4, 5). We detected broad scale influences on the scores
340 of the computed ordinations for Chironomidae composition among streams (PCA),
341 environmental contribution (RDA) and residual distribution without environmental
342 dependence (PRA). The results were plotted in maps with site scores of each stream in
343 the study area, showing the patterns of the first two axes of the computed analysis.
344 Additionally, their associated correlation scalogram are presented with the maximum
345 observed R^2 measuring the amount of variation explained by a given scale in the response
346 data (i.e., **Y**, **E** and **R**) as eight spatial components. All the scalogram presented a
347 significant accumulation of explained variance (R^2) in the broad-scale components.

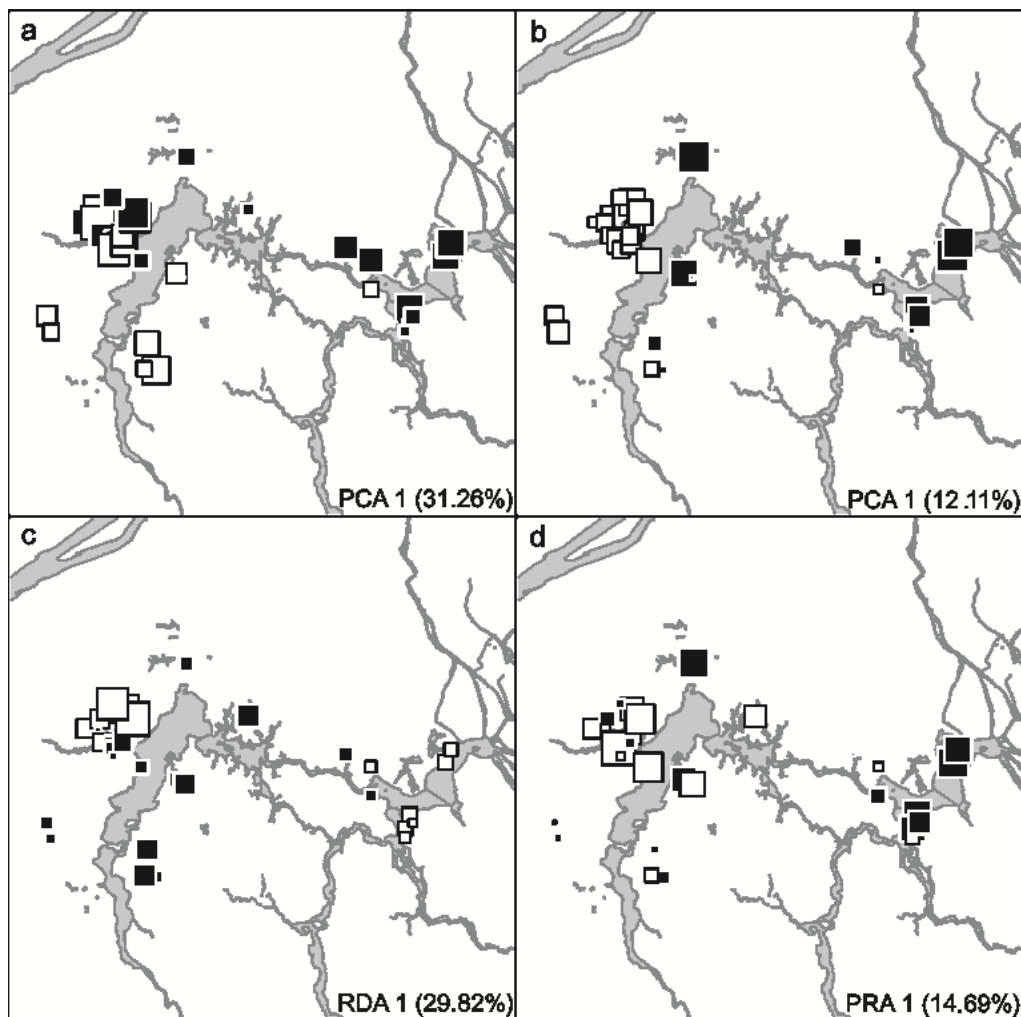


Fig. 4 Maps of the study area with the scores from ordination representing spatial plots for the first two axes of PCA (E: ordination of physical habitat variables) PCA (Y: ordination of Chironomidae assemblage), RDA (E: Redundancy Analysis for Chironomidae species constrained by habitat variables) and PRA (R: The residual analysis without effects of measured environmental variation). Black squares indicate positive values and white squares negative values of the scores for each ordination method.

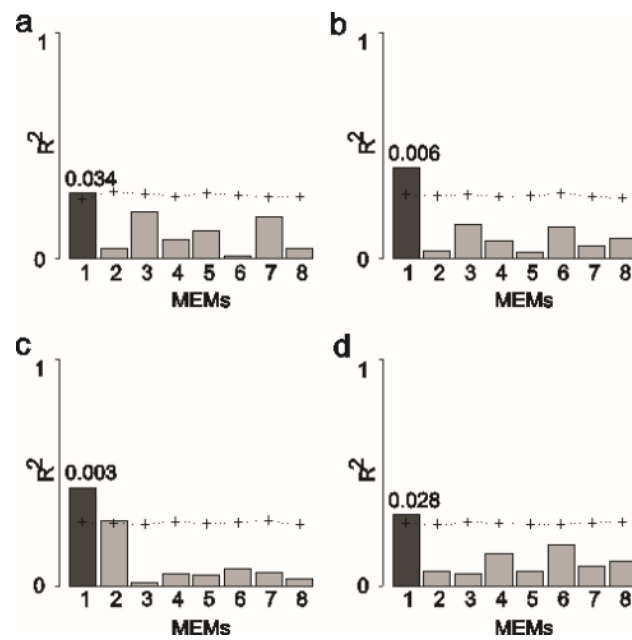


Fig. 5 Scalogram indicating the portion of variance (R^2) explained by Moran's eigenvector maps (MEMs) variables (scale group highlighted in dark grey). Only first axis of ordination methods were applied: a) PCA (environment), b) PCA (species), c) RDA, d) PRA). MEMs variables were accumulated in eight groups. We tested correlations using 999 permutations and p values are given above the highest R^2 . Pointed lines represent the 95% confidence interval.

349

350 Discussion

351 In our study, spatial arrangement of suitable habitat among streams has influenced
 352 Chironomidae distribution and environmental gradients. Thus, a combination of physical
 353 habitat variables and the distance between streams best explained the community
 354 structure. The spatial gradient, determined by stream longitudinal distance, was an
 355 important covariable for assemblage composition. These results show how the
 356 environmental factors governs the river classification and affect insect aquatic
 357 assemblages (Heino et al., 2005). Our results indicate remarkable effects for large-scale
 358 spatial drivers on Chironomidae metacommunity structure. The physical habitat gradient
 359 at broad extents were the main drivers for chironomid distribution and assemblage
 360 structure. However, at regional extents, the detection of significant broad-scale spatial
 361 patterns in residuals also suggests that there are other important large-scale drivers (non-

362 measured environmental data, historical influences at Caxiuanã and Portel Bays,
363 evolutionary or biotic interactions acting in the Chironomidae metacommunities.

364 It should be noted that significant broad-scaled spatial patterns remained in our
365 data after the large-scale effects attributable to the measured environmental gradients,
366 mainly the physical habitat structure expressed by depth and coarse particulate organic
367 matter, were observed in variation partitioning in association with spatial variables. Our
368 study did not find any fine scale structures for chironomid assemblages; however, such
369 patterns were expected, since in stream networks, species are often controlled by local
370 limited dispersal processes, high biotic interactions or habitat disturbance (Urban, 2004;
371 Altermatt, 2013). For the whole metacommunity structure, our findings highlight the low
372 contribution of *species sorting* and high evidence for *mass effects* dynamics as the main
373 processes for Chironomidae distribution. However, it is contrary to our expectations,
374 since we expected that the pure environmental factors were not the main predictors
375 structuring the metacommunities. Therefore, the above patterns can be inferred from
376 natural disturbance effects resulted only in broad scale differences in the physical habitat
377 characteristics, when we expected local drivers for assemblages' distribution.

378 Chironomidae assemblages comprises a set of variable group of species with
379 different responses to environmental and spatial influence. Most of Chironomid taxa are
380 related to live in specific conditions of habitat, such as in high elevation the
381 Orthocladiinae subfamily are dominant. On the other hand, Tanypodinae and
382 Chironominae are common in high stream order and large channel width (Álvarez et al.,
383 2010). Unexpectedly, pure environmental effects were not related to Chironomidae
384 composition and diversity. This finding did not support our hypothesis of strong
385 environmental dependence, because in-stream/riparian characteristic were not
386 considerable predictors to Chironomid species groups, which is common in

387 metacommunity structured by species sorting (Eggermont & Heiri, 2012; Milošević et
388 al., 2013; Chang et al., 2014). This result can be related to the influence of floods on
389 homogenization of habitats and the increasing similarity among stream water chemistry,
390 thereby masking variation in limnological factors in these environments (Thomaz et al.,
391 2007). Although previous studies have reported remarkable patterns in Chironomid
392 distribution along the river continuum, the degree of which variation in species
393 assemblage structure among and within streams did not considered longitudinal patterns
394 within riverine networks. Unlike the physical habitat structure variables, daily tidal flood
395 may constantly bring organic detritus and nutrients, which results in variation in water
396 variables and therefore unfavourable conditions for the establishment of many taxa that
397 are sensitive to these factors and favouring colonisation by good dispersers which can
398 tolerate these changes (evidence for *mass effects* process). These conditions could also
399 influence local diversity, when most species may die and decrease of richness and
400 increase the density of tolerant species in the flood periods, also changing regional
401 composition by dispersal of larvae and adults in the whole catchment (Árva et al., 2015;
402 Durães et al., 2016).

403 Although our study focused on benthic larvae assemblages, it is known that this
404 insect family are quite good dispersers with two modes of dispersion, an active dispersal
405 (adults) and passive dispersal mode (drifted larvae) (Heino & Mykrä, 2008; Kärnä et al.,
406 2015). As expected, from our results the overland distances were the most important
407 factor and strongly correlated with Chironomidae assemblage structures, when we
408 described spatial distance influences at the stream network extents. On the other hand,
409 the directional spatial variables contributed less to explain the species distributions. Thus,
410 these patterns highlighted that the most dispersal contribution for these stream insects can
411 be associated to between sites overland (e.g., adults) and less within (e.g., larvae) the

412 streams in the riverine network. This approach still has remarkable power to describe
413 spatial patterns in species composition, hence past studies elucidated the significance of
414 dispersal processes in shaping metacommunity structures and also found similar patterns
415 for good dispersers (Árva et al., 2015; Curry & Baird, 2015). Nevertheless, many studies
416 still find that this structure is not characteristic of many aquatic habitats. Because the
417 connectivity of lotic systems tends to be arranged as reaches nested within streams,
418 streams nested within catchments, and catchments within watersheds, the connections
419 between streams in the riverine network depend on the scale of observation, other than
420 being particularly dependent on group dispersal ability (Landeiro et al., 2012; Grönroos
421 et al., 2013).

422 Our observations support the relative *mass effects* influence on Chironomidae
423 metacommunities as a response to tidal disturbance at regional extents. Streams at Portel
424 bay were characterised with high thalweg depth values. Floods also can contribute to
425 dispersal events and homogenise both habitat structure and species composition (Thomaz
426 et al., 2007), which is commonly observed in disturbed stream networks such as our study
427 area, where tidal freshwater backup may act as a weak driver for benthic diversity. Thus,
428 the flood pulse in lowland streams influences biodiversity through geomorphic structure
429 and seasonal flooding, interacting in shaping floodplain aquatic habitats and assemblages.
430 (Villnäs et al., 2013; Starr et al., 2014). At a broad scale extent, our results show that
431 Chironomidae larvae are relatively good dispersers and considering floodplain dynamics
432 of high and low water levels, they can be drifted to many habitats by the daily tidal, which
433 can facilitate dispersal and colonisation of new habitats for many species (Buendia et al.,
434 2014; Greenwood & Booker, 2015). Thus, aquatic insect dispersal is most dependent both
435 on downstream drift, when abundant upstream species are better adapted to good

436 conditions and less affected by tides and upstream adult flight (of abundant downstream
437 species better adapted to neutral conditions) (Greenwood & Booker, 2016).

438 Hence, for aquatic insects in stream assemblages, dispersal flux creates a
439 combination of the two main metacommunity perspectives found in this study. First, the
440 local environment restrictions as the effects of *species sorting* processes, which were the
441 less important component found in our results determines the first. The second
442 perspective is related to *mass effects* at the broad scale of habitat extents, in this case,
443 regional processes (dispersal) depend on the spatial structure of the environment and on
444 the connectivity of the regional species pool (Heino et al., 2015b). Our results show a
445 high influence of environmental components in relation to a broad scale spatial structure,
446 suggesting that tidal disturbance has led to conditions where species distribution is
447 constrained by disperser groups tolerant to unfavourable habitat conditions. Since we did
448 not observe dispersal limitation, we strongly believe that the combination of moderate
449 dispersal (high pure spatial response) and low environmental contribution is the main
450 pattern observed in Chironomidae metacommunities governed by a combination of *mass*
451 *effects* and *species sorting* (Göthe et al., 2013; Heino et al., 2015b).

452 Considering that limited dispersal is absent for Chironomidae assemblages, this
453 suggests that other explanatory factors such as biological interactions and the
454 biogeographical history of the catchment as well as evolutionary processes may be also
455 controlling assemblage structure and distribution (Poff, 1997; Finn & Poff, 2011). For
456 instance, community-based analysis of traits may uncover important patterns of species
457 responses to environmental and spatial variation (Poteat et al., 2015). Besides, species
458 mainly responded to high amounts of organic detritus (CPOM) and it has concordance to
459 the most Chironomidae observed traits and functional groups. We found remarkable
460 patterns in the most abundant taxa *Stenochironomus*, which are likely leaf-mining larvae

461 found in leaf and woody debris and followed by the predator genus *Ablabesmyia*, with a
462 wide distribution at the catchments. The most abundant group consisted of collector-
463 gatherers Chironominae taxa, which collect coarse particulate organic matter (CPOM)
464 and process it from the stream bottom. This explains the high frequency of
465 *Stenochironomus* larvae, which can be directly related to conserved riparian vegetation,
466 mainly in-streams, since this genus depends on vegetation deposited in streams (Corbi &
467 Trivinho-Strixino, 2016). In addition, predator species (piercers and engulfers) from
468 Tanypodinae were the second most abundant taxa. Predatory feeding mode is a constant
469 factor in stream networks and regarding the River Continuum Concept, it is an expected
470 pattern in riverine network ecosystems (Altermatt, 2013). Spatial control in physical
471 habitats suggests a gradient from upland to down land streams; where physical habitat
472 mostly increased the distance of streams mainly for summarize the main drivers for the
473 two sub regions for Chironomidae assemblages. Moreover, previous studies obtained
474 similar results, regarding spatial processes and *species sorting* as the main factors
475 influencing metacommunity structuring at broad spatial extents (Heino et al., 2010;
476 Bennett & Gilbert, 2016).

477 **Conclusion**

478 Our results supported the hypothesis that the context of spatial factors influence
479 metacommunity structure and physical habitat in regional extents. Regarding dispersal
480 dynamics, we found that habitat heterogeneity and distance among streams were
481 important components for structuring Chironomidae assemblages at broad regional
482 extents. However, our results should be examined carefully, since the amount of non-
483 explained variation by environment remained relatively high, which may be related to
484 biotic interactions and biogeographical patterns not explored in this study. These factors
485 can be inferred from the main regional natural disturbance (i.e. the tidal flooding in

486 streams) which could have shaped habitat and assemblage adjustments (e.g., species
487 migration and biological interactions). In summary, because Chironomidae assemblages
488 are ubiquitous and small body sized invertebrates; their dispersal ability contributes
489 significantly to assembly structure. Their dependence on demographic features such as
490 population size, abiotic and biological interactions, may regulate the number of potential
491 dispersal events among streams. Thus, future studies should also integrate the effects of
492 scales in assemblage patterns, because when dispersal limitation is discrete, *species*
493 *sorting* and *mass effects* may arise as the main perspectives for structuring chironomid
494 metacommunities.

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CAPÍTULO III

Environmental influence on diversity of aquatic insect communities and functional trait composition in Amazonian small streams

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* Manuscrito com formatação para ser submetido ao periódico Ecological Entomology

1 **Environmental influence on diversity of aquatic insect communities and functional**
2 **trait composition in Amazonian small streams**

3

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15

16 **Running title:** environmental influence on stream trait functional composition

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19

20 **Abstract**

21 Amazonian streams are characterized by their diverse habitats and high species richness,
22 which are ideal models for testing *Habitat Templet* premises and studying functional trait
23 patterns in aquatic insect communities. Our main objectives were to evaluate the structure
24 of aquatic insect communities and functional trait composition according to
25 environmental gradients among streams at Rio Tapajós basin, Pará state, Brazil. We
26 analysed local patterns in diversity and by multivariate methods, we tested the influence
27 of physical habitat and water variables on community and functional assemblage
28 structure. We performed Distance-based Redundancy analyses (dbRDA) to test effects of
29 both environmental dataset on community taxonomical composition. In addition, we
30 summarized by RLQ analysis the functional community structure that was also influenced
31 by environmental predictors. Substratum properties, stream size, pH and electrical
32 conductivity were the most important predictors in determining beta diversity variation.
33 We found that functional traits in assemblages were grouped into three ecological groups
34 defined by variations in wood debris, depth, width and electrical conductivity among
35 streams. In summary, the aquatic insect community was driven by niche dynamics,
36 resulting from a combination of suitable habitat conditions within and among streams and
37 the convergence of species traits along the environmental conditions.

38

39 **Keywords:** Aquatic macroinvertebrates, Habitat Templet, niche dynamics

40

41

42 **Introduction**

43 A recurrent issue in riverine ecology is to describe how habitats can support
44 different species composition and how species can coexist within and among streams
45 (Vinson & Hawkins, 1998; Heino, 2009). To address these questions, mainly niche-based
46 approaches have been extensively applied to explain and predict species distributions
47 according to key features of the environment (Poff, 1997; Auerbach & Poff, 2011). Also,
48 studies have described the roles of functional and evolutionary patterns to ecological
49 processes responsible for the coexistence of species in assemblages (Townsend &
50 Hildrew, 1994a; Usseglio-Polatera *et al.*, 2000). Species coexistence, often, have been
51 related to differences in their life-history traits, the availability of resources and other
52 ecological interactions, mainly considering the contribution of species traits variation and
53 their “syndromes” as a proxy for responses to environmental filters (Southwood, 1977;
54 Poff & Ward, 1990; Townsend & Hildrew, 1994a; Poff *et al.*, 2006).

55 To test hypothesis about the environmental influence on functional community
56 structure, we need to define the key aspects of environment at a determined scale that
57 influences the species distribution (Brown, 2007). Nevertheless, the aquatic ecosystems
58 have complex ecological dynamics (e.g. biotic and abiotic interactions) and can be
59 considered at many spatial scales ranging from regional contexts (whole basins and
60 drainages), mesoscales habitats (pool-riffle sequences within streams) and microhabitats
61 (substrate composition) (Brown, 2003; Swan & Brown, 2011). Therefore, regarding these
62 issues in predicting species composition in lotic systems, studies have proposed that
63 functional classifications of species into groups with similar biological and ecological
64 traits are expected to respond similarly along specific environmental gradients (Usseglio-
65 Polatera *et al.*, 2000; Tomanova & Usseglio-Polatera, 2007; Colzani *et al.*, 2013).

66 The “Habitat Templet” model was the primary theoretical supporting trait-based
67 approach in stream ecology proposed by Southwood (1977). In this model, the similarity
68 in environmental conditions is the main constraint for functional trait composition, which
69 should converge in similar habitats, even if regional-scale processes is acting for species
70 pools dissimilarity (Townsend & Hildrew, 1994a). Then, this hypothesis has been
71 supported by numerous studies that explained trait composition of populations or stream
72 communities in terms of environmental gradients (Díaz *et al.*, 2007; Tomanova &
73 Usseglio-Polatera, 2007; Heino, 2008). Thus, the relationship between functional traits
74 and environmental factors is considered a good indicator to understand community
75 structure and predict which species will be able to avoid some environmental filters in
76 different habitats (Usseglio-Polatera *et al.*, 2000; Heino *et al.*, 2007; Saito *et al.*, 2014).

77 These premises were supported for many aquatic communities, which were
78 structured by many environmental gradients among local and regional streams (Heino,
79 2005). They are taxonomically well-described groups among the aquatic biota, also
80 widespread in many lotic ecosystem and constitute assemblages highly abundant and
81 diverse (Jacobsen *et al.*, 2008a). Also, they are commonly the main group of aquatic
82 organisms to respond a wide range of stressors (Malmqvist, 2002). Therefore, these
83 organisms are considered good indicators to respond to local conditions and temporal
84 changes within stream. Yet, their functional importance in freshwater ecosystems have
85 been mostly related to their diverse array of feeding habits for many groups (Merritt &
86 Cummins, 2007).

87 Habitat heterogeneity along streams has been recognized as the main driver on
88 taxonomical and functional structure of aquatic communities, mainly by influencing their
89 metabolism, feeding and behaviour (Resh *et al.*, 1988; Heino, 2005; Heino *et al.*, 2007).
90 According to theoretical references in the Habitat Templet, initially proposed by

91 Southwood (1997), traits composition are filtered by environmental conditions that
92 determine local species assemblages. Besides, the premises of functional equivalence of
93 assemblages supports that the same species and functional trait combinations are able to
94 colonize similar habitats (Hubbell, 2005). Then, taxonomic and functional structure
95 should exhibit similar responses along local environmental gradients (Heino *et al.*, 2007).
96 By contrast, if among habitats there is high variation in community composition (e.g.
97 species turnover), the taxonomical component may exhibit distinct response to
98 environment and the functional trait structure will remain constant (Dimitriadis &
99 Koutsoubas, 2011). These premises support communities with weaker correspondence
100 between taxonomic and functional structure (Finn & Poff, 2005). While these patterns for
101 habitat conditions by functional traits is quite well understood for many aquatic systems
102 in temperate zones, few patterns for aquatic insects assemblages in tropical streams are
103 well known (Boulton *et al.*, 2008). Regarding this issues, we aimed to evaluate
104 community composition and functional trait responses to local environmental gradients
105 among streams. Thus, we expected that habitat heterogeneity among each stream have
106 insect communities support different trait composition, regardless the taxonomic local
107 composition (Tomanova & Usseglio-Polatera, 2007). We tested the following hypothesis,
108 (i) patterns of taxonomical community structure and functional trait composition of
109 aquatic insects is influenced by the same environmental factors, (ii) the habitat acts
110 filtering specific composition of aquatic insect traits (i.e. correlations between
111 environmental factors and traits).

112 **Material and Methods**

113 *Study area*

114 This study was performed at eight stream sites in pristine forested areas located inside the
115 protected area of Floresta Nacional do Tapajós (Fig. 1). We collected aquatic insects and

116 measured environmental factors in June 2015 at dry season. The area is covered by dense rain
117 forest and located in the watershed of Tapajós River, located at south-west region of Pará State,
118 Brazil. The forests are characterised by "terra firme", or upper level forest (80%) and a small
119 floodplain area with several "igapó" (flooded forest) areas (20%). The climate of the region,
120 according to the Köppen classification, is tropical monsoon climate "Am" with a short dry season
121 from June to September. (Brasil, Ministério do Meio Ambiente, Instituto Chico Mendes de
122 Conservação da Biodiversidade – ICMBio).

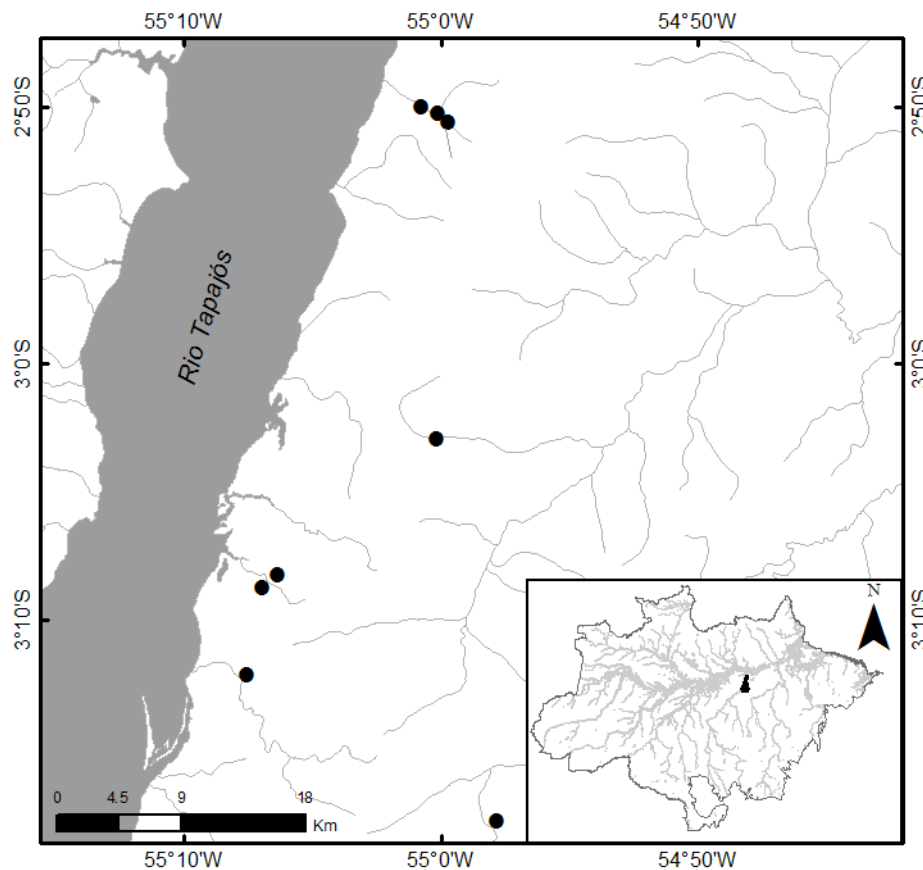


Fig 1. Study area with eight stream sites at Floresta Nacional do Tapajós (Flona Tapajós), Santarém/Belterra, Pará, Brazil.

123 *Biological sampling and processing*

124 Insects were collected using a circular net (diameter=20cm; mesh size = 250 μ m)
125 with 20 subsamples covering 150 m of each stream site. Within the stream site, we
126 performed a screening at each riffle and pool zones with 20 substrates subsamples. In

127 addition, we computed the substrate composition for each subsample considered as
128 percentage of sand (XSAND), leaf bank (XLF), silt, (XSILT), coarse and particulate
129 organic material (XMOP), roots (XRO). All specimens were sorted in the field and
130 preserved in alcohol 85%. We identified the specimens at genus and morphotype level
131 when possible using the available literature considering the limited knowledge on
132 Neotropical aquatic insect fauna (Hamada *et al.*, 2014; Trivinho-Strixino, 2014). The
133 identified material was stored in the Zoological Collection at Universidade Federal do
134 Pará, Belém, Brazil.

135 *Environmental data*

136 For each site, we measured three times the dissolved oxygen, conductivity, pH
137 and temperature. In addition, we measured physical characteristics and features of
138 habitats following Peck *et al.* (2006). For each stream, a 150 m long site was subdivided
139 into ten continuous sections, 15 m long, with 11 cross-sectional transects. Measurements
140 were made at varying levels of resolution across sections and transects, but the response
141 variables were all analysed as stream site summaries (e.g., means, percentages or
142 maxima). The habitat structure matrix included variables grouped in major categories,
143 such as stream channel morphology (e.g., slope, sinuosity, depth, wetted and bankfull
144 width, incision, bank angle), stream habitat features (substrate size, flow types, presence
145 of wood in the channel), riparian structure (e.g., canopy cover, vegetation type).
146 Subsequently, physical habitat metrics were derived from these dataset and calculated
147 according to (Kaufmann *et al.*, 1999).

148 Finally, only a smaller set of habitat variables was selected for further analysis,
149 based on ecological relevance and their past use in studies with aquatic insects in
150 Amazonian streams (e.g. Couceiro *et al.* 2011; Couceiro *et al.* 2012; Datry *et al.* 2016;
151 Juen *et al.* 2016). The selection process consisted of removing variables from the

152 environmental component, the ones that (a) had more than 90% of zero values, (b) were
 153 highly correlated with other variables (Pearson correlations $r > 0.7$) and (c) were
 154 redundant with other variables. We used Principal Component Analysis (PCA) to reduce
 155 data dimensionality to avoid artificial inflation on fitting further multivariate models.
 156 Then, variables within groups with the highest contribution for the components and
 157 without collinearity were selected and our environmental component (**R**) include nine
 158 variables (Table 1; Table S1 in Appendix 1).

159 **Table 1.** Environmental variables considered from streams at Floresta Nacional do Tapajós.

Name	Code	Average	SD	min	max
<i>Physical habitat metric variables</i>					
Mean Substrate Diameter (mm)	LSUB_DMM	19.870	17.990	6.380	60.870
Mean wetted width/ depth (m/m)	XWD_RAT	8.340	2.840	5.380	13.140
Woody Debris (pieces/ 100m)	CIT_100	18.210	7.300	8.000	32.380
<i>Water variables</i>					
Negative log hydrogen ion concentration	pH	4.840	0.270	4.490	5.400
Electrical conductivity ($\mu\text{S}/\text{cm}$)	Cond	17.550	3.200	12.130	20.630
Dissolved oxygen (mg/ L)	OD	7.830	3.850	4.130	16.470
<i>Substrate composition</i>					
% sand + fines (< 2 mm)	XSAND	0.230	0.120	0.140	0.500
% leaf litter	XLF	0.440	0.120	0.300	0.620
% coarse and particulate organic material	XMOP	0.220	0.090	0.110	0.380

160

161 *Functional trait composition*

162 To test our hypothesis of environmental influence on functional trait composition
 163 of aquatic insect communities, we developed a categorical matrix (**Q**) with species-traits
 164 including functional and morphological traits with qualitative information representing
 165 life history, mobility, ecology, morphology and behaviour of aquatic insects as defined
 166 by Poff et al. (2006). We considered traits from all taxa, usually computed in studies to
 167 define some biological attributes previously linked to environmental conditions of aquatic
 168 insect assemblages (Cummins, 1973; Finn & Poff, 2005; Poff *et al.*, 2006; Merritt &
 169 Cummins, 2007; Merritt *et al.*, 2008). Then, we analysed six trait groups for each taxa
 170 identified using the available literature considering the limited knowledge about
 171 functional traits available for Neotropical fauna (Cummins *et al.*, 2005; Tomanova *et al.*,

172 2006; Tomanova & Usseglio-Polatera, 2007; Colzani *et al.*, 2013). We computed trait
173 state within the six functional that are variables recognized independent of immature
174 instar as follows, grouping two trophic traits (i.e. “food” and “guilds”), the respiration
175 mode, two morphological adaptations (body shape and specific adaptations to flow) and
176 mobility mode (See trait matrix in Table S2, S3, S4 – Appendix 1). These traits were
177 chosen to reflect different aspects of stream physical habitat conditions and key physical
178 and chemical characteristics of aquatic ecosystems (e.g. food resources and oxygen
179 availability) (Townsend & Hildrew, 1994a).

180 *Statistical analysis*

181 Prior to constrained ordinations the environmental variables (**R**) were transformed
182 (column values divided by the column's standard deviation) to meet normality criteria.
183 We applied Hellinger transformation to species abundance matrix (**L**: insect composition)
184 in order to best fit beta diversity variation in ordination methods (Legendre & Gallagher,
185 2001). To test our first hypothesis of environmental influence on taxonomical community
186 composition among streams, we performed Distance-based redundancy analysis (db-
187 RDA) based on Bray-Curtis distance. This test has the flexibility to choose an appropriate
188 dissimilarity measure to summarize the relationships between environment and
189 assemblages. In addition, there is not restrictions to the number of variables that can be
190 included in RDA. (Legendre & Anderson, 1999). We tested the null hypothesis of no
191 relationship, using permutation with 9999 runs.

192 To test our main hypothesis of local environmental variables influencing the
193 functional traits composition, we simultaneously analysed the matrices of environmental
194 variables (**R**: physical habitat and water variables), community composition (**L**: 135 taxa)
195 and taxa traits (**Q**: six functional traits). We performed RLQ analysis and fourth-corner
196 approach to summarize the relationships between functional composition of traits and the

197 environmental factors (Dolédec *et al.*, 1996; Dray & Legendre, 2008; Dray *et al.*, 2014).
198 RLQ is an extension of co-inertia analysis that searches simultaneously for linear
199 combinations of variables in **Q** and linear combinations of variables in **R**, maximizing
200 covariance and weighting per abundance in **L** matrix. We tested the null hypothesis that
201 both traits and environment do not influence species distributions (i.e., the links L-Q and
202 R-L are significant) (Dray & Legendre, 2008). Fourth-corner analysis can be used to test
203 the associations between individual traits and environmental variables (Brown *et al.*,
204 2014). We tested the specific environment-trait (relationships between **Q** and **R**) with the
205 Fourth-corner performing bivariate tests to associations between one trait and one
206 environmental variable at a time (Dray *et al.*, 2014). We applied permutation methods
207 using adjusted p values (Holm's method) for multiple comparisons and a significant level
208 $\alpha = 0.05$. We performed statistical analysis with the packages *vegan* (capscale) and *ade4*
209 (*rlq*, *fourthcorner*) in R version 3.3.0 (R Core Team, 2016).

210 **Results**

211 *Overall community structure among streams*

212 We collected 5468 aquatic insects (Coleoptera, Diptera, Ephemeroptera,
213 Hemiptera, Lepidoptera, Megaloptera, Odonata, Plecoptera, Trichoptera) identified in
214 135 taxa and categorized with six groups of functional traits (See Table S2, S3, S4 in
215 Appendix 1). An average of 74 genera and 685 individuals were collected per stream.
216 Diptera and Coleoptera were the richest orders, with 48 and 19 genera, respectively.
217 Ephemeroptera and Diptera were the most abundant orders, with 1564 and 1467
218 individuals, respectively. Among the most common genera, the following twenty
219 represented 67% of the total relative abundance, *Miroculis*, *Leptonema*, *Macrogynoplax*,
220 *Farrodes*, *Anacroneuria*, *Campylocia*, *Gyretes*, *Macronema*, *Parapoynx*, *Riethia*,

221 *Phaenopsectra, Limnophila, Hagenulopsis, Zonophora, Chimarra, Endotribelos,*
222 *Macrostemum, Helicopsyche, Paratanytarsus, and Simulium.*

223 *Relationships among environmental variables and community structure*

224 We found significant responses from community composition to environmental
225 changes provided by the results of Distance-based Redundancy Analysis (Table 2). Then,
226 part of our first hypothesis was corroborated. Our results support the environmental
227 influences on community composition and controlling species distribution. Physical
228 habitat and water variables explained more than 50% of variance in the community
229 structure. The variables of substrate groups did not have relationships to the community
230 matrix. Then, the explanatory variables of physical habitat were woody debris and mean
231 substrate diameter, while for water variables, pH and electrical conductivity were the
232 variables significantly correlated to the first two axis of the Redundancy Analysis (See
233 Fig. 2; Table 2).

234 *Relationship between traits composition and environmental variables*

235 Our results corroborated the hypothesis of environmental influence on traits
236 resulting in patterns of taxa and functional traits (RLQ and Fourth-Corner analysis) at
237 local scales among the streams studied (Table S5, S6, S7 and S8 – Appendix 1, Fig. 3).
238 The first two axes of RLQ analysis explained 92.55% of the total variance
239 (axis1=71.03%; axis2=21.52%). Both RLQ and Fourth-Corner analysis in combination
240 (SRLQ = 0.694; p= 0.036) highlighted the patterns between environmental gradient and
241 trait distribution. Permutations tests on Fourth-Corner models (Pseudo-F and Pearson r
242 for one quantitative variable and one qualitative variable) showed that the overall
243 functional trait structure was significantly correlated with the environmental variables
244 (Model 2: p= 0.021; Models 4: p= 0.027). We found significant bivariate associations
245 between the first two RLQ axes for taxa traits (QAxis 1/ QAxis 2) and the environmental

246 variables (Fourth-Corner Analysis). The mean wetted width/depth and woody debris were
247 negatively correlated with the first axis. For the second axis, only the electrical
248 conductivity was negatively correlated. However, with the same method, we did not find
249 significant bivariate associations between the first two RLQ axis (AxcR1/AxcR2) for
250 direct environmental gradients and functional traits (i.e. specific association
251 trait/environmental variable) (See Table S8 in Appendix 1).

252 *Functional composition and structure*

253 We found three groups of habitat structure, the first with high values for electrical
254 conductivity, the second with high values for width, depth and wood debris, the third with
255 high values for substrate diameter, pH and low dissolved oxygen. Our trait-based
256 approach explained a significant proportion of the community response to these habitat
257 structures. We found that the aquatic insect taxa could be approximately grouped also
258 into three trait-based groups according to habitat gradients. The first group of streams
259 supported specific groups of taxa with distinct trait habitats such as predators (e.g.
260 *Polyplectropus*, *Cerrotina*, *Aeschnosoma* and most Diptera predators) and collector-
261 filterers (e.g. *Chimarra*, *Leptonema*, *Macrostemum* and *Simulium*). The fauna associated
262 to habitat in the second group of streams were collector-gatherers (e.g., *Americabaetis*,
263 *Cryptonympha* and *Waltzoyphius*), shredders (*Anacaena*, *Farrodes*, *Hydrodessus* and
264 *Miroculis*) and scrapers (e.g. *Askola*, *Hydrosmilodon* and *Pheneps*), with in-stream
265 habitat conditions characterized by shallow and well oxygenated waters with presence of
266 coarse detritus. While, some of the piercer's taxa were low represented in these
267 environments (e.g. *Paratrephes*, *Tenagobia*). Most of Diptera (Chironomidae,
268 Psychodidae) taxa, especially *Ablasbesmyia*, were associated to streams in the third group
269 with high values of coarse substrate diameter (e.g. sand and gravel), with high pH, and
270 low dissolved oxygen concentration.

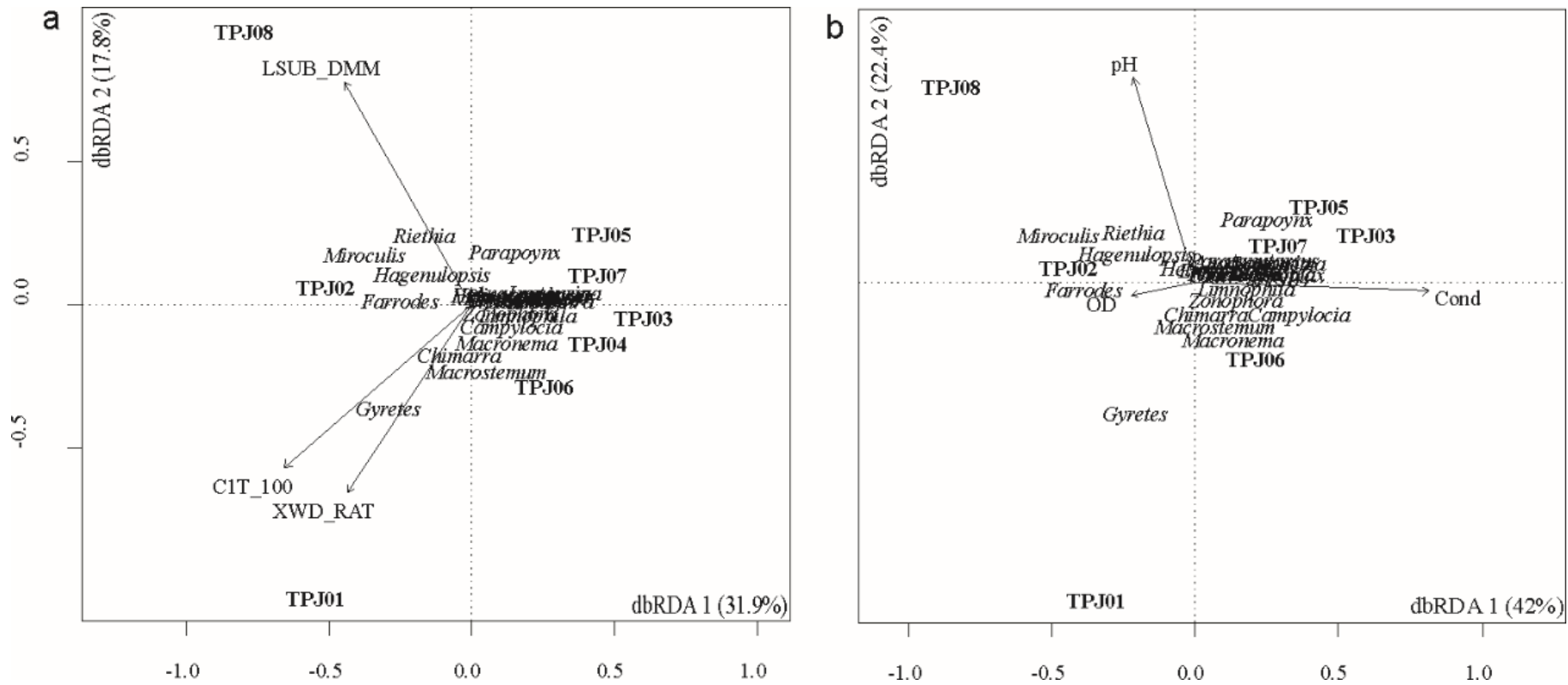


Fig 2. Results for Distance-based RDA ordination based on Bray–Curtis resemblance matrix: (a); physical habitat (b) water variables.

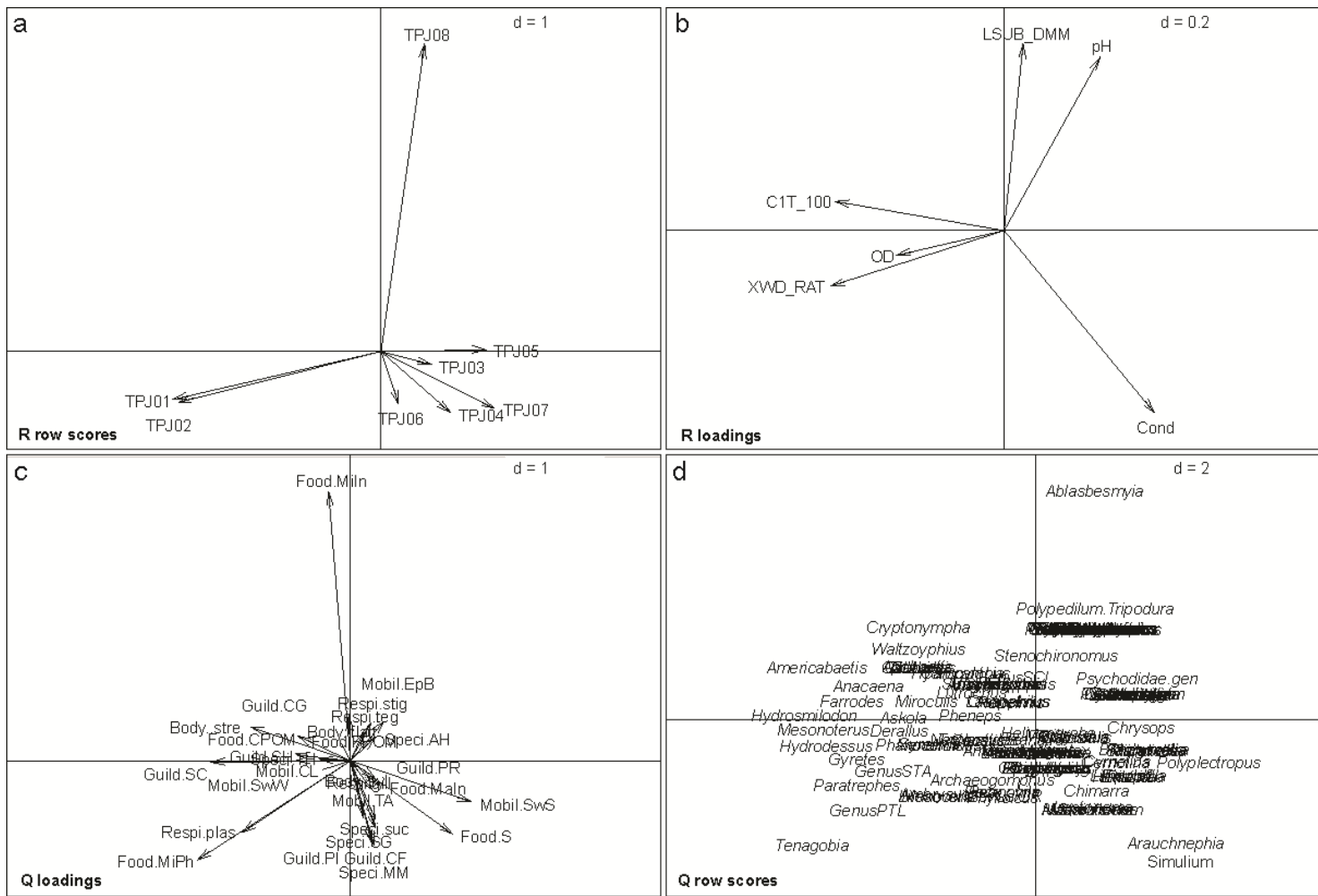


Fig 3. RLQ results: (a) covariation of sites, (b) environmental variables, (c) species traits (d) community composition.

273

274 **Table 2.** Distance-based Redundancy Analysis (db-RDA) results using Bray-Curtis distance.

Variables	RDA 1	RDA 2	Total explanation	F	p
<i>Physical Habitat</i>			0.564	1.932	0.037
LSUB_DMM	-0.485	0.853		2.608	0.044
C1T_100	-0.716	-0.570		2.468	0.042
XWD_RAT	0.476	-0.711		0.721	0.322
Proportion explained	0.319	0.178			
<i>Water Variables</i>			0.711	3.293	0.008
pH	-0.263	0.874		2.938	0.035
Cond	0.996	-0.035		5.539	0.004
OD	-0.275	-0.053		1.399	0.261
Proportion explained	0.420	0.224			
<i>Substrate Composition</i>			0.391	0.855	0.623
XSAND	0.701	-0.370			
XLF	0.167	0.895			
XMOP	-0.443	-0.815			
Proportion explained	0.234	0.108			

275

276 **Discussion**

277 Variation in community structure and functional trait composition for aquatic
278 insects in small riverine landscapes can be defined by the habitat heterogeneity within
279 and among streams. This patterns have been corroborated by the hypothesis that
280 community composition and species traits exhibit direct relationship with local
281 environmental conditions (Townsend & Hildrew, 1994b; Malmqvist, 2002). Local habitat
282 attributes, such as stream channel morphology, riparian structure, substrate size and
283 presence of wood in the channel are known to have great influence on aquatic insect
284 assemblages (Sponseller *et al.*, 2001; Heino *et al.*, 2005; Juen *et al.*, 2016). In streams,
285 the changes in variables of physical habitat have been accounted to be more related to
286 local functional composition than to pure assemblage patterns, considering that the
287 environment select attributes regardless its taxonomical variation (Poff & Ward, 1990;
288 Finn & Poff, 2005).

289 Regarding the patterns in our results, our hypothesis of patterns of taxonomical
290 community structure and functional trait composition of aquatic insects are influenced by
291 the same environmental factors was partially corroborated. Redundancy Analysis

292 suggested that variation in community composition among streams was in function pH,
293 electrical conductivity, substrate size, width and depth of streams. This ordination is
294 robust to estimate differences among communities constrained by environmental
295 predictors, and is based on dissimilarities of relative abundance among sites. Conversely,
296 RLQ analysis for trait composition, also weighed by taxa abundance, showed similar
297 patterns for functional response to pH, electrical conductivity, woody debris, width and
298 depth of streams. Both components were structured by similar environmental gradients,
299 and while we found high variance in community composition, the functional have lower
300 total variance. It supports that among streams the environmental heterogeneity may be
301 structuring spatial turnover on community structure. Then, these patterns is supported for
302 habitat-heterogeneity that is strongly related to species diversity and spatial heterogeneity
303 resulting in high variation in taxonomic composition (González-Megías *et al.*, 2011). Our
304 hypotheses were partially supported since we found environmental influences on
305 community structure and trait composition of aquatic insects among streams. For
306 Amazonian small streams, local heterogeneity in habitat contributes with beta diversity,
307 which was in this study structured by environmental gradients, mainly in variation of
308 mean substrate diameter, woody debris, electrical conductivity and pH (Datry *et al.*,
309 2016). Moreover, trait variables have been shown to be effective to describe community
310 patterns, because they often summarize biological interactions (e.g. predation,
311 competition) at micro and mesohabitat scales (Jonsson *et al.*, 2001). Community structure
312 pattern can also be evaluated at drainage scale, where species are conditioned by
313 environmental filters acting on traits related to dispersal and life history (e.g. locomotion
314 modes, resistance forms and dispersal) (Heino, 2005). Then, considering RLQ
315 ordinations, the trait composition in the community, showed distinct patterns structured
316 by the variation of mean wetted width/depth and woody debris and electrical

317 conductivity. Our second hypothesis was partially corroborated, because we found none
318 habitat component uniquely acting to structure specific insect traits, but contributing
319 mainly for the whole community.

320 Few patterns on trait-community approach can be accounted for empirical studies
321 at non-impacted streams in tropical forests (Tomanova *et al.*, 2006; Tomanova &
322 Usseglio-Polatera, 2007). We recognize that our comparisons are mainly explained by
323 observations in the proportions of trait modalities biased by species in temperate zones.
324 Then, this issue is about the assignment of a taxon to functional categories that can lead
325 to imprecise characterization of biological/ecological trait composition. Because many
326 traits considered depended on the availability of food resource, which is linked to
327 variation in conditions between streams, seasons and habitats heterogeneity (Charvet *et*
328 *al.*, 2000). Despite this bias, our trait-assemblage analysis considered local environmental
329 attributes for Amazonian streams (i.e. high species richness and substrate composition)
330 in order to find patterns in aquatic insect assemblages from tropical streams (Cummins *et*
331 *al.*, 2005; Tomanova & Usseglio-Polatera, 2007).

332 The proportion of functional feeding habits is considered a good indicator and
333 from our results grouped most of functional traits, revealing patterns quite known to
334 describe community structure and stream habitats (Cummins, 1988; Cummins *et al.*,
335 2005). They highlighted many trait states occurring together as tightly-linked syndromes
336 that have apparently strong taxonomic affinities (Finn & Poff, 2005; Poff *et al.*, 2006).
337 Shredders, collector-gatherers and predators comprised convergent assemblages, which
338 were mostly associated to other traits, such as food resource, body form, specific
339 adaptation to flow and mobility and attachment to substratum. Considering the
340 environmental effects, we found convergent trait assemblages (shredders and collector-
341 gatherers), presented by RLQ results (Q loadings and row score), in streams with high

342 dissolved oxygen. These assemblages often occur associated to shallow high-flowing
343 habitats, where individuals have to expend more energy to resist the flow constraints
344 (Tomanova *et al.*, 2006). In contrast, epi- and endobenthic burrowers (Most of predators
345 and Diptera taxa) were found mainly in deep slowly flowing stream reaches, where these
346 habitat commonly have moderate mineral substratum (sand and gravels) easier to
347 penetrate (Moya *et al.*, 2007).

348 Environmental gradients and substrate heterogeneity have been supporting
349 hypotheses for streams with higher species richness and abundance because they allow
350 changes in the functional composition and distribution of communities (Townsend &
351 Hildrew, 1994a; Couceiro *et al.*, 2011). Moreover, the abundance of aquatic insects
352 streams have been considered dependent on food availability and heterogeneous stream
353 habitats (Poff *et al.*, 2006). According with our expectation, taxonomic richness among
354 streams was concordant to functional structure mainly influenced by substrate
355 heterogeneity. From this results it is possible to disentangling the community structure
356 according to both taxonomical attributes and functional composition (Jonsson &
357 Malmqvist, 2003).

358 The functional community composition and FFG structure revealed some patterns
359 in the taxa studied and could be summarized according to their patterns in community
360 structure, such as species richness and abundance (Merritt *et al.*, 2008). First, shredders
361 (e.g. *Miroculis*) was the most abundant feeding group found and it has been indicating
362 autotrophic/heterotrophic aquatic systems, where these organisms are strongly linked to
363 the variation in the riparian zone (Cummins *et al.*, 2005; Poff *et al.*, 2006; Poisot *et al.*,
364 2013). Our results corroborate this fact, since we found among streams high percentage
365 of woody debris and vegetal substrates ranging from coarse particulate organic matter
366 (CPOM) to fine particulate organic matter (FPOM). The second most abundant group

367 was gathering-collectors (e.g. *Campylocia*, *Riethia*, *Hagenulopsis*, *Endotribelos* and
368 *Helicopsyche*). In natural communities, these taxa indicate environments with
369 heterogeneous substrates and channel stability with habitats covered by cobbles, boulders,
370 large woody debris and rooted vascular plants (Cummins *et al.*, 2005). Thus, we found
371 relationships among these collector-gathering taxa and variation in woody debris and
372 substrate size. Rooted vascular were frequent in most stream at riparian zone contributing
373 to the canopy cover and channel stability (e.g. *Euterpe oleracea* M. – Arecaceae).

374 Although small streams in the same regional context often are physical and
375 chemically similar, they also can differ markedly accordingly to habitat heterogeneity
376 (Allan & Castillo, 2007; Lecraw & Mackereth, 2010). Our sampling sites were naturally
377 acid streams with discrete gradients for other limnological variables. This conditions in
378 an evidence that when pH is lower, it is accompanied by a number of other chemical
379 changes, and the organism response is due to various physiological strategies behavioural
380 (Lewis, 2008; Baudier *et al.*, 2015). In summary, we found that a set of specific local
381 conditions (physical habitat and water variables) were the constraints for species diversity
382 and abundance. Additionally, similar set of conditions had strong influence on functional
383 composition. This is due to ecosystem processes may be relatively unaffected due to
384 species substitutions with similar traits (Dangles *et al.*, 2004). Our patterns in community
385 composition and functional traits can be related to the local conditions in-streams often
386 found in Amazonian streams, which were typical black acidic waters with low values of
387 electrical conductivity and high variance in substratum characteristics (Junk *et al.*, 2010).
388 Moreover, for most tropical stream communities these in-streams conditions are
389 considered key factors for explaining the variance in community structure and ecosystem
390 function at different scales (Jacobsen *et al.*, 2008b).

391

392 **Conclusion**

393 As expected, our trait-based approach showed that functional traits was strictly
394 dependent on local conditions, in this way the habitat conditions affected functional
395 composition. Habitat gradients mainly showed similar effects in shaping both trait and
396 taxonomical patterns in aquatic insect communities. Despite the low number of analysed
397 streams, our analyses provided important information for the understanding of
398 simultaneous variation in functional trait composition and the community composition
399 among Amazonian streams. Our study corroborated the habitat templet hypothesis for the
400 main patterns found for trait composition in the aquatic insect communities among the
401 Amazonian streams. Then, we were able to highlight that among streams the width, depth,
402 wood debris, acidity and electrical conductivity were the most important predictors of
403 trait distribution at the stream scale. However, our approach failed to disentangle
404 significant direct associations among each trait and environmental variable. These results
405 may be due low habitat spatial scale of both trait variance and environmental predictors.
406 Thus, we recommend future research addressing these issues, also applying traits as
407 quantitative measures to account the unique features of Neotropical aquatic diversity.

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- 588

CAPÍTULO IV

Regional context structuring aquatic insect communities in Amazonian streams:
responses for species replacement, richness difference and functional composition

Gilberto Nicacio, Neusa Hamada & Leandro Juen

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1 **Regional context structuring aquatic insect communities in Amazonian streams:**
2 **responses for species replacement, richness difference and functional composition**

3

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15

16 **Abstract**

17 Habitat structure and geographical distances have been considered the main determinants
18 of species diversity and distribution in natural communities. The first are strong related
19 with environmental gradients and niche mechanisms, while geographical distances and
20 dispersal limitations have been the support for the neutral models for community
21 structure. We tested variation in community composition of Ephemeroptera, Trichoptera,
22 and Plecoptera between distinct ecological gradients at Amazonian interfluves. We
23 computed beta diversity by dissimilarities from Sorensen index and evaluated how
24 regional and habitat factors interact to structure species composition in stream network
25 between Amazonian interfluves. We performed multiple regression on dissimilarity
26 matrices - MRM to test spatial and environmental influences on assemblages. We also
27 analysed differences in functional composition at regional scales using non-constrained
28 ordination analyses. We found that dissimilarity in species composition between sites was
29 most contributed by species replacement and related to both geographical and
30 environmental distance. Our results provide first empirical evidences for trait approach
31 distribution and functional similarity of aquatic insect assemblages among regions in
32 Amazonian basin. In summary, the species replacement generated community
33 dissimilarities and were associated to geographical distances, environmental distances
34 and non-dispersal limitation among streams at Amazonian interfluves.

35

36 **Key-words:** EPT, beta diversity, spatial factors, environmental distance

37

38 **Introduction**

39

40 Habitat structure and spatial distribution have been considered the main
41 determinants of species diversity and distribution in natural communities (Pedruski and
42 Arnott 2011). The first are strong related with environmental gradients and have
43 corroborated models of niche mechanisms, which rules the assemblages by the effects of
44 habitat conditions, functional organization and species interactions (Lake 2000; Dangles
45 and Malmqvist 2004). On the other hand, geographical distances and dispersal limitations
46 have been the support for the neutral models for community structure (Astorga et al.
47 2012). These models do not consider niche influences on communities and highlighted
48 that all species assemblages consist of ecologically equivalent individuals distributed
49 across a fixed number of species derived from the regional species pool (Hubbell 2001;
50 Willig et al. 2003). However, in spite of this duality, both processes have been elucidated
51 relative contribution to several mechanisms proposed to explain community composition
52 among and within local assemblages with regarding the scale (geographical distances and
53 specific dispersal limitations) of analysis proposed (Thompson and Townsend 2006;
54 Adler et al. 2007; Rosindell et al. 2011).

55 Together, these theories have vastly increased many models applied to describe
56 patterns about species distributions and community structure, which have been supported
57 their main assumptions from studies applying traditional niche-based approaches
58 regardless neutrality effects (Leibold et al. 2004; Pavoine and Bonsall 2011). Among
59 them, predictions about neutral model focused mainly the effects of stochastic dispersal
60 events and competition among ecologically equivalent species (Tilman 2004; Cadotte and
61 Fukami 2005). They found that neutral processes is more effective within groups of
62 species with similar ecological traits, mainly at local neutral communities structured by

63 low variation in functional composition, whereas niche dynamics acts between groups to
64 influence community dissimilarities (Hubbell 2005; Pavoine 2012). Moreover, at regional
65 scale, communities are strong niche structured, where species are similar in fitness, the
66 dispersal limitation has no effect on competitive displacements, leading assemblages to
67 exhibit remarkable species replacement, which contrast patterns often found for many
68 neutral models (Resh et al. 1988; Cadotte 2006). Otherwise, for many local assemblages,
69 when there is coexistence under strong niche structure, the same ecological context lead
70 communities to different traits composition, environmental gradients and particular
71 richness differences, which often invalidate neutrality (Jonsson and Malmqvist 2003;
72 Kneitel and Chase 2004; Purves and Turnbull 2010).

73 Considering the above patterns, aquatic ecologists have found that variation in
74 community structure of aquatic assemblages across regional extent seem to be a function
75 of changes in many environmental predictors, supporting strong niche influences (Heino
76 and Mykrä 2008; McCauley et al. 2008; Engen et al. 2011; Arrieira et al. 2015). The
77 physical environment represent the main constrain leading for shifts in species
78 distribution and community dissimilarity (Dunbar et al. 2010). However, the components
79 of beta diversity in aquatic insect have been poorly disentangled, the majority of the
80 studies focus on the relative role of large scale to support dispersal limitation and niche
81 dynamics (e.g. Costa and Melo 2008; Heino et al. 2013). Among tropical streams,
82 empirical studies with natural communities between large geographical extents have
83 rarely been explicitly disentangled environmental and spatial causes of variation in
84 community composition of aquatic invertebrates (Ligeiro et al. 2010; Siqueira et al.
85 2015).

86 In view of this, some caveats can be highlighted for tropical aquatic ecosystems
87 such as which patterns contribute most to variation in species composition among streams

88 (i.e. species replacement and richness difference), considering large geographical
89 distance and regional habitat specificity. Hence, we aim to investigate at which scales,
90 the components of beta diversity are affected by geographical distance (similarly to the
91 distance decay of similarity) using assemblage dissimilarity (partitioning beta diversity
92 into its spatial turnover and nestedness) to explain community structure (Nekola and
93 White 1999; Baselga 2010). In addition, considering the local effects of habitat conditions
94 on niche dynamics, we want to answer whether the taxonomic component and functional
95 composition in aquatic insect assemblages will be different, since Amazonian regional
96 drainages often has unique conditions of habitats. Large rivers in Amazon basin are
97 recognized to isolate important land areas fact relevant for biodiversity, and are known to
98 create biogeographic patterns within and among the main interfluves (Juen and De Marco
99 2012).

100 To explore environmental gradients in high diverse streams, such as in Amazonia,
101 we assessed composition dissimilarity (beta diversity) into its spatial turnover and
102 nestedness. Then, if richness difference (nestedness) among streams is the main response
103 to habitat heterogeneity, we expect that species loss result in reductions in ecosystem
104 function. In contrast, species replacement (turnover) among highly diverse assemblages
105 should buffer communities by greater levels of complementarity and redundancy, and
106 therefore less affected by the loss of single species (Hubbell 2005). Hence, to address
107 these premises, we aim to analyse two aquatic insect communities from forested streams
108 in two distinct environmental contexts and accounted the contributions of regional
109 specificity to species replacement and richness difference along spatial and environmental
110 gradients.

111 Because of different spatial distribution of communities within and among
112 regions, we established two main hypotheses of community dissimilarity among streams.

113 First, the variation in community composition will be in function of geographical
114 distances. Second, the environmental gradients for local (stream) and regional (basins)
115 specificity generates patterns of richness difference among regions (Nekola and White
116 1999; Soininen et al. 2007). Then, we expect that local habitat conditions strongly affect
117 richness differences among regions and evidence regional niche influence. In addition,
118 we considered that isolated ecoregions (e.g. Amazonian interfluves) have unique
119 environmental conditions and this should lead traits in communities to match different
120 aspects of ecosystem functioning. Hence, we hypothesized that functional composition
121 regarding community dissimilarity should be specific for each region. We believe that
122 Ephemeroptera, Trichoptera and Plecoptera communities in these streams should be
123 effective for testing these hypotheses, as they vary significantly between environmental
124 gradients in both taxonomic structure and functional composition (Bispo et al. 2006; Feld
125 and Hering 2007). Therefore, we want to test the existence of regional patterns of
126 ecological dissimilarities and functional equivalence among streams of aquatic insect
127 communities represented by Ephemeroptera, Trichoptera and Plecoptera assemblages.
128 For many tropical streams, these insect groups are high diverse and include the majority
129 of the functional feeding group taxa in these ecosystems.

130 **Material and Methods**

131 *Study area*

132 The study area includes sixteen stream sites located in two pristine forested
133 regions, eight for each region (Fig. 1). They are located in the Floresta Nacional do
134 Tapajós (Flona Tapajós), Santarém/Belterra and Floresta Nacional de Carajás (Flona
135 Carajás), Parauapebas/Canaã dos Carajás, both in Pará state, Brazil. We collected
136 biological data and measured environmental factors in June 2015 and September/October

137 2015. The streams are within recognized distinct ecoregions with remarkable landscape
138 and geological features.

139 The Flona Tapajós (located at the Tapajós river basin) is situated at the lowland
140 interfluvial Tapajós-Xingu, and this ecoregion lies in central-eastern Brazil, south of the
141 Amazon River. In contrast, the Flona Carajás (located at Tocantins river basin) is at
142 eastern Amazonian Forest, where the landscape has high elevation ranges from sea level
143 next to Amazon River, at 600 m.a.s.l. in the uplands of Serra dos Carajás. The forest of
144 both regions are characterised by "terra firme", or upper level forest and they are covered
145 by dense rain forest (Sioli 1984). The climate of both regions, according to the Köppen
146 criteria, is tropical monsoon climate "Am" with a dry season from June to October and a
147 wet season from November to May (Alvares et al. 2013).

148 *Biological sampling and sample processing*

149 Ephemeroptera, Plecoptera and Trichoptera (EPT) were collected using a circular
150 net (diameter = 18 cm, mesh size = 250 μ m) covering 150 m of each stream site. We
151 performed screening at each riffle and pool zones with 20 substrate subsamples at each
152 stream as replicate of sites. Specimens were sorted in the field and preserved in 85%
153 alcohol. We identified the specimens at genus level when possible using available
154 literature considering the limited knowledge available for Neotropical fauna (Domínguez
155 et al. 2006; Hamada et al. 2014). The specimens were stored in the Zoological Collection
156 at Universidade Federal do Pará, Belém, Brazil.

157 *Environmental data*

158 We considered three stream physical characteristics feature of the habitats (mean
159 wetted width/ depth; mean substrate diameter/Elevation) measured following Peck et al.
160 (2006). For each stream site, we sampled water variables, such as dissolved oxygen,

161 conductivity, pH and temperature. For each stream, a stretch of 150 m long was
162 subdivided into 10 continuous sections of 15 m long, with 11 cross-sectional transects.
163 Measurements were made at varying levels of resolution across sections and transects,
164 but the response variables were all analysed as stream site summaries (e.g. means,
165 percentages or maxima). Habitat structure variables included measures of stream channel
166 morphology (e.g. slope, sinuosity, depth, wetted and bankfull width, incision, bank
167 angle), stream habitat features (substrate size, flow types, presence of wood in the
168 channel). Subsequently, physical habitat metrics were derived from the dataset, according
169 to Kaufmann et al. (1999). Finally, six habitat variables were selected (Table 1, Table S1
170 – Appendix 1), based on ecological relevance and their past use in studies on community
171 diversity of aquatic insects in Amazonian streams (Couceiro et al. 2011; Couceiro et al.
172 2012; Datry et al. 2016; Juen et al. 2016; Martins et al. 2017).

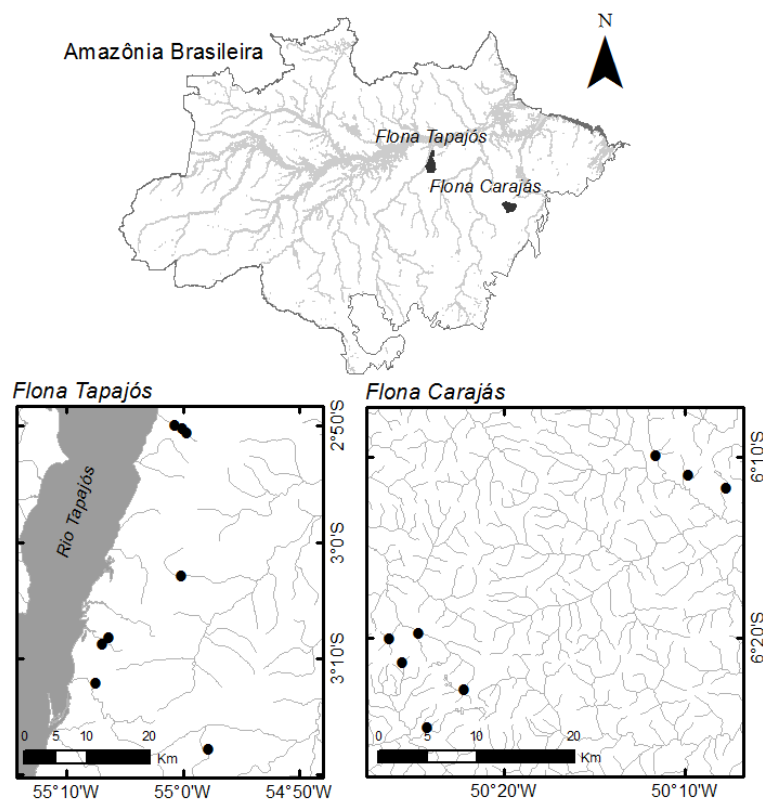


Fig 1. Study area: a) Floresta Nacional do Tapajós (Flona Tapajós), Santarém/Belterra; Floresta Nacional de Carajás (Flona Tapajós), Parauapebas/Canaã dos Carajás, Pará, Brazil.

173 **Table 1.** Environmental variables considered as predictors for variation in community composition of
 174 aquatic insects from streams at Floresta Nacional do Tapajós and Floresta Nacional de Carajás, Pará, Brazil.

Name	Code	Average	SD	min	max
<i>Physical habitat metric variables</i>					
Mean substrate diameter (mm)	xsub	44.248	11.962	20.000	61.905
Mean wetted width / depth (m/m)	xwd	9.501	2.862	5.381	14.906
<i>Water variables</i>					
Negative log hydrogen ion concentration	pH	5.897	1.190	4.493	8.120
Electrical conductivity (µS/cm)	Cond	22.408	18.063	3.000	78.000
Temperature (°C)	T	23.977	1.636	20.900	25.833
Dissolved oxygen (mg/L)	OD	6.854	2.861	4.133	16.467

175

176 *Functional trait composition for Ephemeroptera, Plecoptera and Trichoptera (EPT)*

177 To test our hypothesis that functional composition regarding community dissimilarity
 178 should be specific for each region, we developed a matrix of genus-traits (**T**: EPT
 179 functional composition) adapted from available literature (Cummins et al. 2005;
 180 Tomanova et al. 2006; Tomanova and Usseglio-Polatera 2007; Colzani et al. 2013). The
 181 traits considered here were characteristics from all taxa, usually used in previous studies
 182 to define some biological attributes of the aquatic insect assemblages (Poff et al. 2006;
 183 Merritt et al. 2008). Then, we computed six trait groups expressed as twenty syndromes
 184 for each taxa identified using data available in current literature considering the limited
 185 knowledge for Neotropical fauna (Tomanova et al. 2006; Tomanova and Usseglio-
 186 Polatera 2007; Colzani et al. 2013). We grouped trophic traits (i.e. “food” and “guilds”),
 187 respiration mode, morphological adaptations (body shape and specific adaptations) and
 188 mobility (See trait matrix in Tables S3, S4, S5 – Appendix 1).

189 *Data analysis*

190 To test our main hypothesis, we expressed variation in species composition as
 191 beta diversity and its components and functional composition as a complementary metric
 192 to untangling the different aspects of streams between the two regions. To define spatial
 193 influences on communities, we used pairwise-distances between sites from geographical
 194 coordinates measured as Euclidean (straight-lines) distances. We constructed

195 dissimilarity matrices with methods based on presence/absence and approaches proposed
196 according to Baselga (2010) and calculated the Sorensen-based multiple-site dissimilarity
197 (β_{sor}), the Simpson-based multiple-site dissimilarity (β_{sim}), the Nestedness-based
198 multiple-site dissimilarity (β_{nes}). For all streams and among region, we measured
199 distance matrices for overall variation in community composition (beta diversity - β_{sor}),
200 species replacement (turnover - β_{sim}) and richness difference (nestedness - β_{nes}). To test
201 our hypothesis of geographical distance effects on biotic dissimilarities in communities,
202 we tested the existence of regional patterns of beta diversity, as could be expected by the
203 biogeographic history of Amazonian interfluves, we considered our community dataset
204 into two groups (Carajás and Tapajós region). To test our first hypotheses, we performed
205 Multiple regression on dissimilarity matrices (Lichstein 2007), using Sørensen index, and
206 tested its relationship with the spatial and environmental component (measured as
207 Euclidean matrix).

208 To summarize only environmental patterns, we performed Principal Components
209 Analysis (PCA) on environmental variables (**E**) calculated on the correlation matrix. Prior
210 to analyses, the variables were transformed (centered and divided by their standard
211 deviation) to meet normality criteria. Previously to elaborate the dissimilarity analysis
212 matrices (**Y**: EPT composition), we applied presence/absence transformation. In addition,
213 non-metric multidimensional scaling (NMDS) was performed to plot the overall patterns
214 in community composition. To investigate the patterns in functional composition among
215 regions, we performed the Hill and Smith ordination method on the qualitative genus-
216 traits matrix weighed by scores of genera abundance matrix (scores from Correspondence
217 Analysis) in order to obtain the trait scores that represent spatial functional variation
218 among streams and regions. To test our third hypothesis, we performed Procrustes
219 analysis to estimate the degree of association between the two ordination-based matrices

220 of traits from the different regions. This analysis is appropriate to match the trait
221 composition weighted by distinct abundances of each stream (Peres-Neto & Jackson
222 2001). Procrustes analysis aims to find match between ordinations generated with the
223 matrix association resulted from specific changes in species composition and local
224 species abundance. Procrustes analysis produced an m^2 -statistic that was transformed into
225 an r-statistic ($r = \text{square root of } (1-m^2)$). The r-statistic allow support the match between
226 the two ordinations (Peres-Neto & Jackson 2001, Lisboa et al. 2014).

227 **Results**

228 The Principal Component Analysis (PCA) showed that streams within both
229 regions (Flona Carajás and Tapajós) form very distinct environmental patterns and
230 highlighted site-specific spatial clusters. A clear trend for formation of clusters habitats,
231 which are differentiated by distinct variables, is displayed in this ordination (Fig. 2).

232 *Overall Community composition*

233 We recorded 6,704 immatures of Ephemeroptera, Trichoptera and Plecoptera,
234 3,717 specimens were collected at Flona Carajás and 2,987 at Flona Tapajós (Tables S2,
235 S3, S4 – Appendix 1). We identified 54 taxa representing 32 Ephemeroptera, 21
236 Trichoptera and 2 Plecoptera genera. The overall richness difference between regions was
237 an average of 19.87 genera at Flona Carajás and in 24.65 genera per stream.

238 Each study region had its own unique genus of EPT and a richness difference
239 between regions of 17 genera (Flona Carajás) and 14 genera (Flona Tapajós). Exclusively
240 for the first region, we reported the following genera *Atopsyche*, *Brasilocaenis*, *Caenis*,
241 *Callibaetoides*, *Hydrosmilodon*, *Leentvaaria*, *Leptohyphes*, *Leptohyphodes*, *Notalina*,
242 *Notidobiella*, *Paracloeodes*, *Paramaka*, *Polycentropus*, *Terpides*, *Traverhyphes*,
243 *Tricorythodes*, and *Ulmeritoides*. While for Flona Tapajós the genera with exclusive

244 occurrence were *Amazonatolica*, *Americabaetis*, *Apobaetis*, *Aturbina*, *Austrotinodes*,
 245 *Campsurus*, *Cloeodes*, *Cryptonympha*, *Cyrnellus*, Genus A, *Hydrosmilodon*,
 246 *Simothraulopsis*, *Tricorythopsis* and *Waltzoyphius* (Table S2 – Appendix 1).

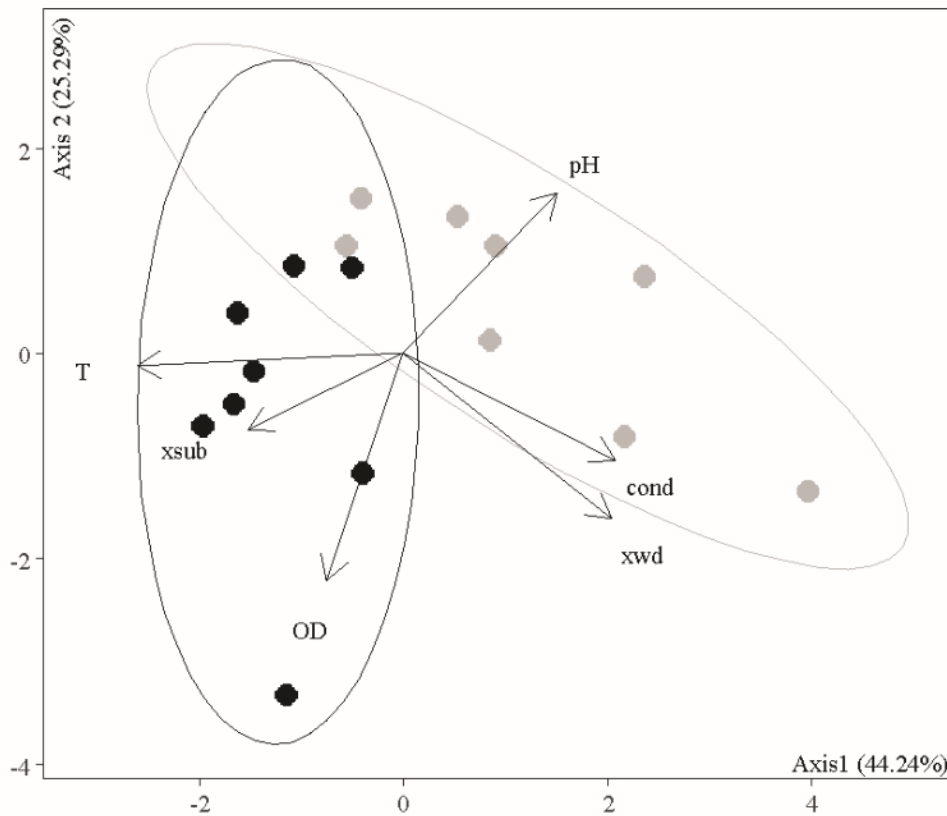


Fig. 2 Results for Principal Component Analysis (PCA): Environmental variables. Black dots represents Floresta Nacional do Tapajós and grey dots represents Floresta Nacional de Carajás. Variable codes: Mean substrate diameter (xsub), mean wetted width/depth (xwd), negative log hydrogen ion concentration (pH), electrical conductivity (Cond); temperature (T), dissolved oxygen (OD) .

247

248 *Components of beta diversity between regions and among streams*

249 Overall, assessing multiple-site dissimilarities among streams, the whole dataset
 250 showed high variation in community composition (β SOR= 0.751), and disentangling
 251 contributions we found most effect of species replacement and (β SIM= 0.677) and low
 252 influence of richness difference (β NES= 0.073). The estimated overall beta diversity was
 253 considerable higher for Carajás region (β SOR= 0.594) than for Tapajós (β SOR= 0.502)
 254 indicating that beta diversity contributes quite evenly for community dissimilarity in both

255 areas. When we partitioned this overall beta diversity into its components, species
 256 replacement and richness differences, the turnover still was the processes responsible for
 257 most of the beta diversity in streams at Carajás ($\beta_{SIM}= 0.506$, $\beta_{NES}= 0.087$) and Tapajós
 258 ($\beta_{SIM}= 0.420$, $\beta_{NES}= 0.083$). We found remarkable significant correlation between the
 259 regional scale and the overall estimated community beta diversity (Table 2). Considering
 260 only the dissimilarities among streams within each region, we yielded weak responses of
 261 beta diversity components to geographic distances using pairwise measures (Euclidean
 262 distance among streams). However, considering species replacement (β_{sim}) and richness
 263 difference (β_{nes}) separately, we found only significant correlation for turnover and
 264 geographic distance among streams at Flona Carajás (Table 2).

265 **Table 2.** Results for Multiple regression on distance matrices. Relationships between geographical
 266 distances and community dissimilarity (β_{sor} , β_{sim} and β_{nes}) for aquatic insect assemblages from streams
 267 at Floresta Nacional do Tapajós and Floresta Nacional de Carajás, Pará, Brazil.

	β_{sor}	β_{sim}	β_{nes}
Flona Tapajós	0.082	0.053	0.201
Flona Carajás	0.294	0.345*	0.004

268 Levels of statistical significance (under 999 random permutations): *P < 0.05.

269

270 *Community similarity X Similarity between functional composition*

271 The non-metric multidimensional scaling (NMDS), based on Sørensen index for
 272 presence/absence matrix of Ephemeroptera, Trichoptera and Plecoptera composition,
 273 highlighted high variation in community composition that was separated at distinct spatial
 274 groups restricted by their regional distribution (Fig. 3). Considering the species
 275 distribution within each region, we found higher dissimilarity in community composition
 276 among the streams at Flona Carajás, while among streams at Flona Tapajós the
 277 dissimilarities among assemblages were lower. However, the overall variation in
 278 functional composition were very similar among the traits composition and clear
 279 congruence was found in the functional matrices between the two regions (Fig. 4).

280 The Procrustes analysis, based on scores of Hill and Smith method (functional
281 traits weighted by community abundance), resulted (m_{12} statistic= 0.009; $r = 0.949$; $p <$
282 0.001) in congruence of the trait-genus matrix with similar patterns of functional
283 composition between streams at Flona Carajás and Tapajós. The congruence was not
284 associated with geographic or environmental distances and hence related purely to trait
285 weighed by abundances and the biotic interactions among functional groups. To visualize
286 the functional composition patterns and the species distribution, we computed plots of
287 ordination scores (Fig. 4).

288 The results of multiple regression on dissimilarity matrices (MRM) retained
289 individual relationships among the environmental variables and the Sørensen
290 dissimilarity matrix. The overall species replacement among streams was individually
291 correlated with elevation, temperature and pH. They were significant correlated with the
292 model including the geographical distance as explanatory variables (Table 3).

293 **Discussion**

294 Our main results showed two contrasting patterns of taxonomic community
295 composition and functional organization among streams, supporting neutral and niche
296 dynamics for aquatic ecosystems. The main responses were found for environmental and
297 geographic distances with effects for community dissimilarity and functional
298 composition. First, variation in community composition were caused by species
299 replacement and this pattern was the same observed in communities at the different
300 environmental contexts within and among regions as expressed by the regression methods
301 applied. In contrast, among the streams, the different taxonomic composition showed low
302 variation within the regions but we found remarkable spatial pattern of dissimilarities
303 among regional assemblages. Unexpectedly, a clear pattern in congruence of functional
304 composition among streams between the two regions was also found. Thus, this result

305 suggests that although both regions are affected by geographical distance and independent
 306 taxonomic composition they respond to specific regional changes in environmental
 307 conditions.

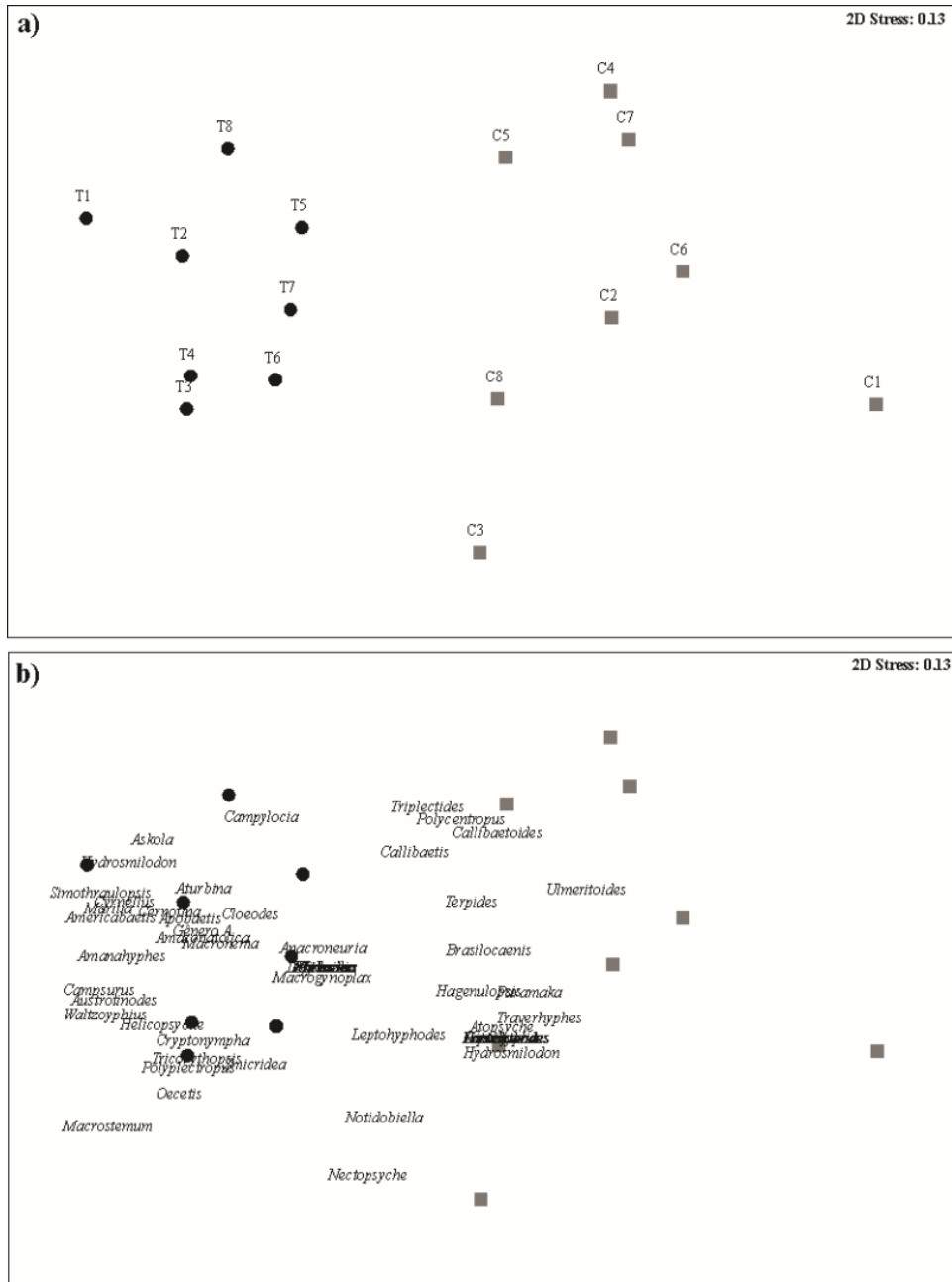


Fig 3. Non-metric multidimensional scaling (NMDS) results for Ephemeroptera, Trichoptera, Plecoptera assemblages (Sørensen dissimilarity, stress: 0.13). a) Plots showing the community dissimilarity between the two study regions (circles: Floresta Nacional do Tapajós; squares: Floresta Nacional de Carajás); b) Genera contribution to dissimilarity patterns among assemblages.



Fig 4. Ordination plots showing the taxonomic assemblages and functional composition of Ephemeroptera, Trichoptera, Plecoptera assemblages: a,b) streams at Flona Tapajós; c,d) streams at Flona Carajás, respectively.

309

310 **Table 3.** Results for Multiple regression on distance matrices. Relationships between the community
 311 dissimilarity matrix (Sørensen dissimilarity) and the explanatory variables for aquatic insect assemblages
 312 (Ephemeroptera, Trichoptera, Plecoptera) from streams at Floresta Nacional do Tapajós and Floresta
 313 Nacional de Carajás, Pará, Brazil.

Variables	Code	R ²	F-test	p
<i>Individual response</i>				
Geographic distance	Xy	0.497	116.774	0.001
Mean wetted width / depth (m/m)	Xwd	0.001	0.072	0.812
Mean Substrate Diameter (mm)	Xsub	0.001	0.050	0.842
Elevation	Elev	0.438	92.160	0.001
Electrical conductivity (µS/cm)	Cond	0.027	3.240	0.129
Dissolved oxygen (mg/L)	OD	0.002	0.264	0.680
Temperature (°C)	T	0.112	14.846	0.006
Negative log hydrogen ion concentration	pH	0.381	72.522	0.001
<i>Model with environmental and spatial distances</i>				
xy + elev + T + pH	-	0.511	60.865	0.001

314 Overall, the genera recorded in this study are indicative of well-preserved aquatic
315 ecosystems. They are often found predominant in pristine first order streams in regions
316 of dense vegetation cover and the predominance of leaf substrates (Bispo et al. 2006;
317 Suga and Tanaka 2013). Besides, we did not found relationships between local stream
318 conditions (e.g. substrate size, electrical conductivity, stream width) and community
319 dissimilarity, which could be related to this factors acts strongly structuring local patters
320 than regional species replacement (Hamerlík et al. 2014). On the other hand, we believe
321 that the explicit responses in community dissimilarity were found for pH and elevation
322 extremes, when then they highlighted the spatial habitat heterogeneity found between the
323 two regions. Moreover, combining all significant factors in our study, we found high
324 contribution in explaining community dissimilarity. Then, the species replacement in
325 insect assemblages among streams was supported by a combination of local and regional
326 variables. Specific environmental gradients are known to controlling community
327 composition and determining the similarity among assemblages for aquatic fauna (Heino
328 et al. 2003a). Yet, when few habitat variables show low effects in the community
329 dissimilarity, this condition is reported to be due to absence of effective environmental
330 gradients required to increase species replacement and dissimilarities may be related to
331 dispersal processes (Monaghan et al. 2005; Tucker et al. 2016).

332 Hypothesis about variations in community dissimilarity and their causes are best
333 explained when the main arrays in species distribution is taken in account, which often
334 are enlightened by different ecological processes that often is not only different but also
335 opposite (Baselga 2010; Saito et al. 2015). As expected, disentangling our community
336 dissimilarity in components we found some causes for variation in assemblage structure
337 among streams (differences in components of beta diversity) (Monaghan et al. 2005;
338 Legendre 2014). Then, we focused only in our main cause, the species replacement, in

339 order to underlie key environmental process acting on community dissimilarity. This
340 approach helped us to understand specific contexts controlling the aquatic insect
341 distribution between and along the environmental gradient at Flona Carajás and Tapajós.

342 Considering the regional specificity, the most important explanatory variables
343 determinant of species replacement among regions were elevation and pH, which
344 commonly represents good predictors for Ephemeroptera, Trichoptera and Plecoptera
345 distribution (Bispo et al. 2006). Between regions, besides the spatial distribution of
346 streams, the species replacement were most structured by regional conditions that was
347 presented in Principal Component Analysis. While, the streams at Flona Carajás are
348 located in high altitude catchments and can be characterized with high values of electrical
349 conductivity and slightly neutral waters. The habitats in streams at Flona Tapajós have
350 remarkable low electrical conductivity values and acid waters distributed in lowland
351 drainages. These specificity are known to create habitat heterogeneity and contribute
352 significantly for species turnover among regional contexts (Datry et al. 2016).
353 Highlighting the influence of elevation, the high value in overall beta diversity and
354 species replacement observed for Carajás region can be explained by the relevance of
355 dispersal limitation in structuring these assemblages. Elevation can act as barrier and lead
356 selective differentiation between the faunas among streams as suggested by the high
357 turnover patterns, mainly at Carajás region.

358 From our results, generalizations should be made cautiously, because of our
359 limited environmental gradient and absence of intermediate regions to explore other
360 regional patterns, which are required for detailed gradient analysis when partitioning the
361 components of beta diversity (Gering et al. 2003; Legendre 2014; Saito et al. 2015).
362 Despite this fact, we recognized environmental influence on the low effects of richness
363 difference (nestedness) and high contribution of species replacement (spatial turnover)

364 found. Therefore, for the aquatic insect distribution, some ecological implications in our
365 finds may be highlighted and some contributions of environmental deterministic
366 processes, dispersal limitation and endemic effects can be summarized.

367 The large amount of variation in environmental conditions within and among
368 regions was computed in our Principal Component Analysis and this pattern is supported
369 by community dissimilarity with low richness difference but strong turnover effects
370 among streams reflecting habitat heterogeneity (Heino et al. 2015a; Heino et al. 2015b).
371 Unexpectedly, the gradients of elevation (high difference in altitude among regions,
372 approximately 40-550 m) were not an effective limiting factor for genera distribution and
373 the spatial turnover processes supported this in community structure. Contrary for most
374 studies that highlighted altitude as a restriction for species distribution, the taxa recorded
375 in this study had not dispersal limitations within and among regional contexts (Altermatt
376 et al. 2013; de Mendoza et al. 2015).

377 Contrasting the patterns, we found low nestedness contribution in assemblage
378 distribution that are indicative of endemic process affecting centres of speciation between
379 the regions (Heino 2011). Carajás and Tapajós regions comprise known large landscapes
380 separated by large rivers (Tapajós and Xingu interfluves), and these features are
381 recognized to create biogeographic endemic areas for many biological groups (e.g.
382 insects, frogs, birds and mammals) (Gascon et al. 2000; Hayes and Sewlal 2004; Juen and
383 De Marco 2012). Considering these interfluves and the regional habitat heterogeneity,
384 Carajás region had the highest variation in community composition, also environmental
385 characteristics, than Tapajós and this patterns supports the mains differences in species
386 replacement within and between regions.

387 Many studies pointed out that habitat heterogeneity is the main factor regulating
388 regional variation in beta diversity, and in our dataset, the landscape features were able

389 for explaining most of community patterns. Hence, considering the geographic distance
390 from one region to other, the community dissimilarity between Carajás and Tapajós may
391 be the result of a combination between environmental factors and non-dispersal limitation
392 in structuring these assemblages. The exclusive genera found may be replacing those
393 occurring in each region and vice-versa with low richness differences (nestedness)
394 patterns pointing out the relevance of landscape variables (Jonsson and Malmqvist 2003).

395 Partitioning the taxonomic composition and considering spatial patterns among
396 assemblages, some patterns are made evident when we analyse them in ordination plots.
397 For instance, the non-metric multidimensional scaling explain the genera distribution
398 among the regions, which evidenced the environmental contribution in community
399 composition (Costa and Melo 2008; Patrick and Swan 2011). When describing
400 assemblage distribution we found that each insect Order contributed distinctly for species
401 replacement. Then, we can highlight the distribution and species replacement of
402 Ephemeroptera assemblages (e.g. *Callibaetoides*, *Brasilocaenis*, *Hydrosmilodon*, and
403 *Ulmeritoides*) was most related to streams at Carajás region. In contrast, beta diversity
404 patterns for most Trichoptera genera were most evident along habitats at Tapajós basin.
405 These observations highlights typical stream environments along black waters drainages,
406 where specific habitats are created for aquatic biota. Tapajós region is known to have a
407 high discharge of litter material produced in riparian forests that amounting as leaf debris
408 in streams decomposing and creating unique conditions for aquatic fauna (Bonetto and
409 Sioli 1975). As expected, the functional composition across these habitats were
410 represented by collector-gatherers that displayed higher relative proportion (e.g.
411 *Miroculis*) and it supports that these organisms are associated the CPOM and FPOM
412 processing, which in turn may be used as food. Furthermore, the shredders (e.g.

413 *Campylocia*, *Nectopsyche* and *Phylloicus*) showed contribution to functional patterns in
414 most Tapajós streams.

415 The aquatic insect distribution among streams have been accounted according to
416 substrate heterogeneity (Beisel et al. 1998). Nevertheless, in our study we found that the
417 substrate size were not associated to species replacement in both regional contexts. Albeit,
418 we believe that among all streams, the microhabitats (i.e. substrates) displayed a nearly
419 similar combination of substrate size that contributed evenly to community organization.
420 Hence, weak ecological distances were found to discriminate assemblage dissimilarity,
421 since composition seems mainly depended on the characteristics of the mesohabitat
422 sampled (Beisel et al. 2000). On the other hand, substrate heterogeneity has been
423 considered as a key factor to shape similar functional composition among streams
424 dominated by species replacement structuring faunal assemblages (Feld and Hering
425 2007). In addition, some studies have found that individuals that show similar
426 morphological and functional characteristics are allowed to colonize more than one
427 substrate type, but in general, the substrates show distinct taxonomical assemblages but
428 functionally convergent (Erman and Erman 1984; Brown 2003). Our results corroborate
429 that functional composition may be quite similar in streams that share microhabitat
430 conditions, despite increasing geographical scales (Costa and Melo 2008). Hence, we
431 believe that functional metrics provide good comparisons among communities at
432 homogeneous conditions in streams than the exclusive taxon approaches to detect
433 microhabitat gradients (Reid et al. 2010).

434 Although we did not correlated directly the habitat conditions with functional
435 composition, we can infer environmental effects on genera traits among stream, since we
436 found congruence among trait matrices and this pattern can be accounted to habitat
437 filtering for similar groups with similar traits (Southwood 1977; Townsend and Hildrew

438 1994). These patterns suggest response to neutral processes that is more effective within
439 groups of species with similar ecological traits, as we found with ordination methods and
440 Procrustes analysis comparing the functional composition between the two regions (Resh
441 et al. 1988; Heino et al. 2003b; Heino et al. 2009; Heino 2009). In addition, the main
442 patterns found in species composition, the species replacement, also contributed to this
443 scenario, where low dispersal limitation are structuring these assemblages highlighting
444 more effect of neutral distribution among the streams, mainly comparing local
445 communities evidenced by low variation in functional composition. However, niche
446 dynamics were supported among regional gradients between groups and influencing most
447 of community dissimilarities (Adler et al. 2007; Pavoine and Bonsall 2011).

448 **Conclusion**

449 Our main results supported that regional effects of environmental heterogeneity
450 were key factors for species replacement and endemic patterns structuring community
451 composition of Ephemeroptera, Trichoptera and Plecoptera. Moreover, the streams
452 showed distinct habitat heterogeneity between the basins (Tapajós and Carajás regions),
453 that are distributed along many different ecosystem attributes with unique landscape
454 conditions (e.g. lowland stream networks, high-elevated streams). The variations in
455 species replacement were related to remarkable variations in landscape features, but in
456 contrast, functional composition was not divergent with taxon similarity among regions
457 that may be related to microhabitat distribution. Besides, the regional environmental
458 conditions are maintaining functional congruence for similar habitats, even with different
459 taxonomical composition, as a result for related trait community dynamics albeit
460 geographical distances.

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1 CONCLUSÃO GERAL

2 A variação ambiental apresentou influência estruturando a composição taxonômica
3 e funcional das comunidades de insetos aquáticos em riachos amazônicos. Além disso,
4 vimos que a distribuição das espécies ocorre de acordo com as características locais e
5 regionais em que os riachos foram encontrados. Em geral, foi possível destacar que as
6 comunidades variaram em sua composição, principalmente de acordo com os efeitos de
7 variáveis limnológicas como a temperatura, pH, condutividade elétrica e oxigênio
8 dissolvido. Ao contrário do esperado, a maioria das variáveis da estrutura física do habitat
9 foram pouco explanatórias para a estrutura das comunidades, uma vez que um grande
10 número de variáveis foi mensurado, mas pouco efeito foi encontrado sobre a fauna nos
11 locais estudados. Este resultado pode estar relacionado a ausência de gradientes robustos
12 dessas variáveis nesses ecossistemas, uma vez que todas as áreas foram similares quanto
13 ao estado de preservação das florestas ripárias.

14 Quando consideramos, a variação na composição taxonômica das comunidades em
15 uma escala geográfica ampla vimos que as comunidades foram dissimilares em resposta
16 ao efeito da distância geográfica. Nos riachos localizados entre regiões isoladas foram
17 afetados principalmente pelas características da paisagem, como por exemplo gradientes
18 de elevação. Contudo, em relação à composição funcional, os padrões mais robustos
19 foram aqueles de comunidades locais que diferiram entre os riachos, e opostamente foram
20 similares em um contexto regional. Assim, corroborando hipóteses e premissas de
21 redundância funcional das comunidades que são estruturadas por grupos tróficos, a qual
22 foi o caso das comunidades de insetos na maioria dos ecossistemas avaliados, o que
23 sugere a ocorrência de comunidades de espécies funcionalmente equivalentes, suportando
24 as premissas da Teoria Neutra.

25 No primeiro estudo, avaliamos como as comunidades de Chironomidae estão
26 sendo abordadas em estudos de monitoramento dos ecossistemas aquáticos e encontramos
27 padrões regionais na literatura científica em relação aos avanços das principais
28 ferramentas utilizando a diversidade e abundância do grupo. Muitos dos estudos avaliados
29 em ambientes impactados foram realizados principalmente em regiões do Hemisfério
30 Norte, onde deram suporte para o desenvolvimento de estudos em diferentes linhas de
31 pesquisa com esses insetos e outros macroinvertebrados. Além disso, contribuíram com
32 avanços nos estudos taxonômicos, mas também na aplicação de índices multimétricos
33 para mensurar a qualidade ambiental em áreas impactadas por atividades antropogênicas.

34 No segundo capítulo testamos hipóteses da Teoria de Metacomunidades e
35 analisamos a contribuição da variação ambiental e da variação geográfica sobre as
36 comunidades de Chironomidae e a estrutura física do habitat. Encontramos baixa
37 contribuição da estrutura do habitat e da escala espacial sobre a composição de táxons, o
38 que deu suporte para considerar a distribuição das comunidades sob o efeito conjunto de
39 de “species sorting” e “mass effects”. Além disso, testamos se a parte da composição das
40 comunidades não explicada pelas variáveis do habitat também foram geograficamente
41 estruturada e encontramos correlação significativa o que indica efeitos de outros
42 mecanismos atuando nas comunidades como eventos históricos, climáticos e o próprio
43 efeito da inundação por marés comum na região. Assim, sugerimos que considerar os
44 efeitos de características regionais (e.g. clima, marés) é necessário para obtenção de
45 diferentes respostas além dos resultados puramente relacionados ao habitat.

46 No terceiro capítulo utilizamos uma abordagem de variação de traços funcionais
47 das comunidades para avaliar o efeito da variação na estrutura do habitat sobre os traços
48 biológicos dos insetos aquáticos em escala local. Encontramos respostas da variação na
49 estrutura funcional das comunidades em relação a variação total das variáveis do habitat.

50 Apesar da correlação ambiente-traços, nenhuma relação específica entre um traço e uma
51 variável do habitat foi observada. Apesar disso, as premissas de “Habitat Templet” foram
52 suportadas e encontramos dependência dos traços funcionais da comunidade com a
53 variação ambiental local. Sugerimos que em escala local, os efeitos dessas variáveis do
54 habitat atuam em conjunto para estruturar a composição local dos traços das comunidades
55 de insetos aquáticos, por outro lado, a variação na composição taxonômica é favorecida
56 pelo aumento da heterogeneidade ambiental entre os diferentes locais.

57 No quarto capítulo encontramos que as distâncias ecológicas das comunidades e
58 dos ambientes foram métricas importantes para avaliar a variação na composição de
59 táxons de Ephemeroptera, Trichoptera e Plecoptera entre regiões com diferentes aspectos
60 da paisagem. Encontramos que as comunidades apresentaram dissimilaridade na
61 composição de gêneros e ambas as comunidades foram resultadas pela substituição de
62 espécies dentro e entre cada região. Além disso, encontramos resultados de efeitos
63 regionais da variação ambiental sobre a composição taxonômica das assembleias dentro
64 e entre regiões. Contudo, em contraste com a dissimilaridade da composição taxonômica,
65 encontramos congruência funcional entre as comunidades das regiões. Esses resultados
66 sugerem que regionalmente as comunidades são formadas principalmente por
67 substituição espécies e são funcionalmente equivalentes, o que corrobora as premissas
68 equivalência funcional das populações propostas pela Teoria Neutra.

69 Análises sobre os efeitos conjuntos dos fatores espaciais e ambientais
70 estruturadores das comunidades locais e regionais contribuem para o entendimento e a
71 compreensão da distribuição dos insetos aquáticos em ambientes heterogêneos, como os
72 que caracterizam a maioria das regiões hidrográficas da Bacia Amazônica. Além disso,
73 destacamos que a composição funcional das comunidades é afetada principalmente em
74 escalas locais, podendo ser redundante entre regiões quando composição das

75 comunidades é formada por substituição de espécies funcionalmente equivalentes. Assim,
76 corroboramos que os ecossistemas aquáticos com similaridade de habitat tendem a
77 convergir as comunidades em seus traços biológicos.

78 Destacamos que ainda existem lacunas no que se refere ao uso das abordagens de
79 análises espaciais e diversidade funcional em estudos sobre a estrutura das comunidades
80 de insetos aquáticos. Estes ainda são sub-representados na maioria dos estudos de
81 priorização para a conservação de ecossistemas na Região Amazônica em comparação
82 aos grupos de invertebrados terrestres. Além disso, novos métodos para a mensuração e
83 escolha de traços funcionais dos grupos de insetos aquáticos na Amazônia ainda
84 necessitam de avanços e refinamentos quanto a escolha dos mesmos. Uma vez que, a
85 maioria destes, é geralmente, baseada na composição da fauna de ecossistemas de regiões
86 temperadas que diferem não apenas nas condições ambientais onde ocorrem quanto na
87 relação que os insetos têm com seus habitats. Assim, para obtenção de respostas mais
88 robustas da variação da composição das comunidades e suas relações com o ambiente,
89 estudos devem considerar além das abordagens de composição taxonômica, as
90 características funcionais dos insetos aquáticos. Também, deve-se considerar a ampla
91 heterogeneidade ambiental da paisagem amazônica que pode ser mensurada desde a
92 escala local (riachos) até as suas características regionais (bacias de drenagem).