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Habitat segregation among freshwater shrimp species in an Amazonian rainforest stream system

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Abstract

1. Resource partitioning is a stabilising 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 generalisations 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. Fish-assemblage composition also affected shrimp densities. Two of the three species of shrimp showed some degree of habitat specialisation, 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 catchments 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, interactions with fish seem 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
apparent competition, habitat dimensions, predator composition, resource partitioning, catchment

1 | INTRODUCTION

Mechanisms relating to how closely related species achieve stable co-existence 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 2000s, but particular assemblages have their own dynamics and can respond differently to a variety of mechanisms. Resource partitioning, intraspecific variation, and frequency-dependent predation, for instance, 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 partitioning is frequently cited as a stabilising mechanism that can alone provide long-term coexistence among species, although, in some cases, this mechanism can be insufficient to promote coexistence. In order for coexistence to be possible, other mechanisms, such as minimising average fitness differences, density-dependent events and life-history trade-offs have to act along with resource partitioning (Chesson, 2000; MacArthur, 1958; Mordecai, Jaramillo, Ashford, Hechinger, & Lafferty, 2016). Moreover, niche partitioning enables morphological, physiological, and behavioural 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 may outweigh interspecific effects, possibly allowing coexistence without niche segregation (Chesson, 1991). However, stable coexistence probably requires substantial ecological differences among species that are manifest as differences in their niches (Chesson, 1991, 2000; Leibold, 1995).

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 dimensions (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), where intraspecific effects were suggested as the key factor of species coexistence, although it is not known if habitat features have the potential to maintain diversity among freshwater shrimp species in tropical streams.

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. Although the principal shrimp predators probably vary with the size of the shrimp, most native fish species are potential predators of small shrimp, since they feed mostly on small invertebrates. 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 a reliable 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.

In this study, we examined the influence of habitat variation on the densities of Amazonian freshwater shrimp species in small rainforest streams and whether species show habitat segregation. We also assessed the effect of fish-assemblage composition and of catchment identity on the relationships between species abundance and environmental variables. Catchment differences related to connectivity can affect fish assemblages in small rainforest streams because of historic and biogeographic effects on colonisation (Mendonça et al., 2005). Here, we examined differences between two catchments in shrimp species relationships to habitat features that might result from differences in environmental complexity (Holt & Chesson, 2018).

2 | METHODS

2.1 | Study system

This study was carried out in *terra firme* streams in Ducke Forest Reserve, which is located 26 km north of the city of Manaus (2°56′S, 59°54′W at the administrative headquarters) and covers an area of *c.* 10,000 ha (Figure 1). Ducke Forest Reserve 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 streams). 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- or second-order streams were sampled, 15 belonging to the eastern catchment and 16 to the western (Figure 1),
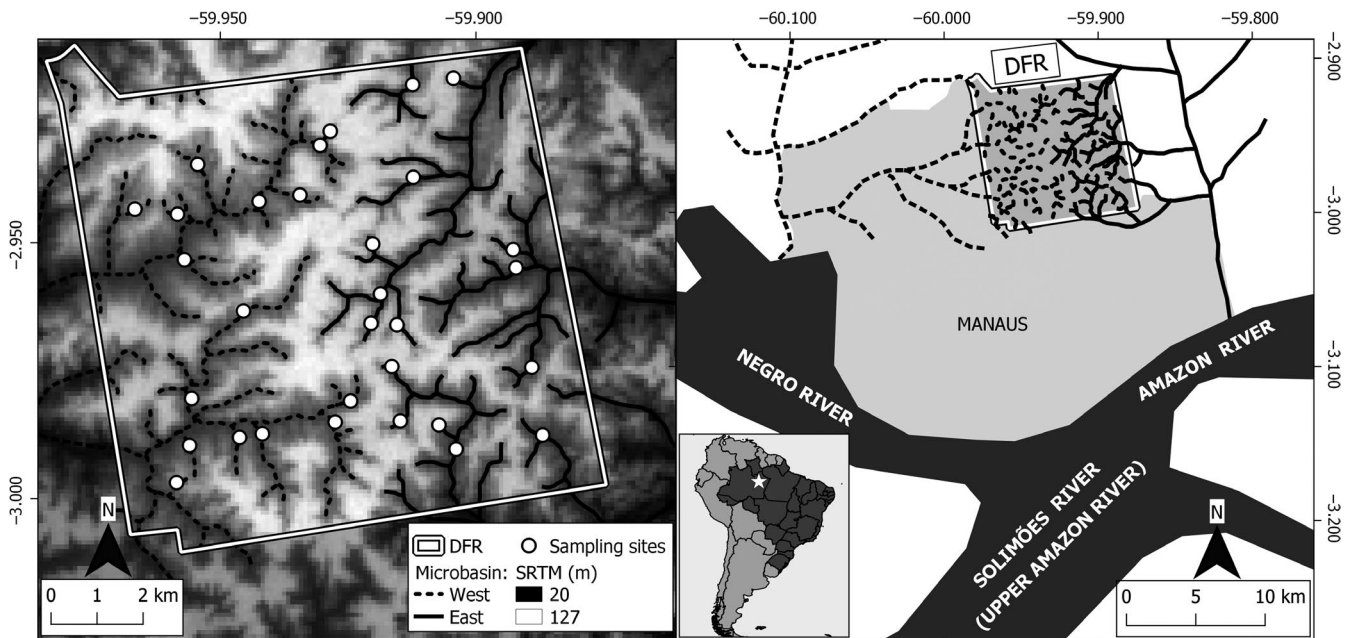
FIGURE 1 Location of Ducke Forest Reserve (DFR). The left figure shows the distribution of 31 sampling sites (white closed circles) in streams divided between two catchments, East (streams shown as continuous lines) and West (streams shown as dashed lines). SRTM,

between May and July 2018. Sampling sites were chosen to coincide with 38 permanent study plots established by the INPA Graduate Program in Ecology and coordinated by the Biodiversity Research Program of Western Amazonia (PPBio). The sample units corresponded to fixed reaches of 50 m 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 activities. Water chemical characteristics were measured in the middle of the stream reach (25 m from the start) using a multi-parameter water-quality meter (HORIBA®—U-52). Channel hydraulic characteristics and habitat physical structure were measured in four transverse transects spaced 16 m apart along the sample reach. Channel morphometry at the position of each of the four transects was represented by the total channel width 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 categorised as sand, clay, pebble, coarse 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 centre of each transect.

After estimating the environmental attributes, the 50-m reach was surrounded at its boundaries with 5-mm 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 in each stream reach. Shrimps could not be reliably identified in the field, so they were kept in well-aerated water in plastic bags and later killed by anaesthesia in alcohol diluted in stream water and then fixed in 70% alcohol. Specimens were identified to the lowest possible taxonomic level with the aid of specialised guides (Kensley & Walker, 1982; Melo, 2003). Fish were captured and kept in plastic containers with stream water and battery-operated 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 fish from Ducke Forest Reserve (Espírito-Santo, Magnusson, Zuanon, & Emilio, 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. To evaluate multicollinearity, tolerance 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 >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 coarse litter) were analysed. 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, in previous studies (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 Table 1.

TABLE 1 Mean values of environmental variables in sample sites

Environmental Variables

Sites	Catchment	pH	Temp. (°C)	Cond. (μS/cm)	O₂ (mg/L)	Cur. vel. (m/s)	Width (m)	Depth (m)	Area (m²)	Discharge (m³/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**	0.00	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	4.54	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

Note: Bold values represent min and max of environmental variables in each catchment.

Abbreviations: CL, clay; Cond., electric conductivity; Cur. vel., current velocity; FL, fine litter; LT, coarse litter; MC, macrophyte; RT, roots; SA, sand; Temp., temperature; TR, trunk; PB, pebble.

Multiple regressions were used to determine the relationships among the number of individuals of the shrimp 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 were 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.
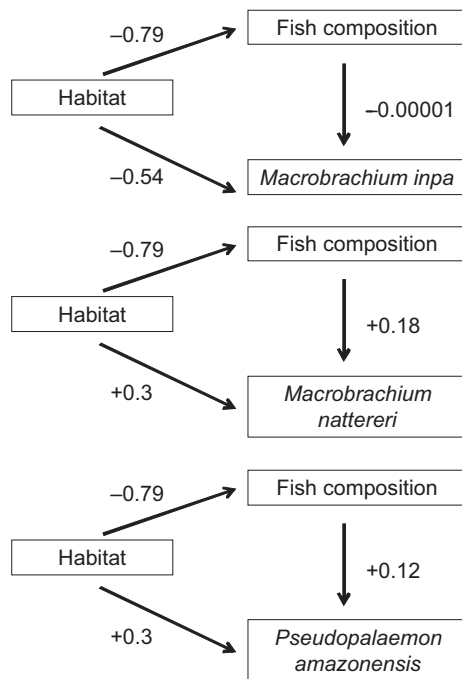
FIGURE 2 Path analyses of the effects of environmental variables (Habitat) directly on the densities of three species of shrimp and indirectly through fish composition in survey plots. The numbers associated with arrows represent path coefficients. The magnitude of the indirect effect is estimated by multiplying the path coefficient between habitat and fish composition by the path coefficient between fish composition and shrimp density. In the original analyses, the environmental variables (pH, temperature, current velocity, water depth, proportional cover of sand substrate, proportional cover of litter substrate) were entered individually, but for clarity of presentation their path coefficients were summed to represent the composite variable *Habitat*

2.3.1 | Specialisation 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 (stream reaches) along the gradients. The significance of the test was based on the χ^2 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 axis was used to summarise the composition of fish assemblages among the plots (Table S3) 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 could be considered a proxy of biological interactions between fish and shrimp, mostly potential predation and competition.

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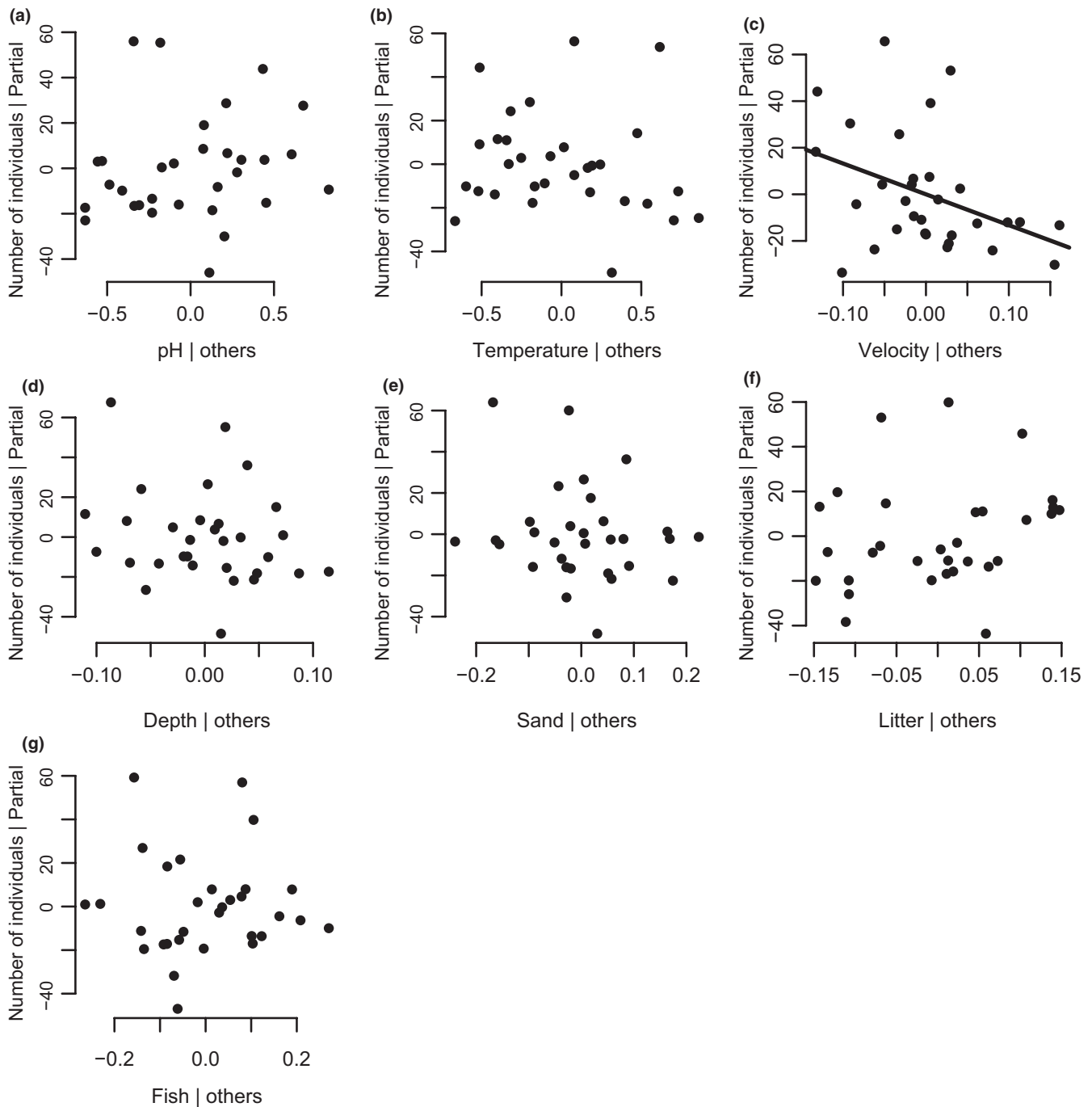
TABLE 2 Path analysis summary of magnitudes of direct and indirect effects (through fish composition) of the environmental variables

| Path analysis		
Macrobrachium inpa	*Macrobrachium nattereri*	*Pseudopalaemon amazonensis*
Path coefficients	Path coefficients	Path coefficients
Habitat–shrimp = −0.54	Habitat–shrimp = +0.3	Habitat–shrimp= +0.3
Habitat–fish–shrimp = +0.000008	Habitat–fish–shrimp = −0.14	Habitat–fish–shrimp= −0.09
General effect = −0.54	General effect = +0.16	General effect= +0.21
R^2 = −0.55	R^2 = +0.48	R^2 = +0.42

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; g, multivariate fish-composition axis) for *Macrobrachium inpa*

fish composition) of the environmental variables. Here, habitat represented the sum of the effects of all environmental features investigated.

Due to the low number of sample units, interactions were also included in simple models with the variables individually.

2.3.3 | Catchment effect

To test whether the effect of predictor variables on the number of individuals depended on the effect of the catchments (East or West), an interaction model was constructed through multiple regressions.

3 | RESULTS

We captured four Palaemonidae shrimp species, *Macrobrachium inpa*, *Macrobrachium nattereri*, *Pseudopalaemon amazonensis*, and Morphospecies 1 (an apparently undescribed species of *Pseudopalaemon*). *Macrobrachium inpa* was the most
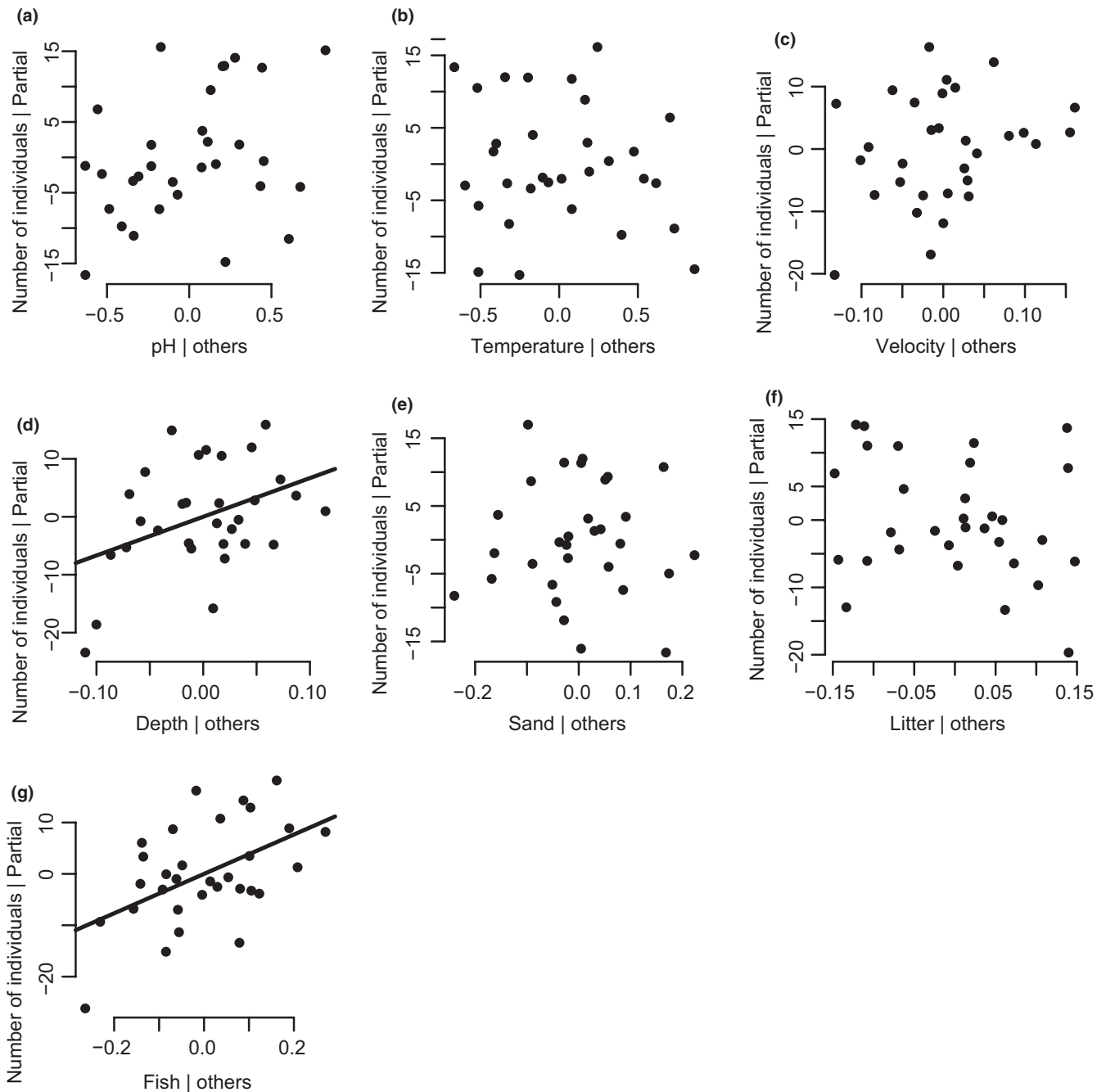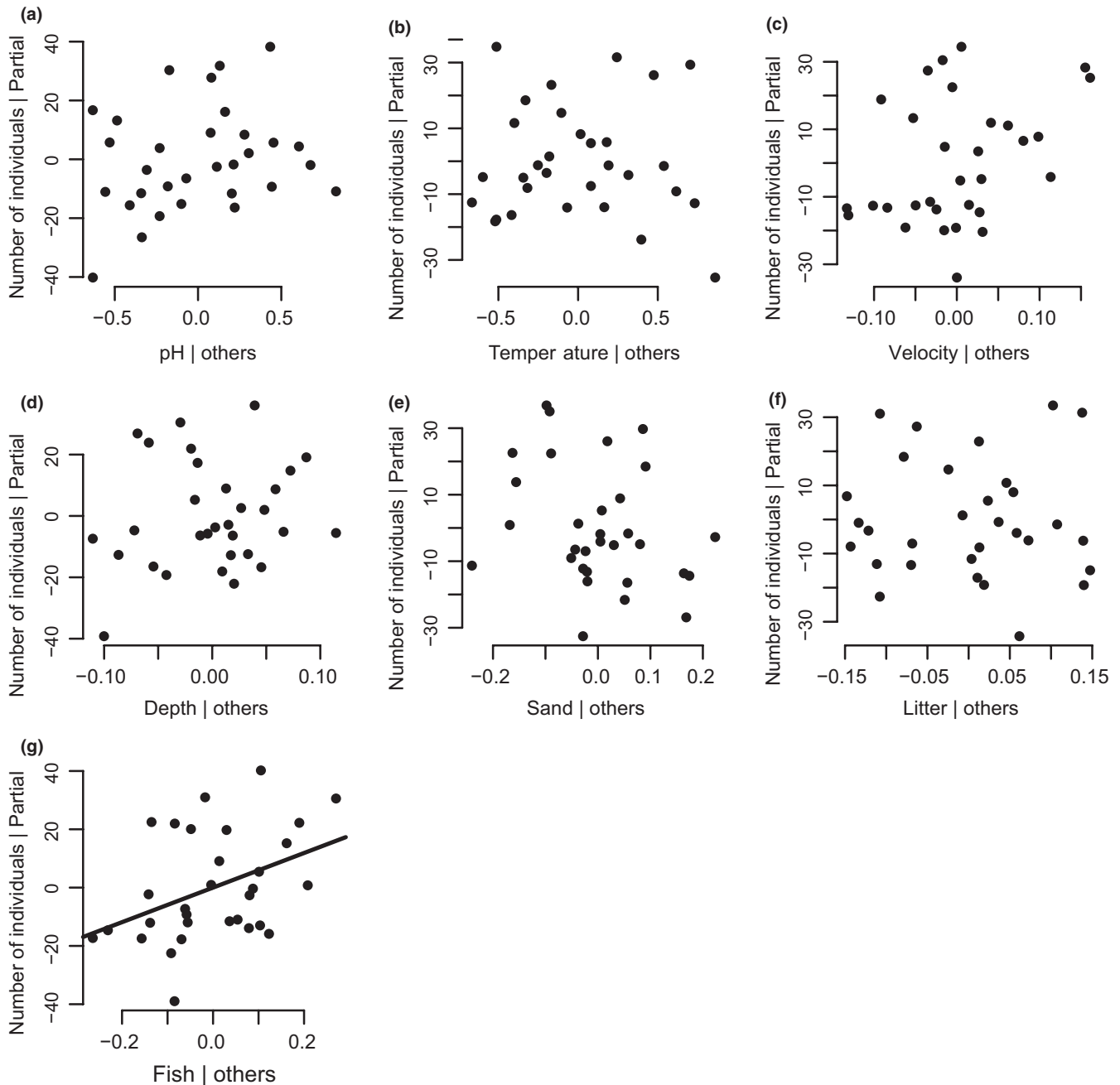
FIGURE 4 Partial-regression plots of the relationships between number of individuals and predictors (a, pH; b, temperature; c, velocity; d, depth; e, sand; f, litter; g, multivariate fish-composition axis) for *Macrobrachium nattereri*

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 2; 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 (Table S4), *M. inpa* was negatively related to current velocity ($t = -2.515$; $p = 0.01$) and channel depth ($t = -2.086$; $p = 0.04$). Analysed independently, fish composition did not significantly influence the distribution of this species ($t = 1.435$; $p = 0.16$). In the complete model (habitat + fish composition—Table S5), this species maintained a significant relationship with current velocity ($t = -2.017$; $p = 0.05$; Figure 3c), but not with any other variable (Figure 3a,b,d,e,f,g). 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 ($p \geq 0.07$), although the low probability associated with the null hypothesis indicated a probable type II error in two cases. When analysed 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 channel depth ($t = 2.121$; $p = 0.04$; Figure 4d) and also with fish composition ($t = 2.817$; $p = 0.009$; Figure 4g), but not with any other variable (Figure 4a,b,c,e,f).

3.3 | Pseudopalaemon amazonensis

Without the inclusion of fish composition, *P. amazonensis* did not show significant relationships with any habitat element ($p \geq 0.11$). Singly,

FIGURE 5 Partial-regression plots of the relationship between number of individuals and predictors (a, pH; b, temperature; c, velocity; d, depth; e, sand; f, litter; g, multivariate fish-composition axis) for *Pseudopalaemon amazonensis*

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 5g) and not with any other variable (Figure 5a,b,c,d,e,f).

3.4 | Specialisation and habitat segregation

Specialisation was detected for *M. inpa* along the current-velocity gradient (D_{KS} = 0.198; *p* = 0.01; Figure 6a,b) and for *P. amazonensis* along the pH (D_{KS} = 0.213; *p* = 0.01; Figure 6c,d) and channel depth (D_{KS} = 0.165; *p* = 0.05) gradients (Figure 6e,f; more information can be found in Table S6). pH (Figure 7a,b,c) and current velocity (Figure 7d,e,f) significantly segregated the distributions of the

three species (KS test, *p* ≤ 0.05), indicating that these habitat aspects have the greatest potential to differentiate the niches of the species. There was also evidence of segregation along the depth gradient between *M. nattereri* and *P. amazonensis* (*p* = 0.07), but the overlap was higher than for the other variables (Table S7).

3.5 | Catchment effect

Catchment 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 8a; Table 3), but not with any other
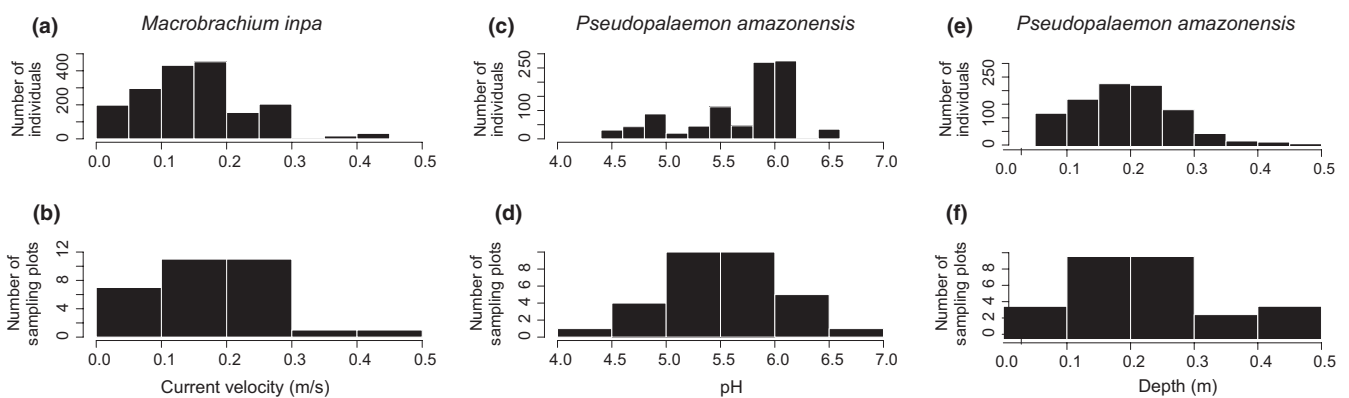

FIGURE 6 Distributions of individuals of specialist species (use, upper plots) and sampling plots (availability, lower plots) for *Macrobrachium inpa* (a, b), *Pseudopalaemon amazonensis* (c, d), and *Pseudopalaemon amazonensis* (e, f) along gradients in current velocity, pH, and depth
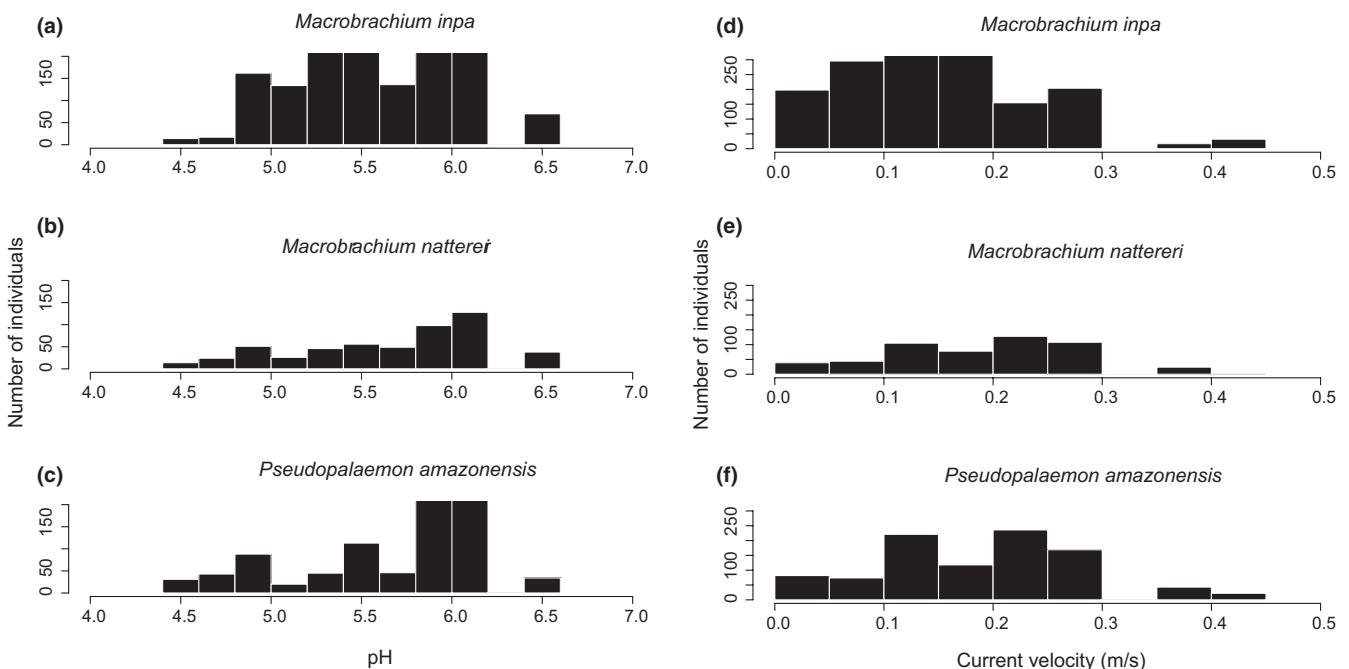

FIGURE 7 Relative use of different values of pH and current-velocity gradients by *Macrobrachium inpa* (a, d), *Macrobrachium nattereri* (b, e), and *Pseudopalaemon amazonensis* (c, f)

variable (Figure 8b–g). Simple regressions detected a similar result to the multiple interaction model, in which only the relationship between *M. nattereri* and pH changed between catchments ($t = -2.394$; $p = 0.02$). Sand proportion also had a low probability associated with the null hypothesis ($t = -1.958$; $p = 0.07$; Figure 8e), 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 ($t = -0.836$; $p = 0.41$).

4 | DISCUSSION

This is the first study demonstrating habitat partitioning among rainforest-stream 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). Among the hydraulic characteristics, stream velocity is usually the most influential habitat variable and a key factor related to shrimp distribution and composition (Girard et al., 2014; Richardson & Cook, 2006). As a general pattern, *M. inpa* was more abundant in shallow locations with lower current velocities, while *M. nattereri* and *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 in fact generalists in relation to substrate or, we think more likely, because any segregation between the species among substrates occurs at much smaller scales than the 50-m stream segments used as sampling units in this study.
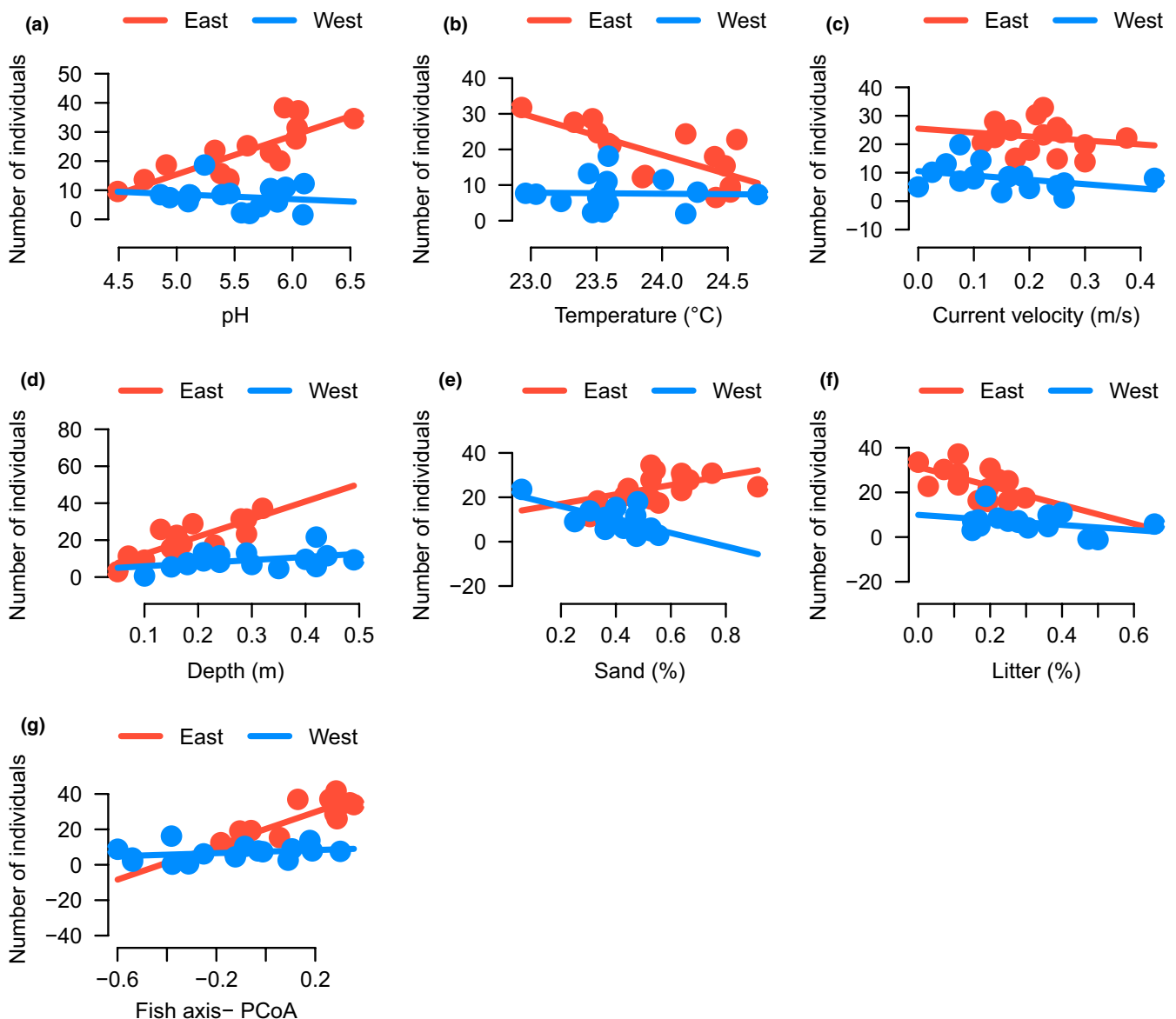

FIGURE 8 Plots of interaction models of catchment effects on number of *Macrobrachium nattereri* individuals with predictor variables (a, pH; b, temperature; c, current velocity; d, depth; e, sand; f, litter; g, multivariate fish-composition axis)

TABLE 3 Summary of results of interaction models of catchment effects on the relationships between predictor variables and number of individuals of each species

Predictors: covariate	Partial regression	
	Statistics parameters	
	t	P
Macrobrachium inpa		
pH: catchment	1.295	0.215
Temperature (°C): catchment	0.373	0.715
Current velocity (m/s): catchment	0.713	0.487
Depth (m): catchment	−0.528	0.605
Sand (%): catchment	−1.448	0.168
Litter (%): catchment	−0.737	0.472
Fish axis: catchment	−0.340	0.739
Macrobrachium nattereri		
pH: catchment	−2.128	**0.05**
Temperature (°C): catchment	1.687	0.112
Current velocity (m/s): catchment	−0.030	0.976
Depth (m): catchment	−1.320	0.206
Sand (%): catchment	−1.958	0.069
Litter (%): catchment	0.867	0.399
Fish axis: catchment	−1.594	0.131
Pseudopalaemon amazonensis		
pH: catchment	0.303	0.766
Temperature (°C): catchment	−0.353	0.729
Current velocity (m/s): catchment	−0.158	0.877
Depth (m): catchment	−0.448	0.660
Sand (%): catchment	−0.675	0.510
Litter (%): catchment	0.736	.473
Fish axis: catchment	0.156	.878

Note: Bold values indicate low probability associated with null hypothesis.

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 interactions with fish are probably more important to shrimp distributions in rainforest streams than habitat variation.

Two of the three species showed habitat specialisation, mainly related to hydraulic features. Specialisation is expected to be stronger in stable habitats (Büchi & Vuilleumier, 2014) so habitat specialists thrive in less-disturbed and less-fragmented environments (Devictor, Julliard, & Jiguet, 2008), such as Amazonian rainforest streams in this area. Habitat segregation was evident along current-velocity and pH gradients, where species showed less overlap than expected by chance. Current velocity is among the variables with the strongest potential to differentiate habitat use by rainforest-stream shrimp (Girard et al., 2014; Iwata et al., 2003). Commonly, shrimp responses to habitat features are linked to predation, competition, food availability, and/or physiological constraints (Covich, Crowl, Johnson, Varza, & Certain, 1991; Crowl & Covich, 1994; De Silva & De Silva, 1988; Rabeni & Minshall, 1977). For Amazonian stream shrimp, there is lack of information on species ecology and, therefore, we were unable to clarify how these factors specifically affect species segregation. However, substrate features tend to vary with stream velocity, so feeding strategies and refuges may be associated with species segregation. 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, 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 utilisation between some species than others, and those species were found to share a strong relationship with fish-assemblage composition. Therefore, the segregation recorded could be more a result of apparent competition than direct interactions among the shrimp species.

Apparent competition characterises 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 also 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). *Macrobrachium nattereri* and *Pseudopalaemon amazonensis* were strongly related to fish-assemblage composition and differ very little in habitat utilisation, so apparent competition seems to be stronger between them. However, these species also differ most in size, shape, 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, destabilising 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 catchments, with the exception of *M. nattereri*. The divergent behaviour in relation to pH between catchments observed for *M. nattereri* may indicate intraspecific variation or the existence of a cryptic species.

We conclude that the distributions of small rainforest-stream shrimps in 50-m stream reaches 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 biological interactions are also an important modulator of potential interactions in these assemblages. Only one species of shrimp appeared to be affected by catchments, and pH was the only variable that affected this species differently between catchments.

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

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