Temporal changes in streamflow regime and host-related factors affect parasitism of freshwater prawn in Southeast Brazil

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Abstract

1. Understanding how changes in hydrological regime and intrinsic host factors drive parasite loads and dynamics remains a challenging issue in aquatic parasitology. Many host-parasite systems have shown that host-related factors can influence parasitism in freshwater systems. Temporal changes in the hydrological regime are also one key factor that could alter the streamflow and habitat area and indirectly affect the interactions between ectoparasite and host. However, there are still few studies on the combined effects of both streamflow regime and intrinsic host factors to investigate variations in parasite loads on stream ecosystems.

2. Here, we used a cymothoid-palaemonid prawn model to test whether host-related traits and the temporal changes in streamflow and area caused by the rainfall regime could influence ectoparasite loads in stream habitats. Prawns were collected seasonally over 4 years in a tropical stream in southeast Brazil. We also tested the hypothesis of whether the prawn body size covaries with cymothoid body size, and also whether this change between sex and seasons.

3. We found a strong relationship between the ectoparasite and host body sizes, which confirms Harrison's rule of this host-ectoparasite system. Our best model showed an effect of host body size, host sex, and host molt stage, but not host age, on ectoparasite loads. Prawn females have higher ectoparasite loads than males, and there was a positive association with the ecdysis stage. Our model also predicts that decreased rainfall could increase parasitism in dry seasons by reducing the natural flow regime and habitat area in these tropical stream systems.

4. Our findings show that temporal variability in streamflow is a key environmental factor combined with host-related characteristics to drive the parasite dynamics of a cymothoid-prawn system in stream habitats.

5. Identifying how the interactions between aquatic invertebrates and parasites respond to the variability in hydrological conditions can help to understand how infections and parasitism may affect the benthic invertebrates play in stream systems.

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 and Poulin, 2020). Although the relevance of parasites in ecosystem functions and conservation has risen in recent years (Poulin, 2021; Gagne *et al*. 2022), this subject 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). For example, most studies on parasitic isopod crustaceans are limited to localities in the Caribbean, Indo-Pacific and Mediterranean (e.g., Smit *et al*. 2019; Welicky *et al*., 2019), with few in the Neotropical freshwater region (Wunderlich *et al*. 2011; Andrade *et al*. 2020; Ribeiro and Horch, 2023). Furthermore, freshwater ecosystems are among the most diverse parasite species (Poulin, 2016), and face increasing high anthropogenic pressure and hydrological disturbance (Boos *et al*. 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.

The history of host-parasite interaction involving epicaridean isopods and prawns has been observed in fossils from the early Cretaceous and the late Jurassic (163–110 Mya), indicating a long evolutionary association (Klompmaker *et al*. 2021; Lima *et al*. 2023). Since then, the dynamic of host-parasite systems is driven by host-related factors that can influence the likelihood of infection on several scales of observation (Poulin, 2007; Castrillo, 2018; Schmid-Hempel, 2021). For example, host body size often correlates positively with parasite abundance or parasite species richness (Poulin, 2007; Kamiya *et al*. 2014a). Also, the parasite body size can increase with the host body size; a pattern termed “Harrison’s rule” (Harrison, 1915; Maestri *et al*. 2020). Although this rule has been reported in several taxa (Poulin, 2007), we still lack knowledge on whether Harrison's rule holds among seasons and between host sex, and also for cymothoid isopods (Welicky *et al*. 2019). Other host characteristics 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 and Forbes, 2012). In crustaceans, the molting stage is a key growth factor, while it can expose hosts to parasite infections (Duneau and Ebert, 2012) or reduce the likelihood of parasite penetration (Izhar *et al*. 2020). Furthermore, these host factors can also correlate with changes in the hydrological regime, which might increase susceptibility to parasitic infections and alter the dynamics of the disease (Groner *et al*. 2018; Xu *et al*. 2020).

Temporal changes in the hydrological regime act as a strong drive to sustain and alter the structure of benthic invertebrate communities (Poff and Zimmerman, 2010; Northington and Webster, 2017; Poff *et al*. 2018; Herbst *et al*. 2019; Palmer and Ruhi, 2019), as well as the infectious disease and parasite dynamics in freshwater ecosystems (Altizer *et al*. 2006; Groner *et al*. 2018; Schmid-Hempel, 2021; Tadiri and Ebert, 2023). Variability in temperature and rainfall are important aspects in understanding host-parasite interactions (Marcogliese, 2016; Shearer and Ezenwa, 2020), and can alter host susceptibility and exposure to parasites, and as a consequence, it can increase or decrease parasite loads (Groner *et al*. 2018; Vestbo *et al*. 2019; Shearer and Ezenwa, 2020). In rivers and stream habitats, the rainfall regime plays a central role because it can change the streamflow and reduce the habitat area of the stream many times (Paull *et al*. 2012; Botter *et al*. 2013). As a consequence, this reduction in streamflow might increase host density and the chances of parasite encounters and transmission (Brunner and Ostfeld, 2008; Paull *et al*. 2012; Shearer and Ezenwa, 2020). Furthermore, most studies have concentrated on the effects of increasing temperature rather than altered hydrology (Marcos-López *et al*. 2010; Lõhmus and 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 streamflow changes and habitat area, to better understand how these hydrological changes correlate with host-related factors to affect parasite loads over space and time (Poulin, 2007; Kamiya *et al*. 2014b; Cattadori *et al*. 2019; Poulin, 2021; Tadiri and Ebert, 2023).

To test whether the hydrological changes and host-related factors affect the parasite infestation, in this study we examined the effects of host size, sex, age, molt stage, rainfall, streamflow, habitat area, and their interactions on ectoparasite loads using the palaemonid prawn, *Macrobrachium brasiliense* (Heller, 1862), and a cymothoid isopod, *Telotha henselii* (Von Martens, 1869), as our model.

Cymothoid isopods are a diverse group of parasitic crustaceans with a broad distribution throughout the world (Williams and Boyko 2012). Most cymothoids are parasites of marine, freshwater, and brackish teleosts (Smit *et al*. 2014), but also may parasitise freshwater palaemonid prawns in tropical South American river systems (Wunderlich *et al*. 2011; Andrade *et al*. 2020). Adults of *Telotha henselii* are a well-known haematophagous ectoparasites cymothoid on fish, mostly found on skin and gills, and juvenile males use palaemonid prawns as optional intermediate hosts besides final hosts (Trilles and Öktener 2004; Wunderlich *et al*. 2011; Andrade *et al*. 2020; Anaguano-Yancha and Pilatasig, 2022; Fujita *et al*. 2023). Therefore, the cymothoid-palaemonid system is a tractable model that could facilitate our understanding of how changes in the hydrological regime and host-related factors can influence host-ectoparasite interactions in freshwater ecosystems.

Here, we investigate the cymothoid isopod in palaemonid prawns from freshwater streams in the Brazilian Southern. First, we analyse the effects of host-related factors on parasite infestation. Since host-related traits are crucial to driving parasite dynamics, we expect a potential effect of body size, sex, age, and molt stage on cymothoid isopod infestations in *M. brasiliense* populations inhabiting a stream habitat with hydrological variation during the seasons and years. We predict that a reduction in streamflow and habitat area in dry seasons could indirectly facilitate the chances of parasite encounters and transmission due to the greater aggregation of hosts during this season. Thus, 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 examine the hypothesis of whether the body size of prawns correlates with the body size of cymothoids (i.e., a pattern termed “Harrison’s rule”), and whether this pattern could vary between sex and seasons (dry vs. wet). Since previous studies have shown that host body size positively covaries with parasite body size, we expected to find similar parasite-specific patterns in this study.

2. METHODS

2.1. Study area and sampling design

As part of a long-term study of ecology and parasitism, palaemonid prawns (*Macrobrachium brasiliense*) were collected at three sites in the Águas Claras stream, the Pardo River basin (21 ° 18 30 S, 47 ° 36 16 W), during 1995 to 1998 in southwest Brazil (Figure 1). The Pardo River has a drainage basin of 10.694 km^2 and a course of approximately 550 km, with the dry season occurring between April and September and the wet season between October and March (Alves *et al.* 2018). We collected prawns over four years from January 1995 to June 1998 monthly and bimonthly, except in 1996 and 1997, which we collected in a month only each year. The years 1996 and 1997 were excluded from the hydrological variation analysis, but we kept to examine the correlation between prawn body size and cymothoid body size. Prawn samples were obtained from three sites at the same time, for 2 hours each by two people, during the day. At each site, the prawns were collected manually by sweeping sieves (50 cm in diameter and 4 mm mesh size) near the riverbank, in places with marginal aquatic vegetation from the stream. The prawns were kept in plastic boxes with water from the stream sites until their arrival in the laboratory, where the specimens were euthanised by thermal shock (at 3°C, for 30 min), fixed and preserved in 70% ethanol.

2.2. Measures of host-related trait and rainfall data

At the laboratory, the prawn specimens were identified according to Melo (2003) and examined to check the presence of isopod cymothoids externally. 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 telson) with a calliper of 0.05 mm precision, and weighing (W, weight – with a digital balance of 0.01 g, in grams), and also characterized according to the age, sex, and molt stage. In this study we consider age in function of the developmental phase (juvenile and adult), using as a proxy the size at onset of morphological sexual maturity at 9 mm CL for males and 8 mm CL for females (Nogueira *et al*. 2019); sex by checking the presence of the appendix masculina in the endopod of the second pair of pleopods (Nogueira *et al*. 2020); and molt stages (intermolt, premolt, and molting or ecdysis) determined by inspection of the exoskeleton hardness, especially the carapace (Drach and Tchernigovtzeff 1967).

The monthly rainfall, streamflow, 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 streamflow (m^3/s), and area (m^2). 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}).

The three different measures were used to test whether current (immediate effect) or prior (delayed effect) rainfall was more strongly associated with ectoparasite loads. Together, changes in streamflow and habitat area are associated with changes in rainfall.

2.3. Parasitological screening

The palaemonid prawns were examined and the ectoparasites found were collected 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 categorised in terms of infestation levels as follows: 0 = no infestation; 1=low infestation; 2-3=high infestation (Horton and Okamura, 2001; Kawanishi *et al*. 2016). The prevalence was calculated as the proportion of prawns infected by cymothoid isopods in relation to the total number of hosts analysed, 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).

2.4. Data analysis

We used generalised linear models (GLM) to test for the relationship between prawn body size and cymothoid body size (i.e. a pattern called “Harrison's rule”), and whether this pattern can vary between sex and seasons (dry vs. wet). To estimate the effects of host traits (i.e., total length, sex, age, and molt stage) and hydrological factors (i.e., rainfall, streamflow, and habitat area), on ectoparasite abundances (i.e., response variable), we fit generalised linear mixed models (GLMMs), using Poisson and negative binomial distributions (Zuur *et al*. 2013). Host traits, hydrological factors 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 and 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 using the R performance packages (Lüdecke *et al*. 2021). After the choice of 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).

3. RESULTS

We found a general prevalence of 16.4 % of a total of 1,012 prawns collected over two years (Table 1). The body size between cymothoid and prawn was positively correlated regardless of sex and seasons (GLM: estimate ± se: 0.054 ± 0.007, $p < 0.0001$, $R^2_{adj} = 0.709$). However, we did not find a significant difference of this pattern (i.e. positive correlation) in our model between sex (GLM: estimate ± se: 0.003 ± 0.011, Wald = 0.298 p = 0.766; Figure 2a) and seasons (GLM: estimate ± se: 0.013 ± 0.016, Wald = 0.828, p = 0.408; Figure 2b). We also found a significant effect of host traits on the abundances of ectoparasites (Figure 3, Table 2), in relation to the size of the host's body (one to three parasites in prawns size ≤ 35.0 mm TL – Figure 3a); host sex (parasitism in female hosts more abundant than in males – Figure 3c); and the stage of molt of the host (parasite abundance following this hierarchical sequence of stages of molt: intermolt > ecdysis > premolt – Figure 3d). However, no effect of age on parasitism was found (parasite abundance did not differ between juveniles and adults – Figure 3b, Table 2). In 1995, the prevalence of ectoparasites was twice in autumn and winter (i.e. 16.6 and 18.9%, respectively) rather than in spring and summer (i.e. 11.9 and 9.2%, respectively; Table 1). This pattern was also observed in 1998, with a higher prevalence in autumn (i.e. 34.1%) and a lower prevalence in summer (i.e. 14.2%; Table 1). The abundance of ectoparasites varied between seasons, with the highest isopod infestation in prawns (i.e. two to three parasites per infested prawn) in the autumn seasons in both years (Figure 4a, Table 1), but there are no differences between the two years in our model (Wald = -1.849; p = 0.064; Table 2, Figure 4b). Of the five models that we compared, the one that included three hydrological factors such as concurrent rainfall (R_t), streamflow, and habitat area received the most support (Table 2). Of all fixed variables included in the GLMM models, season showed high multicollinearity with VIF > 10 (Table 3). We found that the highest isopod infestations (i.e. two to three parasites per infested prawn) were observed in dry rather than wet seasons (Figure 5). 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 ectoparasite infestation, presenting the largest inclusive R^2

(Figure 6A and B), structure coefficient (Figure 6C) and negative beta weight (Figure 6D). Host length, sex (female) and ecdysis contributed positively to the predictors (Figure 6C-D).

4. DISCUSSION

Our results reveal a combined effect of hydrological factors and host-related characteristics as a key driver of seasonal variation in parasite loads and dynamics of a cymothoid-palaemonid prawn system. We also found strong evidence of the Harrison rule (HR) in the ectoparasite host system evaluated in this study. Our results demonstrated the importance of size in this parasite-host system, which states that both body sizes (parasite and host) tend to be positively and significantly correlated (Harrison, 1915; Clayton *et al*. 2016; Maestri *et al*. 2020). Although the pattern has often been corroborated in several parasite taxa (Nagler *et al*. 2017; Maestri *et al*. 2020), for cymothoid isopods, there is still little example to support this rule (see Welicky *et al*. 2019). Our results also corroborated the data registered by Welicky *et al*. (2019) and Kottarathil *et al*. (2019) with other cymothoid isopod species, where a positive and significant correlation was confirmed between the sizes of these parasites and the size of the fish. However, depending on the host-parasite system, the adaptive significance of this match size may vary (Poulin, 2007; Clayton *et al*. 2016; Lim *et al*. 2022; Lisnerová *et al*. 2022). Lim *et al*. (2022), also confirm Harrison’s rule in Nomadinae (cleptoparasitic insects), supporting that body size dynamics influence host shifts of cleptoparasitic bees. Although this pattern between the size of the ectoparasites and their hosts has been well supported in many systems, recently an interesting work demonstrated that some environmental factors (e.g., temperature and precipitation) also affect this pattern, leading to a deceptive correlation between the sizes of the fleas and their hosts across assemblages (Maestri *et al*. 2020). Although we have found a positive correlation between the sizes of the cymothoids and their prawns, we did not observe a significant difference of this pattern between seasons and sex in our study.

Heterogeneity in host-related factors (e.g., size, sex, age, and molt stage) can strongly influence parasite transmission, susceptibility, tolerance, and resistance to infection (Johnson and Hoverman, 2014; Izhar *et al*. 2020; Clark *et al*. 2021; Schmid-Hempel, 2021). We found that host-related traits that involved body length, sex, and molt stage (but not host age), influenced the abundance and dynamic of ectoparasites. The host body size 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*. 2014b; Schmid-Hempel, 2021). The theory suggests that large-bodied hosts should have more parasites (Poulin, 2007; Walker *et al*. 2017). Furthermore, body size correlates with other host traits that affect the likelihood of acquiring infections (Cooper *et al*. 2012; Blasco-Costa and Poulin 2013; Schmid-Hempel, 2021), such as longevity.

The host sex has also been an important factor in explaining sex-biased parasitism (Poulin and Forbes, 2012). In many parasite-host systems, males are more parasitised than females (Cozzarolo *et al*. 2019), an expressive contrast to our study, where 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 (e.g. Sheridan *et al.*, 2000). One potential explanation of a female bias might be caused by differences in immunity and exposure to parasites between the sex (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 favours sex-biased parasitisms (Poulin, 2007; Christe *et al*. 2007). For example, ovigerous females are more cryptic than males (Nogueira *et al*. 2019), which could favour higher exposure to parasites (i.e. to manca exposure) during the dry seasons in our study.

Although we did not find an effect of host age on ectoparasite abundance, age has been correlated with parasite variation among 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*. However, a decrease in susceptibility in older fish has also been suggested to affect host infestation outcomes (Tinsley *et al*. 2020; Bailey *et al*. 2021). For example, the severity of the disease was greater in young than in older adults due to an ontogenetic decline in susceptibility in older individuals (Bailey *et al*. 2021).

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 parasite abundance 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 and Ebert, 2012) or reduce the likelihood of parasite infestations (Izhar *et al*. 2020). Furthermore, these host factors can also vary with environmental changes, which might increase susceptibility to parasitic infections and alter the disease dynamic (Groner *et al*. 2018; Xu *et al*. 2020). For example, in the American lobster (*Homarus americanus*), increasing seawater temperatures can lead to less molting during summer, when lobsters are more susceptible to peaks of epizootic shell disease (Groner *et al*. 2018).

In addition to these host-related factors, hydrological factors can also exert a strong effect on parasitism in freshwater ecosystems (Altizer *et al*. 2006; Paull *et al*. 2012). Freshwater organisms are exposed to variable rainfall regimes and streamflow, potentially altering their behaviour and subsequently parasite loads among hosts (Paull *et al*. 2012; Reynolds *et al*. 2019). Our results showed that the highest prevalences and abundances of ectoparasites were found in dry rather than wet seasons. Rainfall has been suggested to be a key driver of seasonality in parasitism (Aneesh *et al*. 2013; Gagne and Blum, 2016; Jemi *et al*. 2020; Shearer and Ezenwa, 2020). Some authors registered higher parasite loads associated with low rainfall, suggesting a gradual increase in host susceptibility during the dry season (Gagne and Blum, 2016; Shearer and Ezenwa, 2020). Cymothoids parasitizing fish also were more abundant during the autumn season (i.e., dry season to India), suggesting that this season can facilitate the ectoparasite infestation (Aneesh *et al*. 2013; Jemi *et al*. 2020). Another interesting study showed that drought in stream fish communities can intensify parasitic copepod infestations (Medeiros and Maltchik, 1999). Furthermore, recent work suggests that the reproductive peaks of cymothoids in the free-swimming stage (called 'mancae') occurred in autumn (Fujita *et al*. 2023), which could support our study where a more intense infestation of the prawns by juvenile cymothoid isopods during dry seasons. Another important aspect is the effect of low rainfall that can reduce river flow and habitat area during the dryest seasons and promote an increase in parasite transmission and encounter with prawns, probably the same as occurs with ectoparasite loads (Paull *et al*. 2012; Shearer and Ezenwa, 2020). This reduction in streamflow and habitat area can affect host behaviour and aggregation into stream habitats, increasing the chances of acquiring the parasite through host contact (Paull *et al*. 2012; Reynolds *et al*. 2019; Schmid-Hempel, 2021). Studies have shown that a high density of hosts 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 because they are also more clumped together across the environment, which results in hosts experiencing a higher infection level (Brunner and Ostfeld, 2008; Paull *et al*. 2012). For example, in an interesting experiment with fish, the parasite transmission rate was higher in shoals exposed to interrupted flow (Reynolds *et al*. 2019). According to these authors, a significantly higher ectoparasite gyrodactylid transmission rate was observed in interrupted flow, resulting in a higher parasite prevalence when compared to a system with continuous water flux. Furthermore, some authors have observed that slow water flow in downstream may be able to accumulate more free-living infective stages, 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 and Byers, 2023). However, during the wet seasons, excessive rainfall 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 helminths and crustacean parasitic (especially in 'mancae' of cymothoids) (Stromberg 1997; Altizer *et al*. 2006). In addition, low levels of resource availability and environmental stress caused in dry seasons can lead to poor host body conditions and immune function, with an increase in parasite prevalence and intensity (Marshal *et al*. 2008; Shearer and Ezenwa, 2020). Furthermore, a study that integrates differences between types of stream habitat and resource supplementation regimes on parasite dynamics could yield new broadly applicable strategies to help parasitism management and conservation in freshwater ecosystems (Civitello *et al*. 2018). Although our study was not designed to address host body condition differences among the seasons, we suggest the need for additional experiments to test the hypothesis that host body conditions should change among the seasons, modifying thus the ectoparasite-host dynamics.

Overall, our study supports that changes in hydrological factors combined with host-related factors can influence host-parasite dynamics in stream ecosystems. More studies are needed to understand how hydrological disturbances as a result of climate change that have occurred in the last decades can impact the natural flow regime and the benthic invertebrate communities in the stream ecosystems. Aspects such as those are very relevant for the conservation of stream biota and also promote a better understanding of their parasite biodiversity.

AUTHOR CONTRIBUTIONS

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

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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. Total length (*TL*, mm) of *Macrobrachium brasiliense* prawn, *Telotha henselii* cymothoid isopod, and their parasitological indices for each season/year. Average±standard deviation (=Mean±SD).

Season/Year	**Total length Male**		**Total length Female**		**Prevalence**	**Mean Intensity**	**Intensity range**	**Total length Parasite**	
1995	n	Mean±SD	n	Mean±SD	%	Mean±SD	Min-Max	n	Mean±SD
Winter	81	15.3±4.8	167	15.1±3.8	18.9	1.04±0.20	1-2	47	4.4±1.1
Spring	82	17.5±4.3	120	15.7±3.6	11.9	1	1	24	5.3±1.5
Summer	59	15.3±4.5	71	15.7±3.6	9.2	1.08±0.29	1-2	12	3.2±1.1
Autumn	99	14.2±3.8	100	15.5±3.8	16.6	1.12±0.41	1-3	33	3.8±0.8
Total	321	15.5±4.5	458	15.4±3.7	14.9	1.06±0.27	1-3	116	4.3±1,3
1998									
Winter	-	-	-	-	-	-	-	-	-
Spring	-	-	-	-	-	-	-	-	-
Summer	43	28.3±17.1	105	19.7±9.5	14.2	1.23±0.44	1-2	21	2.8±0.8
Autumn	16	31.7±11.8	69	23.9±8.2	34.1	1.24±0.51	1-3	29	3.4±0.8
Total	59	29.2±15.7	174	21.3±9.4	21.5	1.24±0.48	1-3	50	3.2±0.8
TOTAL	380	17.7±8.9	632	17.1±6.5	16.4	1.11±0.35	1-3	166	3.9±1.3

Table 2. Results of generalised linear mixed models describing the total abundance of ectoparasites (i.e., response variables) as a function of host-related traits (host body size, host sex, host age, and host molt stage) and hydrological factors (rainfall, streamflow, and habitat area). 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. The bold terms are statistically significant. 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**
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**
Rainfall (Rt)	**-0.003**	**0.001**	**-2.887**	**0.003**	**-0.005**	**-0.001**
Streamflow	**-0.985**	**0.300**	**-3.275**	**0.001**	**-1.575**	**-3.957**
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

Table 3. 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). We excluded those with VIF > 10 (bold).

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

Figure Captions

Figure 1. Map of the study area showing the geographic location of the Águas Claras stream, the Pardo River basin (Serra Azul municipality, São Paulo State, Brazil), where the freshwater prawns *Macrobrachium brasiliense* and the cymothoid *Telotha henselli* were captured at three sites over four years (1995, 1996, 1997 and 1998).

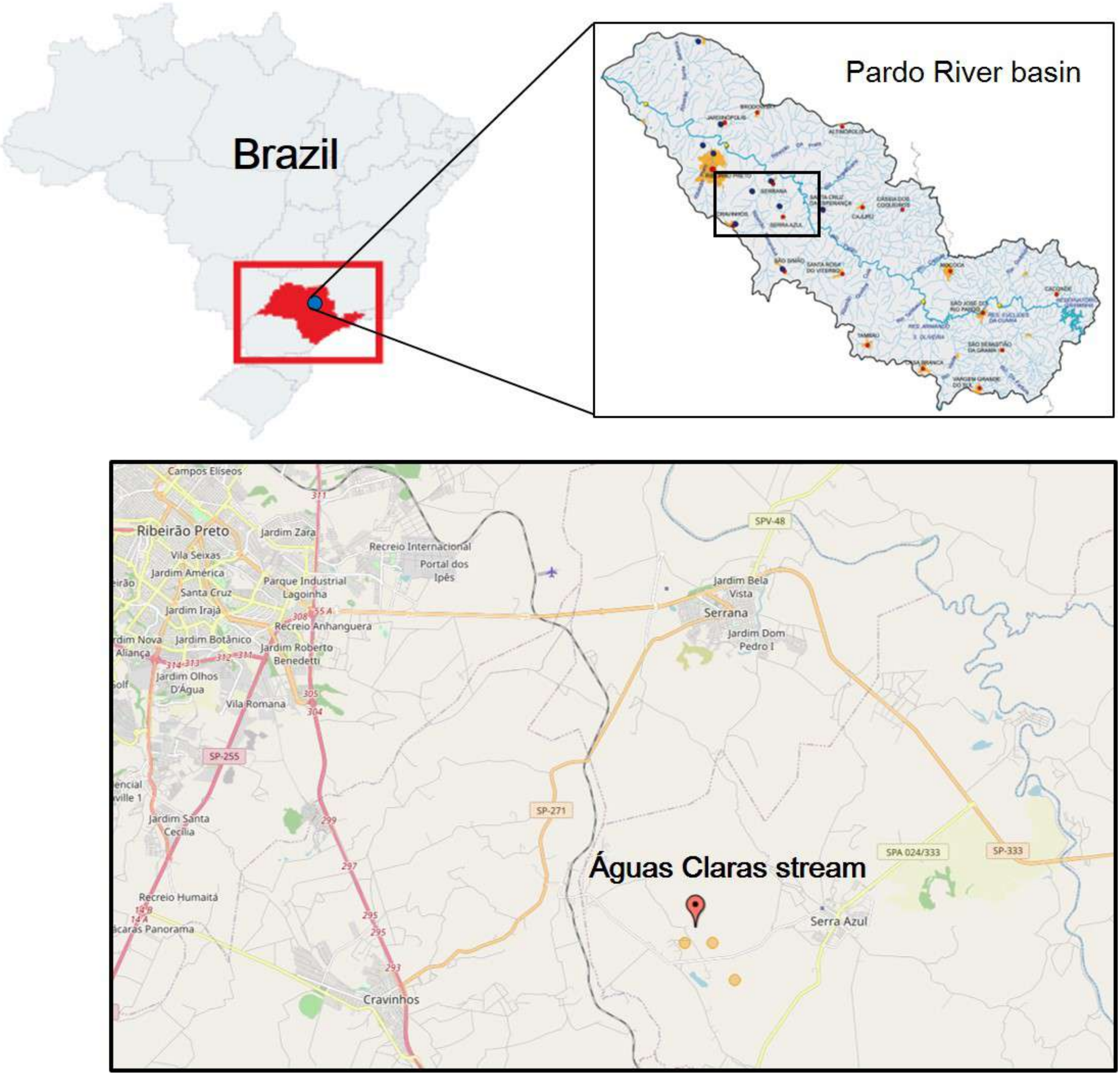
Figure 2. Relationship between host size and parasite size based on the generalised linear model (GLM) between sex (GLM: estimate ± se: 0.003 ± 0.011, Wald = 0.298 p = 0.766; Fig. 2a) and seasons (GLM: estimate ± se: 0.013 ± 0.016, Wald = 0.828, p = 0.408; Fig. 2b).

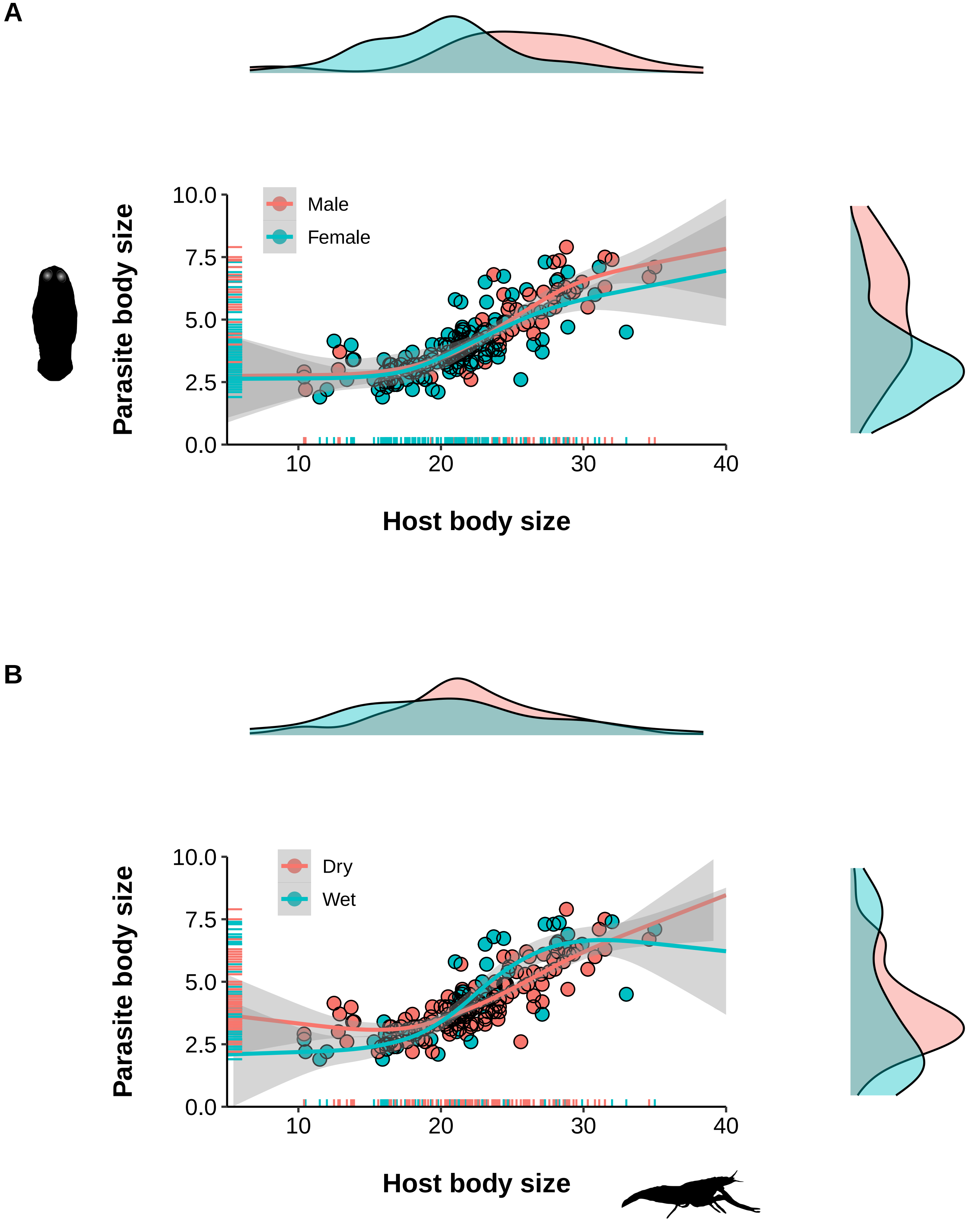
Figure 3. Variation in the total abundance of ectoparasites on *Macrobrachium brasiliense* between host size (a), host age (b), host sex (c) and host molt stage (d).

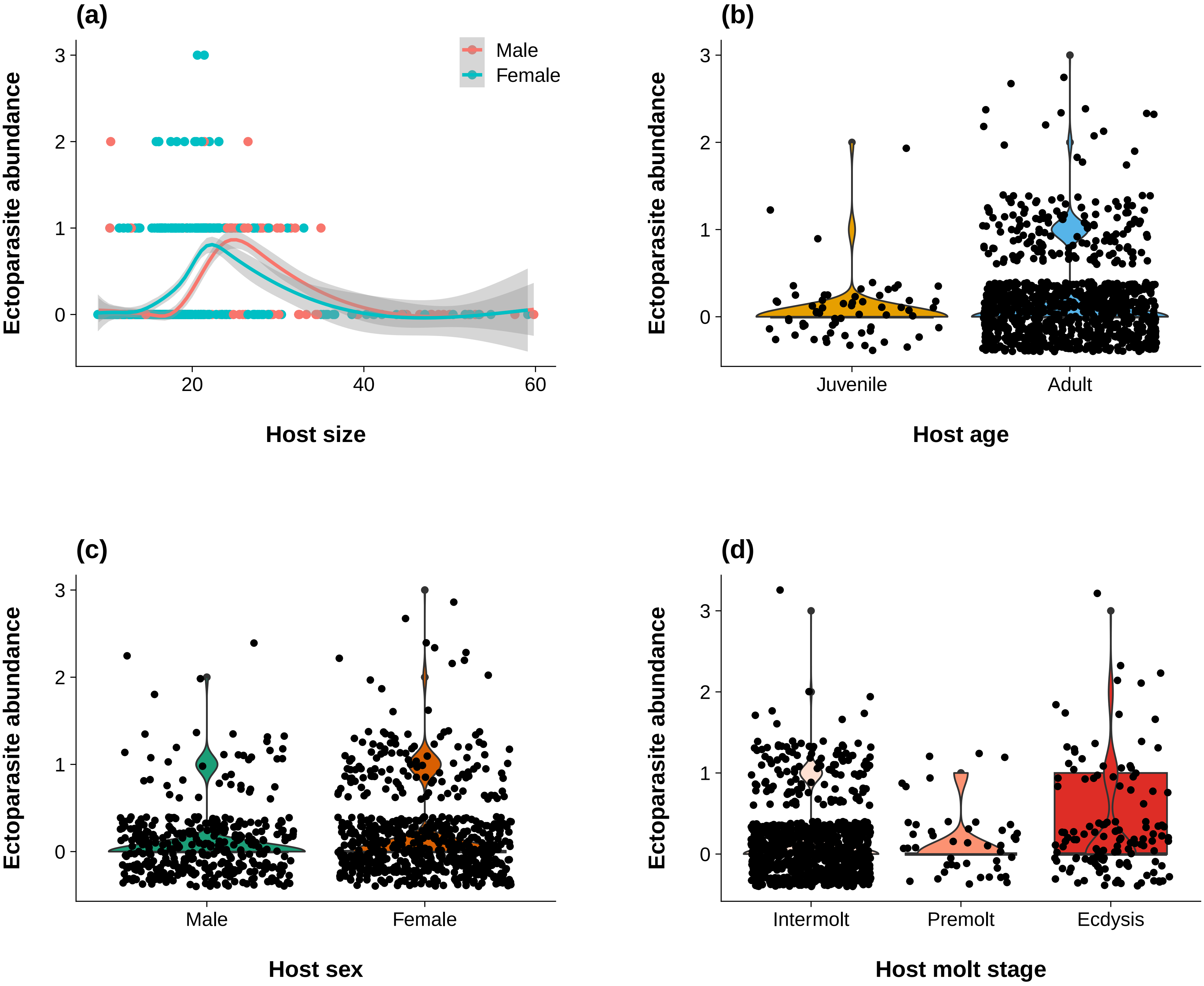
Figure 4. Variation in total ectoparasite abundance on *Macrobrachium brasiliense* between seasons (a) and years (b).

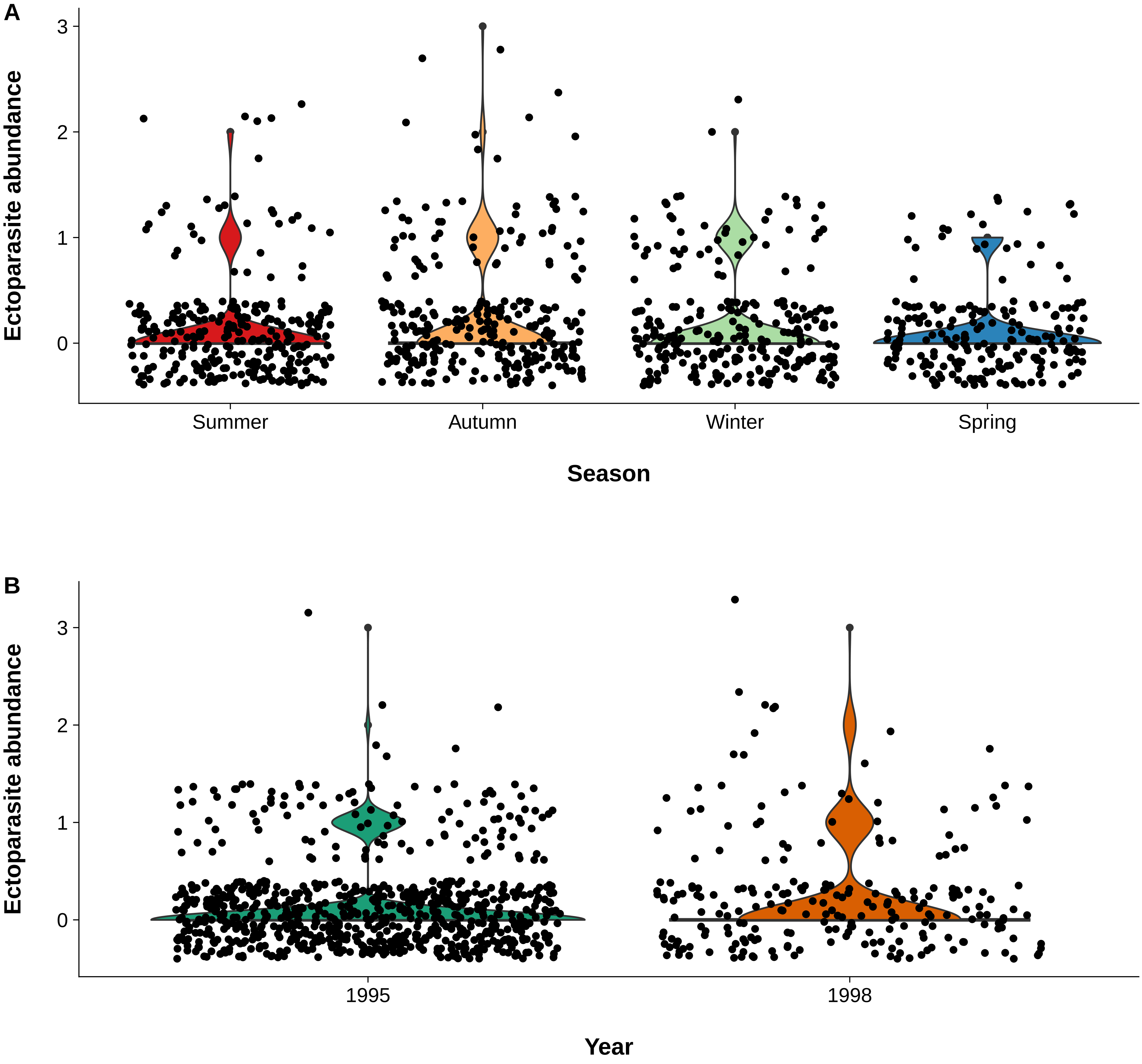
Figure 5. Variation in the total abundance of ectoparasites on *Macrobrachium brasiliense* between dry and wet seasons based on rainfall (mm).

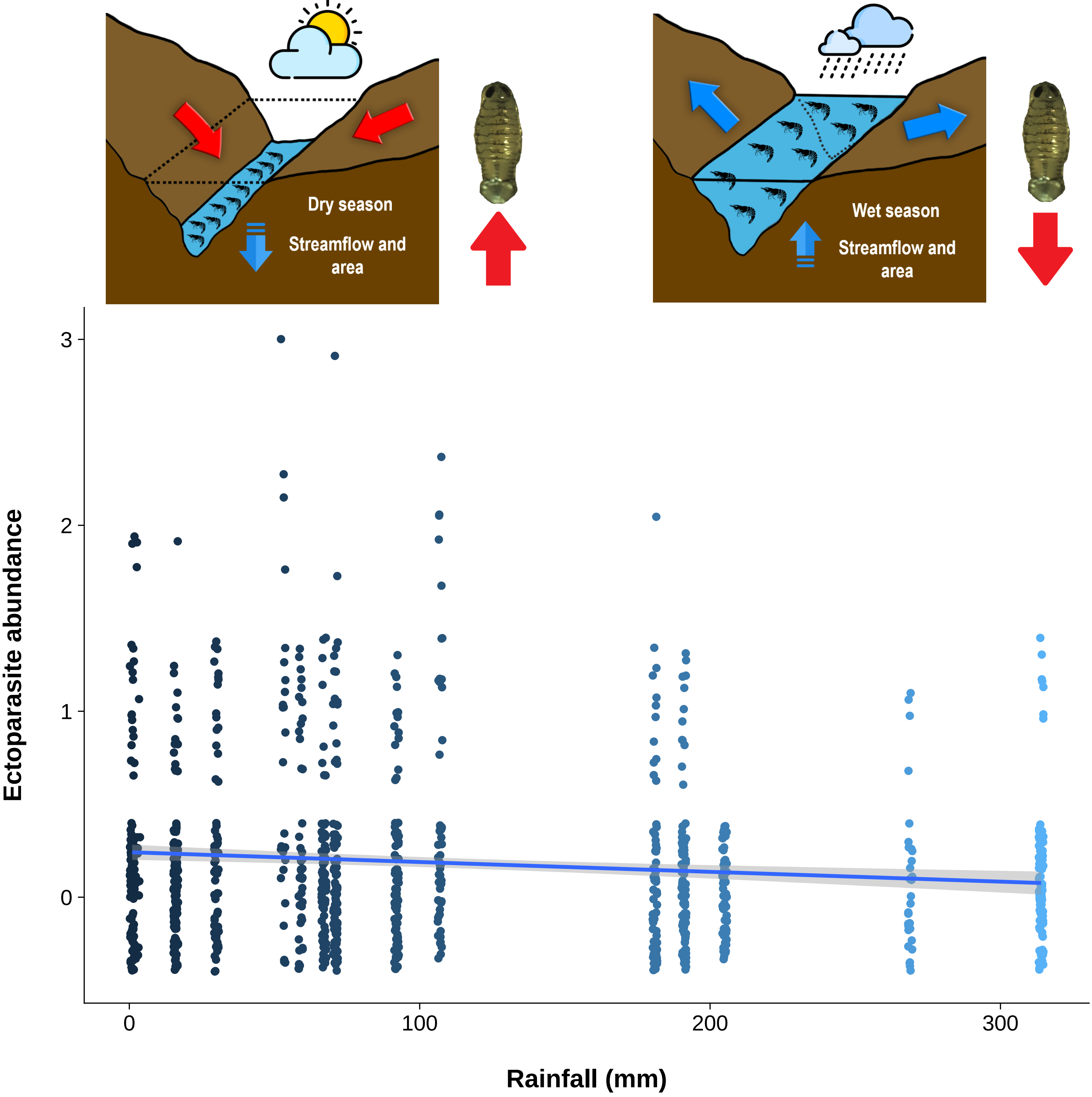
Figure 6. Forest plots for comparison of part R^2 (coefficient of determination) for model predictors (A), inclusive R^2 (B), structure coefficients (C) and beta weights (D) including confidence intervals (CI) for the ectoparasite infestation model.

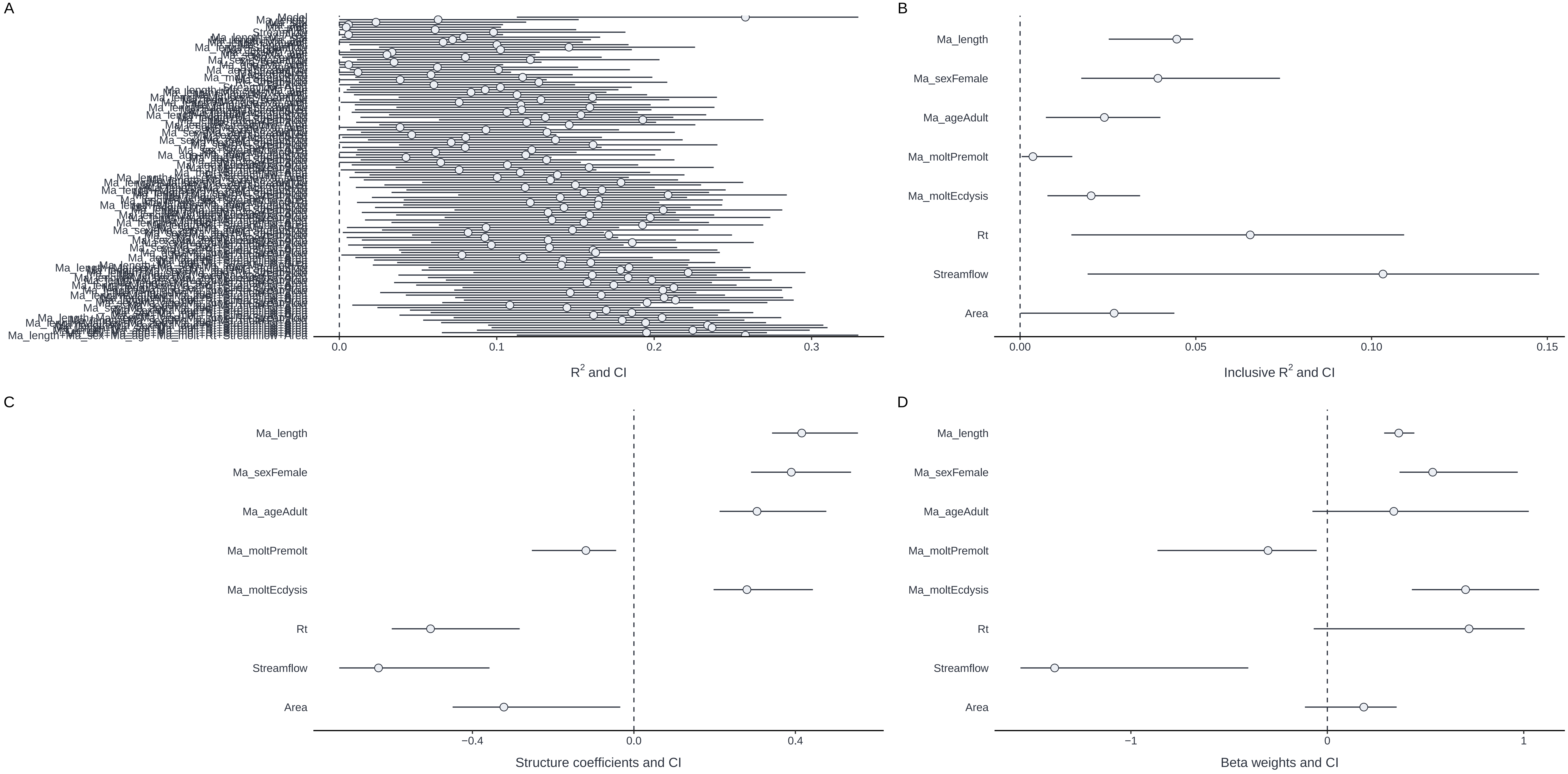

Brazil
Pardo River basin
Águas Claras stream
Ribeirão Preto
Serrana
Serra Azul
Cravinhos
Jardim Bela Vista
Jardim Dom Pedro I
Campos Elíseos
Jardim Zara
Recreio Internacional
Portal dos Ipês
Parque Industrial Lagoinha
Recreio Anhanguera
Jardim Roberto Benedetti
Vila Romana
Jardim Santa Cecília
Recreio Humaitá
SP-255
SP-271
SPV-48
SPA 024/333
SP-333


A
Male
Female
Parasite body size
10.0
7.5
5.0
2.5
0.0
10
20
30
40
Host body size
B
Dry
Wet
Parasite body size
10.0
7.5
5.0
2.5
0.0
10
20
30
40
Host body size


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


A
Ectoparasite abundance
3
2
1
0
Summer
Autumn
Winter
Spring
Season
B
Ectoparasite abundance
3
2
1
0
1995
1998
Year


Dry season
Streamflow and area
Wet season
Streamflow and area
Ectoparasite abundance
3
2
1
0
0
100
200
300
Rainfall (mm)


A
Model
Ma_length+Ma_sex+Ma_age+Ma_molt+Rt+Streamflow+Area
0.0
0.1
0.2
0.3
R^2 and CI
B
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
C
Ma_length
Ma_sexFemale
Ma_ageAdult
Ma_moltPremolt
Ma_moltEcdysis
Rt
Streamflow
Area
−0.4
0.0
0.4
Structure coefficients and CI
D
Ma_length
Ma_sexFemale
Ma_ageAdult
Ma_moltPremolt
Ma_moltEcdysis
Rt
Streamflow
Area
−1
0
1
Beta weights and CI