Instituto Nacional de Pesquisas da Amazônia – INPA

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

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Manaus, Amazonas

Junho, 2019

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Orientador: Dr. William Magnusson

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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).

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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.

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"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.

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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 a 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 particionam 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.

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Capítulo I.

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Habitat segregation among freshwater shrimp species in Amazonian rainforest streams

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RESEARCH ARTICLE

Habitat segregation among freshwater shrimp species in Amazonian rainforest streams

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Abstract

1. 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 along habitat dimensions 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.

2. 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.

3. 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.

4. 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.

1 INTRODUCTION

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

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

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

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

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

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

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

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

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

2 METHODS

2.1 Study system

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

2.2 Study design and sample collection

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

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

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

2.3 Data analysis

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

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

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

2.3.1 Specialization and habitat segregation

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

$$X^2 = 4D^2 \frac{n1n2}{n1 + n2},$$

where *D* represents the test coefficient, and *n1* and *n2* correspond to the number of units in each distribution. We generally used the number of plots (31) for both *n1* and *n2*, because shrimp in each plot are not independent of the mean value of the gradient in the plot. For two species found in only 30 of the 31 plots, *n2* was 30. The second test

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

2.3.2 Fish-assemblage composition

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

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

2.3.3 Watershed effect

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

3 RESULTS

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

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

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

3.1 *Macrobrachium inpa*

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

3.2 *Macrobrachium nattereri*

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

3.3 *Pseudopalaemon amazonensis*

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

3.4 Specialization and habitat segregation

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

3.5 Watershed effect

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

4 DISCUSSION

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

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

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

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

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

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

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

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

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

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

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

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DATA AVAILABILITY

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

CONFLICT OF INTEREST

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

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TABLES

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

		Environmental Variables																
Sites	Watershed	pH	Temp. (°C)	Cond. (µS/cm)	O_2 (mg/L)	Cur. vel. (m/s)	Width (m)	Depth (m)	Area (m^2)	Discharge (m^3/s)	SA %	CL %	LT %	FL %	MC %	RT %	TR %	PB %
AC11	West	5.1	23.23	**0.024**	6.21	0.075	2.9	0.3	1.05	0.08	**0.56**	**0.00**	0.31	0.03	0.08	**0.00**	0.03	**0.00**
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	**0.00**	0.19	0.00	0.05	0.00
AC13	West	5.11	**24.73**	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	**1.36**	0.15	0.26	0.03	0.53	0.00	0.36	0.00	**0.00**	0.06	0.05	0.05
AC15	West	**6.1**	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	**0.00**	0.00
AC16	West	**4.86**	**23.04**	0.014	6.88	0.1	1.47	0.18	0.34	0.03	0.39	0.00	0.17	0.00	0.08	**0.17**	0.17	**0.17**
AC22	West	5.12	22.96	**0.01**	**3.63**	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	**8.95**	**0.00**	1.9	0.42	1.00	**0.00**	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	**0.425**	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	**0.39**	0.00	0.00	0.00
BO14	West	5.56	23.47	0.013	5.24	0.262	**2.75**	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	**0.06**	0.00	**0.66**	0.00	0.23	0.00	0.03	0.00
BO16	West	6.09	23.55	0.012	4.74	0.15	1.64	**0.1**	**0.18**	0.03	0.475	0.00	**0.15**	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	**0.21**	0.12
BO22	West	5.72	23.59	0.012	5.01	0.2	3.23	**0.49**	**1.94**	**0.39**	0.43	**0.14**	0.17	**0.11**	0.09	0.03	0.06	0.03
BR21	East	5.33	24.4	0.01	3.75	0.25	2.59	**0.32**	0.99	0.25	0.53	**0.00**	0.22	0.08	0.08	**0.00**	0.08	**0.00**
IP11	East	**6.53**	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	**0.00**	0.00
IP12	East	4.91	23.47	**0.008**	3.97	0.137	1.55	0.16	0.31	0.04	0.64	0.00	**0.25**	0.03	0.06	0.00	0.00	0.00
IP13	East	5.93	**24.57**	0.01	4.58	0.225	1.53	0.13	0.24	0.05	0.53	**0.14**	0.11	**0.00**	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	**0.12**	0.06	0.00	0.08	0.00

IP15	East	5.81	24.52	0.01	4.5	**0.115**	1.03	0.1	0.13	0.02	0.64	0.00	0.11	0.08	**0.00**	0.00	0.16	0.00
IP21	East	**4.49**	23.51	**0.011**	3.84	0.225	**2.98**	0.29	**1.08**	0.24	0.67	0.00	0.11	0.06	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	**0.31**	0.00	0.17	0.11	**0.36**	0.00	0.05	0.00
TI14	East	5.38	24.52	0.011	4.41	0.2	**0.93**	**0.05**	**0.06**	**0.01**	0.53	0.00	0.25	0.03	0.08	**0.11**	0.00	**0.11**
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	**2.21**	0.3	2.03	0.23	0.59	0.18	**0.92**	0.00	0.03	0.00	0.06	0.00	0.00	0.00
UB11	East	5.61	**22.93**	0.009	**7.9**	0.167	1.14	0.07	0.11	0.02	0.44	0.03	0.11	0.03	0.17	0.00	**0.22**	0.00
UB21	East	4.72	23.33	0.01	5.72	**0.375**	2.65	0.28	0.9	**0.34**	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	**0.00**	0.08	0.14	0.00	0.03	0.00

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

‡Abbreviations: Temperature (Temp.); Electric conductivity (Cond.); Current velocity (Cur. vel.); Sand (SA); Clay (CL); Litter (LT); Fine Litter (FL); Macrophyte (MC); Roots (RT); Trunk (TR); Pebble (PB).

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

Path Analysis		
Macrobrachium inpa	*Macrobrachium nattereri*	*Pseudopalaemon amazonensis*
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

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

	Partial Regression		
		Statistics parameters	
	Predictors: covariate	*t*	*p*
Macrobrachium inpa			
	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
Macrobrachium nattereri			
	pH: watershed	-2.128	**0.05**
	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
Pseudopalaemon amazonensis			
	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

†Bold values indicate low probability associated with null hypothesis.

FIGURES

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

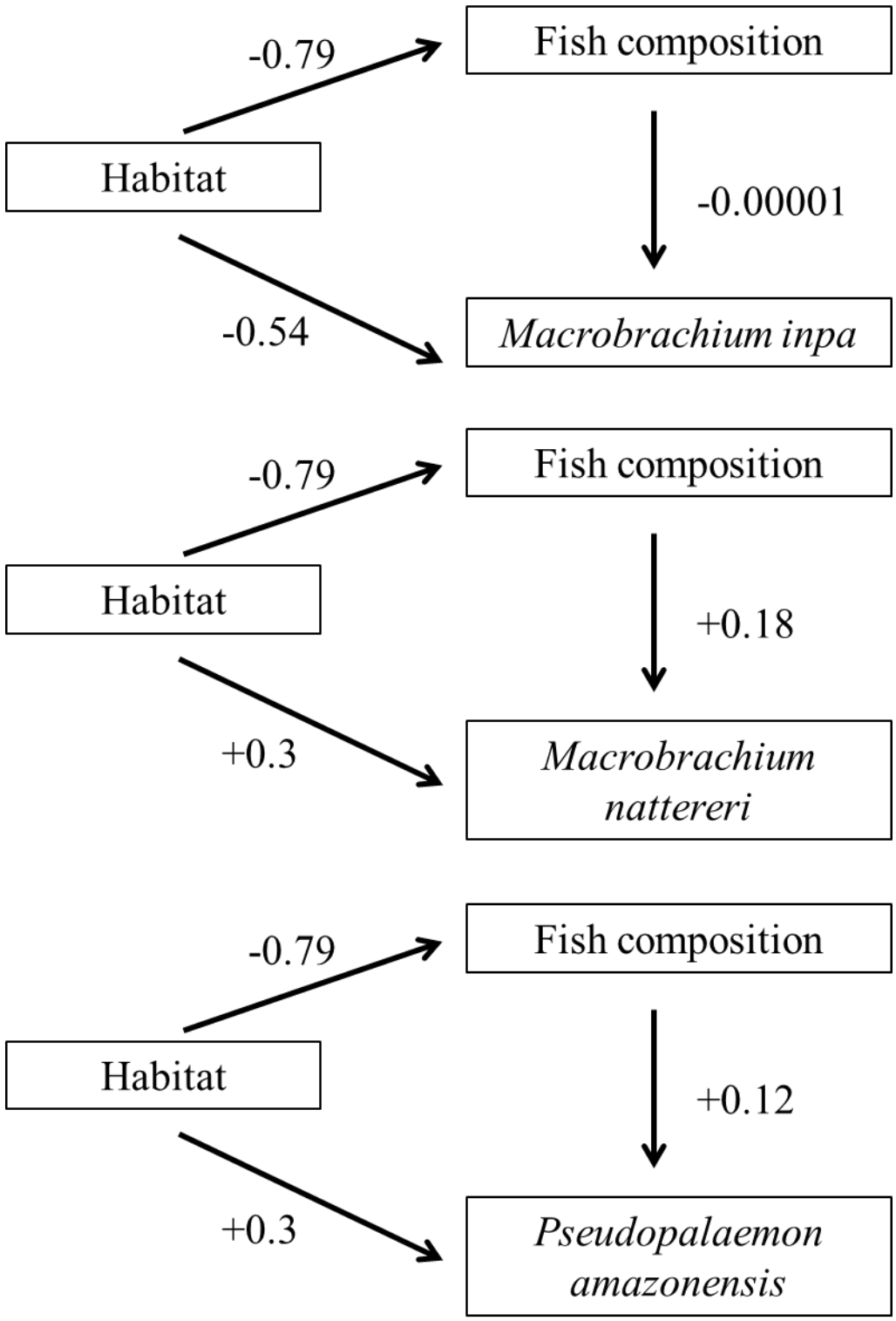


Figure 2. Partial-regression plots of the relationships between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for *Macrobrachium inpa*.

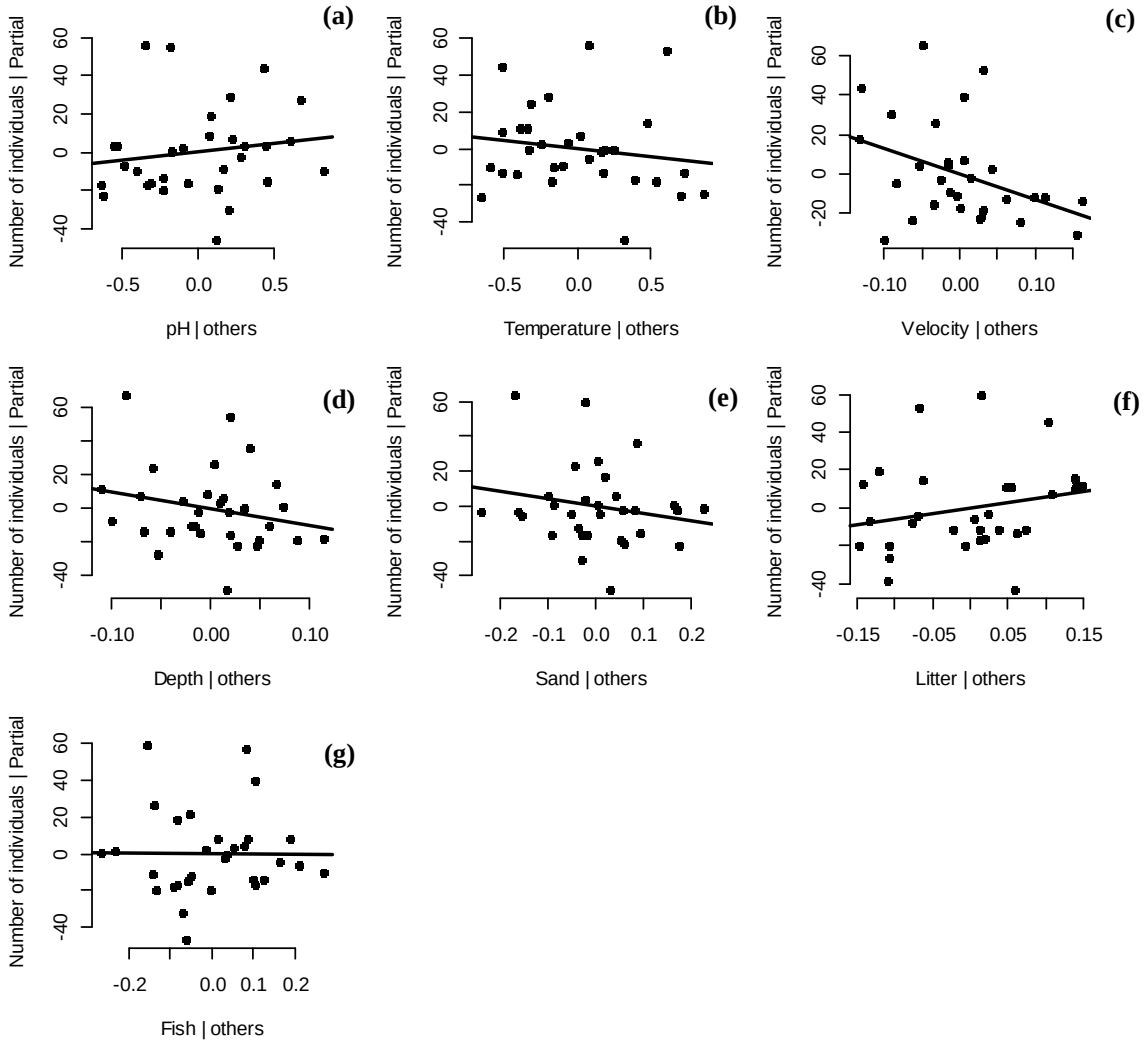


Figure 3. Partial-regression plots of the relationships between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for *Macrobrachium nattereri*.

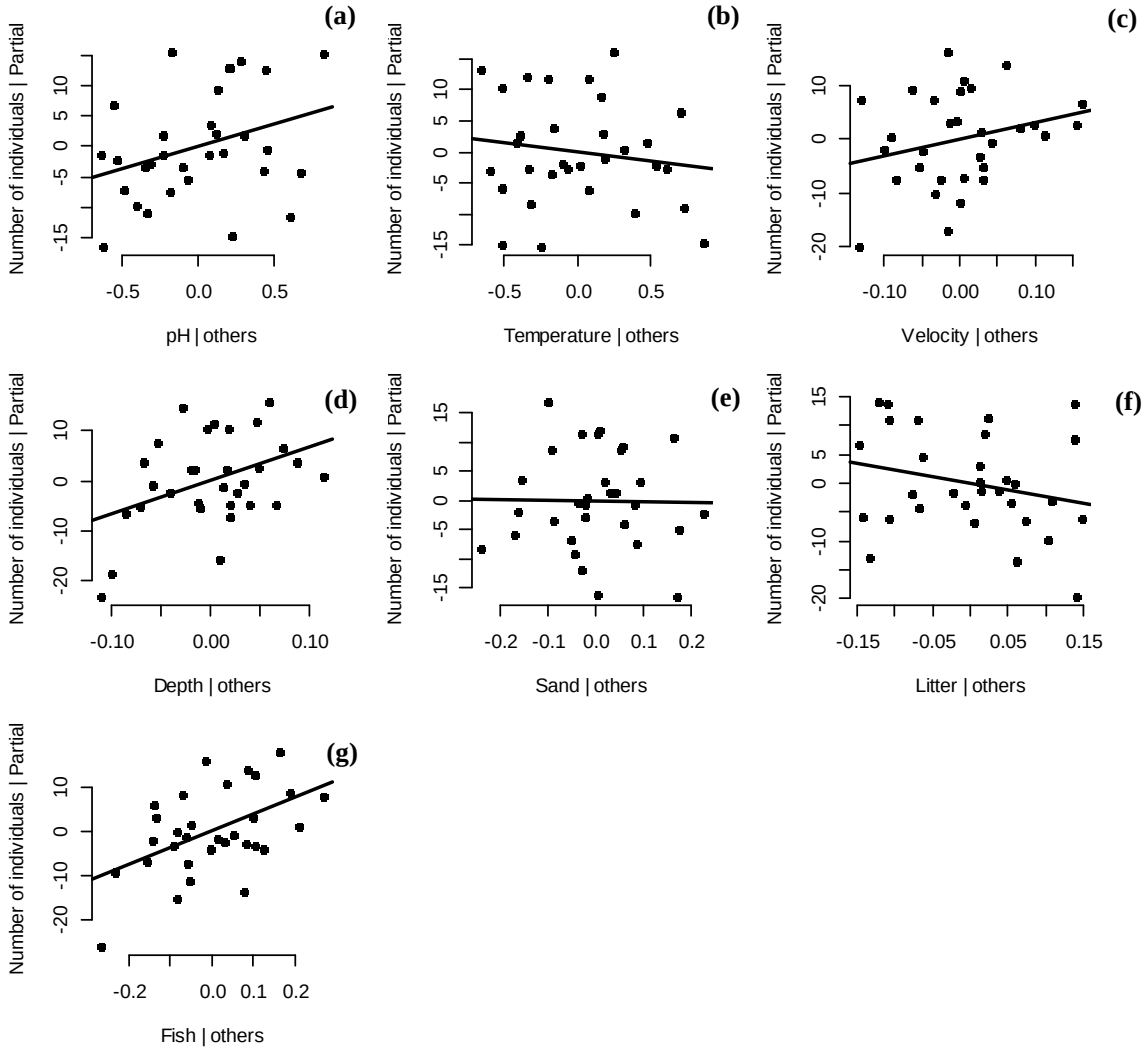


Figure 4. Partial-regression plots of the relationship between number of individuals and predictors (a – pH, b – Temperature, c – Velocity, d – Depth, e – Sand, f – Litter and g – Fish) for *Pseudopalaemon amazonensis*.

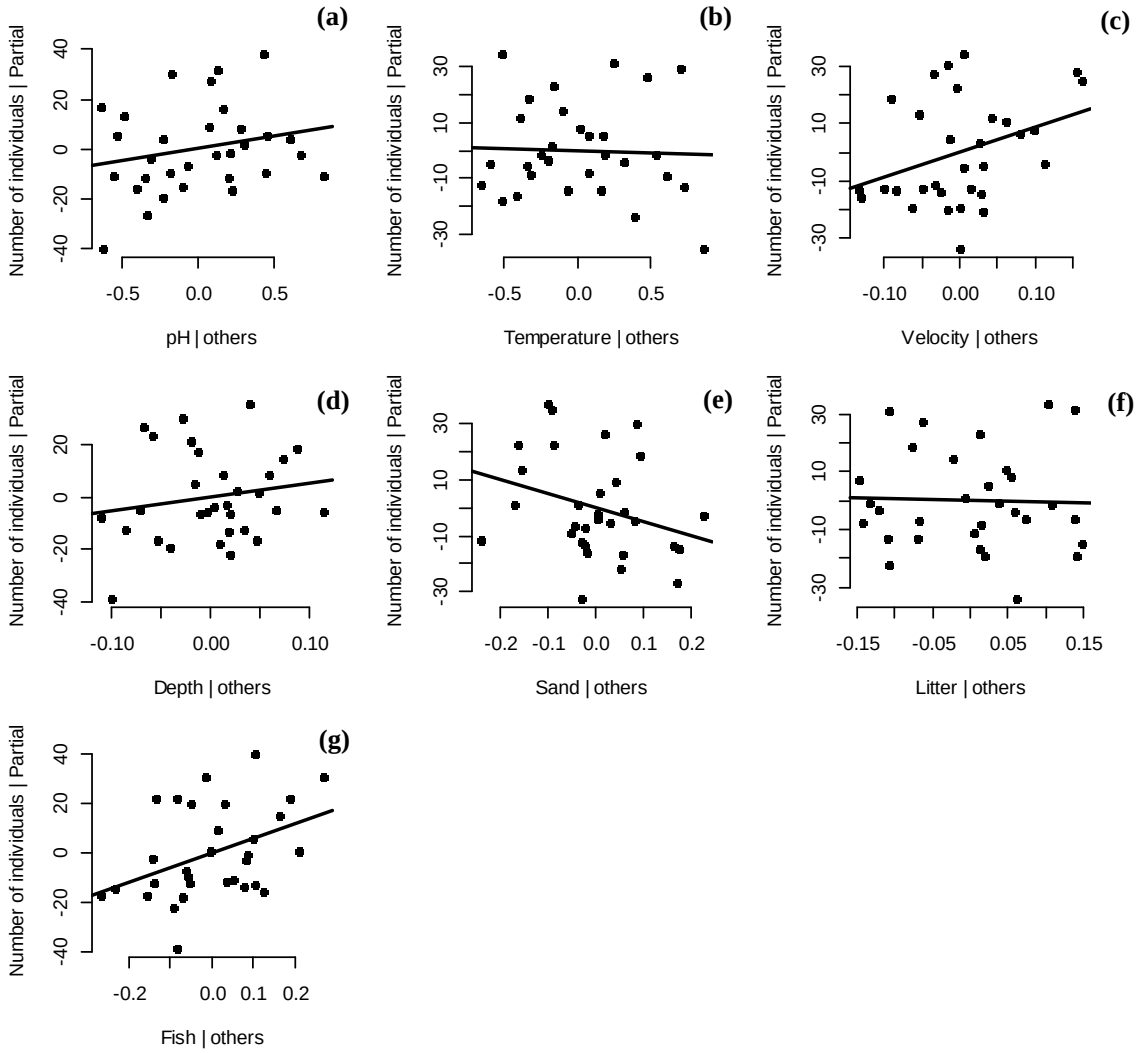


Figure 5. Distributions of individuals of each species (use) and sampling plots (availability) along gradients in current velocity, pH and depth.

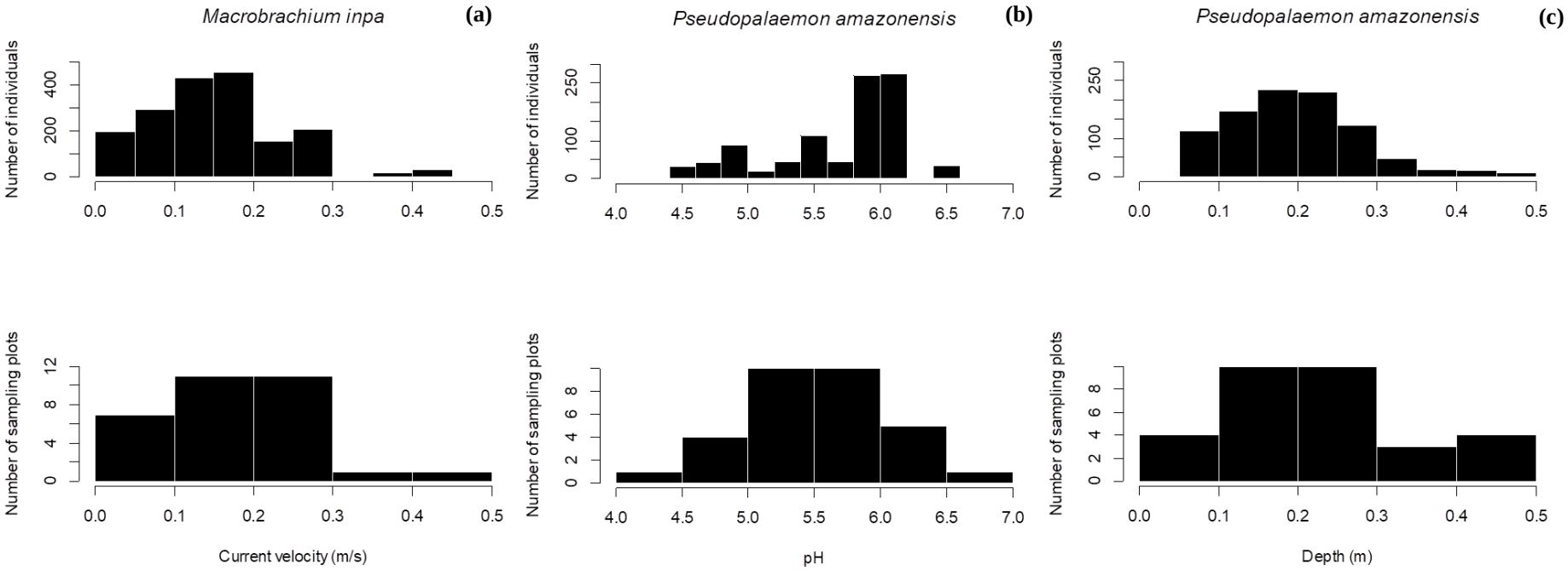


Figure 6. Relative use of different values of current-velocity and pH gradients by three rainforest-stream shrimp species.

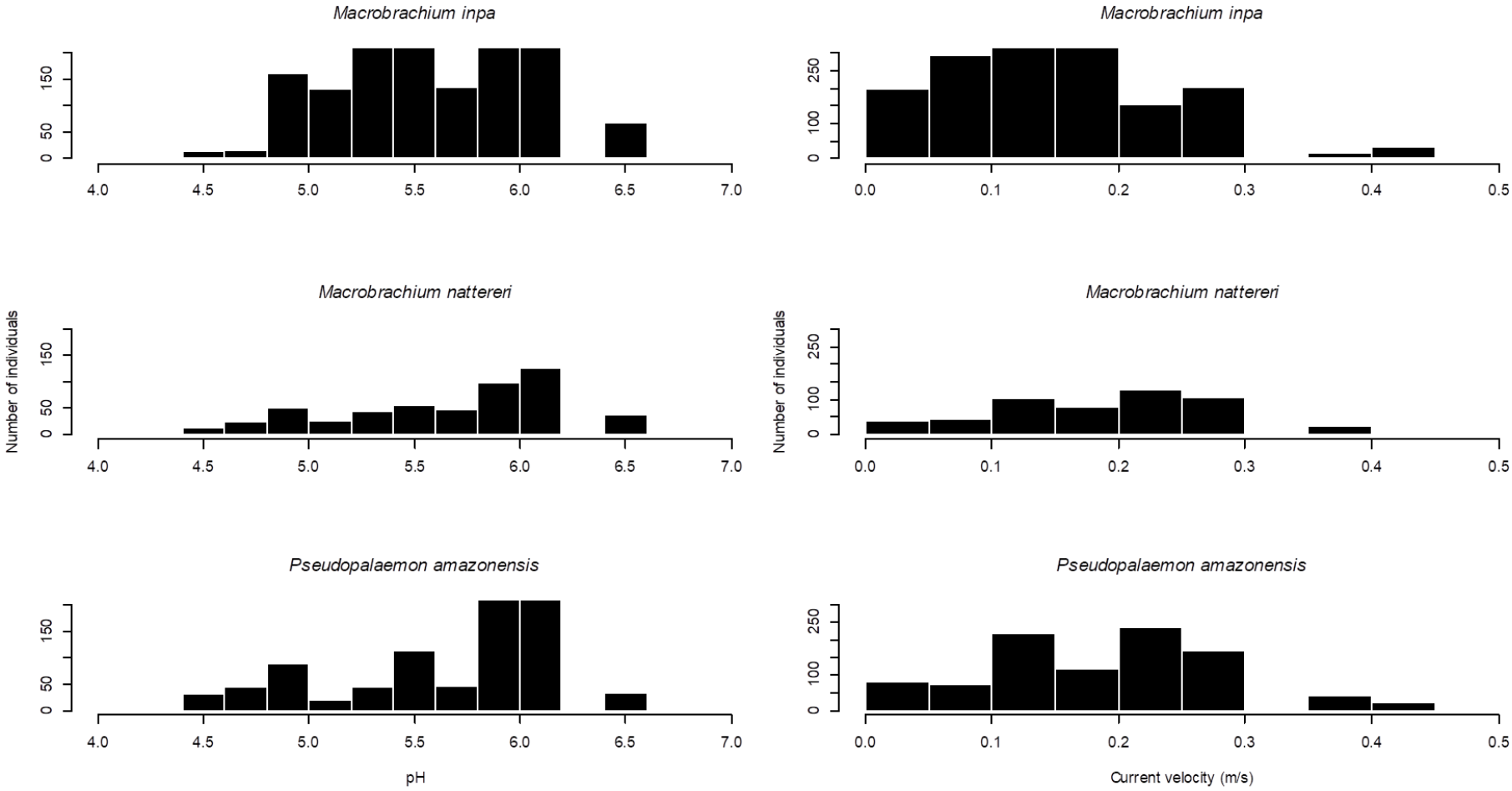
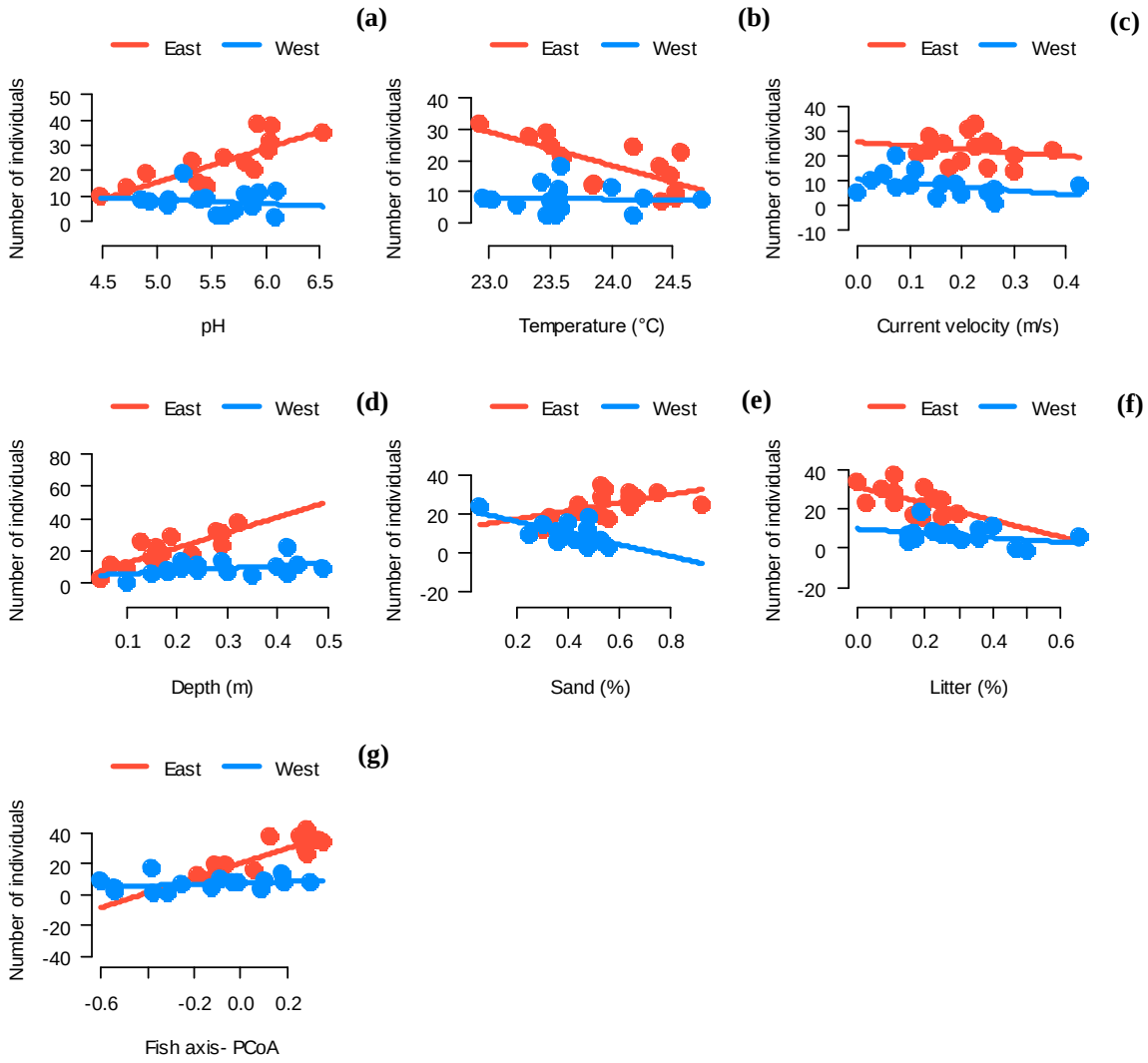


Figure 7. Plots of interaction models of watershed effects on number of *Macrobrachium nattereri* individuals with predictors (a – pH, b – Temperature, c – Current velocity, d – Depth, e – Sand, f – Litter and g – Fish axis).



SUPPORTING INFORMATION

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

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

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

	Multicollinearity Test		
		Collinearity coefficients	
	Predictors	TOL	R^2
pH			
	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	
Temperature			
	pH	0.7876	
	Current velocity (m/s)	0.5598	
	Depth (m)	0.2441	
	Sand (%)	0.5210	0.2856
	Litter (%)	0.4249	
	Fish	0.2025	
Current velocity			
	pH	0.7203	
	Temperature (°C)	0.7145	
	Depth (m)	0.3012	
	Sand (%)	0.4420	0.4403
	Litter (%)	0.4925	
	Fish	0.3030	
Depth			
	pH	0.7047	
	Temperature (°C)	0.7371	
	Current velocity (m/s)	0.7126	
	Sand (%)	0.4390	0.7634
	Litter (%)	0.4278	
	Fish	0.6740	
Sand			
	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	
Litter			
	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	0.7997
	Temperature (°C)	0.7222	
	Current velocity (m/s)	0.8468	
	Depth (m)	0.7962	
	Sand (%)	0.4420	
	Litter (%)	0.4561	

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

	Partial Regression		
		Statistics parameters	
	Environmental variables	*t*	*p*
Macrobrachium inpa			
	pH	0.773	0.4473
	Temperature (°C)	-0.796	0.4336
	Current velocity (m/s)	-2.515	**0.0190**
	Depth (m)	-2.086	**0.0478**
	Sand (%)	-0.942	0.3555
	Litter (%)	1.189	0.2462
Macrobrachium nattereri			
	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
Pseudopalaemon amazonensis			
	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

†Bold values indicate low probability associated with null hypothesis.

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

	Partial Regression		
		Statistics parameters	
	Predictors	*T*	*p*
Macrobrachium inpa			
	pH	0.752	0.459
	Temperature (°C)	-0.773	0.447
	Current velocity (m/s)	-2.017	**0.055**
	Depth (m)	-1.135	0.268
	Sand (%)	-0.916	0.369
	Litter (%)	1.113	0.277
	Fish	-0.025	0.979
Macrobrachium nattereri			
	pH	1.702	0.102
	Temperature (°C)	-0.738	0.467
	Current velocity (m/s)	1.304	0.205
	Depth (m)	2.121	**0.044**
	Sand (%)	-0.076	0.940
	Litter (%)	-1.218	0.235
	Fish	2.817	**0.009**
Pseudopalaemon amazonensis			
	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	**0.043**

†Bold values indicate low probability associated with null hypothesis.

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

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

†Bold values indicate low probability associated with null hypothesis.

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

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

†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.