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Integrating climate and host richness as drivers of global parasite diversity

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Abstract

Aim: Climate and host richness are essential drivers of global gradients in parasite diversity, and the few existing studies on parasites have mostly investigated their effects separately. The advantages of combining these factors into a single analytical framework include unravelling the relative roles of abiotic and biotic drivers of parasite diversity. We compiled a dataset of helminths of amphibians to investigate the direct and indirect effects of temperature seasonality, annual precipitation, precipitation seasonality and host richness as drivers of parasite diversity at the global scale. Our analyses focus not only on the least studied group of vertebrates regarding macroecology of parasite diversity, but also the host group most sensitive to climatic conditions, especially temperature seasonality and water availability.

Location: Global.

Time period: 1955–2017.

Major taxa studied: Helminth parasites of amphibians.

Methods: We used piecewise structural equation modelling on a global dataset of helminths of amphibians, comprising 613 populations of 319 anuran species and 94 populations of 43 salamander species from 10 zoogeographical realms.

Results: We found that precipitation seasonality and host richness both affect parasite diversity positively, but the latter presented a stronger effect. Additionally, we found that both temperature seasonality and total precipitation indirectly affected parasite richness through their respective negative and positive effects on host richness.

Main conclusions: Future studies on global gradients in parasite diversity should include both direct and indirect effects of climatic factors as drivers of parasite diversity. Integrating multiple predictors into a single statistical framework that measures both direct and indirect effects increases our theoretical understanding of the relative importance of and interactions among different diversity drivers at the macroecological scale. The indirect effects of temperature seasonality and total precipitation on parasite diversity are an interesting new insight brought by our study, with implications for future studies dealing with host–parasite coextinctions due to climate change.

KEYWORDS

amphibians, climate, helminths, host diversity, parasite diversity, piecewiseSEM, precipitation, temperature

1 | INTRODUCTION

Understanding why biological diversity is distributed unevenly across Earth's ecosystems persists as an essential goal in macroecology and biogeography. Despite many unresolved issues, there is a growing consensus that no single factor can account for biodiversity gradients; therefore, studies considering multiple explanations promote a greater understanding of how different mechanisms determine species diversity at the macroecological scale (Belmaker & Jetz, 2015; Rodrigues et al., 2017). For broad geographical patterns, most studies rely on the effects that area, time, productivity, biotic interactions, mean temperature and climate stability have on the balance between species appearing and their exclusion over evolutionary time (reviewed in Fine, 2015). However, these studies are biased toward certain taxonomic groups (e.g., birds and mammals) or geographical areas (e.g., temperate zone) (Beck et al., 2012). Surprisingly, whether these major diversity drivers also affect symbiont and particularly parasite diversity remains largely unexplored (Stephens et al., 2016).

There is usually a strong correlation between species richness and climatic components leading to various hypotheses of how climate affects species diversity (Currie et al., 2004; Field et al., 2009). However, macroecological studies on parasite diversity are primarily focused on host-related drivers and latitudinal gradients (Poulin, 2014; Morand, 2015; but see Guernier et al., 2004; Preisser, 2019). Most studies found a positive association between host and parasite diversity regardless of host and parasite taxa (Kamiya et al., 2014a). This relationship is considered analogous to the role of habitat heterogeneity for free-living organisms where high diversity is generated by high turnover (Johnson et al., 2016), or to the bottom-up control of diversity where species diversity at higher trophic levels is constrained by diversity at the lower level (Krasnov et al., 2007). In relation to latitudinal gradients, there is considerable heterogeneity in the relationship between parasite diversity and latitude, with some studies supporting it and others not. When latitudinal effects are detected, there seems to be a weak but positive association between latitude and parasite richness at least for metazoan parasites (see meta-analysis by Kamiya et al., 2014a).

Temperature and precipitation belong to the core of some prominent climate-based explanations, but how they affect parasite diversity remains largely unexplored (but see Guernier et al., 2004; Preisser, 2019). For instance, according to the climate stability hypothesis, the absence of marked climatic extremes has a positive effect on net speciation rates by lowering extinction rates and promoting specialization (Fine, 2015; McKenna & Farrell, 2006). However, evolutionary processes such as speciation require hundreds of thousands of years to occur. Especially at short temporal scales (e.g., thousands of years), precipitation and temperature are more likely to affect diversity by influencing species persistence due to physiological constraints that limit species ranges (but see Araújo et al., 2008). In this context, ectotherms such as amphibians seem to be notably limited by tolerance to low temperatures and extremes (Wells, 2007).

Even though the broad-scale drivers of diversity such as climate stability and water availability are correlated with latitude, using the actual variables instead of latitude as a proxy represents a superior approach for linking biodiversity patterns to mechanisms (Hawkins & Diniz-Filho, 2004). Additionally, host-related drivers such as local richness may interact with climatic factors as drivers of parasite diversity (Rohde, 1999). To disentangle the respective roles and interactions of climate and host-related factors, it is desirable to have geographically widespread groups of hosts and parasites and include both direct and indirect effects of climate through an influential host-related attribute that itself responds to climatic gradients. Host richness is an adequate candidate for this host-related factor due to its consistent relationship with parasite diversity (Kamiya et al., 2014b) and responsiveness to climate.

Identifying the drivers of diversity gradients has often been guided by human interest over the future of biodiversity and the urge to establish its status (Gaston, 2000). Some estimates suggest that parasitic organisms, notably parasitic worms (helminths) and arthropods, constitute 30 to 50% of the animal tree of life (see Poulin, 2014). Therefore, investigating what drives parasite diversity represents a major step towards understanding what affects a substantial portion of existing species. Additionally, parasite diversity is a potentially good measure of parasite pressure on hosts, being related to key factors such as host diversification, energetic demands and body condition (reviewed in Bordes & Morand, 2009).

Using the major broad-scale drivers of diversity and considering their interactions with important host-related factors is a promising approach to explore what determines parasite diversity at the macroecological scale. Using a novel global dataset on helminths of amphibians, we used structural equation modelling to investigate the direct and indirect effects of temperature seasonality, precipitation seasonality, total precipitation and host richness as drivers of parasite alpha diversity. We highlight that, to our knowledge, no previous study on global parasite diversity has used amphibians as models, therefore our study besides bringing a new approach to the study of parasite diversity at broad spatial scales, explores an unprecedented group of hosts. We chose our climatic variables based on key climatic conditions required for both amphibian and helminth reproduction and survival (Goater et al., 2014; Wells, 2007).

Given that both climate and host richness are essential drivers of parasite diversity through space and time, we might expect that global changes might affect parasites in two different ways. Future projections forecast (a) an increase in climate instability (i.e., extreme values of temperature, precipitation and drought: Fischer & Knutti, 2015) and (b) an increase in the loss of amphibians worldwide (Nowakowski et al., 2018), which, consequently, could have a strong negative effect on parasite diversity (see e.g., Carlson et al., 2017). Additionally, although most studies on negative impacts of amphibian parasites are focused on microparasites such as the chytrid fungus, helminths can cause substantial damage to their host (see Koprivnikar et al., 2012 and references therein). Therefore, our study could help to predict the conditions under which amphibians may face higher helminth parasite pressure.

Regarding the direction of the effects, our predictions are: (a) annual precipitation has a positive effect on host and parasite richness,

(b) temperature and precipitation seasonality affect negatively both host and parasite richness, and (c) host richness has a positive effect on parasite richness. A great novelty in our approach is that it considers whether climate affects parasite diversity indirectly by influencing host richness. We particularly emphasize the importance of our predictor variables as major biological drivers of amphibian diversity due to their ectothermic metabolism, permeable skin and reproductive mode tied to water availability in most species.

2 | METHODS

2.1 | Database

We compiled a comprehensive dataset on helminths parasitizing amphibians by conducting a systematic search of the literature published between 1970 and 2018 in the Google Scholar (scholar.google.com) and Web of Science (isiknowledge.com) databases. To find published references, we combined the keywords 'Helminth* OR Parasite*' with scientific and common names of different orders of amphibians: 'Amphibia* OR Anura* OR Frog* OR Toad* OR Caudata* OR Urodela* OR Salamander* OR Newt* OR Gymnophiona OR Caecilian*'. To be included in our dataset, we considered the following inclusion criteria: (a) focus on the whole helminth community, (b) specify the sampling locality (ideally with geographical coordinates), and (c) provide the number of analysed hosts (minimum of five hosts). We disregarded studies describing new helminth species or focusing only on particular parasite groups. We also excluded surveys combining data from different localities separated from each other by more than 100 km, and studies that did not report host sample size. We removed hosts that were collected out of their native ranges to control for potential confounding variables associated with this condition. A list of the data sources is given in Supporting Information Appendix S1 – Data sources. We updated host scientific names and taxonomic classification according to the Amphibian Species of the World 6.0 online database (https://amphibiansoftheworld.amnh.org/).

We restricted our analysis to helminths found in the lumen of the gut, lungs and urinary bladder for the following reasons: (a) in contrast to other organs and structures, most studies in our database surveyed the parasites in these organs, (b) most of these parasites are identified down to the species level, (c) most of these parasites have amphibians as their final hosts, which strengthens the associations between parasite diversity and factors related to amphibians. When not reported in the original papers, the site of infection of each helminth species was obtained from the literature. The full dataset is available at https://doi.org/10.5061/dryad.4mw6m907s.

2.2 | Predictor variables

We obtained temperature seasonality (standard deviation *100), precipitation seasonality (coefficient of variation), annual precipitation and host richness for each locality to test their effects on parasite diversity, here defined as the number of parasite species per host population. We chose these climatic variables based on our model organisms. As ectotherms, amphibians are particularly sensitive to temperature fluctuations and have little control over water loss. Additionally, most amphibians require standing water or moist habitats to reproduce (Wells, 2007). Similarly, we expect helminths to be sensitive to these conditions during their environmental stages (see Pietrock & Marcogliese, 2003). Therefore, these variables may be explicitly linked to physiological tolerance for both groups of organisms. At first, we also included mean annual temperature in the model, but it was strongly correlated to temperature seasonality ($r = −.86$, $p < .05$). Thus, we kept temperature seasonality in the final model because it had a much stronger effect on amphibian richness in our model.

The climatic variables were acquired from WorldClim version 2 based on data from 1970 to 2000 (Fick & Hijmans, 2017). Host richness was generated for each locality by combining primary geographical range data for different amphibian species. All amphibian diversity maps were acquired from the Mapping the World's Biodiversity initiative (BiodiversityMapping.org; see Jenkins et al., 2013; Pimm et al., 2014 for details). Local host richness was then computed as the number of host species whose distributions overlapped the sampled locality. All rasters containing the data were standardized for a spatial resolution of 10 min (*c.* 340 km^2). We created grids of one squared degree per cell and calculated a mean coordinate for all populations sharing the same grid for extracting the predictor and dependent variables. Populations from the same species within the same grid were combined.

2.3 | Data analysis

We fitted a piecewise structural equation model (piecewiseSEM; Lefcheck, 2016) to test the direct and indirect effects of temperature seasonality, precipitation seasonality, annual precipitation and host diversity as drivers of parasite diversity. One of the main advantages of SEM models is that they allow evaluation of networks of direct and indirect effects among variables. Our piecewise SEM model encompasses two underlying structured equations that represent (a) the effects of temperature seasonality, precipitation seasonality and annual precipitation on host richness, and (b) the effects of the same climate variables and host richness on parasite richness. Both were fitted using linear mixed models (LMMs). The main advantage of mixed models is the possibility of including the hierarchical structure of the data as a random factor. For both models, the random structure is represented by the zoogeographical realms categorized following Holt et al. (2013). Additionally, we included the amphibian taxonomic hierarchy (i.e., family, genus and species) as an additional random factor in model (b) to account for the possible dependence of parasite richness on some species-level host characteristics. Predictor climatic variables were standardized, and both host and parasite diversity were log + 1 transformed to fit the model assumptions.

We ran the Moran's *I* test for spatial autocorrelation in both models and found no spatial autocorrelation for model (b). Given that model (a) showed spatial autocorrelation, we included the spatial autocorrelation structure directly in the mixed model. The final models were:

> (a) lme (log_host_richness ~ temperature_seasonality + total_precipitation + precipitation_seasonality, random = ~1|realm, corSpatial (form = ~longitude + latitude), data = dat).

> (b) lmer (log_helminth_richness ~ log_host_richness + temperature_seasonality + total_precipitation + precipitation_seasonality + (1|realm), offset = log(sampling_effort), data = dat).

We found five helminth groups infecting amphibians: acanthocephalans, cestodes, monogeneans, nematodes and trematodes. Due to limitations in the number of records for some groups and the overall low parasite richness in amphibians (see Supporting Information Appendix S2), we did not run separate models for each parasite group. Regarding hosts, we ran separate piecewise SEM models for anurans (frogs and toads) and salamanders, as these represented a major phylogenetic split in our dataset and may respond differently to our climatic variables. We checked for multicollinearity by calculating the variance inflation factor (VIF) for each predictor variable (Quinn & Keough, 2002). There was no indication of multicollinearity in any of our models (all VIF values < 3). The models were fitted using the 'lme4' (Bates et al., 2015), 'nlme' (Pinheiro et al., 2020) and 'piecewiseSEM' (Lefcheck, 2016) packages in the environment R (R Core Team, 2020).

3 | RESULTS

We obtained 424 references, among which 241 were used to compile our database after considering the inclusion criteria (see Supporting Information Appendix S1 – Data sources). The final dataset (available at: https://doi.org/10.5061/dryad.4mw6m907s) contains the richness of endohelminths (trematodes, cestodes, nematodes and acanthocephalans) parasitizing 613 populations (495 after combining populations sharing the same grid) of 319 anuran species, and 94 populations (77 after combining populations sharing the same grid) of 43 salamander species collected from 1955 to 2017; no helminth community survey was available for any caecilian species. We collected data from 29 families of anurans and five families of salamanders. For anurans, most investigated species belong to the Ranidae, Hylidae and Bufonidae families (see Supporting Information Appendix S3), while for salamanders most species belong to the Plethodontidae, Salamandridae and Ambystomatidae families (see Supporting Information Appendix S4).

We obtained data from 10 zoogeographical realms for anurans and five zoogeographical realms for salamanders (Figure 1). All predictor variables displayed a wider range of values for anurans than for salamanders (Table 1). Mean parasite richness was 3.9 (range: 1 to 21) helminth species for frogs and 3.1 (range: 1 to 10) for salamanders. For both amphibian orders, nematodes were the most common parasites followed by trematodes and cestodes in that order (see Supporting Information Appendix S2).

Overall, the model for anuran helminths explained 46% of parasite diversity ($R^2_{Cond} = .46$), among which 10% is attributed to precipitation seasonality and host diversity alone ($R^2_{Marg} = .10$). Temperature seasonality and total precipitation explained 43% of anuran diversity ($R^2_{Marg} = .43$). The model for salamanders did not uncover any effect of climate or host diversity on parasite diversity; therefore, below we focus on the results of the anuran models.

Regarding direct effects, anuran diversity (standardized $\beta = .406$, $p < .05$) and precipitation seasonality (standardized $\beta = .266$, $p < .05$) had a positive effect on helminth richness (Figure 2). Temperature seasonality (standardized $\beta = -.589$, $p < .05$) and total precipitation (standardized $\beta = .279$, $p < .05$) had a negative effect on host richness, which resulted in a respective negative and positive indirect effect on parasite diversity mediated by host diversity (see Figure 2).

4 | DISCUSSION

Based on a comprehensive novel dataset of helminths parasitizing amphibians, we showed that both climate and host diversity affect parasite diversity at the global scale in a complex manner that include direct and indirect relationships. Host diversity is one of the main drivers of parasite diversity, and the responsiveness of amphibian richness to temperature seasonality and annual precipitation reveals that these climatic factors affect amphibian helminth diversity indirectly. Additionally, we found that precipitation seasonality affected parasite richness positively and independently of host diversity, which is probably explained by the reproductive synchrony of different amphibian species imposed by seasonal environments. The negative indirect effect of temperature seasonality on parasite richness has important implications for biodiversity conservation, given that increasing temperature seasonality due to climate change may cause cascading extinctions of amphibians and their parasites. Additionally, our results indicate that amphibian populations inhabiting more seasonal areas face more parasite pressure, given the positive association between precipitation seasonality and helminth richness. Our study also highlights the importance of analytical and theoretical frameworks that encompass multiple predictors and paths in the same model. Besides allowing simultaneous consideration of multiple explanations, it is possible to evaluate direct and indirect effects of distinct predictors.

The positive effect of host diversity on parasite diversity is in accordance with most previous findings (see meta-analysis by Kamiya et al., 2014b). In fact, host diversity is a strong predictor of parasite diversity regardless of taxa or spatial scale (Kamiya et al., 2014b; but see Johnson et al., 2016 for discussion on scale). Johnson et al. (2016) found that this positive association between host and parasite richness is mainly explained by an increase in parasite beta diversity,
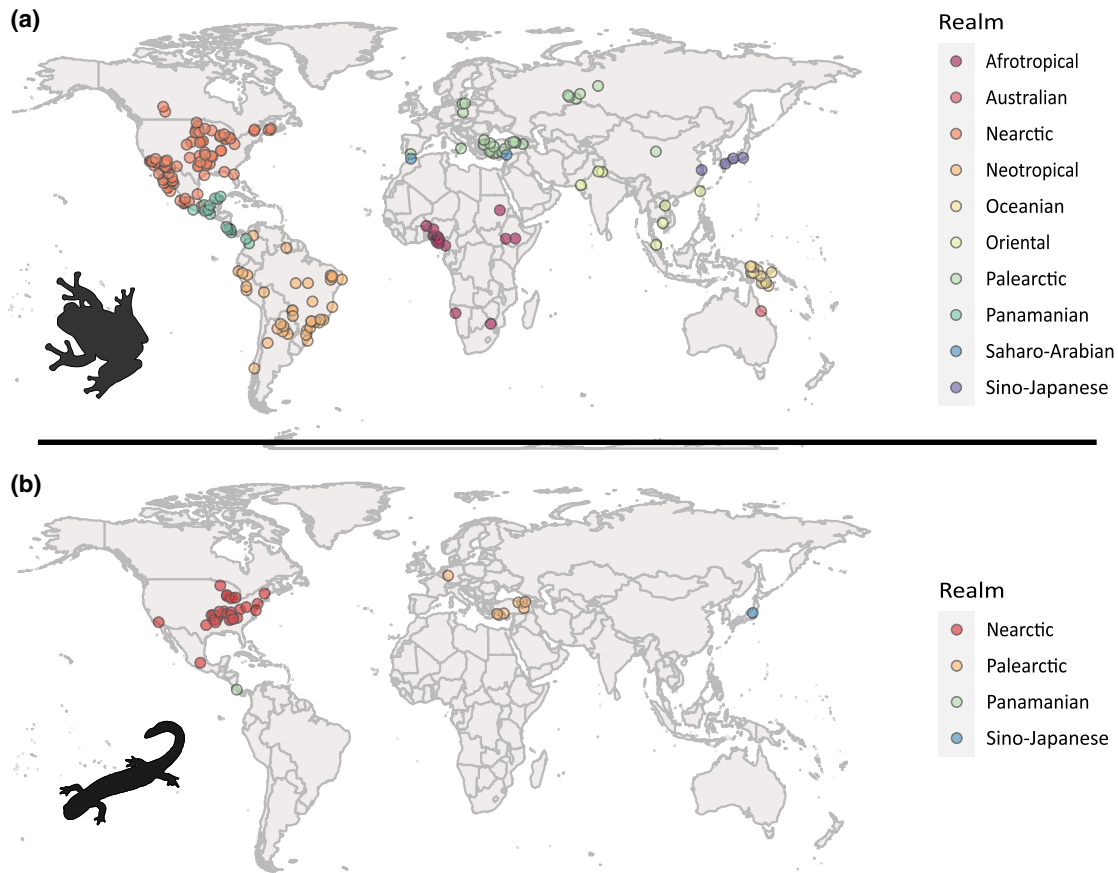
FIGURE 1 Spatial spread and zoogeographical realms of localities in which the anurans (a) and salamanders (b) were collected in the original studies that compose our final database [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Ranges of the raw climatic predictor variables and host richness associated with each host group

Host group	Temperature seasonality (SD*100)	Annual precipitation (mm)	Precipitation seasonality (coefficient of variation)	Host richness
Anurans	18.73–1,409.49	74–5,463	9.78–162.6	1–120
Salamanders	54.99–1,098.29	480–2,674	11–94.72	1–25

resembling the influence of habitat heterogeneity for free-living organisms. Additionally, the spatial co-occurrence of multiple host species (high local host diversity) that are phylogenetically related can promote host-switching by parasites (Pedersen & Davies, 2009; Poulin, 2010). Thus, each host species may begin with its own unique set of parasite species but then exchanges occur among them, thereby increasing the average parasite richness among host species in that locality.

In addition, climate is a strong correlate of species diversity for free-living organisms, especially at large spatial grains and extents (Field et al., 2009). Previous studies on parasites have also emphasized the prominence of climate as an important global predictor of parasite diversity (Dunn et al., 2010; Guernier et al., 2004; Preisser, 2019). Some proposed explanations for how climate affects species diversity are related to the speed of evolutionary processes, the amount of available energy and to species tolerances (see Currie et al., 2004). Especially at short temporal scales such as our study

(1955–2018), the climatic effects we have found are more likely to be associated with the actual species tolerance to contemporary climatic conditions, although we should not underestimate the importance of historical factors (see Araújo et al., 2008; Mittelbach et al., 2007).

The model for anurans revealed a positive effect of precipitation seasonality on helminth richness (Figure 2). We interpret this positive outcome based on the particularities of anuran reproduction. Interspecific parasite transmission requires different host species to have direct or indirect contact, giving parasites the opportunity to infect new host species, therefore increasing intraspecific parasite richness (Poulin & Morand, 2004). Most amphibians rely on standing water or wet environments to reproduce and can stay inactive when wet conditions are not available. Especially in arid environments, most amphibian species rely on standing water to reproduce (Wells, 2007). For such sites, a high precipitation seasonality may indicate that environmental requirements for anuran reproduction
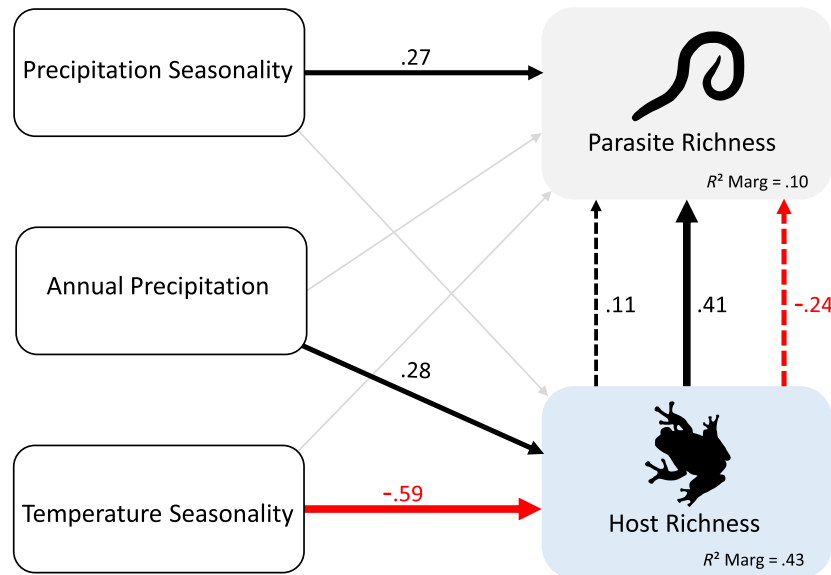
FIGURE 2 Piecewise structural equation model exploring the relationships among temperature seasonality, precipitation seasonality, total precipitation, host richness and parasite richness. Arrows show unidirectional relationships among variables. Black arrows designate positive effects, and red arrows negative relationships. Grey arrows denote non-significant paths ($p > .05$) and arrows with dotted lines represent the indirect effects. Numbers next to arrows represent the standardized regression coefficients, which are also expressed in the thickness of arrows. The indirect standardized coefficients were obtained by multiplying the coefficients of significant paths [Colour figure can be viewed at wileyonlinelibrary.com]

are available only during a short period of the year, and local species may share the same reproductive sites at the same time, increasing the possibility for host-switching.

The importance of temperature and water-related variables as determinants of amphibian diversity is in accordance with other findings (Qian et al., 2007; Rodríguez et al., 2005). The strong negative effect of temperature seasonality on anuran richness (Figure 2) is expected and may indicate that mechanisms related to physiological tolerance to temperature variation are in play. Species inhabiting highly seasonal regions are liable to face extreme climatic fluctuations during the year. This is hypothesized to affect probabilities of extinction, especially for organisms with low dispersal abilities (see Fine, 2015 and references therein). When extended to the past geological history of the planet, this reasoning is at the core of why tropical environments preserve more lineages and hold a high species diversity (see McKenna & Farrell, 2006). Most amphibians rely on standing water to reproduce and have little or no control over water loss (Wells, 2007). These characteristics of amphibian biology may explain their sensitivity to water availability and the positive effect of annual precipitation on amphibian richness.

Helminths did not respond directly to temperature seasonality and annual precipitation, but these variables indirectly affected helminth diversity mediated by host richness (Figure 2). This result has important implications for biodiversity conservation. Parasite diversity declines with biodiversity loss and hosts differ in their extinction susceptibility (Lafferty, 2012). Among vertebrates, amphibians are the most vulnerable group of hosts. This is due to the specific water requirements for reproduction and survival along with low tolerance to temperature extremes (see Wells, 2007). Along with their low

dispersal abilities, these aspects of amphibian biology make them especially susceptible to changes in the temperature and water regimes as a result of climate change (Foden et al., 2013). In fact, some amphibians face local extinction due to severe droughts due to recruitment failure (e.g., Scheele et al., 2012). Therefore, certain parasites of amphibians are likely to go extinct as the diversity of their definitive hosts decreases. This coextinction and loss of interacting and dependent species is a special concern of biological conservation (see Colwell et al., 2012).

The model for salamanders did not detect any effect of climate or host richness on parasite richness. We can think of two possible reasons for this absence of effect. First, this could be explained by the smaller variation in both parasite and host richness among localities, as well as by the much smaller geographical extent of salamander data when compared to that of anurans (Figure 1; Table 1). Additionally, maybe the general taxonomic composition of their helminth fauna is different, and therefore may be driven by other factors.

In a broad dataset such as the one we used, there are some shortcomings we need to consider while interpreting the results. First, there is a noticeable temporal spread in the years in which the hosts were collected (1955–2017). In a recent paper, Tessarolo et al. (2017) discussed the temporal degradation of biodiversity data, which is inevitable due to the dynamic character of natural systems. Old records therefore may present a 'picture' of a state that no longer exists. For instance, some sampling sites may have gone through dramatic changes in land use. Second, it was not possible to control for potential confounding variables such as host sex and age given that most authors did not mention these in the original papers. Third, the means for the climatic variables are based on a narrower

temporal scale than the dataset (1970–2000 for climatic variables against 1955–2017; Fick & Hijmans, 2017). However, none of these factors is likely to generate the significant effects we uncovered; they would be more likely to generate noise rather than bias the results in one particular direction.

5 | CONCLUSION

We found that integrating climate factors and host diversity brings new insights on how different mechanisms jointly influence parasite diversity at the global scale. Recent surveys have highlighted the advantages of bringing ecological theory into parasite studies (Johnson et al., 2016; Stephens et al., 2016), along with a growing interest in identifying drivers of parasite diversity at multiple scales (Morand, 2015; Poulin, 2014). Here, we showed that both precipitation and temperature are in play for determining parasite richness through direct and indirect effects mediated by host diversity. When studying parasite diversity, future studies should consider indirect effects associated with how hosts respond to environmental variables and the indirect impact this can have on parasite diversity. Additionally, for broad-scale studies on parasites, we argue that studies should focus on the climatic gradient and host factors instead of latitude as a proxy (Hawkins & Diniz-Filho, 2004), especially when dealing with complex patterns such as interactions among species (see Romero et al., 2018), while also considering the direct and indirect relationships among distinct predictor variables. This understanding, which is relevant for dealing with future co-extinctions due to climate change, would have been lost if we had ignored the interactions between climate and host diversity.

AUTHOR CONTRIBUTIONS

Paulo Mateus Martins: conceptualization, methodology, formal analysis, investigation, data curation, writing – original draft. Robert Poulin: conceptualization, methodology, writing – review and editing. Thiago Gonçalves-Souza: conceptualization, methodology, formal analysis, writing – review and editing, supervision.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.