

Instituto Nacional de Pesquisas da Amazônia – INPA

Programa de Pós-Graduação em Ecologia

Segregação de habitat por espécies de camarões em riachos de terra firme  
na Amazônia

Elmo Pereira da Silva

Manaus, Amazonas

Junho, 2019

Elmo Pereira da Silva

**Segregação de habitat por espécies de camarões em riachos de terra firme  
na Amazônia**

Orientador: Dr. William Magnusson

Coorientadores: Dr. Célio Magalhães

Dr. Jansen Zuanon

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia do Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Mestre em Biologia (Ecologia).

Manaus, Amazonas

Junho, 2019

Elmo Pereira da Silva

**Segregação de habitat por espécies de camarões em riachos de terra firme  
na Amazônia**

Dissertação apresentada à Coordenação do Programa de Pós-Graduação em Ecologia do Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos necessários à obtenção do título de Mestre em Biologia (Ecologia).

Orientador: Dr. William Ernest Magnusson

**BANCA EXAMINADORA**

---

Dra. Thatyla L. B. Farago – 1º Examinador  
Instituto Nacional de Pesquisas da Amazônia – INPA

---

Dr. Victor Lemes Landeiro – 2º Examinador  
Universidade Federal de Mato Grosso – UFMT

---

Dra. Flávia Delgado Santana – 3º Examinador  
Instituto Nacional de Pesquisas da Amazônia – INPA



PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

ATA DA DEFESA PÚBLICA DA  
DISSERTAÇÃO DE MESTRADO DO  
PROGRAMA DE PÓS-GRADUAÇÃO EM  
ECOLOGIA DO INSTITUTO NACIONAL  
DE PESQUISAS DA AMAZÔNIA.

Aos 07 dias do mês de junho do ano de 2019, às 09h00min, no Auditório dos PPG's ATU/CFT/ECO, Campus III, INPA/V8. Reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Cristhiana Paula Röpke**, do Instituto Nacional de Pesquisas da Amazônia – INPA, o(a) Prof(a). Dr(a). **Tiago Henrique da Silva Pires**, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). **Victor Lemes Landeiro**, da Universidade Federal de Mato Grosso - UFMT, tendo como suplentes o(a) Prof(a). Dr(a). Flávia Delgado Santana, do Instituto Nacional de Pesquisas da Amazônia – INPA, e o(a) Prof(a). Dr(a). Thatyla Luana Beck Farago, do Instituto Nacional de Pesquisas da Amazônia – INPA sob a presidência do(a) primeiro(a), a fim de proceder a arguição pública do trabalho de DISSERTAÇÃO DE MESTRADO de ELMO PEREIRA DA SILVA, intitulado: "SEGREGAÇÃO DE HABITAT POR ESPÉCIES DE CAMARÕES EM RIACHOS DE TERRA FIRME NA AMAZÔNIA", orientado(a) pelo(a) Prof(a). William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia – INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

APROVADO(A)

REPROVADO(A)

POR UNANIMIDADE

POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a).CRISTHIANA PAULA RÖPKE



Prof(a).Dr(a).TIAGO HENRIQUE DA SILVA PIRES



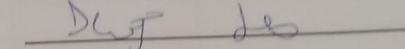
Prof(a).Dr(a). VICTOR LEMES LANDEIRO

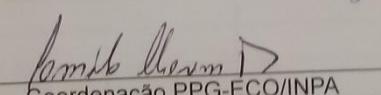


Prof(a).Dr(a). FLÁVIA DELGADO SANTANA



Prof(a).Dr(a). THATYLA LUANA BECK FARAGO



  
Coordenação PPG-ECO/INPA

## Ficha catalográfica

SEDAB/INPA © 2019 - Ficha Catalográfica Automática gerada com dados fornecidos pelo(a) autor(a)  
Bibliotecário responsável: Jorge Luiz Cativo Alauzo - CRB11/908

S586s Silva, Elmo Pereira da  
Segregação de habitat por espécies de  
camarões em riachos de terra firme na Amazônia  
/ Elmo Pereira da Silva; orientador William  
Ernest Magnusson; coorientador Célio Magalhães;  
Jansen Zuanon . -- Manaus:[s.l], 2019.  
60 f.

Dissertação (Mestrado - Programa de Pós  
Graduação em Ecologia) -- Coordenação do  
Programa de Pós-Graduação, INPA, 2019.

1. Partição de recursos. 2. Dimensões de habitat.  
3. Composição do predador. 4. Competição  
aparente. 5. Bacia de drenagem. I. Magnusson,  
William Ernest, orient. II., Célio Magalhães;  
Jansen Zuanon, coorient. III. Título.

CDD: 598

### Sinopse:

Neste estudo, determinou-se a influência de variáveis ambientais associadas à química da água, hidráulica do canal e estrutura física do habitat no número de camarões de riachos de terra firme, para desta forma, trazer evidências de que as espécies particionam o nicho na dimensão de habitat. Aspectos como o efeito de potenciais predadores e de diferentes bacias de drenagem também foram estimados.

**Palavras-chave:** Camarões, segregação de habitat, coexistência, riachos de terra firme, Amazônia.

Aos camarões, cujo sacrifício proporcionou a elaboração deste trabalho, dedico.

## Agradecimentos

Agradeço primeiramente aos órgãos/instituições que fomentaram a execução deste trabalho. Ao CNPq pela bolsa de mestrado concedida, sem ela minha estadia em Manaus não seria possível. Ao PELD pelo financiamento da pesquisa em campo. Ao Projeto Igarapés e CENBAM pelos materiais cedidos para a realização das amostragens em campo e ao PPBio pela manutenção das parcelas de estudo. Ao INPA pela infraestrutura em Manaus, especialmente o laboratório de carcinologia, e na Reserva Ducke. E a secretaria do PPG-Eco pela dedicação.

Agradeço profundamente aos meus queridos orientadores, Dr. William Magnusson (Bill), Dr. Jansen Zuanon e Dr. Célio Magalhães, pela paciência, crítica e sugestões que proporcionaram a elaboração deste trabalho. Sou grato também aos meus companheiros de campo, Gabriel Borba (Gabes), Rayssa Guinato e José Lopes (“Seu” Zé), sem eles a estadia em campo não seria a mesma. Aos meus companheiros de turma (mestrado Eco-2017) e aos queridos docentes do PPG-Eco. E aos amigos incríveis que fiz em Manaus.

Agradeço a toda minha família, em especial meus pais e meu irmão. Aos meus amigos de Pernambuco e da Paraíba, que me incentivaram e me deram suporte durante todo o período do mestrado. A todos que participaram da minha formação acadêmica até o presente momento, meus primeiros professores do colégio, professores de cursos técnicos, professores de graduação, enfim.

Acredito que não conseguirei agradecer apropriadamente todos, mas para aqueles que influenciaram direta ou indiretamente na realização deste trabalho, meu muito obrigado.

*“Our feelings are our most genuine paths to knowledge.”*

**Audre Lorde**

## **Resumo**

Partição de recursos é um mecanismo estabilizante conhecido por manter a diversidade de espécies em vários ambientes. Assembleias de camarões de riachos são estruturadas por características do habitat e predação. Portanto, a segregação na dimensão do habitat poderia facilitar a coexistência entre espécies nessas assembleias, mesmo quando a segregação é resultado de pressão de predação por espécies de peixes. Essas interações ecológicas ocorrem em um ambiente modulado por características biogeográficas, como a conectividade entre drenagens. No entanto, essas generalizações são baseadas principalmente em estudos realizados em regiões temperadas. Investigamos se a abundância de espécies de camarões de riachos de terra firme está relacionada com as dimensões do habitat e se as relações de abundância com o habitat podem ser mediadas pela estrutura da assembleia de peixes e pelo efeito das drenagens. Regressões múltiplas foram usadas para demonstrar possíveis relações entre a abundância de camarões e o habitat, e também com a composição dos peixes. Testes de Kolmogorov-Smirnov foram realizados para evidenciar a especialização e a segregação de habitat entre as espécies. Detectamos efeitos da variação do habitat nas densidades das espécies de camarões, mas as magnitudes dos efeitos foram maiores para algumas espécies que para outras. A composição do predador também afetou as densidades dos camarões. Duas das três espécies mostraram algum grau de especialização de habitat, mas apenas ao longo dos gradientes de velocidade da correnteza, profundidade e pH. Segregação de habitat entre as espécies ocorreu ao longo dos gradientes de velocidade da correnteza e pH. As relações entre densidade e gradientes ambientais diferiram entre bacias apenas para uma espécie e apenas ao longo do gradiente de pH. Nossas descobertas fornecem evidências de que espécies de camarões de riachos tropicais respondem diferentemente aos gradientes ambientais e isso pode facilitar a coexistência entre as espécies. No entanto, a pressão de predação parece ter um efeito mais forte sobre as densidades de espécies e, consequentemente, a segregação de espécies, e também os efeitos diretos dos gradientes ambientais, resultam de competição aparente por esses recursos.

**Palavras-chave:** Partição de recursos, dimensões de habitat, composição do predador, competição aparente, bacia de drenagem.

## **Abstract**

Resource partitioning is a stabilizing mechanism known to maintain species diversity in a variety of environments. Assemblages of stream shrimp species are structured by habitat features and predation. Therefore, segregation in habitat dimension could facilitate coexistence among species in shrimp assemblages even when segregation is a result of predation pressure by fish species. These ecological interactions take place on a background modulated by biogeographic features, such as connectivity among drainages. However, these generalizations are mainly based on studies undertaken in temperate regions. We investigated whether abundances of rainforest shrimp species are related to habitat dimensions, and whether habitat-abundance relationships might be mediated through fish-assemblage structure and the effect of drainages on connectivity. Multiple regressions were used to detect relationships between shrimp-abundance and habitat, and also fish composition. Kolmogorov-Smirnov tests were used to detect specialization and habitat segregation among shrimp species. An interaction model was constructed in order to test the influence of watershed on the relation between abundance of shrimp species and habitat features. We detected effects of habitat variation on densities of shrimp species, but the magnitudes of the effects were larger for some species than others. Predator composition also affected shrimp densities. Two of the three species of shrimp showed some degree of habitat specialization, but only along current-velocity, depth and pH gradients. Habitat segregation among species occurred along the current-velocity and pH gradients. Relationships between density and environmental gradients differed between watersheds for only one species and only along the pH gradient. Our findings provide evidence that rainforest-stream shrimp species respond differently to environmental gradients and this could facilitate coexistence among species. However, predation pressure seems to have a stronger effect on species densities, and consequently species segregation, than direct effects of the environmental gradients, resulting in apparent competition for these resources.

Keywords: resource partitioning, habitat dimensions, predator composition, apparent competition, watershed.

## Sumário

Lista de tabelas .....	12
Lista de figuras .....	13
Introdução geral .....	14
Objetivos .....	19
<i>Geral</i> .....	19
<i>Específicos</i> .....	19
Referências.....	20
RESEARCH ARTICLE .....	26
Abstract.....	27
1 INTRODUCTION.....	28
2 METHODS .....	30
2.1 Study system .....	30
2.2 Study design and sample collection .....	30
2.3 Data analysis .....	31
2.3.1 Specialization and habitat segregation .....	32
2.3.2 Fish-assemblage composition .....	33
2.3.3 Watershed effect.....	33
3 RESULTS .....	33
3.1 <i>Macrobrachium inpa</i> .....	34
3.2 <i>Macrobrachium nattereri</i> .....	34
3.3 <i>Pseudopalaemon amazonensis</i> .....	34
3.4 Specialization and habitat segregation .....	35
3.5 Watershed effect.....	35
4 DISCUSSION .....	35
ACKNOWLEDGMENTS.....	38
DATA AVAILABILITY .....	38
CONFLICT OF INTEREST .....	38
REFERENCES.....	39
TABLES.....	43
FIGURES .....	47
SUPPORTING INFORMATION .....	54
Conclusões .....	61

## **Lista de tabelas**

<b>Table 1.</b> Mean values of environmental variables in sample sites.....	42
<b>Table 2.</b> Path analysis summary of magnitudes of direct and indirect effects (through fish composition) of the environmental variable.....	44
<b>Table 3.</b> Summary of results of interaction models of watershed effects on the relationships between predictor variables and number of individuals of each species.....	45

## **Lista de figuras**

<b>Figure 1.</b> Path analysis for shrimp species through fish composition and environmental variables.....	46
<b>Figure 2.</b> Partial-regression plots of the relationships between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for <i>Macrobrachium inpa</i> .....	47
<b>Figure 3.</b> Partial-regression plots of the relationships between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for <i>Macrobrachium nattereri</i> .....	48
<b>Figure 4.</b> Partial-regression plots of the relationship between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for <i>Pseudopalaemon amazonensis</i> .....	49
<b>Figure 5.</b> Distributions of individuals of each species (use) and sampling plots (availability) along gradients in current velocity, pH and depth.....	50
<b>Figure 6.</b> Relative use of different values of current-velocity and pH gradients by three rainforest-stream shrimp species.....	51
<b>Figure 7.</b> Plots of interaction models of watershed effects on number of <i>Macrobrachium nattereri</i> individuals with predictors (a – pH, b – Temperature, c – Current velocity, d – Depth, e – Sand, f – Litter and g – Fish axis).....	52

## Introdução geral

Entender os mecanismos que afetam à distribuição das espécies tem sido uma das perguntas centrais dos estudos ecológicos que abrangem a estrutura das comunidades (Andrewartha e Birch 1954). A distribuição de uma espécie no espaço pode estar associada ao clima da região, à sua capacidade de movimentação (dispersão), aos aspectos estruturais do ambiente físico em que ela está inserida e à interação com espécies que possuem requerimentos ecológicos similares (Hutchinson 1957; Caughley et al. 1987; Root 1988; Silvertown et al. 1999; McGill 2010). Estes mecanismos variam em importância dependendo do tipo da comunidade, da escala em que as espécies são observadas, do momento, entre outros aspectos (Connell 1983; Gotelli et al. 2010; Chesson 2012). Contudo, autores apontaram que, em escalas ecológicas usualmente estudadas, o habitat e as interações biológicas estão mais correlacionados com as variações na distribuição das espécies (McGill 2010). Além disso, estes mecanismos não atuam necessariamente isolados, uma vez que a forma da distribuição das espécies pode ser resultado da combinação de todos ou alguns deles simultaneamente (Yuan e Chesson 2015; Kohli et al. 2018; Letten et al. 2018). Por isso, estudar os possíveis atributos do habitat e as possíveis interações entre as espécies seria o melhor caminho para entender a ocorrência e abundância dos indivíduos no espaço (Lindenmayer et al. 2015).

Espécies, em geral, não estão distribuídas ao acaso no espaço, uma vez que elas possuem um intervalo de tolerância às variações no ambiente. O conjunto de intervalos ao longo dos eixos representando suas necessidades para sobrevivência e reprodução corresponde ao nicho ecológico (Hutchinson 1957; 1965). Embora seja presumido que as espécies possuam uma totalidade de nichos ecológicos diferentes, podem existir similaridades entre alguns eixos, resultando em competição interespecífica. Sendo assim, a alta proximidade ecológica e filogenética entre espécies dificulta a coexistência entre elas (Chesson 2018). Portanto, espera-se que as espécies particionem os eixos de recursos associados ao nicho; se não, uma excluirá a outra.

Para evitar competição, as espécies podem utilizar recursos diferentes, em locais diferentes ou em momentos diferentes (MacArthur 1958; Hutchinson 1961; Schoener 1968). Contudo, a partição de recursos pode não ser suficiente, ou até mesmo necessária, para promover coexistência (MacArthur 1958). Neste contexto, mecanismos

como a intensificação dos efeitos intraespecíficos quando as espécies são abundantes, e a redução das diferenças relativas de aptidão, sendo esta no sentido de habilidade competitiva e não no evolutivo, também previnem a importância dos efeitos interespecíficos na coexistência (MacArthur 1958; Chesson 2000). Além disso, outros mecanismos, como eventos estocásticos e demográficos, também estão associados à coexistência, porém são menos óbvios (Sale 1978; Warner e Chesson 1985). Competição interespecífica não é o único fator que gera pressão seletiva para o desenvolvimento de mecanismos que promovam coexistência (Diamond 1978). Fatores como predação e limitações morfológicas e fisiológicas também estão associadas a esses mecanismos (Toft 1985; Bull 1991; Walter 1991; Barros et al. 2016).

Existem diversos eixos de recursos associados ao nicho (e.g. habitat, alimento, espaço, tempo) e é presumido que as espécies precisem ou não segregar estes eixos ou não podem coexistir. Entretanto, se a partição é necessária, quantos eixos precisam ser particionados para que a coexistência seja promovida? Alguns autores sugeriram que a partição em três eixos de recursos seria suficiente para que a sobreposição entre os nichos das espécies permitisse coexistência (Schoener 1974; Iglesias-Rios 2004). Contudo, existe uma hierarquia de importância entre as dimensões do nicho, em que o habitat, o alimento e o tempo são os eixos que englobam os demais (Schoener 1974; Pianka 1975). Os eixos associados ao nicho, geralmente, são correlacionados e não independentes, podendo a coexistência ser resultado da partição interativa ou independente das dimensões (Toft 1985). Sendo o habitat a dimensão mais importante do nicho e, em geral, a primeira a ser particionada, seria esperado que a diferenciação de nicho apenas no eixo de habitat fosse suficiente para gerar coexistência, mas isto pode ser verdade ou não, dependendo do tipo de organismo e dos fatores que levaram à partição de recursos entre as espécies (Schoener 1974; Pianka 1975). Presume-se que espécies filogeneticamente similares possuam uma tolerância máxima de sobreposição menor que espécies não similares, e então, as relações de sobreposição de nicho assumem diferentes conformações dependendo dos efeitos de competição interespecífica e do suporte do ambiente físico (Pianka 1974). Além disso, quando espécies ecologicamente similares são observadas coexistindo, não necessariamente elas competem por interferência, mas sim por exploração (Hutchinson 1957; MacArthur e Levins 1967; MacArthur 1970).

Como sugerido por MacArthur (1965), a diversidade de espécies é diretamente proporcional à complexidade estrutural do ambiente físico, tendo em vista que existem

diversos elementos do habitat em que as espécies podem ser mais eficientes. Além disso, espécies com tolerâncias ambientais restritas (especialistas) são mais eficientes no uso de locais particulares do habitat que espécies com tolerâncias mais amplas (generalistas) e, portanto, tendem a ter mais sucesso em ambientes homogêneos, onde o acesso aos recursos é mais previsível (Smith 1982; Futuyma e Moreno 1988; Kassen 2002; Devictor et al. 2008; Verberk et al. 2010). Contudo, não é incomum observar a coexistência entre espécies especialistas e generalistas, embora as especialistas possuam um melhor desempenho no seu habitat “ótimo” (MacArthur e Levins 1964; Morris 1996; Büchi e Vuilleumier 2014). Um ambiente instável, ou pouco previsível, tem potencial de limitar o grau de especialização das espécies, levando à limitação da similaridade entre espécies que coexistem dependendo do grau de competição interespecífica (MacArthur e Levins 1967). A existência de espécies especialistas culmina também no aumento dos efeitos intraespecíficos em detrimento dos interespecíficos, permitindo assim a coexistência (MacArthur 1958). Sendo assim, a coexistência tende a diminuir com a redução da complexidade ambiental (Mordecai et al. 2016; Holt e Chesson 2018).

Nesse sentido, a heterogeneidade em escala local tem potencial de definir a força das relações entre espécies que realmente interagem, e também com o ambiente circundante (Cornell e Harrison 2014; Holt e Chesson 2016). Dependendo da escala em que são observados, riachos amazônicos de terra firme variam em sua complexidade estrutural. Segmentos destes riachos podem ser categorizados em três principais ambientes típicos: corredeiras, água corrente e seções empoçadas. O primeiro possui alta velocidade da correnteza, baixa profundidade e substrato composto basicamente de areia, seixo e raízes; o segundo possui velocidade da correnteza e profundidade médias; e o terceiro possui baixa velocidade da correnteza, alta profundidade e substrato composto por bancos de liteira (Zuanon et al. 2015). Contudo, existem diferentes extratos dentro de cada uma dessas categorias. Existem também gradientes de velocidade e substrato da margem até o centro do riacho e da superfície para o fundo. Por exemplo, a existência de um gradiente de velocidades da correnteza implica no aumento da complexidade estrutural do ambiente e, por conseguinte, no aumento de locais em que espécies especialistas poderiam ser mais eficientes, possivelmente permitindo a coexistência entre espécies filogeneticamente próximas.

O efeito de determinado mecanismo na distribuição e coexistência das espécies pode depender do tipo da comunidade. Nesse sentido, invertebrados aquáticos têm sua

distribuição mais notadamente relacionada a aspectos estruturais do habitat, e também pela presença de potenciais predadores (Fidelis et al. 2008; Anton-Pardo e Armengol 2014; Brito et al. 2018). O tipo de substrato, a velocidade da correnteza e a profundidade do canal têm sido apontados como os mais importantes na determinação de espécies de invertebrados em riachos (Rezende 2007; Fidelis et al. 2008). Poucos estudos evidenciaram a relação de atributos ambientais associados ao habitat com a distribuição e coexistência de espécies de camarões na Amazônia Central (Kensley e Walker 1982; Walker e Ferreira 1985; Henderson e Walker 1986; Walker 2001; Rezende 2007; Kemenes et al. 2010; Gualberto et al. 2012; De Oliveira et al. 2019), permanecendo assim uma lacuna no que diz respeito ao entendimento dos fatores que têm potencial de modular os aspectos populacionais e coexistência destas espécies.

Predação é considerado um dos fatores que mais influencia a estrutura das assembleias de invertebrados aquáticos (Brooks e Dodson 1965; Power 1990; Petrin et al. 2010). Dentre os principais predadores destes organismos, os peixes se destacam, especialmente no seu efeito sobre a assembleia de camarões (McPeek 1990; Salini et al. 1990; Primavera 1997). Além disso, as espécies respondem diferentemente à ação dos predadores, em que algumas podem interagir positivamente e outras negativamente à presença dos mesmos (Johansson e Brodin 2003). Camarões, assim como os demais invertebrados, parecem ser regulados pela presença de peixes, contudo, isso pode depender do comportamento dos peixes e também dos camarões (Primavera 1997; Mace e Rozas 2018).

Bacias de drenagem também podem ser um importante componente estruturador das assembleias aquáticas em riachos amazônicos, devido às diferenças locais entre os riachos, efeitos históricos e biogeográficos (Mendonça et al. 2005). Dessa forma, variações na complexidade ambiental entre bacias têm potencial de modular as relações das espécies com fatores estruturais do habitat (Holt e Chesson 2018). De acordo com Mendonça et al. (2005), em riachos de terra firme as características associadas à química da água geram a maior variação estrutural entre as bacias de drenagem, sendo esperado que estes fatores determinem as relações das espécies com o habitat entre as bacias.

Portanto, entender como o ambiente físico tem potencial de estruturar as assembleias de camarões pode nos ajudar a desvendar porque as espécies estão distribuídas de determinada maneira no espaço e, se elas particionam o habitat conseguindo reduzir o potencial para competição. Neste contexto, este estudo pretende

determinar a influência do habitat na assembleia de camarões, para desta forma trazer evidências de que espécies de camarões de riachos partitionam o nicho no eixo de habitat.

## Objetivos

### *Geral*

Determinar a influência de variáveis ambientais associadas à química da água, hidráulica do canal e estrutura física do habitat na abundância de camarões de riachos de terra firme.

### *Específicos*

1. Determinar se as espécies particionam as dimensões de habitat.
2. Determinar o efeito de predadores potenciais na abundância das espécies.
3. Determinar se as bacias de drenagem exercem efeito sobre as relações das espécies com as variáveis ambientais.

## Referências

- Andrewartha, H. G.; Birch, C. 1954. *The distribution and abundance of animals.* University of Chicago Press, Chicago.
- Anton-Pardo, M.; Armengol, X. 2014. Aquatic invertebrate assemblages in ponds from coastal Mediterranean wetlands. *Annales de Limnologie - International Journal of Limnology.* 50 (3): 217–230.
- Barros, G.; Zuanon, J.; Deus, C. 2016. Effects of species co-occurrence on the trophic-niche breadth of characids in Amazon forest streams. *Journal of Fish Biology.* 90 (1): 326–340.
- Brito, J. G.; Martins, R. T.; Oliveira, V. C.; Hamada, N.; Nessimian, J. L.; Hughes, R. M.; de Paula, F. R. 2018. Biological indicators of diversity in tropical streams: Congruence in the similarity of invertebrate assemblages. *Ecological Indicators.* 85 85–92.
- Brooks, J. L.; Dodson, S. I. 1965. Predation, body size and the composition of zooplankton. *Science.* 150 28–35.
- Büchi, L.; Vuilleumier, S. 2014. Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist.* 183 (5): 612–624.
- Bull, C. M. 1991. Ecology of parapatric distributions. *Annual Review of Ecology and Systematics.* 22 19-36.
- Caughley, G.; Short, J.; Grigg, G. C.; Nix, H. 1987. Kangaroos and climate: an analysis of distribution. *The Journal of Animal Ecology.* 56 (3): 751.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics.* 31 (1): 343–366.
- Chesson, P. 2012. Scale transition theory: Its aims, motivations and predictions. *Ecol Complex.* 10 52–68.
- Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. *Journal of Ecology.* 106 (5): 1773–1794.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *The American Naturalist.* 122 (5): 661–696.
- Cornell, H. V.; Harrison, S. P. 2014. What are species pools and when are they important? . *Annual Review of Ecology, Evolution, and Systematics.* 45 (1): 45–67.

- De Oliveira, L. J. F.; Sant'Anna, B. S.; Hattori, G. Y. 2019. Population biology of the freshwater prawn *Macrobrachium brasiliense* (Heller, 1862) in the Middle Amazon Region, Brazil. *Tropical Zoology*. 32 (1): 19–36.
- Devictor, V.; Julliard, R.; F., J. 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*. 117 507–514.
- Diamond, J. M. 1978. Niche shifts and the rediscovery of interspecific competition: why did field biologists so long overlook the widespread evidence for interspecific competition that had already impressed Darwin? *Amer. Sci.* 66 322–331.
- Fidelis, L.; Nessimian, J. L.; Hamada, N. 2008. Distribuição espacial de insetos aquáticos em igarapés de pequena ordem na Amazônia Central. *Acta Amazonica*. 38 (1): 127–134.
- Futuyma, D. J.; Moreno, G. 1988. The evolution of ecological specialization. *Annual Review of Ecology and Systematics*. 19 207–233.
- Gotelli, N. J.; Graves, G. R.; Rahbek, C. 2010. Macroecological signals of species interactions in the Danish avifauna. *Proceedings of the National Academy of Sciences*. 107 (11): 5030–5035.
- Gualberto, T. L.; Menin, M.; Almeida, L. O. 2012. Population structure, fecundity and ecological aspects of freshwater shrimp species (Decapoda, Palaemonidae) of an urban forest fragment in central Amazonia, Brazil. *Crustaceana*. 85 (10): 1205–1219.
- Henderson, P. A.; Walker, I. 1986. On the leaf litter community of the Amazonian blackwater stream Tarumazinho. *Journal of Tropical Ecology*. 2 1-17.
- Holt, G.; Chesson, P. 2016. Scale-dependent community theory for streams and other linear habitats. *The American Naturalist*. 188 (3): E59–E73.
- Holt, G.; Chesson, P. 2018. The role of branching in the maintenance of diversity in watersheds. *Freshwater Science*. 37 (4): 000–000.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22 415-427.
- Hutchinson, G. E. 1961. The paradox of the plankton. *The American Naturalist*. 95 (882): 137-145.
- Hutchinson, G. E. 1965. *The niche: an abstractly inhabited hypervolume*. Yale University Press, New Haven. 26–78.
- Johansson, F.; Brodin, T. 2003. Effects of fish predators and abiotic factors on dragonfly community structure. *Journal of Freshwater Ecology*. 18 (3): 415-423.
- Kassen, R. 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology*. 15 173–190.

- Kemenes, A.; Forsberg, B. R.; Magalhães, C.; Anjos, H. 2010. Environmental factors influencing the community structure of shrimps and crabs (Crustacea: Decapoda) in headwater streams of the Rio Jaú, Central Amazon, Brazil. *Pan-American Journal of Aquatic Sciences*. 5 (1): 36-46.
- Kensley, B.; Walker, I. 1982. *Palaemonidae shrimp from the Amazon basin (Crustacean: Decapods: Natantia)*. Smithsonian Contribution to Zoology. 1-28
- Kohli, B. A.; Terry, R. C.; Rowe, R. J. 2018. A trait-based framework for discerning drivers of species co-occurrence across heterogeneous landscapes. *Ecography*.
- Letten, A. D.; Dhami, M. K.; Ke, P. J.; Fukami, T. 2018. Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proceedings of the National Academy of Sciences*. 115 (26): 6745–6750.
- Lindenmayer, D. B.; Welsh, A.; Blanchard, W.; Tennant, P.; Donnelly, C. 2015. Exploring co-occurrence of closely-related guild members in a fragmented landscape subject to rapid transformation. *Ecography*. 38 (3): 251–260.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology*. 39 (4): 599-619.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews*. 40 (4): 510–533.
- MacArthur, R. H. 1970. Species packing and competitive equilibrium for many species. *Theoretical Population Biology*. 1 (1): 1–11.
- MacArthur, R. H.; Levins, R. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences*. 51 (6): 1207–1210.
- MacArthur, R. H.; Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*. 101 (921): 377–385.
- Mace, M. M.; Rozas, L. P. 2018. Fish predation on juvenile penaeid shrimp: examining relative predator impact and size-selective predation. *Estuaries and Coasts*.
- McGill, B. J. 2010. Matters of scale. *Science*. 328 (5978): 575–576.
- McPeek, M. A. 1990. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology*. 71 1714-1726.
- Mendonça, F. P.; Magnusson, W. E.; Zuanon, J. 2005. Relationships between habitat characteristics and fish assemblages in small streams of Central Amazonia. *Copeia*. 2005 (4): 751–764.
- Mordecai, E. A.; Jaramillo, A. G.; Ashford, J. E.; Hechinger, R. F.; Lafferty, K. D. 2016. The role of competition - colonization tradeoffs and spatial heterogeneity in promoting trematode coexistence. *Ecology*. 97 (6): 1484–1496.

- Morris, D. W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology*. 77 (8): 2352–2364.
- Petrin, Z.; Schilling, E. G.; Loftin, C. S.; Johansson, F. 2010. Predators shape distribution and promote diversification of morphological defenses in Leucorrhinia, Odonata. *Evolutionary Ecology*. 24 (5): 1003–1016.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences*. 71 (5): 2141–2145.
- Power, M. E. 1990. Effects of fish in river food webs. *Science*. 250 811–814.
- Primavera, J. 1997. Fish predation on mangrove-associated penaeids. *Journal of Experimental Marine Biology and Ecology*. 215 (2): 205–216.
- Rezende, C. F. 2007. Estrutura da comunidade de macroinvertebrados associados ao folhiço submerso de remanso e correnteza em igarapés da Amazônia Central. *Biota Neotropica*. 7 (2): 301-305.
- Root, T. 1988. Environmental factors associated with avian distributional boundaries. *J. Biogeogr.* 15 489–505.
- Sale, P. F. 1978. Chance patterns of demographic change in populations of territorial fish in coral rubble patches at Heron Reef. *Journal of Experimental Marine Biology and Ecology*. 34 233–243.
- Salini, J. P.; Blaber, S. J. M.; Brewer, D. T. 1990. Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Mar. Biol.* 105 363–374.
- Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology*. 49 (4): 704-726.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science*. 185 (4145): 27–39.
- Silvertown, J.; Dodd, M. E.; Gowing, D.; Mountford, O. 1999. Hydrologically-defined niches reveal a basis for species-richness in plant communities. *Nature*. 400 61–63.
- Smith, E. P. 1982. Niche breadth, resource availability and inference. *Ecology*. 63 1675–1681.
- Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia*. 1 1–21.
- Verberk, W.; van der Velde, G.; Esselink, H. 2010. Explaining abundance-occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. *Journal of Animal Ecology*. 79 589–601.
- Walker, I. 2001. The pattern of distribution of the two sibling species *Euryrhynchus amazoniensis* and *E. burchelli* (Decapoda, Palaemonidae) in the Central Amazonian

blackwater stream Tarumã-Mirim, and the problem of coexistence. *Amazoniana*. 16 (3/4): 565–578.

Walker, I.; Ferreira, M. J. N. 1985. On the population dynamics and ecology of the shrimp species (Crustacean, Decapoda) in the Central Amazonian river Tarumã-Mirim. *Oecologia*. 66 264–270.

Walter, G. H. 1991. What is resource partitioning? *J. theor. Biol.* 150 137–143.

Warner, R. R.; Chesson, P. L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist*. 125 (6): 769–787.

Yuan, C.; Chesson, P. 2015. The relative importance of relative nonlinearity and the storage effect in the lottery model. *Theoretical Population Biology*. 105 39–52.

Zuanon, J.; P., M. F.; Espírito-Santo, H. M. V.; Dias, M. S.; Galuch, A. V.; Akama, A. 2015. *Guia de peixes da Reserva Adolpho Ducke*. INPA, Manaus. 12-13

## **Capítulo I.**

Silva, E. P.; Magalhães, C.; Zuanon, J.; Magnusson, W. E.

**Habitat segregation among freshwater shrimp species in Amazonian rainforest streams**

Manuscrito submetido para o periódico *Freshwater Biology*

1 RESEARCH ARTICLE

2

3

4 **Habitat segregation among freshwater shrimp species in Amazonian rainforest  
streams**

5

6

7

8 Elmo Pereira da Silva<sup>1\*</sup>, Célio Magalhães<sup>2</sup>, Jansen Zuanon<sup>1,2</sup> & William Ernest  
9 Magnusson<sup>1,2</sup>

10

11

12 <sup>1</sup>Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da  
13 Amazônia, Manaus, AM, Brazil.

14 <sup>2</sup>Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia,  
15 Manaus, AM, Brazil.

16 \*elmopereira1317@gmail.com

17

18 Keywords: resource partitioning, habitat dimensions, predator composition, apparent  
19 competition, watershed.

20 **Abstract**

21

22 1. Resource partitioning is a stabilizing mechanism known to maintain species diversity  
23 in a variety of environments. Assemblages of stream shrimp species are structured by  
24 habitat features and predation. Therefore, segregation along habitat dimensions could  
25 facilitate coexistence among species in shrimp assemblages even when segregation is a  
26 result of predation pressure by fish species. These ecological interactions take place on a  
27 background modulated by biogeographic features, such as connectivity among  
28 drainages. However, these generalizations are mainly based on studies undertaken in  
29 temperate regions.

30

31 2. We investigated whether abundances of rainforest shrimp species are related to  
32 habitat dimensions, and whether habitat-abundance relationships might be mediated  
33 through fish-assemblage structure and the effect of drainages on connectivity.

34

35 3. We detected effects of habitat variation on densities of shrimp species, but the  
36 magnitudes of the effects were larger for some species than others. Predator  
37 composition also affected shrimp densities. Two of the three species of shrimp showed  
38 some degree of habitat specialization, but only along current-velocity, depth and pH  
39 gradients. Habitat segregation among species occurred along the current-velocity and  
40 pH gradients. Relationships between density and environmental gradients differed  
41 between watersheds for only one species and only along the pH gradient.

42

43 4. Our findings provide evidence that rainforest-stream shrimp species respond  
44 differently to environmental gradients and this could facilitate coexistence among  
45 species. However, predation pressure seems to have a stronger effect on species  
46 densities, and consequently species segregation, than direct effects of the environmental  
47 gradients, resulting in apparent competition for these resources.

48 **1 INTRODUCTION**

49

50 Mechanisms relating to how closely-related species achieve stable coexistence were  
51 well studied in the period between the publication of Hutchinson's (1959) emblematic  
52 paper: "Why are there so many kinds of animals?", and the early 2000's, but particular  
53 assemblages have their own dynamics and can respond differently to a variety of  
54 phenomena. Different mechanisms, such as resource partitioning, intraspecific variation  
55 and frequency-dependent predation, can promote coexistence among species that have  
56 suffered selective pressure from interspecific competition, predation or  
57 morphological/physiological constraints (Chesson, 2000; Hausch, Vamosi, & Fox,  
58 2018; Schoener, 1974; Toft, 1985).

59 Niche segregation is frequently cited as a stabilizing mechanism that can provide  
60 long-term coexistence among species, though, in some cases, this mechanism can be  
61 insufficient to promote coexistence. In order for coexistence to be possible, other  
62 mechanisms, such as minimizing average fitness differences, density-dependent events  
63 and life-history tradeoffs have to act along with resource partitioning (Chesson, 2000;  
64 MacArthur, 1958; Mordecai, Jaramillo, Ashford, Hechinger, & Lafferty, 2016).  
65 Moreover, niche segregation enables morphological, physiological and behavioral  
66 adaptation of individuals, leading to character displacement, which also promotes  
67 coexistence (Brown & Wilson, 1956; Grant, 1972; Walter, 1991).

68 Despite the likely role of resource partitioning in maintaining diversity,  
69 mechanisms that do not require niche differentiation can also promote coexistence  
70 (Hubbell, 2001). For example, lottery models suggest that demographic mechanisms  
71 can control species' density fluctuations, preventing extinction through competition  
72 (Chesson & Warner, 1981). Also, intraspecific predation increases intraspecific effects  
73 in relation to interspecific effects, possibly allowing coexistence without niche  
74 segregation (Chesson, 1991). However, stable coexistence probably usually requires  
75 substantial ecological differences among species that are manifest as differences in their  
76 niches (Chesson, 1991, 2000; Leibold, 1995).

77 The idea that a single mechanism can promote stable coexistence has been  
78 largely criticized, given that interactions of several mechanisms can result in the  
79 coexistence of similar species (Clark et al., 2010; Edwards & Stachowicz, 2010;  
80 Mordecai et al., 2016), so coexistence between species probably results from a  
81 combination of several mechanisms. Coexistence through resource partitioning,

82 normally results from segregation in several niche dimensions, because these  
83 dimensions are rarely independent (Schoener, 1974; Toft, 1985). Partitioning along any  
84 of the three major niche axes seems to be sufficient to separate species (Iglesias-Rios,  
85 2004; Schoener, 1974), but habitat segregation is usually more effective in  
86 differentiating niches than food or time (MacArthur & Pianka, 1966; Schoener, 1974).

87 Little is known about what promotes coexistence among freshwater-shrimp  
88 species, but generally freshwater-shrimp assemblages are structured along  
89 environmental gradients, indicating some sort of niche differentiation in habitat  
90 (Gualberto, Menin, & Almeida, 2012; Kemenes, Forsberg, Magalhães, & Anjos, 2010).  
91 Among habitat features, current velocity is often cited as a major factor that can affect  
92 macroinvertebrate assemblage composition and distributions, including those of shrimp  
93 species (Lee & Fielder, 1984; Pardo & Armitage, 1997; Richardson & Cook, 2006).  
94 Only one study has examined coexistence among shrimp species in Central Amazonian  
95 streams (Walker, 2001) and it is not known which factors have the potential to maintain  
96 diversity among freshwater shrimp species in tropical streams.

97 It is known that predation plays an important role in structuring aquatic-  
98 invertebrate assemblages (Brooks & Dodson, 1965; Petrin, Schilling, Loftin, &  
99 Johansson, 2010; Power, 1990). Aquatic-invertebrate density can be depleted locally by  
100 predator activity and prey species occur at higher densities where predators are absent  
101 (Covich, Crowl, Hein, Townsend, & McDowell, 2009). Fish species are frequently cited  
102 as the most important predators on aquatic invertebrates, especially of shrimp  
103 assemblages (McPeek, 1990; Primavera, 1997; Salini, Blaber, & Brewer, 1990), so  
104 Amazonian shrimp assemblages could be also modulated by the presence of fish in  
105 rainforest streams. However, the principle shrimp-predators probably vary with the size  
106 of the shrimp, so most native fish species are potential predators. Although not closely  
107 related, fish could also be major competitors with shrimp, because many have  
108 overlapping diets. In the absence of information on which species of predators are most  
109 important in different stages of the life cycle, fish-assemblage composition may be the  
110 best way to measure the effect of potential predation or competition on shrimp-  
111 assemblages. Habitat variation also explains fish-assemblage composition in streams  
112 (Dias et al., 2016; Espírito-Santo, Magnusson, Zuanon, Mendonça, & Landeiro, 2009;  
113 Mendonça, Magnusson, & Zuanon, 2005), so effects of habitat on shrimp-abundance  
114 could be confounded by the effect of habitat on fish composition.

115 Fish and other aquatic assemblages in small rainforest streams also differ among  
116 watersheds due to historic and biogeographic effects on colonization (Mendonça et al.,  
117 2005). Holt and Chesson (2018) stated that divergence in environmental complexity  
118 between watersheds is the main element that allows ecological variation among species,  
119 and by doing so, enables a plurality of relations between species and habitat features.

120 In this study, we provide evidence that densities of Amazonian freshwater  
121 shrimp species in small rainforest-streams are related to habitat variation and species  
122 show strong habitat segregation. However, fish-assemblage composition and watersheds  
123 also affect the relationships between species abundance and environmental variables, so  
124 segregation of shrimp along environmental gradients may result from apparent  
125 competition.

126

## 127 **2 METHODS**

128

### 129 **2.1 Study system**

130

131 This study was carried out in *terra firme* streams in Ducke Forest Reserve (RFD), which  
132 is located 26 km north of the city of Manaus ( $2^{\circ} 56' S$ ,  $59^{\circ} 54' W$  at the administrative  
133 headquarters) and covers an area of ~10.000 ha. RFD has many small streams  
134 distributed in two drainage basins (East and West) and seven micro-basins (Acará, Água  
135 Branca, Barro Branco, Bolívia, Ipiranga, Tinga and Uberê). The eastern basin drains to  
136 the Amazon River and the western basin drains to the Negro River.

137

### 138 **2.2 Study design and sample collection**

139

140 Thirty-one first- to second-order streams were sampled, 15 belonging to the eastern  
141 watershed and 16 to the western, between May and July 2018. The sampling sites were  
142 chosen to coincide with 38 permanent study plots established by the INPA Graduate  
143 Program in Ecology (PPG-Eco) and coordinated by the Biodiversity Research Program  
144 of Western Amazonia (PPBio-AmOc). The sample units corresponded to fixed reaches  
145 of 50m in each stream, where environmental attributes were measured, and shrimp and  
146 fish sampled on the same day. Sample collection followed an adaptation of the standard  
147 PPBio protocol for fish (Mendonça et al., 2005).

148 Environmental attributes were estimated before shrimp sampling to avoid  
149 changes in habitat structure caused by collector movement. Water chemical  
150 characteristics were measured in the middle of the sample section (25m from the start)  
151 using a multiparameter water-quality meter (HORIBA® – U-52). Channel hydraulic  
152 characteristics and habitat physical structure were estimated in four transverse transects  
153 spaced 16m apart along the sample reach. Channel morphometry at the position of each  
154 of the four transects was represented by the total channel width, measured with a tape  
155 measure, and by the average depth, measured at nine equidistant points across the  
156 channel width of each transect. Substrate type was registered at each of the nine depth-  
157 measurement points and was categorized as sand, clay, pebble, litter, fine litter, root,  
158 trunk or macrophyte. The current velocity of the stream was estimated using a flow  
159 meter (Global Water Flow Probe® – FP111), which was placed in the middle of the  
160 water column at the center of each transect.

161 After estimating the environmental attributes, the 50m reaches were surrounded  
162 at their boundaries with 5mm stretch-mesh nets, and an additional net was used to  
163 subdivide the reach sequentially at each of the transects to facilitate sampling (Espírito-  
164 Santo, Rodríguez, & Zuanon, 2013). Shrimp and fish were captured simultaneously  
165 through active sampling using fine-mesh hand nets manipulated by two researchers  
166 moving in the downstream-upstream direction. Sampling was carried out in the daytime  
167 and by the same collectors during two hours. Shrimps could not be reliably identified in  
168 the field, so they were kept in well-aerated plastic bags and later killed by anesthesia in  
169 alcohol dilute in stream water and then fixed in 70% alcohol. Specimens were identified  
170 to the lowest possible taxonomic level with the aid of specialized guides. Fish were  
171 captured and kept in plastic containers with stream water and mechanical aerators.  
172 Individuals were identified from field guides (Zuanon et al., 2015) and returned to the  
173 main channel. This method is effective for field identification of RFD fish (Espírito-  
174 Santo, Magnusson, Zuanon, & Emílio, 2011).

175

### 176 **2.3 Data analysis**

177

178 All statistical analyses were performed in *R* statistical software version 3.3.3 (R Core  
179 Team, 2017). Data corresponded to the values of the number of individuals of the  
180 species and the environmental variables in the 31 stream reaches. In order to evaluate  
181 multicollinearity, tolerance (TOL) was tested using the *imcdiag* function of the *mctest*

182 package (Imdad & Aslam, 2018). When collinearity between variables was detected,  
 183 those that generated an independent effect greater than 10% were selected. Due to the  
 184 low number of sample units, only pH, temperature (°C), current velocity (m/s), depth  
 185 (m) and substrate (% sand and litter) were analyzed. These variables were selected from  
 186 those that had tolerance >0.1 based on their variability among the sample units and their  
 187 importance for aquatic assemblages, especially shrimps, according to ecological  
 188 literature (Supporting information, Tables S1 and S2). However, these are correlated  
 189 with other variables and the data for all measured variables, including those not used in  
 190 the analyses, are presented in the Table 1.

191 Multiple regressions were used to determine the relationships among the number  
 192 of individuals of the species and the environmental variables, with the number of  
 193 individuals as the response variable (dependent) and the environmental variables as  
 194 predictors. Although the dependent variables were based on counts, the numbers of  
 195 individuals involved was very large, permitting use of least-squares regressions with  
 196 assumed normal distribution of residuals. To illustrate the partial regressions resulting  
 197 from the multiple regressions, the *car* package (Fox & Weisberg, 2011) was used  
 198 through the *avPlots* function.

199

### 200 2.3.1 Specialization and habitat segregation

201

202 To test whether the distributions of species along the gradients were different from the  
 203 availability of gradient levels in the plots, we used Kolmogorov-Smirnov (KS) tests to  
 204 compare the distribution of the number of individuals along the different gradients with  
 205 the distribution of the number of sample units (reaches of streams) along the gradients.  
 206 The significance of the test was based on the chi-square distribution from the Goodman  
 207 equation (1954):

208

$$209 X^2 = 4D^2 \frac{n_1 n_2}{n_1 + n_2}$$

210

211 where  $D$  represents the test coefficient, and  $n_1$  and  $n_2$  correspond to the number of units  
 212 in each distribution. We generally used the number of plots (31) for both  $n_1$  and  $n_2$ ,  
 213 because shrimp in each plot are not independent of the mean value of the gradient in the  
 214 plot. For two species found in only 30 of the 31 plots,  $n_2$  was 30. The second test

215 compared the distributions across species along resource gradients, but only for those  
216 species pairs in which at least one species was considered to be a specialist based on the  
217 KS tests.

218

### 219 **2.3.2 Fish-assemblage composition**

220

221 A Principal Coordinate Analysis (PCoA) axis was used to summarize the composition  
222 of fish assemblages among the plots using the *vegan* package (Oksanen et al., 2017)  
223 through the *vegdist* function, with the Bray-Curtis distance measure. The first axis,  
224 which extracted most of the variation explained, was chosen to represent fish  
225 composition. Since most abundant fish species captured feed on invertebrates (terrestrial  
226 insects, aquatic insects and crustaceans) and there is a lack of information on predators  
227 of different-sized shrimp, we assumed that the assemblage-composition axis would be  
228 representative of potential predation, though we recognize that it could also represent  
229 the potential for competition between fish and shrimp.

230 Because of the strong relationship between fish composition and some  
231 environmental variables, the effects of the environmental variables were evaluated with  
232 and without fish composition in the model. Path analysis (Wright, 1921) was used to  
233 evaluate the relative magnitudes of direct and indirect effects (through fish composition)  
234 of the environmental variables.

235

### 236 **2.3.3 Watershed effect**

237

238 To test whether the effect of predictor variables on the number of individuals depended  
239 on the effect of the watersheds (east or west); an interaction model was constructed  
240 through multiple regressions. Due to the low number of sample units, interactions were  
241 also included in simple models with the variables individually.

242

## 243 **3 RESULTS**

244

245 Were captured four shrimp species, *Macrobrachium inpa*, *Macrobrachium nattereri*,  
246 *Pseudopalaemon amazonensis* and Morphospecies 1 (an apparently undescribed species  
247 of *Pseudopalaemon*), all from the family Palaemonidae. *Macrobrachium inpa* was the  
248 most frequently found species and accounted for 1787 (54.2%) individuals, followed by

249 *P. amazonensis* (965), *M. nattereri* (530) and Morphospecies 1 (13). Due to the small  
250 number of individuals captured, Morphospecies 1 was not included in the statistical  
251 analyses.

252 Due to differences in relative magnitude between the general effect of the path  
253 analysis and the effect obtained by multiple regressions ( $R^2$ ) of the environmental  
254 variables and fish-assemblage composition with the number of shrimps (Figure 1; Table  
255 2), the regression model was constructed with and without the variable fish composition  
256 for each species individually.

257

258 **3.1 *Macrobrachium inpa***

259

260 Without the inclusion of fish composition (Supporting information, Table S3), *M. inpa*  
261 was negatively related to current velocity ( $t = -2.515$ ,  $p = 0.01$ ) and channel depth ( $t = -$   
262  $2.086$ ,  $p = 0.04$ ). Analyzed independently, fish composition did not significantly  
263 influence the distribution of this species ( $t = 1.435$ ;  $p = 0.162$ ). In the complete model  
264 (habitat + fish composition – Supporting information, Table S4), this species maintained  
265 a significant relationship with current velocity ( $t = -2.017$ ;  $p = 0.05$ ), but not with any  
266 other variable (Figure 2c). Possibly, no significant relationship with channel depth was  
267 found in the complete model because its effect was confounded by the high correlation  
268 between fish composition and depth (path coefficient =  $-0.63$ ).

269

270 **3.2 *Macrobrachium nattereri***

271

272 Without the inclusion of fish composition, *M. nattereri* did not exhibit significant  
273 relationships with any habitat element ( $p \geq 0.07$ ), though the low probability associated  
274 with the null hypothesis indicated a probable type II error in two cases. When analyzed  
275 separately, fish composition significantly influenced the distribution of this species ( $t =$   
276  $3.056$ ,  $p = 0.004$ ). In the complete model, this species showed a significant relationship  
277 with fish composition ( $t = 2.817$ ;  $p = 0.009$ ) (Figure 3g) and also showed a significant  
278 relationship with channel depth ( $t = 2.121$ ;  $p = 0.044$ ).

279

280 **3.3 *Pseudopalaemon amazonensis***

281

282 Without inclusion of fish composition, *P. amazonensis* did not show significant  
283 relationships with any habitat element ( $p \geq 0.11$ ). Singly, fish composition significantly  
284 influenced the distribution of this species ( $t = 2.711$ ;  $p = 0.01$ ). In the complete model,  
285 this species continued to show a significant relationship with fish composition ( $t =$   
286  $2.132$ ;  $p = 0.04$ ) (Figure 4g) and not with any other variable.

287

### 288 **3.4 Specialization and habitat segregation**

289

290 Specialization was detected for *M. inpa* along the current-velocity gradient ( $D_{KS} =$   
291  $0.198$ ;  $p = 0.01$ ) (Figure 5a) and for *P. amazonensis* along the pH ( $D_{KS} = 0.213$ ;  $p =$   
292  $0.01$ ) (Figure 5b) and channel-depth ( $D_{KS} = 0.165$ ;  $p = 0.05$ ) gradients (Figure 5c) (more  
293 information can be found in Supporting information, Table S5). Current velocity and  
294 pH significantly segregated the distributions of the three species (Kolmogorov-Smirnov  
295 test,  $p \leq 0.049$ ), indicating that these habitat aspects have the greatest potential to  
296 differentiate the niches of the species (Figure 6). There was also evidence of segregation  
297 along the depth gradient between *M. nattereri* and *P. amazonensis* ( $p = 0.073$ ), but the  
298 overlap was higher than for the other variables (Supporting information, Table S6).

299

### 300 **3.5 Watershed effect**

301

302 Watersheds did not have a strong effect on the relationships between predictor variables  
303 and the number of individuals for most species. However, for *Macrobrachium nattereri*  
304 a likely interaction was detected for pH, with a low probability associated with the null  
305 hypothesis ( $t = -2.097$ ;  $p = 0.05$ ) (Figure 7a; Table 3). Simple regressions detected a  
306 similar result to the multiple interaction model, in which only the relationship between  
307 *M. nattereri* and pH changed between watersheds ( $t = -2.394$ ;  $p = 0.024$ ). Sand  
308 proportion also had a low probability associated with the null hypothesis ( $t = -1.958$ ;  $p =$   
309  $0.069$ ), and this may indicate a type II error, but the simple-regression model showed a  
310 high probability associated with the null hypothesis for this variable ( $t = -0.836$ ;  $p =$   
311  $0.41$ ) for this variable.

312

## 313 **4 DISCUSSION**

314

315 This is the first study demonstrating habitat partitioning among shrimp species in  
316 Central Amazonia. Of the environmental features investigated, only current velocity and  
317 depth were significantly related to shrimp-species abundance. Stream hydraulic  
318 characteristics have been reported as the main factors determining shrimp-assemblage  
319 variation in other regions (Kemenes et al., 2010; Novak, Bayliss, Garcia, Pusey, &  
320 Douglas, 2017; Richardson & Cook, 2006) and, as a general pattern, *M. inpa* inhabited  
321 shallow locations with lower current velocities. *M. nattereri* while *P. amazonensis* were  
322 more abundant in deeper places with higher current velocities.

323 Substrate variables, especially cover of leaf litter, have often been found to be  
324 important for habitat segregation in aquatic assemblages, such as fish species in forest  
325 streams (Leitão et al., 2015), but we detected no effect of substrate on the densities of  
326 any of the shrimp species. This may be because the shrimp are really generalists in  
327 relation to substrate or, we think more likely, that any segregation between the species  
328 among substrates occurs at smaller scales than the 50m stream segments used as  
329 sampling units in this study.

330 Temperature seems to have little effect on the species we studied, possibly  
331 because of the small variation in this variable in our study site. Depth was a strong  
332 predictor of abundance for some, but not all species. In general, it is evident that shrimp  
333 assemblages in stream systems are structured by habitat variation, but much of this  
334 effect could be mediated through the relationship between habitat variation and fish-  
335 assemblage composition, which was also related to shrimp-abundance. Variation in  
336 shrimp density can be strongly related to fish composition in inland waters (Covich et  
337 al., 2009; Mace & Rozas, 2018) and predation has been frequently reported as a factor  
338 modulating shrimp response to habitat (Covich et al., 2009; Crowl & Covich, 1994).  
339 Thus, we conclude that predation is probably more important to shrimp distributions in  
340 rainforest-streams than habitat variation.

341 Two of the three species showed habitat specialization, mainly related to  
342 hydraulic features. Specialization is expected to be stronger in predictable habitats  
343 (Büchi & Vuilleumier, 2014) so habitat specialists thrive in less-disturbed and less-  
344 fragmented environments (Devictor, Julliard, & Jiguet, 2008), such as Amazonian  
345 rainforest-streams. Habitat segregation was evident along current-velocity and pH  
346 gradients. Current velocity is among the variables with the strongest potential to  
347 differentiate habitat use in rainforest-stream shrimp (Iwata et al., 2003). In general, pH  
348 seems to be a weak factor to explain freshwater shrimp variation. However, given the

349 amplitude of variation along the pH gradient in the study site, it is expected that species  
350 in that system could respond to variation in pH. Depth was also a strong predictor,  
351 although it did not segregate the distribution of all three species. We also detected more  
352 similarities in habitat utilization between some species than others, and those species  
353 were found to share a strong relationship with fish-assemblage composition. Therefore,  
354 the segregation we recorded could be more a result of apparent competition than direct  
355 interactions among the shrimp species.

356 Apparent competition characterizes negative indirect interactions between  
357 species that share a common enemy (Holt, 1977). Assuming that these enemies are  
358 prey-generalists, it is expected that these prey will, in some ways, converge by sharing  
359 such enemies (Holt & Bonsall, 2017; Mittelbach & Chesson, 1987). A common  
360 competitor could have the same effect. Predation, as well as competition, has the  
361 potential to modulate the way species segregate resource dimensions associated with the  
362 niche (Chase et al., 2002; Kotler & Holt, 1989; Sommers & Chesson, 2019). *M. nattereri* and *P. amazonensis* were strongly related to fish-assemblage composition and  
363 differ very little in habitat utilization, so, apparent competition seems to be stronger  
364 between them. However, these species also differ most in size morphology and foraging  
365 mode (Kensley & Walker, 1982), so they are unlikely to be strong competitors.

367 Stable coexistence is dependent on relative intraspecific and interspecific effects  
368 on species density, so, generalist predation can switch the relative importance of  
369 intraspecific and interspecific competition, destabilizing coexistence (Chase et al., 2002;  
370 Chesson, 2000, 2018; Chesson & Kuang, 2008). The pattern observed in this study  
371 indicates that species with distributions strongly related to fish composition may have  
372 coexistence weakened by sharing predation, or competition, for fish. While the causes  
373 of segregation are uncertain, habitat partitioning may be sufficient to facilitate  
374 coexistence among rainforest-stream shrimp.

375 Species seem to respond to habitat variables similarly in both watersheds, with  
376 the exception of *M. nattereri*. The divergent behavior in relation to pH between  
377 watersheds observed for *M. nattereri* may indicate the existence of a cryptic species.

378 We conclude that the distributions of small rainforest-stream shrimps in 50m  
379 segments of stream are affected by habitat variation, mainly in hydraulic features.  
380 However, habitat seems to be more important for some species than others and  
381 segregation occurred only along the current-velocity and pH gradients. The strong  
382 relationship between fish composition and shrimp-species abundances indicates that

383 predation is an important modulator of potential interactions in these assemblages. Only  
384 one species of shrimp appeared to be affected by watersheds and pH was the only  
385 gradient that affected this species differently between watersheds.

386 An outstanding question is why this system has only four species of shrimps? It  
387 seems to be sufficiently heterogeneous to encompass more species. There are about 70  
388 species of fish in the reserve (Zuanon et al., 2015), so fish seem to be able to divide the  
389 niche much more finely. Perhaps there has not been enough time for other species to  
390 colonize the vacant niche, or environmental variance limits species packing (MacArthur  
391 & Levins, 1967; May & MacArthur, 1972; Roughgarden & Feldman, 1975). However,  
392 there are only about 35 species of freshwater shrimp found in Brazil (De Grave et al.,  
393 2015; Magalhães, Campos, Collins, & Mantelatto, 2016), of which about 15 are found  
394 in Central Amazonia (Kensley & Walker, 1982). Therefore, perhaps four species is not  
395 particularly low for that system and it may be that shrimp simply cannot divide the  
396 habitat as finely as fish, or that predation pressure or competition with fish has not  
397 allowed shrimp to divide resources more finely.

398

## 399 **ACKNOWLEDGMENTS**

400

401 We are grateful to Programa de Pesquisa Ecológica de Longa Duração for funding this  
402 project (Grant number: 15/2016; Project: 88887.136282/2017-00 - 441282/2016-4).  
403 Specimens sampling was conducted under permits issued through Sisbio/ICMBio  
404 number 61473-1; cod 29553912. We also want to thank PPBio for the maintenance of  
405 study plots, and CENBAM and Projeto Igarapés for logistic support.

406

## 407 **DATA AVAILABILITY**

408

409 The authors declare that the dataset used in this manuscript is not publicly available but  
410 are available from the corresponding author on reasonable request.

411

## 412 **CONFLICT OF INTEREST**

413

414 The authors of this manuscript have no conflict of interest to declare.

## 415 REFERENCES

- 416  
 417 Brooks, J. L., & Dodson, S. I. (1965). Predation, body size, and composition of  
 418 plankton. *Science*, 150(3692), 28–35. doi:10.1126/science.150.3692.28
- 419 Brown, W. L., & Wilson, E. O. (1956). Character displacement. *Systematic Zoology*,  
 420 5(2), 49–64. doi:10.2307/2411924
- 421 Büchi, L., & Vuilleumier, S. (2014). Coexistence of specialist and generalist species is  
 422 shaped by dispersal and environmental factors. *The American Naturalist*, 183(5),  
 423 612–624. doi:10.1086/675756
- 424 Chase, J. M., Abrams, P. A., Grover, J. P., Diehl, S., Chesson, P., Holt, R. D., . . . Case,  
 425 T. J. (2002). The interaction between predation and competition: a review and  
 426 synthesis. *Ecology Letters*, 5(2), 302–315. doi:10.1046/j.1461-  
 427 0248.2002.00315.x
- 428 Chesson, P. (1991). A need for niches? *Trends in Ecology & Evolution*, 6(1), 26–28.  
 429 doi:10.1016/0169-5347(91)90144-m
- 430 Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of  
 431 Ecology and Systematics*, 31(1), 343–366. doi:10.1146/annurev.ecolsys.31.1.343
- 432 Chesson, P. (2018). Updates on mechanisms of maintenance of species diversity.  
 433 *Journal of Ecology*, 106(5), 1773–1794. doi:10.1111/1365-2745.13035
- 434 Chesson, P., & Kuang, J. J. (2008). The interaction between predation and competition.  
 435 *Nature*, 456(7219), 235–238. doi:10.1038/nature07248
- 436 Chesson, P., & Warner, R. R. (1981). Environmental variability promotes coexistence  
 437 in lottery competitive systems. *The American Naturalist*, 117(6), 923–943.  
 438 doi:10.1086/283778
- 439 Clark, J. S., Bell, D., Chu, C., Courbaud, B., Dietze, M., Hersh, M., . . . Wyckoff, P.  
 440 (2010). High-dimensional coexistence based on individual variation: a synthesis  
 441 of evidence. *Ecological Monographs*, 80(4), 569–608. doi:10.1890/09-1541.1
- 442 Covich, A. P., Crowl, T. A., Hein, C. L., Townsend, M. J., & McDowell, W. H. (2009).  
 443 Predator-prey interactions in river networks: comparing shrimp spatial refugia in  
 444 two drainage basins. *Freshwater Biology*, 54(3), 450–465. doi:10.1111/j.1365-  
 445 2427.2008.02121.x
- 446 Crowl, T. A., & Covich, A. P. (1994). Responses of a freshwater shrimp to chemical  
 447 and tactile stimuli from a large decapod predator. *Journal of the North American  
 448 Benthological Society*, 13(2), 291–298. doi:10.2307/1467247
- 449 De Grave, S., Smith, K. G., Adeler, N. A., Allen, D. J., Alvarez, F., Anker, A., . . .  
 450 Wowor, D. (2015). Dead shrimp blues: a global assessment of extinction risk in  
 451 freshwater shrimps (Crustacea: Decapoda: Caridea). *PLoS ONE*, 10(3), 1–14.  
 452 doi:10.1371/journal.pone.0120198
- 453 Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist  
 454 species along spatial gradients of habitat disturbance and fragmentation. *Oikos*,  
 455 117, 507–514. doi:10.1111/j.2008.0030-1299.16215.x
- 456 Dias, M. S., Zuanon, J., Couto, T. B. A., Carvalho, M., Carvalho, L. N., Espírito-Santo,  
 457 H. M. V., & Tedesco, P. A. (2016). Trends in studies of Brazilian stream fish  
 458 assemblages. *Natureza & Conservação*, 14(2), 106–111.  
 459 doi:10.1016/j.ncon.2016.06.003
- 460 Edwards, K. F., & Stachowicz, J. J. (2010). Multivariate trade-offs, succession, and  
 461 phenological differentiation in a guild of colonial invertebrates. *Ecology*, 91(11),  
 462 3146–3152. doi:10.1890/10-0440.1

- 463 Espírito-Santo, H. M. V., Magnusson, W. E., Zuanon, J., & Emilio, T. (2011). Short-  
 464 term impacts of fish removal from small Amazonian forest streams. *Biotropica*,  
 465 43(5), 529–532. doi:10.1111/j.1744-7429.2011.00800.x
- 466 Espírito-Santo, H. M. V., Magnusson, W. E., Zuanon, J., Mendonça, F. P., & Landeiro,  
 467 V. L. (2009). Seasonal variation in the composition of fish assemblages in small  
 468 Amazonian forest streams: evidence for predictable changes. *Freshwater  
 469 Biology*, 54(3), 536–548. doi:10.1111/j.1365-2427.2008.02129.x
- 470 Espírito-Santo, H. M. V., Rodríguez, M. A., & Zuanon, J. (2013). Reproductive  
 471 strategies of Amazonian stream fishes and their fine-scale use of habitat are  
 472 ordered along a hydrological gradient. *Freshwater Biology*, 58(12), 2494–2504.  
 473 doi:10.1111/fwb.12225
- 474 Fox, J., & Weisberg, S. (2011). An R companion to applied regression (Version 2).  
 475 Sage, Thousand Oaks, CA.
- 476 Goodman, L. A. (1954). Kolmogorov-Smirnov tests for psychological research.  
 477 *Psychological Bulletin*, 51(2), 160–168. doi:10.1037/h0060275
- 478 Grant, P. R. (1972). Convergent and divergent character displacement. *Biological  
 479 Journal of the Linnean Society*, 4(1), 39–68. doi:10.1111/j.1095-  
 480 8312.1972.tb00690.x
- 481 Gualberto, T. L., Menin, M., & Almeida, L. O. (2012). Population structure, fecundity  
 482 and ecological aspects of freshwater shrimp species (Decapoda, Palaemonidae)  
 483 of an urban forest fragment in central Amazonia, Brazil. *Crustaceana*, 85(10),  
 484 1205–1219. doi:10.1163/156854012x651349
- 485 Hausch, S., Vamosi, S. M., & Fox, J. W. (2018). Effects of intraspecific phenotypic  
 486 variation on species coexistence. *Ecology*, 99(6), 1453–1462.  
 487 doi:10.1002/ecy.2346
- 488 Holt, G., & Chesson, P. (2018). The role of branching in the maintenance of diversity in  
 489 watersheds. *Freshwater Science*, 37(4), 000–000. doi:10.1086/700680
- 490 Holt, R. D. (1977). Predation, apparent competition, and the structure of prey  
 491 communities. *Theoretical Population Biology*, 12(2), 197–229.  
 492 doi:10.1016/0040-5809(77)90042-9
- 493 Holt, R. D., & Bonsall, M. B. (2017). Apparent competition. *Annual Review of Ecology,  
 494 Evolution, and Systematics*, 48(1), 447–471. doi:10.1146/annurev-ecolsys-  
 495 110316-022628
- 496 Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography* (Vol.  
 497 1): Princeton University.
- 498 Hutchinson, G. E. (1959). Homage to Santa Rosalia or Why Are There So Many Kinds  
 499 of Animals? *The American Naturalist*, 93(870), 145–159. doi:10.1086/282070
- 500 Iglesias-Rios, R. (2004). A teoria do nicho ecológico: benefícios e malefícios. In:  
 501 Coelho A. S., Loyola R. D., Souza M. B. G. In *Ecologia Teórica: desafios para  
 502 o aperfeiçoamento da Ecologia no Brasil* (pp. 27–41): O Lutador, Belo  
 503 Horizonte.
- 504 Imdad, M. U., & Aslam, M. (2018). Multicollinearity diagnostic measures.
- 505 Iwata, T., Inoue, M., Nakano, S., Miyasaka, H., Doi, A., & Covich, A. P. (2003).  
 506 Shrimp abundance and habitat relationships in tropical rain-forest streams,  
 507 Sarawak, Borneo. *Journal of Tropical Ecology*, 19(4), 387–395.  
 508 doi:10.1017/s0266467403003432
- 509 Kemenes, A., Forsberg, B. R., Magalhães, C., & Anjos, H. (2010). Environmental  
 510 factors influencing the community structure of shrimps and crabs (Crustacea:  
 511 Decapoda) in headwater streams of the Rio Jaú, Central Amazon, Brazil. *Pan-  
 512 American Journal of Aquatic Sciences*, 5(1), 36-46.

- 513 Kensley, B., & Walker, I. (1982). *Palaemonidae shrimp from the Amazon basin*  
 514 (*Crustacean: Decapods: Natantia*) (Vol. 362): Smithsonian Contribution to  
 515 Zoology.
- 516 Kotler, B. P., & Holt, R. D. (1989). Predation and competition: the interaction of two  
 517 types of species interactions. *Oikos*, 54(2), 256–260. doi:10.2307/3565279
- 518 Lee, C. L., & Fielder, D. R. (1984). Swimming reponse to water current stimulus in the  
 519 freshwater prawn, *Macrobrachium australiense* Holthius 1950. *Crustaceana*,  
 520 46(3), 249–256. doi:10.1163/156854084X00153
- 521 Leibold, M. A. (1995). The niche concept revisited: mechanistic models and community  
 522 context. *Ecology*, 76(5), 1371–1382. doi:10.2307/1938141
- 523 Leitão, R. P., Sánchez-Botero, J. I., Kasper, D., Trivério-Cardoso, V., Araújo, C. M.,  
 524 Zuanon, J., & Caramaschi, É. P. (2015). Microhabitat segregation and fine  
 525 ecomorphological dissimilarity between two closely phylogenetically related  
 526 grazer fishes in an Atlantic Forest stream, Brazil. *Environmental Biology of*  
 527 *Fishes*, 98(9), 2009–2019. doi:10.1007/s10641-015-0423-3
- 528 MacArthur, R. H. (1958). Population ecology of some warblers of northeastern  
 529 coniferous forests. *Ecology*, 39(4), 599–619. doi:10.2307/1931600
- 530 MacArthur, R. H., & Levins, R. (1967). The limiting similarity, convergence, and  
 531 divergence of coexisting species. *The American Naturalist*, 101(921), 377–385.  
 532 doi:10.1086/282505
- 533 MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The*  
 534 *American Naturalist*, 100(916), 603–609. doi:10.1086/282454
- 535 Mace, M. M., & Rozas, L. P. (2018). Fish predation on juvenile penaeid shrimp:  
 536 examining relative predator impact and size-selective predation. *Estuaries and*  
 537 *Coasts*. doi:10.1007/s12237-018-0409-4
- 538 Magalhães, C., Campos, M. R., Collins, P. A., & Mantelatto, F. L. (2016). Diversity,  
 539 distribution and conservation of freshwater crabs and shrimps in South America.  
 540 In *A global overview of the conservation of freshwater decapod crustaceans* (pp.  
 541 303–322): Springer.
- 542 May, R. M., & MacArthur, R. H. (1972). Niche overlap as a function of environmental  
 543 variability. *Proceedings of the National Academy of Sciences*, 69(5), 1109–1113.  
 544 doi:10.1073/pnas.69.5.1109
- 545 McPeek, M. A. (1990). Behavioral differences between *Enallagma* species (Odonata)  
 546 influencing differential vulnerability to predators. *Ecology*, 71(5), 1714–1726.  
 547 doi:10.2307/1937580
- 548 Mendonça, F. P., Magnusson, W. E., & Zuanon, J. (2005). Relationships between  
 549 habitat characteristics and fish assemblages in small streams of Central  
 550 Amazonia. *Copeia*, 2005(4), 751–764. doi:10.1643/0045-  
 551 8511(2005)005[0751:rbhcaf]2.0.co;2
- 552 Mittelbach, G. G., & Chesson, P. L. (1987). Predation risk: indirect effects on fish  
 553 populations. In W. C. K. A. Sih (Ed.), *Predation: direct and indirect impacts on*  
 554 *aquatic communities* (pp. 315–332): University Press of New England Hanover,  
 555 NH.
- 556 Mordecai, E. A., Jaramillo, A. G., Ashford, J. E., Hechinger, R. F., & Lafferty, K. D.  
 557 (2016). The role of competition - colonization tradeoffs and spatial  
 558 heterogeneity in promoting trematode coexistence. *Ecology*, 97(6), 1484–1496.  
 559 doi:10.1890/15-0753.1
- 560 Novak, P. A., Bayliss, P., Garcia, E. A., Pusey, B. J., & Douglas, M. M. (2017).  
 561 Ontogenetic shifts in habitat use during the dry season by an amphidromous

- 562 shrimp in a tropical lowland river. *Marine and Freshwater Research*, 68(12),  
563 2275–2288. doi:10.1071/mf16375
- 564 Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., . . .  
565 Wagner, H. (2017). Community Ecology Package.
- 566 Pardo, I., & Armitage, P. D. (1997). Species assemblages as descriptors of  
567 mesohabitats. *Hydrobiologia*, 344(1/2/3), 111–128.  
568 doi:10.1023/A:1002958412237
- 569 Petrin, Z., Schilling, E. G., Loftin, C. S., & Johansson, F. (2010). Predators shape  
570 distribution and promote diversification of morphological defenses in  
571 Leucorrhinia, Odonata. *Evolutionary Ecology*, 24(5), 1003–1016.  
572 doi:10.1007/s10682-010-9361-x
- 573 Power, M. E. (1990). Effects of fish in river food webs. *Science*, 250(4982), 811–814.  
574 doi:10.1126/science.250.4982.811
- 575 Primavera, J. (1997). Fish predation on mangrove-associated penaeids. *Journal of*  
576 *Experimental Marine Biology and Ecology*, 215(2), 205–216.  
577 doi:10.1016/s0022-0981(97)00046-4
- 578 R Core Team. (2017). A language and environment for statistical computing. Vienna,  
579 Austria.
- 580 Richardson, A. J., & Cook, R. A. (2006). Habitat use by caridean shrimps in lowland  
581 rivers. *Marine and Freshwater Research*, 57(7), 695–701. doi:10.1071/mf05160
- 582 Roughgarden, J., & Feldman, M. (1975). Species packing and predation pressure.  
583 *Ecology*, 56(2), 489–492. doi:10.2307/1934982
- 584 Salini, J. P., Blaber, S. J. M., & Brewer, D. T. (1990). Diets of piscivorous fishes in a  
585 tropical Australian estuary, with special reference to predation on penaeid  
586 prawns. *Marine Biology*, 105(3), 363–374. doi:10.1007/bf01316307
- 587 Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*,  
588 185(4145), 27–39. doi:10.1126/science.185.4145.27
- 589 Sommers, P., & Chesson, P. (2019). Effects of predator avoidance behavior on the  
590 coexistence of competing prey. *The American Naturalist*, 193(5), E000.  
591 doi:10.1086/701780
- 592 Toft, C. A. (1985). Resource partitioning in amphibians and reptiles. *Copeia*, 1, 1–21.  
593 doi:10.2307/1444785
- 594 Walker, I. (2001). The pattern of distribution of the two sibling species *Euryrhynchus*  
595 *amazoniensis* and *E. burchelli* (Decapoda, Palaemonidae) in the Central  
596 Amazonian blackwater stream Tarumã-Mirim, and the problem of coexistence.  
597 *Amazoniana*, 16(3/4), 565–578.
- 598 Walter, G. H. (1991). What is resource partitioning? *J. theor. Biol.*, 150, 137–143.  
599 doi:10.1016/S0022-5193(05)80327-3
- 600 Wright, S. (1921). Correlation and causation. *J. Agri. Res.*, 20, 557–585.
- 601 Zuanon, J., P., M. F., Espírito-Santo, H. M. V., Dias, M. S., Galuch, A. V., & Akama,  
602 A. (2015). *Guia de peixes da Reserva Adolpho Ducke*: INPA, Manaus.
- 603

## 604 TABLES

605 Table 1. Mean values of environmental variables in sample sites.

606

Environmental Variables																		
Sites	Watershed	pH	Temp. (°C)	Cond. (µS/cm)	O <sub>2</sub> (mg/L)	Cur. vel. (m/s)	Width (m)	Depth (m)	Area (m <sup>2</sup> )	Discharge (m <sup>3</sup> /s)	SA %	CL %	LT %	FL %	MC %	RT %	TR %	PB %
AC11	West	5.1	23.23	<b>0.024</b>	6.21	0.075	2.9	0.3	1.05	0.08	<b>0.56</b>	<b>0.00</b>	0.31	0.03	0.08	<b>0.00</b>	0.03	<b>0.00</b>
AC12	West	5.39	24.27	0.015	4.4	0.162	2.3	0.18	0.54	0.09	0.47	0.00	0.28	<b>0.00</b>	0.19	0.00	0.05	0.00
AC13	West	5.11	<b>24.73</b>	0.013	4.14	0.025	2.25	0.44	1.29	0.03	0.53	0.00	0.25	0.08	0.03	0.08	0.03	0.08
AC14	West	5.87	23.51	0.016	6.34	0.1	<b>1.36</b>	0.15	0.26	0.03	0.53	0.00	0.36	0.00	<b>0.00</b>	0.06	0.05	0.05
AC15	West	<b>6.1</b>	23.44	0.012	4.12	0.112	1.68	0.21	0.47	0.05	0.4	0.00	0.4	0.06	0.14	0.00	<b>0.00</b>	0.00
AC16	West	<b>4.86</b>	<b>23.04</b>	0.014	6.88	0.1	1.47	0.18	0.34	0.03	0.39	0.00	0.17	0.00	0.08	<b>0.17</b>	0.17	<b>0.17</b>
AC22	West	5.12	22.96	<b>0.01</b>	<b>3.63</b>	0.262	2.08	0.24	0.62	0.16	0.36	0.00	0.28	0.00	0.33	0.000	0.03	0.00
AC23	West	5.24	23.59	0.014	4.4	0.075	2.01	0.42	1.09	0.08	0.48	0.00	0.19	0.00	0.06	0.12	0.12	0.12
BO11	West	5.63	24.18	0.021	<b>8.95</b>	<b>0.00</b>	1.9	0.42	1.00	<b>0.00</b>	0.36	0.00	0.47	0.00	0.06	0.00	0.11	0.00
BO12	West	5.94	24.01	0.011	4.75	<b>0.425</b>	2.08	0.29	0.76	0.32	0.47	0.00	0.36	0.00	0.14	0.00	0.00	0.00
BO13	West	5.46	23.56	0.015	6.2	0.187	1.73	0.21	0.49	0.09	0.31	0.05	0.22	0.03	<b>0.39</b>	0.00	0.00	0.00
BO14	West	5.56	23.47	0.013	5.24	0.262	<b>2.75</b>	0.35	1.25	0.33	0.25	0.03	0.5	0.00	0.19	0.00	0.03	0.00
BO15	West	5.81	23.58	0.019	5.81	0.05	1.94	0.24	0.63	0.03	<b>0.06</b>	0.00	<b>0.66</b>	0.00	0.23	0.00	0.03	0.00
BO16	West	6.09	23.55	0.012	4.74	0.15	1.64	<b>0.1</b>	<b>0.18</b>	0.03	0.475	0.00	<b>0.15</b>	0.02	0.2	0.00	0.05	0.00
BO21	West	4.94	23.57	0.012	5.53	0.25	2.2	0.4	1.12	0.28	0.36	0.06	0.15	0.00	0.00	0.12	<b>0.21</b>	0.12
BO22	West	5.72	23.59	0.012	5.01	0.2	3.23	<b>0.49</b>	<b>1.94</b>	<b>0.39</b>	0.43	<b>0.14</b>	0.17	<b>0.11</b>	0.09	0.03	0.06	0.03
BR21	East	5.33	24.4	0.01	3.75	0.25	2.59	<b>0.32</b>	0.99	0.25	0.53	<b>0.00</b>	0.22	0.08	0.08	<b>0.00</b>	0.08	<b>0.00</b>
IP11	East	<b>6.53</b>	23.59	0.009	4.54	0.137	1.33	0.17	0.28	0.04	0.43	0.08	0.3	0.11	0.08	0.00	<b>0.00</b>	0.00
IP12	East	4.91	23.47	<b>0.008</b>	3.97	0.137	1.55	0.16	0.31	0.04	0.64	0.00	<b>0.25</b>	0.03	0.06	0.00	0.00	0.00
IP13	East	5.93	<b>24.57</b>	0.01	4.58	0.225	1.53	0.13	0.24	0.05	0.53	<b>0.14</b>	0.11	<b>0.00</b>	0.22	0.00	0.00	0.00
IP14	East	6.05	24.18	0.01	6.48	0.212	2.65	0.19	0.63	0.13	0.54	0.00	0.2	<b>0.12</b>	0.06	0.00	0.08	0.00

IP15	East	5.81	24.52	0.01	4.5	<b>0.115</b>	1.03	0.1	0.13	0.02	0.64	0.00	0.11	0.08	<b>0.00</b>	0.00	0.00	0.16	0.00
IP21	East	<b>4.49</b>	23.51	<b>0.011</b>	3.84	0.225	<b>2.98</b>	0.29	<b>1.08</b>	0.24	0.67	0.00	0.11	0.06	0.00	0.00	0.00	0.16	0.00
TI11	East	6.03	23.61	0.016	7.77	0.3	1.73	0.15	0.33	0.1	0.33	0.05	0.19	0.03	0.25	0.06	0.03	0.05	
TI13	East	5.45	23.85	0.008	3.36	0.175	1.41	0.16	0.3	0.05	<b>0.31</b>	0.00	0.17	0.11	<b>0.36</b>	0.00	0.05	0.00	
TI14	East	5.38	24.52	0.011	4.41	0.2	<b>0.93</b>	<b>0.05</b>	<b>0.06</b>	<b>0.01</b>	0.53	0.00	0.25	0.03	0.08	<b>0.11</b>	0.00	<b>0.11</b>	
TI21	East	5.89	23.87	0.009	5.53	0.25	1.95	0.29	0.71	0.18	0.56	0.00	0.19	0.06	0.11	0.06	0.03	0.05	
TI22	East	5.45	24.41	0.008	<b>2.21</b>	0.3	2.03	0.23	0.59	0.18	<b>0.92</b>	0.00	0.03	0.00	0.06	0.00	0.00	0.00	
UB11	East	5.61	<b>22.93</b>	0.009	<b>7.9</b>	0.167	1.14	0.07	0.11	0.02	0.44	0.03	0.11	0.03	0.17	0.00	<b>0.22</b>	0.00	
UB21	East	4.72	23.33	0.01	5.72	<b>0.375</b>	2.65	0.28	0.9	<b>0.34</b>	0.64	0.00	0.07	0.02	0.09	0.00	0.16	0.00	
UB22	East	6.04	24.48	0.009	4.15	0.258	2.05	0.16	0.41	0.11	0.75	0.00	<b>0.00</b>	0.08	0.14	0.00	0.03	0.00	

607

608 †Bold values represent min and max of environmental variables in each watershed.

609 ‡Abbreviations: Temperature (Temp.); Electric conductivity (Cond.); Current velocity (Cur. vel.); Sand (SA); Clay (CL); Litter (LT); Fine Litter

610 (FL); Macrophyte (MC); Roots (RT); Trunk (TR); Pebble (PB).

611 **Table 2.** Path analysis summary of magnitudes of direct and indirect effects (through  
 612 fish composition) of the environmental variables.

613

<b>Path Analysis</b>		
<i>Macrobrachium inpa</i>	<i>Macrobrachium nattereri</i>	<i>Pseudopalaemon amazonensis</i>
Path coefficients	Path coefficients	Path coefficients
Habitat-Shrimp= -0.54 Habitat-Fish-Shrimp= +0.000008 General effect= -0.54 $R^2 = -0.55$	Habitat-Shrimp= +0.3 Habitat-Fish-Shrimp= -0.14 General effect= +0.16 $R^2 = +0.48$	Habitat-Shrimp= +0.3 Habitat-Fish-Shrimp= -0.09 General effect= +0.21 $R^2 = +0.42$

614

615 **Table 3.** Summary of results of interaction models of watershed effects on the  
 616 relationships between predictor variables and number of individuals of each species.  
 617

<b>Partial Regression</b>			
		<i>Statistics parameters</i>	
Predictors: covariate		<i>t</i>	<i>p</i>
<i>Macrobrachium inpa</i>			
pH: watershed		1.295	0.215
Temperature (°C): watershed		0.373	0.715
Current velocity (m/s):			
watershed		0.713	0.487
Depth (m): watershed		-0.528	0.605
Sand (%): watershed		-1.448	0.168
Litter (%): watershed		-0.737	0.472
Fish axis: watershed		-0.340	0.739
<i>Macrobrachium nattereri</i>			
pH: watershed		-2.128	<b>0.05</b>
Temperature (°C): watershed		1.687	0.112
Current velocity (m/s):			
watershed		-0.030	0.976
Depth (m): watershed		-1.320	0.206
Sand (%): watershed		-1.958	0.069
Litter (%): watershed		0.867	0.399
Fish axis: watershed		-1.594	0.131
<i>Pseudopalaemon amazonensis</i>			
pH: watershed		0.303	0.766
Temperature (°C): watershed		-0.353	0.729
Current velocity (m/s):			
watershed		-0.158	0.877
Depth (m): watershed		-0.448	0.660
Sand (%): watershed		-0.675	0.510
Litter (%): watershed		0.736	0.473
Fish axis: watershed		0.156	0.878

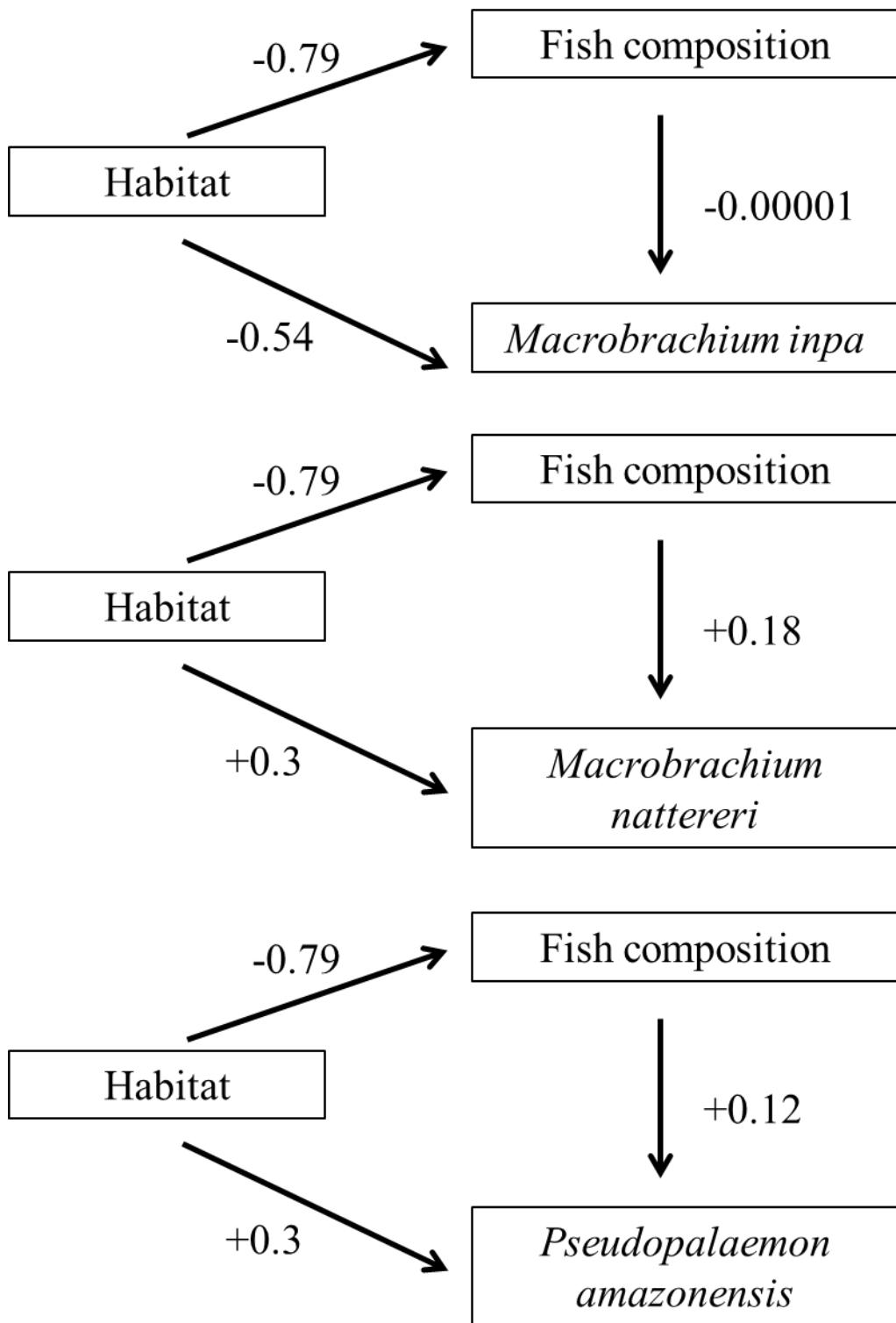
618

619 †Bold values indicate low probability associated with null hypothesis.

620 **FIGURES**

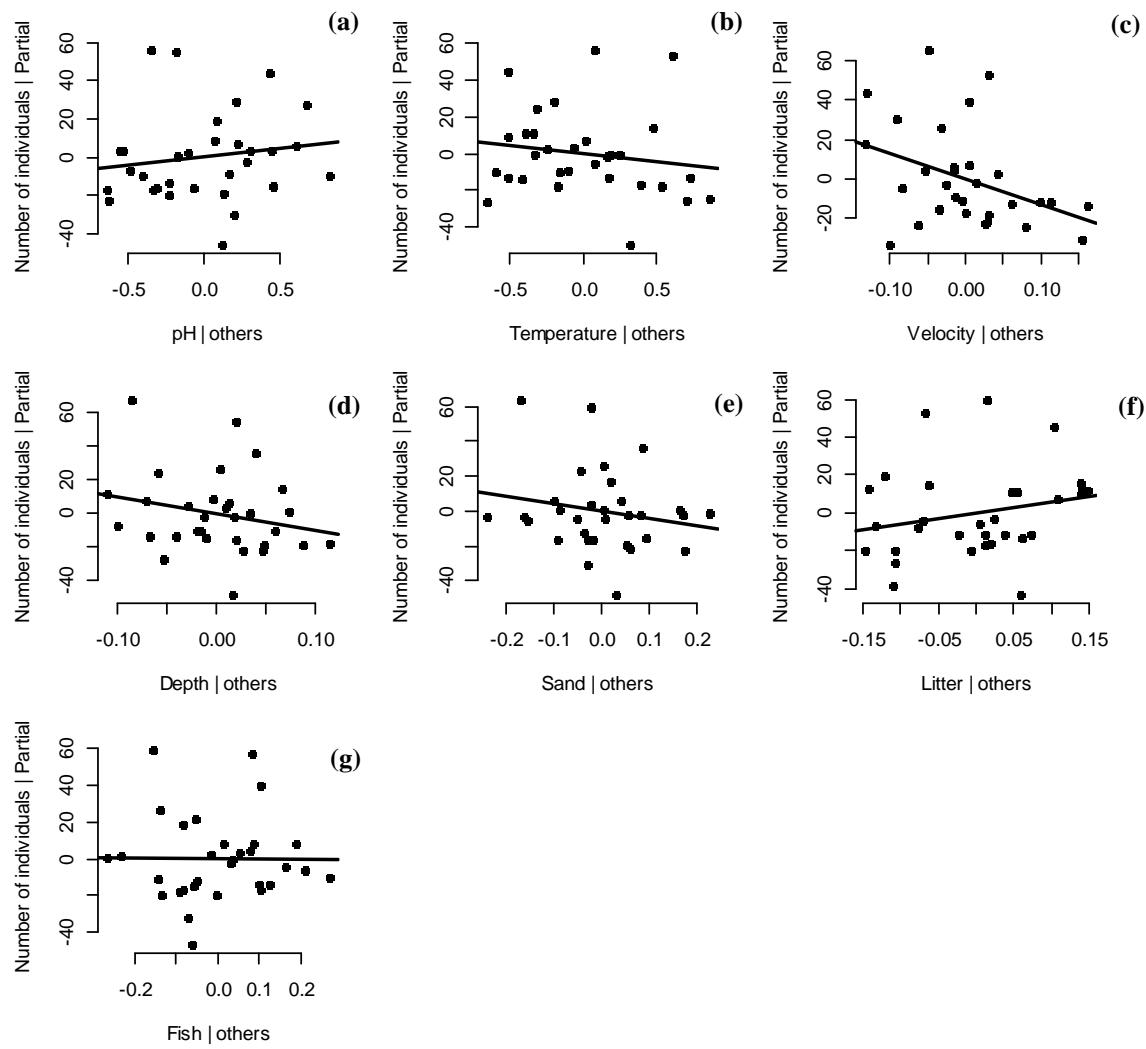
621

622 **Figure 1.** Path analysis for shrimp species through fish composition and environmental  
623 variables.



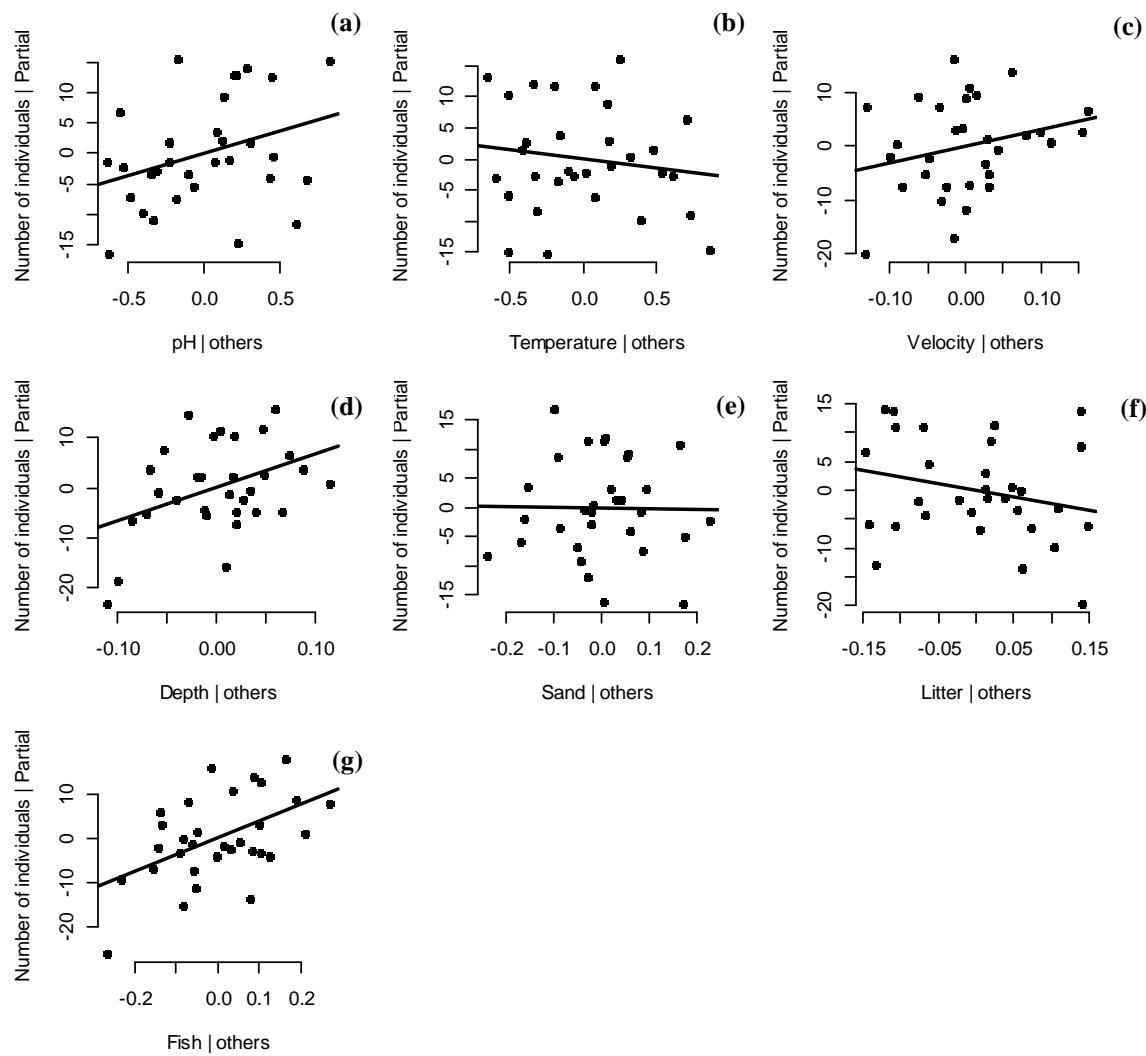
624

625 **Figure 2.** Partial-regression plots of the relationships between number of individuals  
626 and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter  
627 and g – Fish) for *Macrobrachium inpa*.



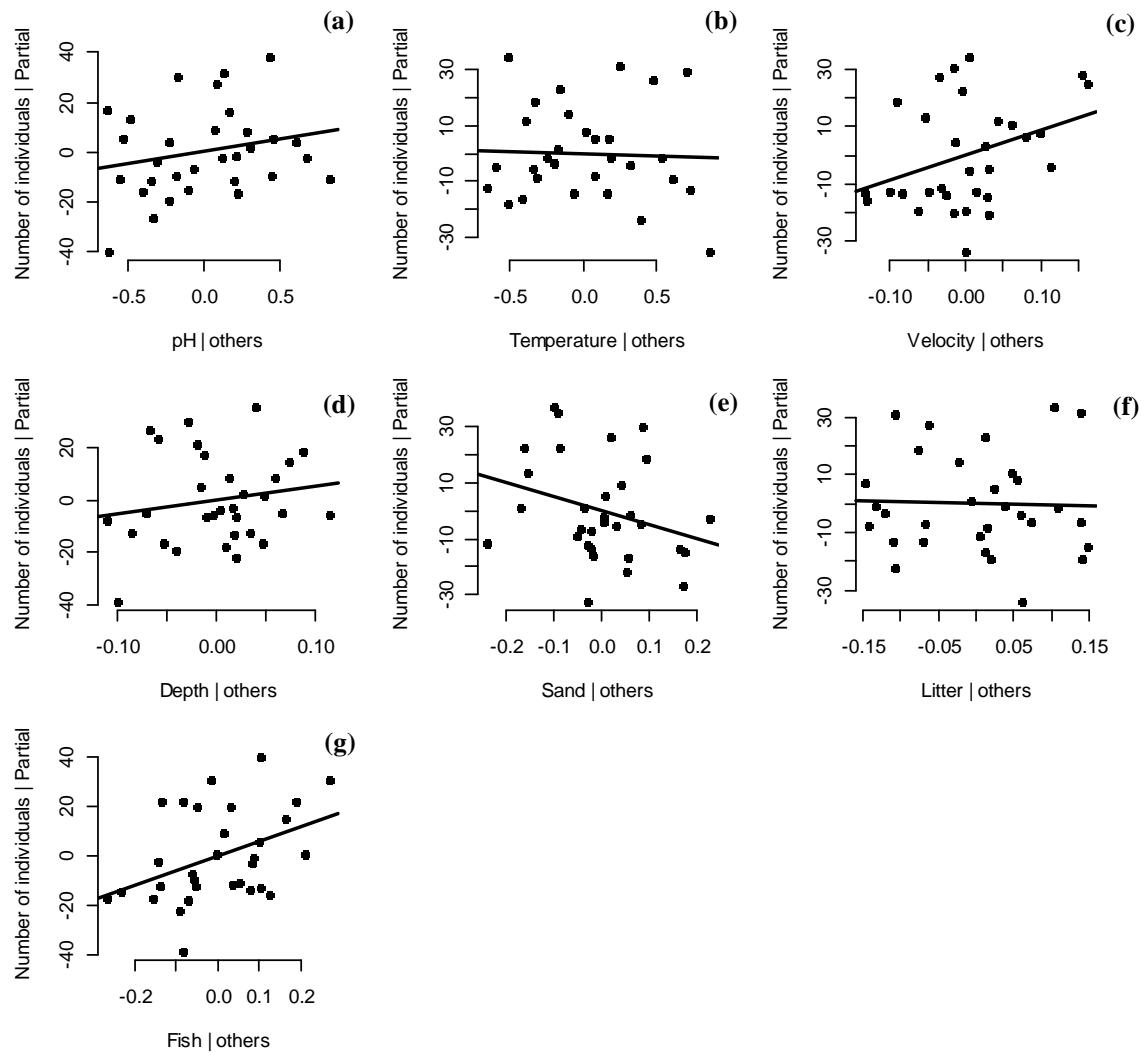
628

629 **Figure 3.** Partial-regression plots of the relationships between number of individuals  
 630 and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter  
 631 and g – Fish) for *Macrobrachium nattereri*.



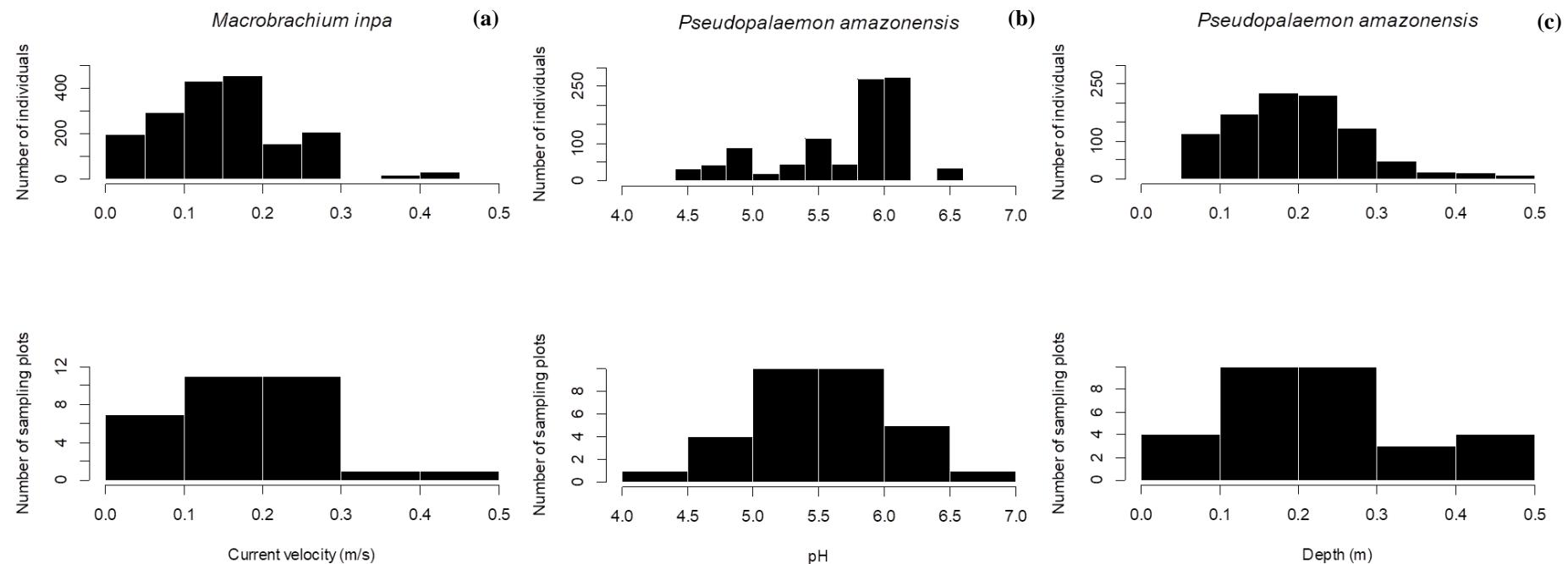
632

633 **Figure 4.** Partial-regression plots of the relationship between number of individuals and  
 634 predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g –  
 635 Fish) for *Pseudopalaemon amazonensis*.



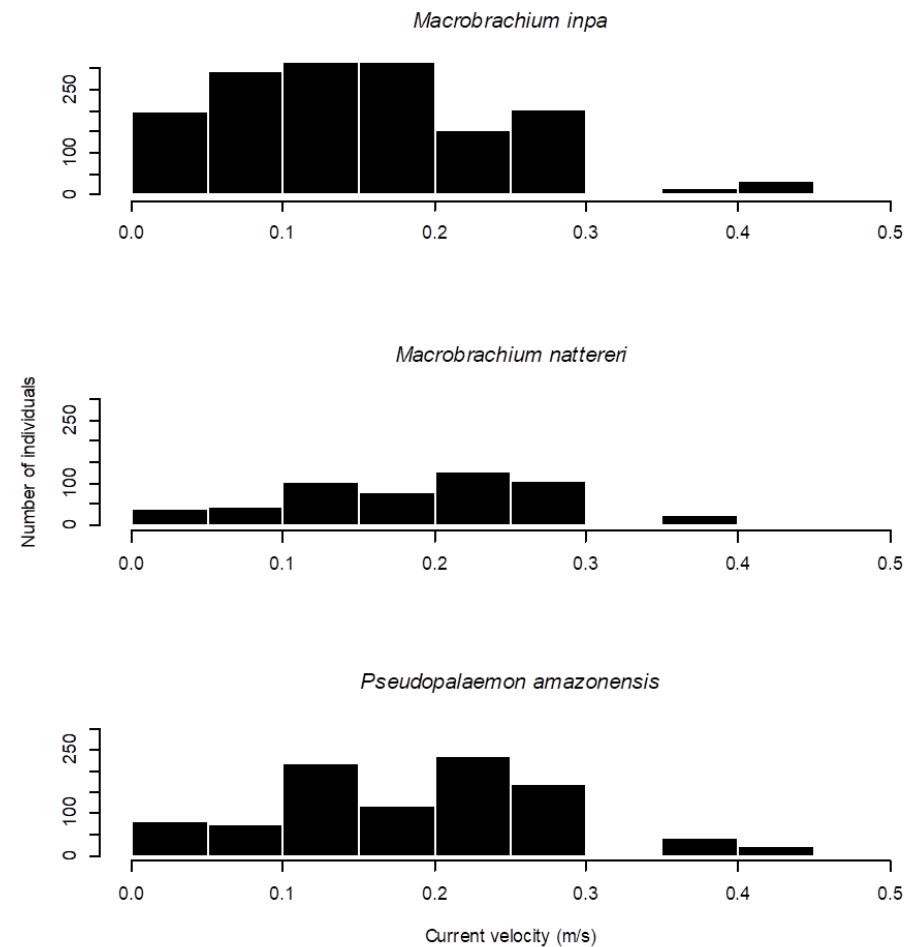
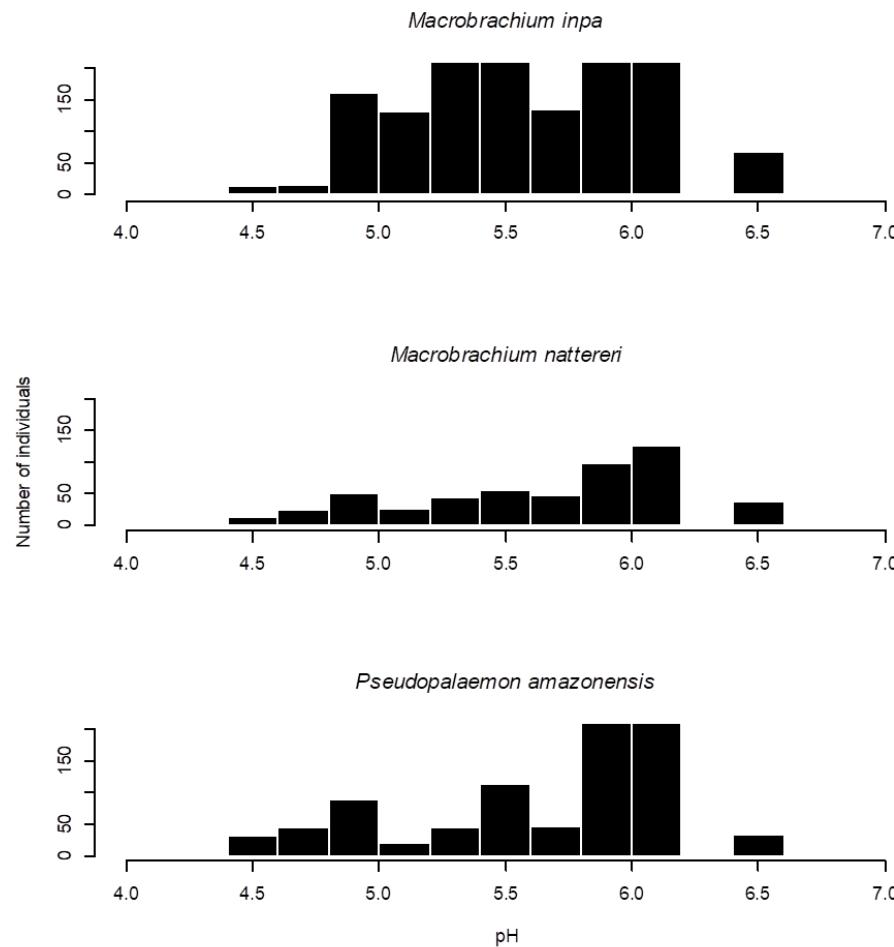
636

637 **Figure 5.** Distributions of individuals of each species (use) and sampling plots (availability) along gradients in current velocity, pH and depth.

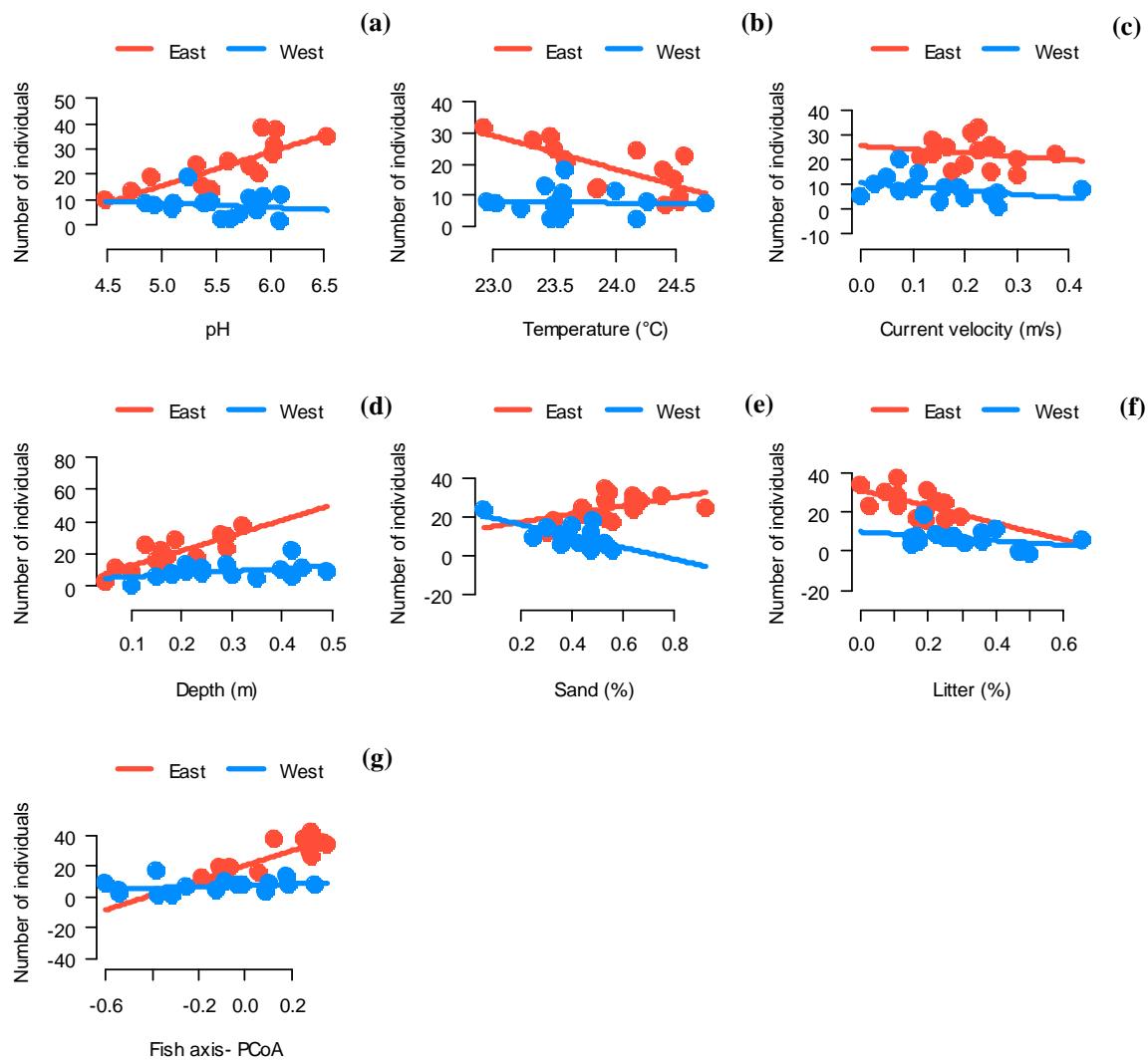


638

639 **Figure 6.** Relative use of different values of current-velocity and pH gradients by three rainforest-stream shrimp species.



641 **Figure 7.** Plots of interaction models of watershed effects on number of  
 642 *Macrobrachium nattereri* individuals with predictors (a – pH, b – Temperature, c –  
 643 Current velocity, d – Depth, e – Sand, f – Litter and g – Fish axis).



644

645 **SUPPORTING INFORMATION**

646

647 **Table S1** Multicollinearity test of environmental variables for each model used in the  
648 study.

<b>Multicollinearity Test</b>			
	Environmental variables	TOL	<i>R</i> <sup>2</sup>
<b>pH</b>	Temperature (°C)	0.8281	
	Current velocity (m/s)	0.8563	
	Depth (m)	0.9523	0.2848
	Sand (%)	0.4556	
	Litter (%)	0.4714	
<b>Temperature</b>	pH	0.8201	
	Current velocity (m/s)	0.8531	
	Depth (m)	0.8178	0.2778
	Sand (%)	0.5329	
	Litter (%)	0.4571	
<b>Current velocity</b>	pH	0.7233	
	Temperature (°C)	0.7276	
	Depth (m)	0.7987	0.1532
	Sand (%)	0.4430	
	Litter (%)	0.4948	
<b>Depth</b>	pH	0.8555	
	Temperature (°C)	0.7418	
	Current velocity (m/s)	0.8494	0.2038
	Sand (%)	0.4436	
	Litter (%)	0.4800	
<b>Sand</b>	pH	0.7373	
	Temperature (°C)	0.8707	
	Current velocity (m/s)	0.8487	0.558
	Depth (m)	0.7990	
	Litter (%)	0.6978	
<b>Litter</b>	pH	0.7392	
	Temperature (°C)	0.7238	
	Current velocity (m/s)	0.9186	0.5439
	Depth (m)	0.8378	
	Sand (%)	0.6762	

649

650 **Table S2** Multicollinearity test of environmental variables and fish composition axis.

<b>Multicollinearity Test</b>			
		<i>Collinearity coefficients</i>	
	Predictors	TOL	R <sup>2</sup>
<b>pH</b>	Temperature (°C)	0.8052	
	Current velocity (m/s)	0.5770	
	Depth (m)	0.2386	
	Sand (%)	0.4535	0.3012
	Litter (%)	0.4426	
	Fish	0.2050	
<b>Temperature</b>	pH	0.7876	
	Current velocity (m/s)	0.5598	
	Depth (m)	0.2441	
	Sand (%)	0.5210	0.2856
	Litter (%)	0.4249	
	Fish	0.2025	
<b>Current velocity</b>	pH	0.7203	
	Temperature (°C)	0.7145	
	Depth (m)	0.3012	
	Sand (%)	0.4420	0.4403
	Litter (%)	0.4925	
	Fish	0.3030	
<b>Depth</b>	pH	0.7047	
	Temperature (°C)	0.7371	
	Current velocity (m/s)	0.7126	
	Sand (%)	0.4390	0.7634
	Litter (%)	0.4278	
	Fish	0.6740	
<b>Sand</b>	pH	0.7234	
	Temperature (°C)	0.8497	
	Current velocity (m/s)	0.5647	
	Depth (m)	0.2371	0.5619
	Litter (%)	0.5952	
	Fish	0.2021	
<b>Litter</b>	pH	0.7318	
	Temperature (°C)	0.7182	
	Current velocity (m/s)	0.6522	
	Depth (m)	0.2395	0.5773
	Sand (%)	0.6169	
	Fish	0.2161	

---

**Fish**

pH	0.7152
Temperature (°C)	0.7222
Current velocity (m/s)	0.8468
Depth (m)	0.7962
Sand (%)	0.4420
Litter (%)	0.4561

---

652 **Table S3** Results of multiple regression of number of individuals on habitat predictors.

653

<b>Partial Regression</b>			
		<i>Statistics parameters</i>	
	Environmental variables	<i>t</i>	<i>p</i>
<i>Macrobrachium inpa</i>			
	pH	0.773	0.4473
	Temperature (°C)	-0.796	0.4336
	Current velocity (m/s)	-2.515	<b>0.0190</b>
	Depth (m)	-2.086	<b>0.0478</b>
	Sand (%)	-0.942	0.3555
	Litter (%)	1.189	0.2462
<i>Macrobrachium nattereri</i>			
	pH	1.896	0.07
	Temperature (°C)	-0.394	0.6970
	Current velocity (m/s)	-0.363	0.7194
	Depth (m)	-0.388	0.7017
	Sand (%)	0.168	0.8679
	Litter (%)	-1.812	0.0825
<i>Pseudopalaemon amazonensis</i>			
	pH	1.349	0.191
	Temperature (°C)	0.024	0.981
	Current velocity (m/s)	0.661	0.515
	Depth (m)	-1.666	0.109
	Sand (%)	-1.189	0.246
	Litter (%)	-0.681	0.502

654

655 †Bold values indicate low probability associated with null hypothesis.

656 **Table S4** Results of multiple regression of number of individuals on habitat predictors  
 657 and fish composition axis.

658

<b>Partial Regression</b>			
		<i>Statistics parameters</i>	
	Predictors	<i>T</i>	<i>p</i>
<i>Macrobrachium inpa</i>			
	pH	0.752	0.459
	Temperature (°C)	-0.773	0.447
	Current velocity (m/s)	-2.017	<b>0.055</b>
	Depth (m)	-1.135	0.268
	Sand (%)	-0.916	0.369
	Litter (%)	1.113	0.277
	Fish	-0.025	0.979
<i>Macrobrachium nattereri</i>			
	pH	1.702	0.102
	Temperature (°C)	-0.738	0.467
	Current velocity (m/s)	1.304	0.205
	Depth (m)	2.121	<b>0.044</b>
	Sand (%)	-0.076	0.940
	Litter (%)	-1.218	0.235
	Fish	2.817	<b>0.009</b>
<i>Pseudopalaemon amazonensis</i>			
	pH	1.103	0.281
	Temperature (°C)	-0.196	0.846
	Current velocity (m/s)	1.817	0.082
	Depth (m)	0.815	0.423
	Sand (%)	-1.469	0.155
	Litter (%)	-0.125	0.901
	Fish	2.132	<b>0.043</b>

659

660 †Bold values indicate low probability associated with null hypothesis.

661   **Table S5** Kolmogorov-Smirnov test coefficients of species' distributions and sampling  
 662   plots (availability) along environmental gradients.  
 663

<b>Kolmogorov-Smirnov Test</b>				
		<i>Statistics parameters</i>		
	Species x resource availability	D	X <sup>2</sup>	p- adjusted
<b>pH</b>	<i>M. inpa</i> x pH availability	0.09	2.06	0.4
	<i>M. nattereri</i> x pH availability	0.12	3.43	0.2
	<i>P. amazonensis</i> x pH availability	0.21	10.88	<b>0.01</b>
<b>Temperature (°C)</b>	<i>M. inpa</i> x Temp. availability	0.10	2.43	0.3
	<i>M. nattereri</i> x Temp. availability	0.09	1.90	0.4
	<i>P. amazonensis</i> x Temp. availability	0.03	0.29	0.9
<b>Current velocity (m/s)</b>	<i>M. inpa</i> x Cur. vel. availability	0.19	9.71	<b>0.01</b>
	<i>M. nattereri</i> x Cur. vel. availability	0.08	1.49	0.5
	<i>P. amazonensis</i> x Cur. vel. availability	0.07	1.18	0.6
<b>Depth (m)</b>	<i>M. inpa</i> x Depth availability	0.13	4.54	0.1
	<i>M. nattereri</i> x Depth availability	0.12	3.73	0.2
	<i>P. amazonensis</i> x Depth availability	0.16	6.55	<b>0.04</b>
<b>Sand (%)</b>	<i>M. inpa</i> x Sand availability	0.12	3.89	0.2
	<i>M. nattereri</i> x Sand availability	0.11	3.29	0.2
	<i>P. amazonensis</i> x Sand availability	0.09	1.89	0.4
<b>Litter (%)</b>	<i>M. inpa</i> x Litter availability	0.11	3.30	0.2
	<i>M. nattereri</i> x Litter availability	0.14	4.61	0.1
	<i>P. amazonensis</i> x Litter availability	0.11	2.93	0.2

664

665   †Bold values indicate low probability associated with null hypothesis.

666 **Table S6** Kolmogorov-Smirnov test coefficients of species' distributions comparison  
 667 along gradients of pH, current velocity and depth.

668

<b>Kolmogorov-Smirnov Test</b>			
		<i>Statistics parameters</i>	
	<i>Species' distribution comparison</i>	<i>D</i>	<i>p</i>
<b>pH</b>	<i>M. inpa</i> x <i>M. nattereri</i>	0.1281	<b>2.9<sup>-6</sup></b>
	<i>M. inpa</i> x <i>P. amazonensis</i>	0.1701	<b>3.3<sup>-16</sup></b>
	<i>M. nattereri</i> x <i>P. amazonensis</i>	0.1018	0.001
<b>Current velocity (m/s)</b>	<i>M. inpa</i> x <i>M. nattereri</i>	0.2698	<b>2.2<sup>-16</sup></b>
	<i>M. inpa</i> x <i>P. amazonensis</i>	0.2587	<b>2.2<sup>-16</sup></b>
	<i>M. nattereri</i> x <i>P. amazonensis</i>	0.0734	0.049
<b>Depth (m)</b>	<i>M. inpa</i> x <i>M. nattereri</i>	0.0938	0.001
	<i>M. inpa</i> x <i>P. amazonensis</i>	0.1037	<b>2.78<sup>-6</sup></b>
	<i>M. nattereri</i> x <i>P. amazonensis</i>	0.0694	<b>0.073</b>

669

670 †Bold values indicate high probability associated with null hypothesis.

## Conclusões

Evidenciamos que camarões de riachos de terra firme na Amazônia central têm sua distribuição estruturada por atributos do habitat, principalmente para as variáveis associadas à hidráulica, embora este seja mais importante para algumas espécies que outras. Como a variação do habitat nesses ambientes não é pronunciada, apenas relações fortes puderam ser observadas na escala estudada. Especialização foi detectada ao longo dos gradientes de velocidade da correnteza, profundidade e pH, em que as espécies especialistas utilizaram intervalos de baixa magnitude ao longo dos gradientes de velocidade da correnteza e profundidade, e intervalos de magnitudes maiores no gradiente de pH. Segregação de habitat foi observada ao longo dos gradientes de velocidade da correnteza e pH, em que as distribuições das espécies exibem menos sobreposição do que esperado ao acaso. Correlações da composição de peixes com a distribuição das espécies indicam que predação também é um importante estruturador dessa assembleia, em que se sugere que competição aparente tenha resultado a segregação observada. Bacias de drenagem estruturaram a relação de uma única espécie, somente em relação ao gradiente de pH.