Temporal changes in streamflow can predict parasitism levels in freshwater prawns better than host traits

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Keywords: Cymothoid; *Macrobrachium*; rainfall; stream discharge; *Telotha henselii*.

Abstract

1. Understanding how changes in the hydrological regime drive parasite loads and dynamics remains a challenging issue in ecological parasitology. Temporal changes in streamflow and rainfall are key hydrological factors that could alter interactions between the parasite and host and affect parasitism levels. However, to investigate the effect of streamflow, rainfall, and its mechanisms, it is important to control host traits that can also influence parasitism levels in freshwater systems.

2. Here, we used a cymothoid-palaemonid prawn model to test the combined effects of streamflow and rainfall accounting for host traits to predict variations in parasite loads in stream ecosystems. We collected the palaemonid prawns monthly for two years and measured the variation of rainfall and streamflow (i.e. stream discharge) at the time of prawn sampling.

3. Our best model showed that streamflow can predict parasitism levels in prawns better than host traits. We found a higher prevalence and abundance of parasites in reduced streamflow compared to increased ones. We also found higher ectoparasite loads in females rather than males and occurring in autumn and winter rather than in spring and summer. Our results also showed that ectoparasite loads also suffer an effect of host body size, sex, and molt stage, but not host age.

4. Our findings show that reduced streamflow can facilitate host finding that favors parasite transmission in dry seasons and increase parasitism levels in stream systems. Temporal variability in streamflow can have a strong influence on parasite loads and dynamics compared to host traits in stream ecosystems.

5. Identifying how interactions between aquatic invertebrates and parasites respond to variability in the hydrological regime can help to better understand and predict disease outbreaks as habitat reduction and disturbance continue in stream ecosystems.

1. INTRODUCTION

Parasites represent a significant component of biodiversity, with key roles in most ecosystems of the world (Poulin, 2007; Hechinger et al., 2011; Timi & Poulin, 2020). Although the relevance of parasites in ecosystem functions and conservation has increased in recent years (Poulin, 2021; Gagne et al., 2022), this topic has been neglected in studies on crustacean biology and ecology, particularly in the neotropical freshwater environment (Wunderlich et al., 2011; Smit et al., 2014; Smit et al., 2019). Moreover, freshwater ecosystems are among the most diverse parasite species (Poulin, 2016) and face increasing high anthropogenic pressure and hydrological disturbance (Poff, 2018; Boos et al., 2019; Palmer & Ruhí, 2019; Zanghi et al., 2023; Rumschlag et al., 2023), which calls for more studies to understand how these environmental changes interact with the properties of hosts to affect parasite infestations and dynamics.

Environmental changes in hydrological regime act as a strong driver to sustain and alter the dynamics of macroinvertebrates and fish communities in freshwater ecosystems (Poff & Zimmerman, 2010; Jellyman et al., 2013; Jellyman et al., 2014; Northington & Webster, 2017; McIntosh et al., 2018; Herbst et al., 2019; Mendes et al., 2021). In rivers and stream habitats, rainfall and/or precipitation play a central role in affecting the interaction between the biota and the physical factors of the stream (Palmer & Ruhí, 2019; McIntosh et al., 2024). Changes in river flow are driven by variation in precipitation, that can change the flow of stream many times (Paull et al., 2012; Botter et al., 2013; Olsson et al., 2024), and influence the dispersal (Miyazono & Taylor, 2013), the predation (Jellyman et al., 2014; McIntosh et al., 2018), community stability (Greig et al., 2022) and food webs (McIntosh et al., 2024). These changes in hydrological regime have also been suggested to affect host-parasite interactions (Marcogliese, 2016; Shearer & Ezenwa, 2020), through parasite transmission mechanisms and host susceptibility to parasites (Blasco-Costa et al., 2013; Penczykowski et al., 2014), which can increase or decrease parasite loads (Altizer et al., 2006; Groner et al., 2018; Vestbo et al., 2019; Shearer & Ezenwa, 2020; Tadiri & Ebert, 2023). For example, some studies have suggested that the reduction in streamflow (i.e., stream discharge) might increase host aggregation and facilitate host finding by the parasite that also is more clumped into the stream (Brunner & Ostfeld, 2008; Paull et al., 2012; Shearer & Ezenwa, 2020). However, most studies have focused on the effects of increasing temperature rather than variation in streamflow and their mechanisms (Marcos-López et al., 2010; Lõhmus & Björklund, 2015; Marcogliese, 2016; Lymbery et al., 2020). Therefore, it is fundamental in aquatic parasitology to disentangle the contribution of these sources of variation, particularly in the hydrological regime, to better understand how these changes in streamflow and rainfall correlate with host traits to affect parasite loads over time (Poulin, 2007; Kamiya et al., 2014; Poulin, 2021; Tadiri & Ebert, 2023).

Furthermore, the dynamic of host-parasite systems is also driven by host traits that can influence the likelihood of infection on several scales of observation (Poulin, 2007; Castrillo, 2018; Schmid-Hempel, 2021). It is important in ecological studies, particularly in stream ecosystems, to control for host trait effects such as host body, sex, age and molt that can affect host exposure and susceptibility to parasite infections commonly found in the field (Altizer et al., 2006; Cattadori et al., 2019; Izhar et al., 2020). For example, host body size often correlates positively with parasite abundance (Poulin, 2007; Kamiya et al., 2014). Other host traits such as host age, sex, and molt are also correlated with parasite variations between individuals within populations (Christe et al., 2007; Ben-Ami, 2019, Izhar et al., 2020), which can be age-dependent (Wunderlich et al., 2022) or sex-biased (Poulin & Forbes, 2012). In crustaceans, the molting stage is a key growth factor, while it can expose hosts to parasite infections (Duneau & Ebert, 2012) or reduce the likelihood of parasite penetration (Izhar et al., 2020). Thus, it is important to account for the role of host traits when investigating the effects of streamflow and rainfall on parasite dynamics, because these traits could confound the results and interpretations of the focal predictors that freshwater ecologists seek to uncover (Timi & Poulin, 2020).

Here, we investigate the influence of the hydrological regime, such as streamflow and rainfall, on the accounting for host traits on parasitism levels in a species of palaemonid prawn from freshwater streams in the Brazilian Southern. To test whether the hydrological regime can affect parasite infestation, in this study we examined the effects of streamflow (Q, m^3/s), rainfall, seasons, host size, sex, age, molt stage, and their interactions on prevalence and abundances of a cymothoid isopod, *Telotha henselii* (Von Martens, 1869) parasitizing the palaemonid prawn *Macrobrachium brasiliense* (Heller, 1862), as our model. We predict that a reduction in streamflow in dry seasons could indirectly facilitate the chances of parasite encounters and transmission due to greater aggregation of hosts and free-swimming parasites during this season. Therefore, we also expect that prawns collected in dry seasons (i.e., low rainfall and reduced streamflow) would have higher levels of cymothoid isopod infestation than in wet seasons (i.e., high rainfall and normal streamflow). Finally, we also expected that the host traits may have a potential additive effect on parasitism levels. Since host traits are crucial to driving parasite dynamics, we expect a potential additive effect of body size, sex, age, and molt stage on cymothoid isopod infestations in *M. brasiliense* populations.

2. METHODS

2.1. Host-parasite model system

Cymothoid isopods are a diverse group of parasitic crustaceans with a broad distribution throughout the world (Williams & Boyko 2012). Most cymothoids are parasites of marine, freshwater, and brackish teleosts (Smit et al., 2014), but can also parasitize freshwater palaemonid prawns in tropical South American river systems (Wunderlich et al., 2011; Andrade et al., 2020). Cymothoids can also cause damage and affect the growth of their hosts

(Smit et al., 2019; Rose et al., 2020). Adults of *Telotha henselii* are well-known hematophagous cymothoid ectoparasites on fish, mostly found on skin and gills, and juvenile males use palaemonid prawns (e.g., *Macrobrachium brasiliense*) as optional intermediate hosts besides final hosts (Trilles & Öktener 2004; Wunderlich et al., 2011; Andrade et al., 2020; Anaguano-Yancha & Pilatasig, 2022; Fujita et al., 2023). These cymothoids also exhibit protandrous hermaphroditism in which male reproductive organs develop first (i.e. that can attach to the prawn), and when parasitizing a fish host, they transform into a sexually mature female (Cook & Munguia, 2015; Rose et al., 2020). Therefore, the cymothoid-palaemonid system is a tractable model that could facilitate our understanding of how changes in streamflow and host traits can influence host-ectoparasite interactions and the presence of juvenile cymothoids in freshwater ecosystems.

2.2. Study area and sampling design

As part of a long-term study of ecological parasitology, palaemonid prawns were collected for two years (i.e., 1995 and 1998), in a stream of first and second order (Águas Claras stream) from the Pardo River basin (21° 18’ 30’’ S - 47° 36’ 16’’ W), in southwest Brazil (Figure 1). The Águas Claras stream is a tributary of the Pardo River that has a drainage basin of 10,694 km^2 and a course of approximately 550 km, with the dry season occurring from April to September and the wet season from October to March (Alves et al., 2018). The bottom of the stream bottom was mainly composed of sand and the depth rarely exceeds 1 m. We collected prawns monthly from three sites at the same time, for 2 hours each by two people from 10:00 am to 12:00 soon. At each site, the prawns were manually collected by sweeping sieves (50 cm in diameter and mesh size of 4 mm mesh size) near the riverbank, in places with marginal aquatic vegetation consisting mainly of species of Hydrocharitaceae (aquatic herbs), Juncaceae (reeds), and Pontederiaceae (water hyacinths) from the stream (Mantelatto & Barbosa, 2005).

Prawns were individualized in plastic bags while still in the field and kept in thermic box on crushed ice until they arrived in the laboratory, where the specimens were euthanized by thermal shock (at 3°C, for 30 min), fixed, and preserved in 70% ethanol.

2.3. Measures of host traits

In the laboratory, the prawn specimens were identified according to Melo (2003). Posteriorly, prawns were submitted to biometry based on body measures (CL, carapace length – from the base of the rostral spine to the opposite region of the carapace; and TL, total length – comprising total body size, from the base of the rostral spine to the extremity of the telson), with a 0.05 mm precision caliper; and weigh (W, total wet weight – with a digital balance of 0.01 g), and also characterized according to the age, sex, and molt stage. In this study, we consider age as a function of the developmental phase (juvenile and adult), using as proxies: 1) the size at onset of morphological maturity for males and females (9 and 8 mm CL, respectively, according to Nogueira et al., 2019); 2) sex of each exemplar, by checking the presence of the appendix masculine in the endopod of the second pair of pleopods (Nogueira et al., 2020); and 3) molt stage (intermolt, premolt, and molting or ecdysis) determined in each specimen by exoskeleton hardness inspection, especially the carapace (Drach & Tchernigovtzeff 1967).

2.4. Streamflow and rainfall measurements

The monthly rainfall, streamflow (i.e. stream discharge), and habitat area data were obtained from an archival hydrological data set from the Department of Waters and Electric Energy of the State of São Paulo (DAEE, 2023). We used a rainfall station near the sampling sites to obtain total rainfall (mm), average monthly stream discharge (Q, m^3/s), velocity (m/s), depth (m), width (m) and area (m^2). We used the streamflow (Q) based on the velocity-area method at the time of prawn sampling. We used three rainfall variables; total rainfall (mm) for the month in which the sample was collected (R_t), total rainfall for the month before sample collection (R_{t-1}), and total rainfall two months before sample collection (R_{t-2}). Three different measures were used to test whether current (immediate effect) or previous (delayed effect) rainfall was more strongly associated with ectoparasite loads. Together, changes in the rainfall regime are associated with changes in streamflow.

2.5. Parasitological screening

The palaemonid prawns were examined and the ectoparasites found were removed from each animal and measured to obtain the total length (TL) under a stereomicroscope (Zeiss® Stemi® SV-6) attached to a computer image analysis system using Zeiss® KS-100 3.0 software (0.01 mm precision). Posteriorly, the ectoparasites were fixed in 70% ethanol and subsequently identified through specific characteristics (e.g., 2nd pereopod showing five spines in the inner margin of the propodus and the 6th pereopod showing four spines in the propodus and one in merus), according to Lemos de Castro (1985) and Andrade et al. (2020). The abundance of ectoparasites was considered as the total number of cymothoid isopods in each host individual, which can be categorized in terms of infestation levels as follows: 0 = no infestation; 1 = low infestation; and 2-3 = high infestation (Horton & Okamura, 2001; Kawanishi et al., 2016). The prevalence was calculated as the proportion of prawns infected by cymothoid isopods with the total number of hosts analyzed, and the mean intensity was calculated as the total number of cymothoids in a sample of infected host species divided by the number of infected individuals of the host species in the sample (Bush et al., 1997).

2.6. Data analysis

We used generalized linear models (GLM) to test the relationship between streamflow (i.e. stream discharge, Q) and parasitological indices (i.e., prevalence and parasite abundances), and whether this pattern can vary between sexes. To estimate the effects of streamflow, rainfall, habitat area, and host traits (i.e., total length, sex, age, and molt stage) on ectoparasite abundances (i.e., response variable), we fit generalized linear mixed models (GLMMs), using Poisson and negative binomial distributions (Zuur et al., 2013). Streamflow, habitat area, rainfall, year, host traits, and their interaction were the main predictors, while month and year were included as random intercepts. Individual IDs (i.e., prawn ID) nested within each month were used as random factors in all models. We used prawn ID as an observation-level random effect to control overdispersion in our parasite count data (Zuur & Ieno, 2016). Before fitting the model, we evaluated the multicollinearity of the predictors using the variance inflation factor (VIFs) with the R performance packages (Lüdecke et al., 2021), and excluded those with VIFs >10, which represent high multicollinearity among predictors (Borcard et al., 2011). We also used diagnostic plots to test for normal distribution and equal variance of residuals with the R package DHARMA (Hartig, 2022).

We used the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) to select the best competitive model with R performance packages (Lüdecke et al., 2021). After choosing the best model, we used the semipartial coefficients of determination (partR2) to check the variation to individual predictors of this model (Stoffel et al., 2021). The partR2 can decompose the variance of R^2 into components uniquely explained by individual predictors (Stoffel et al., 2021). GLM and GLMM analyses were performed in R v. 4.2.1 (R Development Core Team, 2022) with packages lme4 (Bates et al., 2015) and glmmTMB (Magnusson et al., 2020), respectively.

3. RESULTS

We found that streamflow can predict parasitism levels in prawns better than host traits (Table 1). Of the models that we compared, the one that included streamflow (Q), concurrent rainfall (R_t), and habitat area received the most support (Table 1). We found a higher prevalence (GLMM: estimate ± se: –0.756 ± 0.167, $p < 0.001$, $R^2_{adj} = 0.72$; Figure 2A) and abundance (GLMM: estimate ± se: –0.625 ± 0.203, $p < 0.002$, $R^2_{adj} = 0.77$; Figure 2B) of parasites in reduced streamflow (i.e., $Q < 2$) compared to increased ones (i.e., $Q > 2$; Figure 2). We also found a significant difference between males and females in total abundance to streamflow (GLMM: estimate ± se: 0.951 ± 0.307, $p = 0.002$; Figure 2B), but not in prevalence (GLMM: estimate ± se: –0.101 ± 0.345, $p = 0.769$; Figure 2A). The higher parasite infestations (i.e., two to three parasites per infested prawn) were observed in lower rainfall (dry season) rather than in higher rainfall (wet season) (Figure 3).

Overall, we found a prevalence of 16.4 % of a total of 1,012 prawns collected over two years (Table 3). In 1995, the prevalence of ectoparasites was higher in winter and autumn (18.9% and 16.6%, respectively) rather than in spring and summer (11.9 and 9.2%, respectively - Table 3). For 1998, the prevalence in autumn was also higher (34.1%) than in the summer (14.2%; Table 3). The mean intensity of the infection was slightly higher in 1998 than in 1995 (Table 3). The abundance of ectoparasites varied between seasons, with a higher infestation (i.e., two to three parasites per infested prawn) in the autumn of both years (Figure 4a, Table 3), but there are no differences between the two years in our model (Wald = –1.849; $p = 0.064$; Table 1, Figure 4b). We also found higher ectoparasite loads in females than in males in autumn/winter than in spring/summer.

Our results also showed a significant effect of host traits on ectoparasite abundances (Figure 5, Table 1), with the size of the host's body (one to three parasites in prawns size ≤ 35 mm TL – Figure 5a; Table 1); host sex (parasitism in female hosts more abundant than in males

– Figure 5c; Table 1); and host molt stage (parasite abundance following this hierarchical sequence of stages of molt: intermolt > ecdysis > premolt – Figure 5d; Table 1). However, no effect of age on parasitism was found (the abundance of parasites did not differ between juveniles and adults – Figure 5b; Table 1).

Of all fixed variables included in the GLMM models, season was excluded because it showed high multicollinearity with VIF > 10 (Table 2). The relative importance of the predictors used in the GLMM was decomposed to check the variation with the individual predictors of the best model (Figure 6). Of three hydrological factors, streamflow seems to be the best predictor of the ectoparasite infestation model, presenting the largest inclusive R^2 (Figure 6A), negative structure coefficient (Figure 6B) and negative beta weight (Figure 6C), while host length, sex (female), and molt (ecdysis) contributed positively to the predicted model (Figure 6A-C; Table 1).

4. DISCUSSION

Our results reveal that the effect of streamflow on parasitism levels surpasses those of host traits. Changes in hydrological regime act as a strong drive to sustain and alter the dynamic of benthic invertebrate communities (Poff et al., 2018; McIntosh et al., 2018; Herbst et al., 2019; Palmer & Ruhi, 2019), as well as infectious disease and parasite dynamics in freshwater ecosystems (Altizer et al., 2006; Paull et al., 2012; Penczykowski et al., 2014; Groner et al., 2018; Tadiri & Ebert, 2023). Freshwater organisms are exposed to variable rainfall regimes that lead to changes in streamflow, and can affect their behaviour and the interaction between host and parasite in stream ecosystems (Paull et al., 2012; Penczykowski et al., 2014; Reynolds et al., 2019).

The effect of variation in rainfall regime that leads to a temporal reduction in streamflow can facilitate host finding by cymothoid parasites and, consequently, increase parasitism levels in a more confined environment (Paull et al., 2012; Penczykowski et al., 2014; Shearer & Ezenwa, 2020). Some mechanisms have been suggested to explain the influence of hydrological regime such as streamflow on successful transmission of parasites during this period (Sousa & Grosholz, 1991; Penczykowski et al., 2014; Smit et al., 2019). This reduction in streamflow can affect host behaviour and aggregation, increasing the probability of contact between parasite and host (Paull et al., 2012; Reynolds et al., 2019; Schmid-Hempel, 2021). Studies have shown that a high density of hosts in a more confined stream, as also shown by our results, can accelerate contact between those most susceptible, as well as intensify the risk of infection for host individuals (Lafferty et al., 2015; Buck et al., 2017). The same can occur with parasites and their transmission stages because they are also more clumped together across the environment, resulting in hosts experiencing a higher infection level (Brunner & Ostfeld, 2008; Paull et al., 2012; Davenport et al., 2024). Furthermore, a recent study showed that disease outbreaks in a freshwater zooplankton are closely linked to the concentration of the transmission stage in the environment (i.e., mean spore concentration increased prior to disease outbreaks in hosts; Davenport et al., 2024), reinforcing our prediction that high aggregation of free-swimming parasites in reduced streamflow can favor the higher infestation of isopods in the prawns. With the reduction in depth/width in the stream with a lower flow/discharge, the incidence of light is high (Bernhardt et al., 2022), which can facilitate the attack of the manca juveniles (i.e., free-swimming parasites) on the prawn hosts. Manca juveniles are positively phototaxic (i.e., they spend the day on the surface) and possess large eyes that help the parasite locate the shadows of potential prawns at the bottom of the sand where they are foraging (Smit et al., 2019). However, depending on the parasite species and system, the increase in light can also reduce the infectivity of parasites that use spores to transmit (Shaw et al. 2020). Studies have shown that parasites respond to host and environmental cues (e.g. light) in ways that bring them into the habitat (i.e., a few centimeters of an appropriate host's "active space") commonly frequented by their potential hosts (Rea & Irwin, 1994; Goater et al., 2014; Cook & Munguia 2015; Shaw et al. 2020). An interesting study also showed that males in parasitic crustaceans were more active in light with reduced activity in darkness (Hunt et al., 2021), with light being their dominant stimulus (Bandilla et al., 2007). This makes sense because in low-flow habitat, manca juveniles are probably closer to prawns, which might increase their visual capacity to detect the hosts.

In addition, streamflow velocity can be another mechanism that drives parasite transmission success (Sousa & Grosholz, 1991; Reynolds et al., 2019). Fast streamflow might decrease the capacity of the parasite (i.e., manca juveniles) to detect and attach to the hosts (Smit et al., 2019). For example, in an interesting experiment with fish, the parasite transmission rate was higher in shoals exposed to interrupted flow (Reynolds et al., 2019), resulting in a higher parasitic prevalence compared to a continuous water flux system. Furthermore, some studies have shown that slow water flow downstream can accumulate more infective stages of free-living, which can influence the probability of host and parasite encounter, resulting in high parasitism in this part of the stream (Blasco-Costa et al., 2013; Resetaris & Byers, 2023). In contrast, during the wet seasons, excessive rainfall and streamflow can drag away and reduce the abundance of the free-living infective stages of the parasites due to higher water volume, a fact verified in several helminth and crustacean parasites, especially in mancae of cymothoids (Stromberg, 1997; Altizer et al., 2006). Our results are consistent with the above pattern, showing that the higher prevalences and abundances of ectoparasites were found in dry (slow-flowing) rather than wet (fast-flowing) seasons.

Few published studies have shown strong evidence for the role of rainfall and/or precipitation as a key driver of seasonality in parasitism in freshwater and terrestrial ecosystems (Aneesh et al., 2013; Hiestand et al., 2014; Gagne & Blum, 2016; Jemi et al., 2020; Shearer & Ezenwa, 2020). Although these studies have shown the influence of rainfall on parasite infections, the mechanisms for this were not well elucidated. Some authors recorded higher parasite loads associated with low rainfall, suggesting a gradual increase in host susceptibility and exposure to helminth infections during the dry season (Gagne & Blum, 2016; Shearer & Ezenwa, 2020). In aquatic ecosystems, cymothoids parasitizing fish were also more abundant during the autumn season (i.e., dry season in India), suggesting that this season can facilitate the infestation of ectoparasites (Aneesh et al., 2013; Jemi et al., 2020). Another interesting study showed that drought in stream fish communities can intensify parasitic crustacean infestations (Medeiros & Maltchik, 1999), which could support our study, with a more intense infestation of prawns by these juvenile cymothoid isopods during the dry seasons. Precipitation also has a profound effect on the free-living stages of terrestrial mammal helminths because some parasites use aquatic invertebrates as their intermediate hosts (Hiestand et al., 2014; Carlson et al., 2017). This point also suggests a more complex interaction and certain dependence that some terrestrial animals have with freshwater ecosystems and their changes. Furthermore, changes associated with rainfall and/or precipitation in parasitism can vary depending on key host traits (Shearer & Ezenwa, 2020).

We also found an effect of host traits on parasite infestation. Previous studies have found a positive relationship between ectoparasite infestation and host traits, suggesting heterogeneity in transmission, susceptibility, tolerance, and resistance to determine parasite infections (Johnson & Hoverman, 2014; Izhar et al., 2020; Clark et al., 2021; Schmid-Hempel, 2021). We found that body length, sex, and molt stage (but not host age), influenced the abundance of ectoparasites. The size of the host body is a critical characteristic that influences several host-parasite systems (Poulin, 2007; Schmid-Hempel, 2021). For example, parasite abundance (or loads) often correlates positively with host body size (Kamiya et al., 2014; Schmid-Hempel, 2021). Furthermore, body size correlates with other host traits that affect the likelihood of acquiring infections (Cooper et al., 2012; Blasco-Costa & Poulin, 2013; Schmid-

Hempel, 2021), such as longevity. The host sex has also been an important factor in explaining sex-biased parasitism (Poulin & Forbes, 2012). In many parasite-host systems, males are more parasitized than females (Cozzarolo et al., 2019), however, in our study female prawns have a higher abundance of ectoparasites than males. In general, the prevalence or intensity of parasites in arthropods is also higher in males than females (Klein et al., 2004), but in some studies it was not observed (see Sheridan et al., 2000). A potential explanation of a female bias might be caused by differences in immunity and parasite exposure between the sexes (Poulin, 2007, Cozzarolo et al., 2019; Schmid-Hempel, 2021). Males and females are likely to exhibit differences in behaviour and spatial aggregation in the host population (Nogueira et al., 2019; Bardera et al., 2020), which can influence parasite exposure and susceptibility and favor sex-biased parasitism (Poulin, 2007; Christe et al., 2007).

Another key factor that can interfere with infestation levels is the molting process (Groner et al., 2018; Izhar et al., 2020). Our results suggest that the abundance of parasites was positively associated with the ecdysis stage. In crustaceans, the molting stage is a key growth factor, while it can expose hosts to parasite infections (Duneau & Ebert, 2012) or reduce the likelihood of parasite infestations (Izhar et al., 2020). Although we did not find an effect of host age on the abundance of ectoparasites, age has been correlated with parasite variation between individuals within invertebrates (Ben-Ami, 2019, Izhar et al., 2020) and vertebrates host populations (Wunderlich et al., 2022). For example, Izhar et al. (2020) found that older adults have better immune responses than younger adults and juveniles of *Daphnia magna*. Finally, our host trait data suggested an additive effect on parasite infestation and underscores the importance of controlling these traits in ecological studies of host-parasite systems.

In addition, the shortage in resource availability during the dry season (i.e. in a more confined environment), could also lead to poor host body conditions and immune function, with an increase in parasite prevalence and intensity (Marshal et al., 2008; Shearer & Ezenwa, 2020). Another important gap that could be considered is a potential combined effect of streamflow and habitat size on the variation of aquatic populations and their parasites. Habitat size has been suggested to drive many important ecological processes (McIntosh et al., 2018; McIntosh et al., 2024). However, it is unclear how this combined effect could influence host-parasite dynamics. Furthermore, a study that integrates different stream habitats, local environmental factors, and resource availability in ecological parasitology could produce new broadly applicable strategies to help parasitism management and conservation in freshwater ecosystems (Civitello et al., 2018; Hasik & Siepielski, 2022). Although our study was not designed to address the influence of the variation in resource availability and habitat size, we suggest the need for additional experiments to test the hypothesis that host body conditions should change between smaller and larger habitats, thus modifying the ectoparasite-host dynamics.

In conclusion, our study demonstrated that changes in streamflow combined with host traits can influence host-parasite interactions and affect the risk of parasitism in stream ecosystems. More studies are needed to understand how variation in streamflow and habitat structure as a result of climate change and hydrological disturbances can impact the natural flow regime and affect how benthic macroinvertebrates communities will overcome the risk of parasitism in a stream ecosystem that changes. Our findings also revealed that additive effects of streamflow and host traits in predicting the parasitism levels are relevant and should be considered in future studies in freshwater ecosystems.

AUTHOR CONTRIBUTIONS

Conceptualization, data interpretation, writing: AW, EM, and MP. Conducting the research, data analysis, and preparation of figures and tables: AW, MP.

ACKNOWLEDGEMENTS

We thank members of the CRUSTA's research group (Gustavo Y. Hattori, Lucimari M. Seto, and Fabiano G. Taddei), during field expeditions to Águas Claras stream (Serra Azul municipality, SP), and help with their biometry. MAAP thanks to 'Fundação de Amparo à Pesquisa do Estado de São Paulo' – FAPESP, which indirectly funded this work during the execution of the *Arenaeus* Project (# 1995/09495-2) and to the 'Conselho Nacional de Desenvolvimento Científico e Tecnológico' – CNPq, due to the research fellowship grant (# 303286/2016-4 and # 305957/2019-8). ACW also thanks São Paulo State University (UNESP/PROPe) for a postdoctoral research fellowship (Edital 13/2022 - Programa Unesp de Pós-Doutorado- Chamada Pública para Seleção de Bolsistas - Apoio a Grupos de Pesquisa) and indirectly to FAPESP (# 2017/16650–5) due to previous financial support to statistical courses (e.g., Mixed effects modelling) that makes possible the data analyses in this study. We also thank the Associate Editor and two anonymous referees for their helpful comments that improved the quality of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data supporting the findings of this study are available upon request from the corresponding author.

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Table 1. Results of generalized linear mixed models describing the total abundance of ectoparasites (i.e., response variables) as a function of streamflow (Q, m^3/s), rainfall (mm), habitat area, years, and host traits (host body size, host sex, host age, and host molt stage). Parameter estimates, standard error (SE), Wald z-values, p-value, and 95% confidence interval for the parameters of explanatory variables describing variation in ectoparasite abundances are provided. Bold values indicate significant variables. The confidence intervals (CI) that exclude zero are also reported in bold.

Parameter	**Parameter estimate**	**SE**	***z*-value**	***p*-value**	**95% CI**	
					Lower	**Upper**
Intercept	–3.354	0.610	–5.499	**<0.001**	**–4.550**	**–2.159**
Streamflow (Q)	–0.985	0.300	–3.275	**0.001**	**–1.575**	**–3.957**
Rainfall (Rt)	–0.003	0.001	–2.887	**0.003**	**–0.005**	**–0.001**
Habitat area	0.409	0.175	2.328	**0.019**	**0.064**	**0.754**
Year	–0.244	0.132	–1.849	0.064	–0.503	0.014
Host body size	0.051	0.007	6.893	**<0.001**	**0.036**	**0.065**
Host sex (Female)	0.546	0.186	2.925	**0.003**	**0.180**	**0.912**
Host age (Adult)	0.459	0.608	0.755	0.755	–0.732	1.651
Host molt stage (Premolt)	–0.333	0.424	--0.786	0.432	–1.165	0.498
Host molt stage (Ecdysis)	0.511	0.200	2.551	**0.010**	**0.118**	**0.904**

Table 2. Variable inflation scores used to select variables included in the GLMM models. Predictor terms (term), variance inflation factor (VIF) and 95% confidence interval for VIF (VIF 95% CI). Bold values indicate exclusion of VIF > 10

Term	**VIF**	**VIF 95% CI**	
		Lower	**Upper**
Streamflow (Q)	9.51	8.11	11.24
Rainfall (Rt)	5.68	5.09	6.35
Habitat area	8.58	7.66	9.63
Season	**98.92**	**87.71**	**111.59**
Year	6.48	5.80	7.26
Host sex	1.04	1.01	1.20
Host body size	1.06	1.02	1.19
Host age	1.07	1.03	1.19
Host molt stage	1.04	1.01	1.22

Table 3. Variation of the parasitism indices of the *Telotha henselii* cymothoid isopod on *Macrobrachium brasiliense* prawn with seasons, years, and host traits. Where: Mean ± SD = average ± standard deviation.

Season/Year	**Total length Male**		**Total length Female**		**Prevalence**	**Mean Intensity**	**Intensity range**
1995	n	Mean ± SD	n	Mean ± SD	%	Mean ± SD	Min-Max
Winter	81	15.3±4.8	167	15.1±3.8	18.9	1.04±0.20	1-2
Spring	82	17.5±4.3	120	15.7±3.6	11.9	1	1
Summer	59	15.3±4.5	71	15.7±3.6	9.2	1.08±0.29	1-2
Autumn	99	14.2±3.8	100	15.5±3.8	16.6	1.12±0.41	1-3
Total	321	15.5±4.5	458	15.4±3.7	14.9	1.06±0.27	1-3
1998							
Winter	-	-	-	-	-	-	-
Spring	-	-	-	-	-	-	-
Summer	43	28.3±17.1	105	19.7±9.5	14.2	1.23±0.44	1-2
Autumn	16	31.7±11.8	69	23.9±8.2	34.1	1.24±0.51	1-3
Total	59	29.2±15.7	174	21.3±9.4	21.5	1.24±0.48	1-3
TOTAL	380	17.7±8.9	632	17.1±6.5	16.4	1.11±0.35	1-3

Figure Captions

Figure 1. Map of the study area showing the geographic location of the Águas Claras stream (below square), the Pardo River basin (above square, São Paulo State, Brazil), where the freshwater prawns *Macrobrachium brasiliense* (Heller, 1862) and the cymothoid *Telotha henselli* (Von Mertens, 1869) were captured at three sites simultaneously over two years (1995 and 1998).

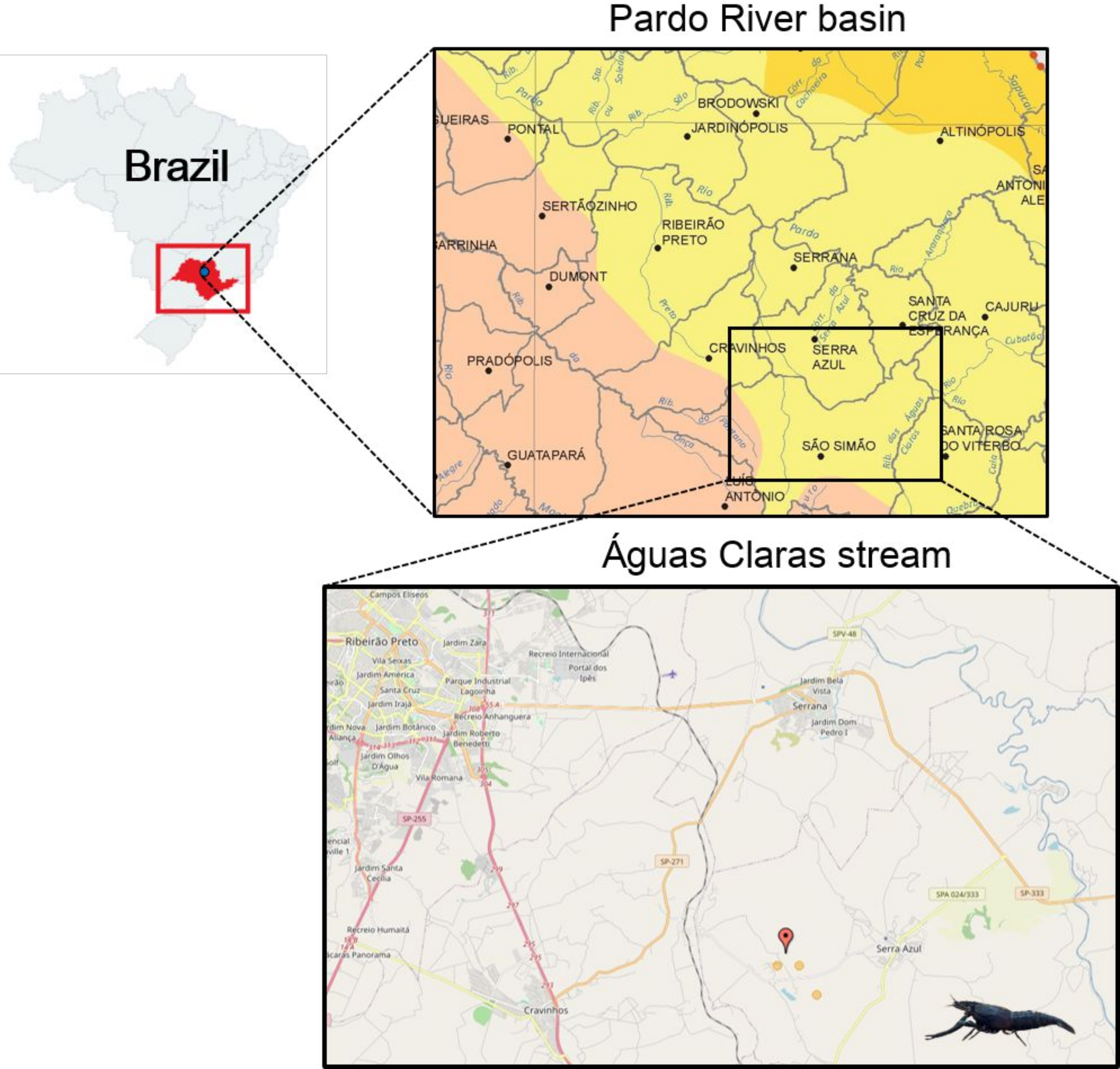
Figure 2. Influence of streamflow (m^3/s) on prevalence (a) and total abundance (b) per month of parasitism on freshwater prawns *Macrobrachium brasiliense* (Heller, 1862) between male and female in the Águas Claras stream during the two years. Rug marks represent the distribution of the data along the y and x axes. R^2 and significance values are given in the text.

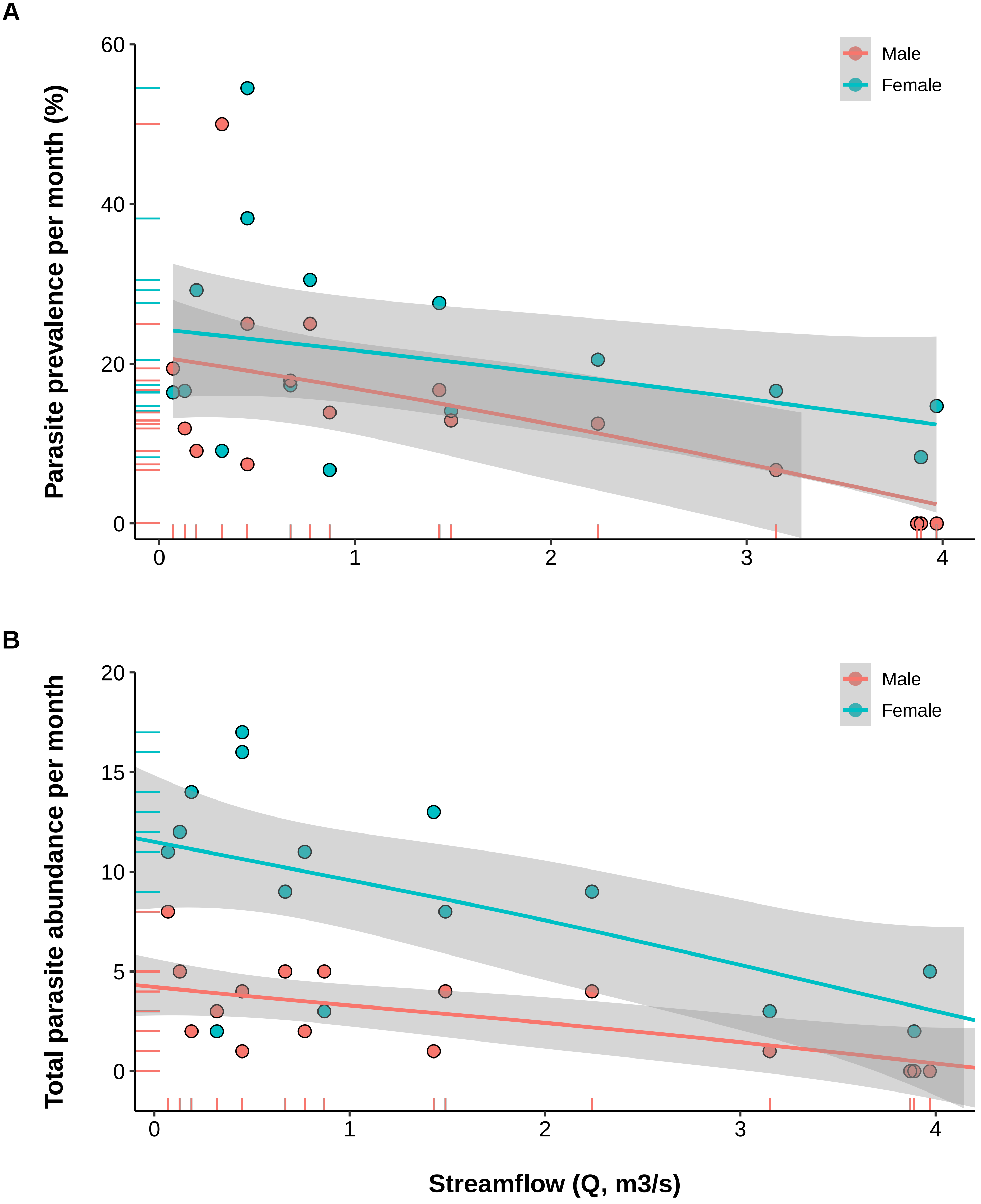
Figure 3. Variation in the total abundance of ectoparasites in *Macrobrachium brasiliense* (Heller, 1862) between the dry and wet seasons based on the variation of the rainfall in the month (mm). On top, a diagram representing our prediction about the effect of dry and wet seasons on the variation in parasitism levels with streamflow (m3/s).

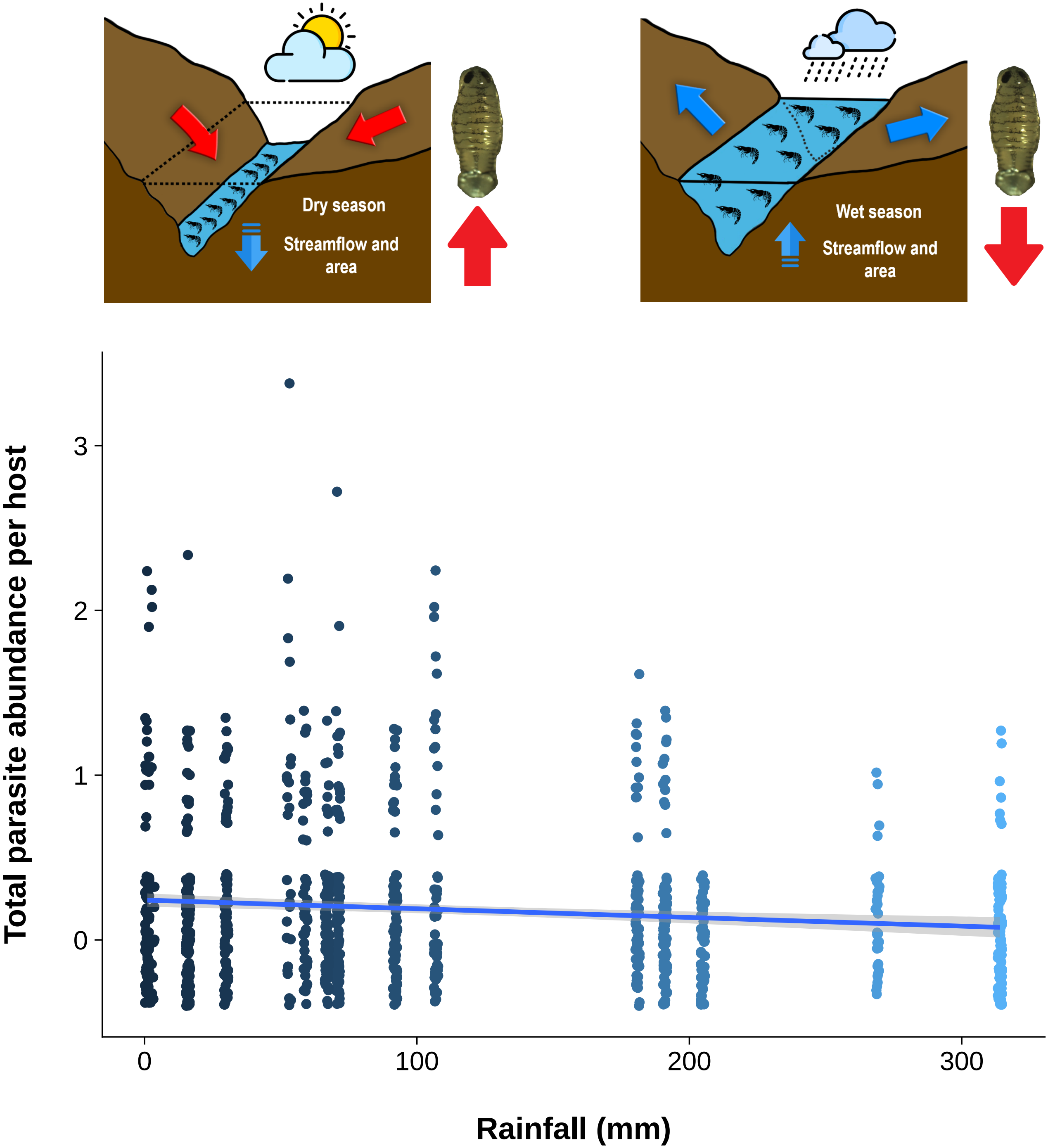
Figure 4. Variation in total ectoparasite abundance on *Macrobrachium brasiliense* (Heller, 1862) between seasons (a) and years (b). Violin plots show the distribution and probability density for each season and year.

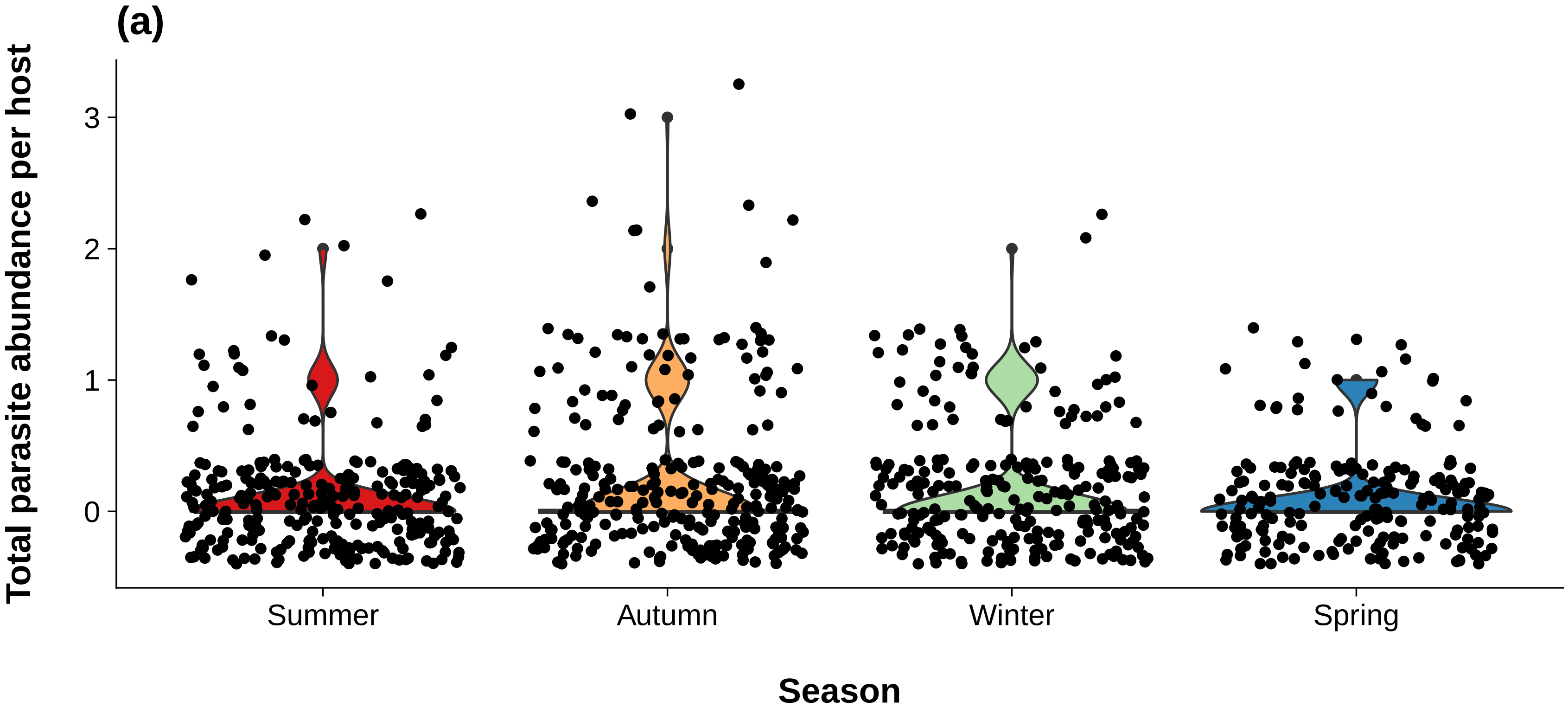
Figure 5. Variation in the total abundance of ectoparasites on *Macrobrachium brasiliense* (Heller, 1862) between host size (a), host age (b), host sex (c), and host molt stage (d). Violin plots show the distribution and probability density for each host trait.

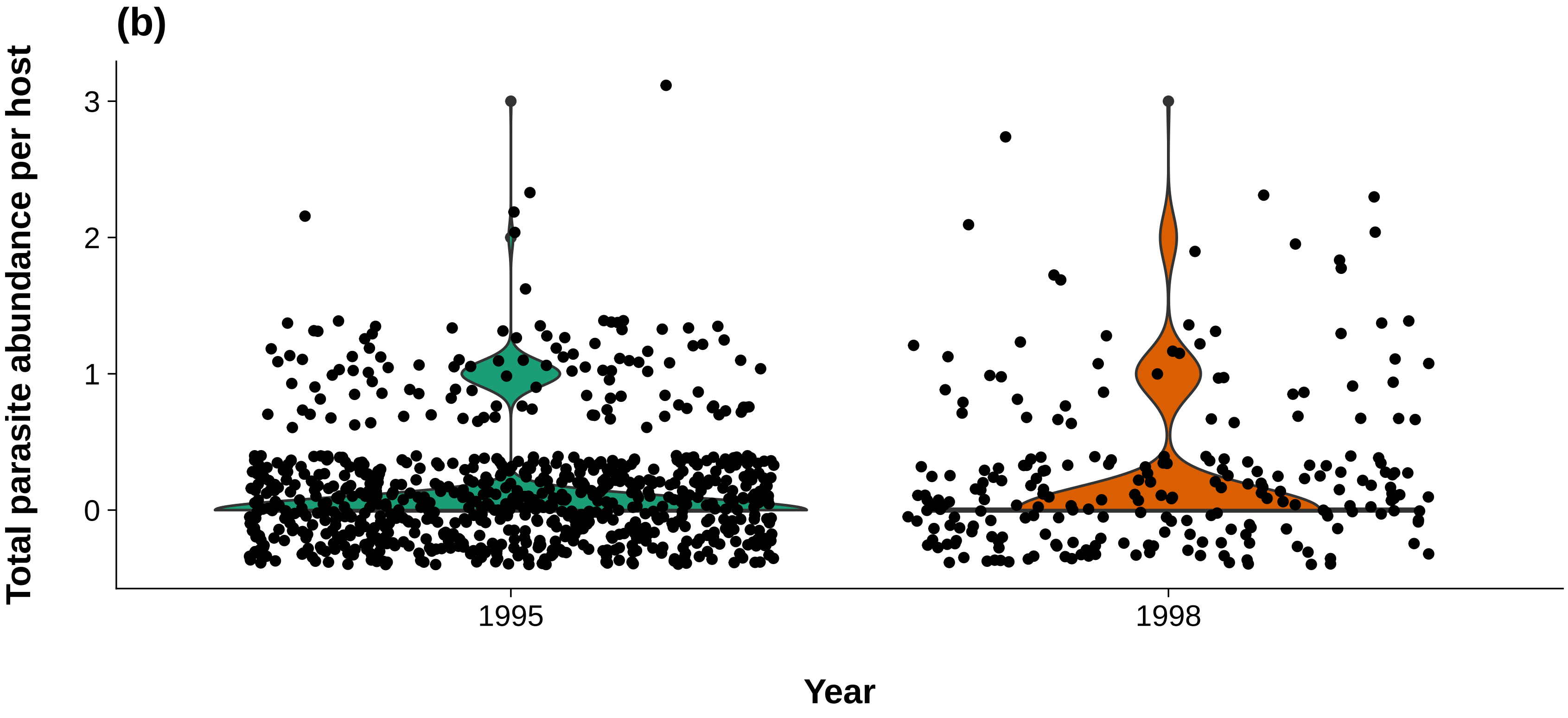
Figure 6. Forest plots for the comparison of part R^2 (coefficient of determination) for the model inclusive R^2 (A), structure coefficients (B) and beta weights (C) including confidence intervals (CI) for the ectoparasite infestation model. Total rainfall (Rt) and streamflow (Q).

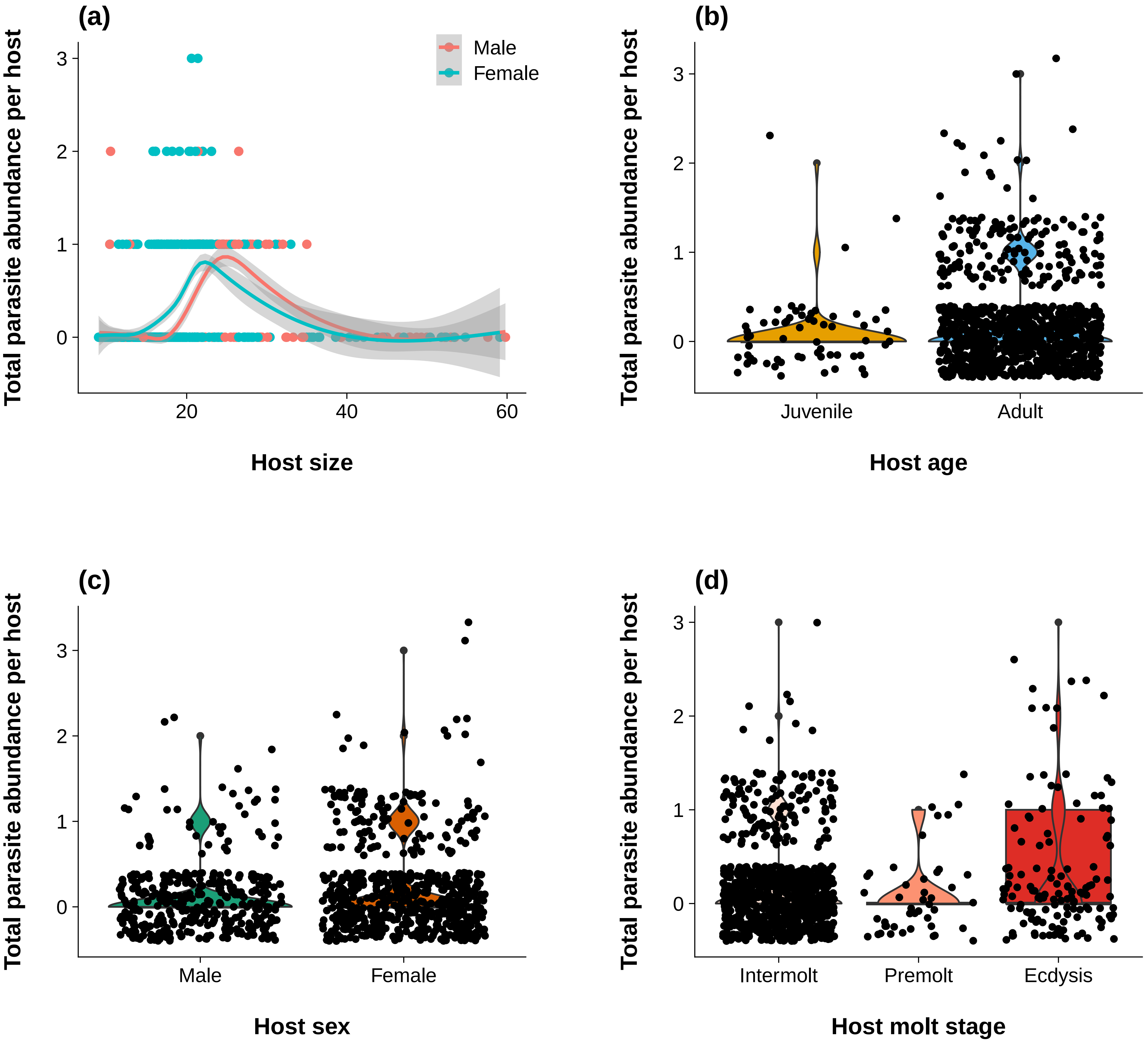

Pardo River basin
Brazil
BRODOWSKI
PONTAL
JARDINÓPOLIS
ALTINÓPOLIS
SERTÃOZINHO
RIBEIRÃO PRETO
SERRANA
DUMONT
SANTA CRUZ DA ESPERANÇA
CAJURU
CRAVINHOS
SERRA AZUL
PRADÓPOLIS
SÃO SIMÃO
SANTA ROSA DO VITERBO
GUATAPARÁ
LUÍS ANTÔNIO
Rio Pardo
Rib. Preto
Rib. das Águas Claras
Águas Claras stream
Ribeirão Preto
Serrana
Serra Azul
Cravinhos
SP-255
SP-271
SP-333
SPV-48
SPA 024/333

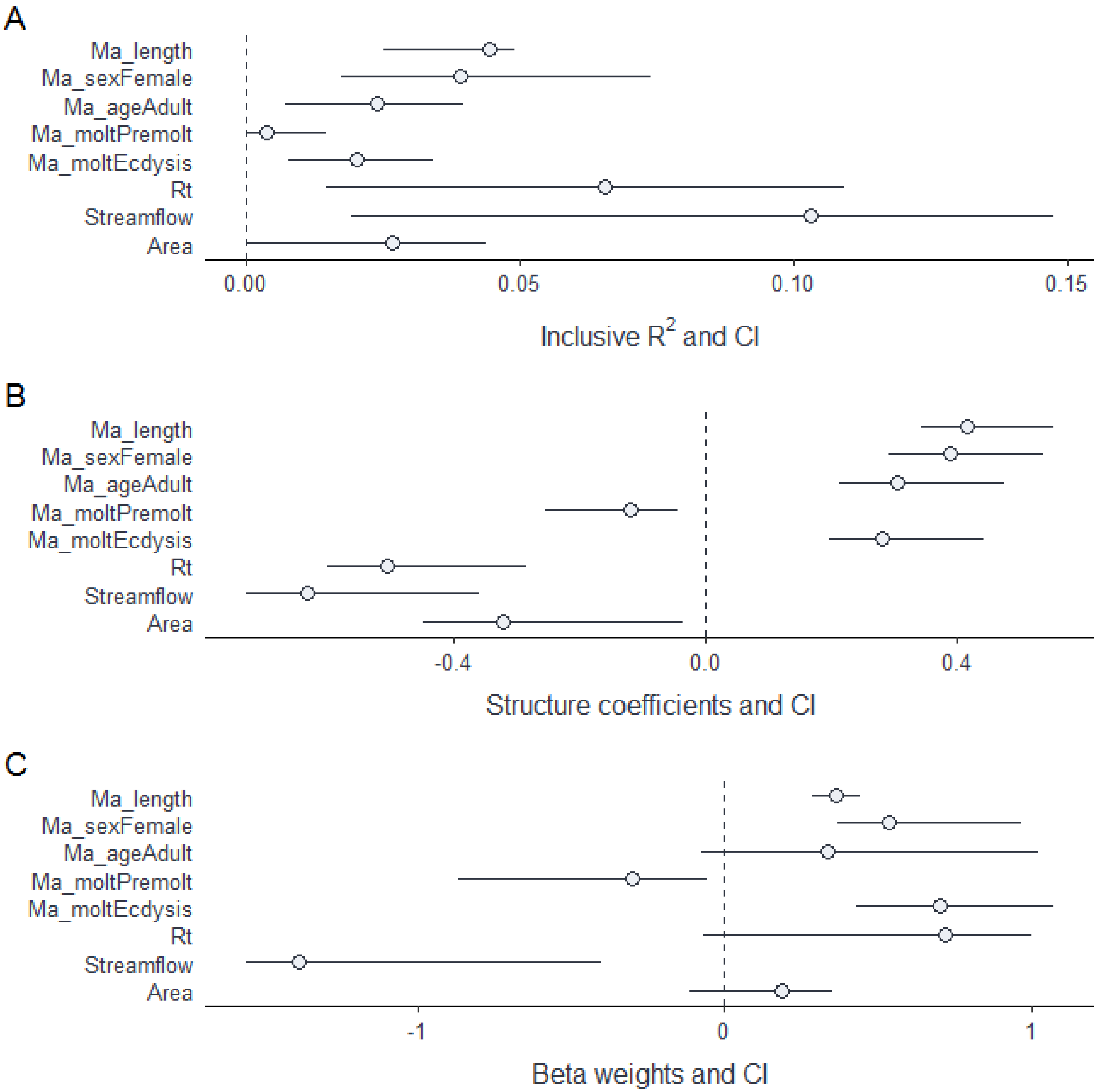

A
Parasite prevalence per month (%)
60
40
20
0
0
1
2
3
4
Male
Female
B
Total parasite abundance per month
20
15
10
5
0
0
1
2
3
4
Male
Female
Streamflow (Q, m3/s)


Dry season
Streamflow and area
Wet season
Streamflow and area
Total parasite abundance per host
0
1
2
3
0
100
200
300
Rainfall (mm)


(a)
Total parasite abundance per host
3
2
1
0
Summer
Autumn
Winter
Spring
Season


(b)
Total parasite abundance per host
3
2
1
0
1995
1998
Year


(a)
Male
Female
Total parasite abundance per host
3
2
1
0
20
40
60
Host size
(b)
Total parasite abundance per host
3
2
1
0
Juvenile
Adult
Host age
(c)
Total parasite abundance per host
3
2
1
0
Male
Female
Host sex
(d)
Total parasite abundance per host
3
2
1
0
Intermolt
Premolt
Ecdysis
Host molt stage


A
Ma_length
Ma_sexFemale
Ma_ageAdult
Ma_moltPremolt
Ma_moltEcdysis
Rt
Streamflow
Area
0.00
0.05
0.10
0.15
Inclusive R^2 and CI
B
Ma_length
Ma_sexFemale
Ma_ageAdult
Ma_moltPremolt
Ma_moltEcdysis
Rt
Streamflow
Area
-0.4
0.0
0.4
Structure coefficients and CI
C
Ma_length
Ma_sexFemale
Ma_ageAdult
Ma_moltPremolt
Ma_moltEcdysis
Rt
Streamflow
Area
-1
0
1
Beta weights and CI