

Research



Cite this article: Martins PM, Poulin R, Gonçalves-Souza T. 2021 Drivers of parasite β -diversity among anuran hosts depend on scale, realm and parasite group. *Phil. Trans. R. Soc. B* **376**: 20200367. <https://doi.org/10.1098/rstb.2020.0367>

Accepted: 9 June 2021

One contribution of 15 to a theme issue 'Infectious disease macroecology: parasite diversity and dynamics across the globe'.

Subject Areas:
ecology

Keywords:
 β -diversity, parasite macroecology, temperature, precipitation, climate, spatial distance

Authors for correspondence:
Paulo Mateus Martins
e-mail: paulomateusms@gmail.com
Thiago Gonçalves-Souza
e-mail: tgoncalves.souza@gmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5557135>.

Drivers of parasite β -diversity among anuran hosts depend on scale, realm and parasite group

Paulo Mateus Martins^{1,2}, Robert Poulin³ and Thiago Gonçalves-Souza²

¹Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, and ²Laboratório de Síntese Ecológica e Conservação da Biodiversidade [Ecological Synthesis and Biodiversity Conservation Lab], Departamento de Biologia, Universidade Federal Rural de Pernambuco (UFRPE), Recife, Pernambuco, Brazil
³Department of Zoology, University of Otago, Dunedin, New Zealand

PMM, 0000-0003-2780-2604; RP, 0000-0003-1390-1206; TG-S, 0000-0001-8471-7479

A robust understanding of what drives parasite β -diversity is an essential step towards explaining what limits pathogens' geographical spread. We used a novel global dataset (latitude -39.8 to 61.05 and longitude -117.84 to 151.49) on helminths of anurans to investigate how the relative roles of climate, host composition and spatial distance to parasite β -diversity vary with spatial scale (global, Nearctic and Neotropical), parasite group (nematodes and trematodes) and host taxonomic subset (family). We found that spatial distance is the most important driver of parasite β -diversity at the global scale. Additionally, we showed that the relative effects of climate concerning distance increase at the regional scale when compared with the global scale and that trematodes are generally more responsive to climate than nematodes. Unlike previous studies done at the regional scale, we did not find an effect of host composition on parasite β -diversity. Our study presents a new contribution to parasite macroecological theory, evidencing spatial and taxonomic contingencies of parasite β -diversity patterns, which are related to the zoogeographical realm and host taxonomic subset, respectively.

This article is part of the theme issue 'Infectious disease macroecology: parasite diversity and dynamics across the globe'.

1. Introduction

Understanding how biotic and abiotic processes drive the spatial variation of biodiversity is still an important goal of biogeography and macroecology. For years, biodiversity studies were primarily focused on what drives the number of species found at the local scale, or α -diversity [1]. However, during the last decades, there has been a renewed interest in the variation in species composition among sites, or β -diversity [2]. β -Diversity acts as a link between local (α) and regional (γ) diversities [2–4], making its study crucial to determine what drives diversity at broad scales. In β -diversity studies, species turnover refers to the replacement of species among sites due to environmental, geographical and historical differences [5,6].

The usual approach for studying species turnover includes measuring the rate at which species composition changes across space [7,8]. In general, compositional similarity among sites tends to decrease (or dissimilarity tends to increase) with spatial distance. The proposed explanations for such distance-decay relationships include deterministic responses of species to biotic and abiotic conditions (i.e. niche-based processes) and spatial processes that influence the ability of organisms to find suitable environments, such as dispersal ability and its interaction with habitat configuration and history [8,9]. In the study of parasite turnover, niche-based processes are inferred from the effects of host-related and environmental variables, while geographical distance is generally used as a proxy for spatial processes such as dispersal limitation.

Current evidence suggests that parasite turnover at broad scales is mostly affected by host diversity and climate, with a minor effect of spatial distance

[10–14]. Since many parasites release larvae and eggs into the environment, climate has an impact on parasite survival, emergence and infectivity during these stages [15,16]. Furthermore, hosts are the ultimate resources for parasites, so parasite diversity often tracks host diversity in parallel with the consumer–resource relationship for free-living organisms [17]. As a result, the available studies indicate that at large scales, parasite geographical distribution is primarily constrained by niche-based processes mediated by environmental variation and host composition.

Despite some exceptions [18], most large-scale studies on parasite β -diversity are either focused on ectoparasites, mammals or cold regions (particularly the Palearctic), most likely due to data availability. However, the observed patterns and identified drivers of parasite diversity are likely to change in response to all those factors. Berkhout *et al.* [10], for example, found that host composition explained a greater proportion of β -diversity in parasites infecting fish than parasites infecting mammals and birds, and proposed that differences in dispersal capacity between hosts could explain this variation. Similarly, even when collected from the same host group, different parasite groups may respond differently or to varying degrees to the same variables [10], probably because parasite groups with different life cycles may respond to environmental variables in different ways.

Additionally, our understanding of how these drivers vary among zoogeographic realms and spatial scales remains limited. First, each realm represents a distinct combination of past historical events and species pool [19], which may result in region-specific species–environment relationships [20]. For instance, the range of temperature is exceptionally high in northern zoogeographical realms. Thus, because most species have a low tolerance to this condition, temperature (especially extremes) tends to be critical at limiting species' geographical spread in cold regions [21]. Based on the evidence that region- or system-specific relationships may affect the general findings, our ability to make broad statements about what governs parasite β -diversity at broad spatial scales is limited. As a result, assessing novel groups of hosts and parasites, as well as distinct realms, is critical for advancing parasite macroecological theory.

Regarding spatial scale, we know of no study investigating how parasite β -diversity drivers vary with spatial scale. However, the current synthesis in community ecology recognizes that biodiversity patterns result from a combination of niche and neutral processes whose relative importance varies with scale [22,23]. The importance of niche-based processes is evidenced by the observed associations between species composition and environmental conditions such as climate, even after controlling for spatial distance [21,24,25]. By contrast, the neutral theory [26] predicts that dispersal limitation increases with spatial distance, resulting in an increase in species dissimilarity regardless of environmental differences [23,27,28]. For some organisms, niche-based processes are stronger at smaller spatial scales, while dispersal tends to be limiting at larger scales. For example, Gonçalves-Souza *et al.* [29] observed that at the biogeographic scale, geographical distance explained the most variation in arthropod composition, whereas microhabitat variation was more important at the metacommunity scale (but see [30]). This framework has currently advanced to a more predictive theory where both spatial and taxonomic scales represent useful information to explain broad-scale biodiversity patterns.

Based on a novel global dataset (latitude ranging from -39.8 to 61.05 and longitude ranging from -117.84 to 151.49) on helminths of anurans, we investigate how including different taxonomic and spatial scales improves our understanding of the relative importance of climate, host composition and spatial distance as drivers of helminth β -diversity in anuran hosts. Our main question addresses how the relative roles of these factors as drivers of helminth turnover vary in relation to (i) spatial scale (global and regional), (ii) realm (Nearctic and Neotropical) and (iii) parasite group (nematodes and trematodes). We predict that (i) niche-based processes (here represented by a combination of climate and host composition) will be more critical than dispersal limitation (here represented by spatial distance) at the realm scale (Nearctic and Neotropical), (ii) climatic extremes will be more important in the Nearctic than in the Neotropical realm, (iii) trematodes will be more responsive to climate than nematodes because they are more sensitive and mostly rely on free-living aquatic infective stages and (iv) host composition will be a strong determinant of parasite β -diversity at all scales. Additionally, we investigated how selecting different host taxonomic subset (all anurans, Bufonidae, Hylidae and Ranidae) affect the general trends.

2. Methods

(a) Host–parasite dataset

We updated a global dataset on helminths parasitising anurans used for a previous study [31] through a systematic review of the literature published between 1970 and 2020 in the Google Scholar (scholar.google.com) and Web of Science (isiknowledge.com) databases. As for the first study, we combined the keywords 'Helminth* OR Parasite*' and keywords associated with different anuran groups: 'Amphibia* OR Anura* OR Frog* OR Toad*'. To be included in the final dataset, studies had to be surveys of parasites within a given amphibian population or community, and they had to: (i) provide a list of parasite taxa found in the hosts sampled, (ii) specify the number of analysed hosts and (iii) specify the sampling location. We removed surveys describing new parasite species or focused on only a subset of the helminth community. We also excluded studies that combined parasite data from localities separated by more than 100 km. We opted to keep only hosts collected within their native ranges to avoid possible confounding factors connected with introduction to new areas.

We limited our analysis to nematodes and trematodes detected in the lumen of the gastrointestinal tract based on the following reasoning: (i) all compiled studies analysed the gut for parasites, (ii) it avoids generating artificial differences in parasite species composition based on surveys of different infection sites and (iii) most gut helminths are identified down to the species level. When not reported in the original papers, the infection site of each helminth species was obtained from the literature. Hosts and parasites had their scientific names updated following, respectively, the Amphibian Species of the World 6.0 [32] and the GBIF Backbone Taxonomy [33] datasets. For studies without coordinates, we used Google Maps (maps.google.com) to obtain approximate latitudes and longitudes of the sampling localities provided by the authors.

(b) Spatial units and predictor variables

We used hierarchical clustering to group sampling sites that were distant from each other by less than 100 km. Clusters were created using the agglomeration method Unweighted Pair Group

Method with Arithmetic Mean (UPGMA). We opted for this method instead of grouping by random grids to avoid arbitrarily splitting nearby localities that likely belong to the same community. We used these clusters as grouping variables and obtained the coordinates of the centroid of each cluster of localities. Then, we used those coordinates to obtain the climatic variables for each cluster. To test parasite responses to climate, we first chose variables that measured temperature and precipitation extremes. These were the maximum temperature of the warmest month, the minimum temperature of the coldest month, the precipitation of the wettest month and the precipitation of the driest month. Furthermore, we used variables measuring temperature and precipitation variability that were uncorrelated with the first four. These were the mean diurnal range (mean of monthly (max temp – min temp)) and precipitation seasonality (coefficient of variation). Global rasters for these variables were obtained from WorldClim version 2 [34] with a spatial resolution of 10 min (approx. 340 km²). All climatic variables were standardized and checked for collinearity.

To assess the effect of host assemblage on parasite β -diversity, we used a dissimilarity matrix of host composition. To get host composition per site, we first downloaded the amphibian distribution polygons provided by the International Union for Conservation of Nature [35]. We considered that an anuran species occurred in a given locality when its respective polygon overlapped that site's coordinates. We ended up with a list of anuran species for each locality after the removal of duplicate entries having the clusters as grouping variables. We then generated host dissimilarity matrices using the Jaccard index. Throughout this paper, spatial distance (in km) is used as a proxy for dispersal limitation [14].

(c) Dealing with uneven sampling effort

For parasite studies, sampling sites can have at least three critical dimensions of sampling effort: the number of analysed host individuals, the number of analysed host species and which host species were analysed. If not appropriately treated, differences in these dimensions can produce undesirable artefacts that could lead to incorrect conclusions regarding diversity drivers. As a way of dealing with this issue, we took the following approach. First, given that recorded parasite richness of a host population increases with the number of analysed hosts, we only included host populations that had at least five surveyed individuals. Second, during the model fitting process, we gave a proportionally higher weight to locations with a higher number of individual hosts sampled. We set the 'weightType' to 'custom' in the 'formatsitepair' function, which is the function that generates the site-pair table required for fitting a Generalized Dissimilarity Model within the 'gdm' package [36].

Finally, we recognize that pairwise dissimilarity in parasite diversity can be high when disparate groups of hosts are analysed. Given that host–parasite relationships tend towards specificity, such comparison would cause an apparent turnover in parasite species induced by sampling phylogenetically disparate host species rather than other biological processes. To see if comparing different host species affected dissimilarity in the overall dataset, we ran separate nematode analyses for the Bufonidae, Ranidae and Hylidae families in the Nearctic realm. We chose those families because each appears in at least 15 data points in our dataset.

(d) Data analysis

To investigate the effects of climate, host compositional dissimilarity and geographical distance on nematode and trematode turnover, we adopted the generalized dissimilarity modelling (GDM) approach. GDM was originally formulated as a nonlinear extension of the matrix regression procedure that accommodates

two types of nonlinearity that are common in ecological datasets: (i) the curvilinear relationship between environmental distance and compositional dissimilarity and (ii) the non-stationarity in rates of species turnover along environmental gradients [37]. The nonlinearity is accommodated in GDM models by a flexible function that measures the turnover along a gradient based on splitting the response in *I-splines*, which function as partial regressions [37]. The maximum height of each plotted *I-spline* represents the total amount of turnover in relation to a given gradient, while all other predictors are kept constant, resulting in partial regression fits that demonstrate the importance of each predictor's effect on species turnover [11,37]. Higher coefficients express higher rates of compositional change along a given gradient [11,37].

We ran separate GDM to different spatial subsets of our dataset to investigate whether the relative roles of our predictors vary from the regional to the global scale and among distinct parasite groups. We restricted the regional analysis to the Nearctic and Neotropical realms, given that they were the best-sampled realms. This restriction to the best-sampled regions is an attempt to mitigate the effects of high variability due to uneven sampling and geographical coverage, which is especially severe in regions with fewer data points. To investigate whether the relative roles of our predictors also vary with the parasite group, we ran different GDMs at each scale with varying subsets of the parasite data. We ended up with nine GDMs: global (nematodes and trematodes), Nearctic (nematodes and trematodes) and Neotropical (nematodes and trematodes) (plus the separate analyses on Bufonidae, Hylidae and Ranidae). We also ran the main analyses after removing parasites that only occurred in one cluster (i.e. singletons) to check whether our results were disproportionately influenced by rare species (see electronic supplementary material, table S1).

The response matrix for all GDMs was a dissimilarity matrix of helminths per cluster based on the Raup–Crick index, whereas the predictors were the spatial distance between clusters, and pairwise dissimilarity matrices of host composition and climate. Variable and model significance, as well as variable importance, were calculated by the matrix permutation method using the 'gdm.VarImp' function [36]. The importance of each variable is calculated by contrasting the per cent change in deviation explained by the full model to the per cent change in deviation explained by a model fit with that variable permuted [36]. Non-significant variables were removed, and GDM models calculated. We ran the GDM models using the 'gdm' package [36] in the R environment [38]. The default of three *I-splines* was used to calculate the models [11,14].

We performed a *k*-fold cross-validation procedure for each model to evaluate the performance of our models in predicting parasite turnover. This method randomly divides the observations into *k* sets (or folds) of roughly equal size [39]. The first fold is used as a validation set, and the method is then applied to the remaining *k* – 1 sets [39]. Following that, the mean squared error on the observations in the held-out fold is calculated [39]. This method is repeated *k* times, with each validation set containing a unique set of observations and estimates of error, which are then averaged to evaluate model performance [39]. We performed the cross-validation with the 'sgdm' package's *n*-fold cross-validation procedure using the default of 10 folds [40].

3. Results

The full dataset contains 162 clusters with 134 species of nematodes and 96 clusters with 69 species of trematodes, covering 330 host populations of 205 anuran species from 26 families occurring in sites spread in all continents (figure 1). Throughout this paper, the strength of effect of a variable relates to the sum of its corresponding fitted

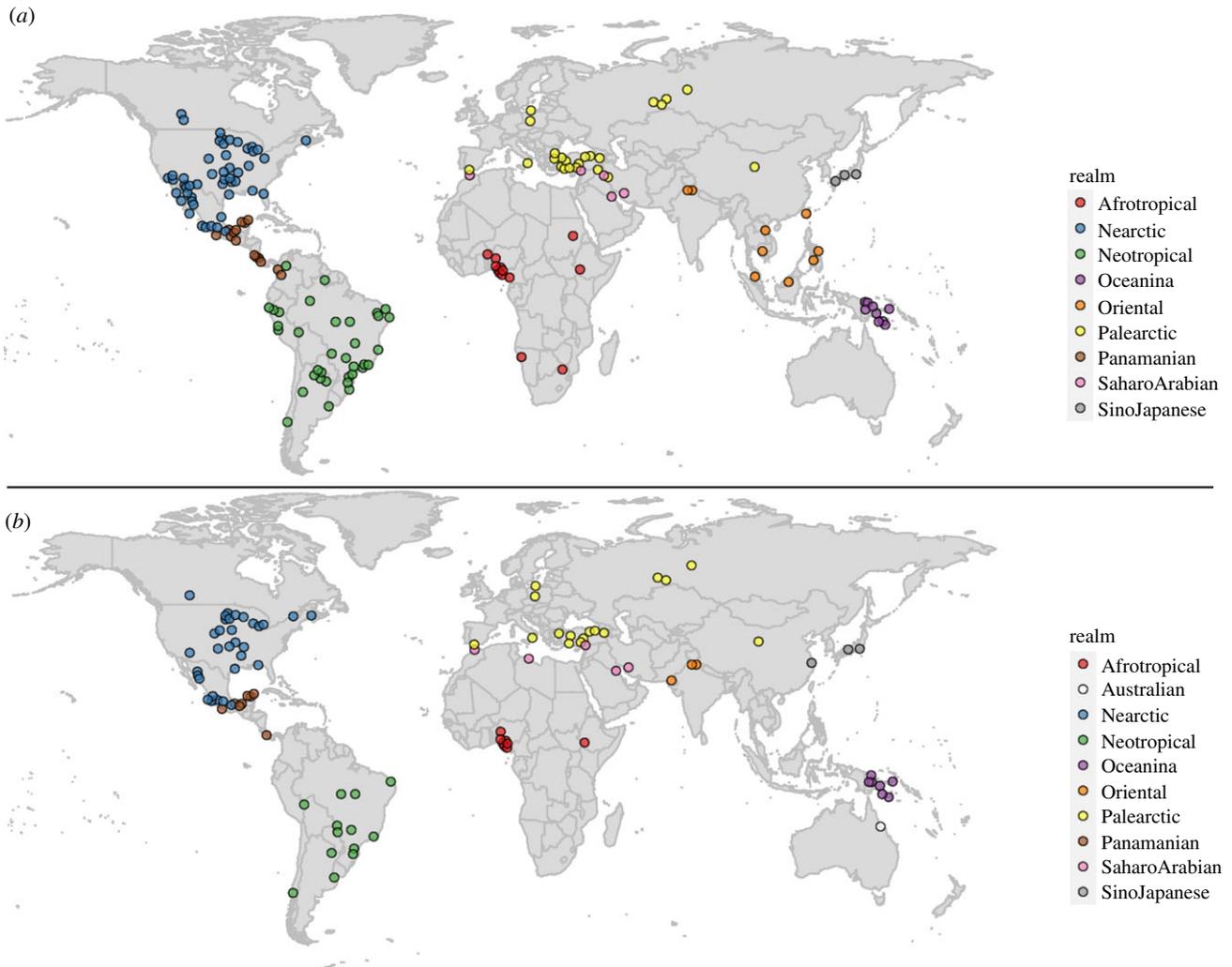


Figure 1. Geographical spread of clusters used for the nematode (a) and trematode (b) GDM models. Zoogeographical realms were delimited after Holt *et al.* [19]. (Online version in colour.)

I-spline coefficients (partial regressions), which measures the rate of parasite turnover in response to our predictors. We show the sum of the coefficients in table 1, while the fitted curves for each model are presented in electronic supplementary material, figures S1–S9. Sample sizes and number of host and parasite species for all data subsets are found in electronic supplementary material, table S2. The mean and ranges for climatic predictors are shown in electronic supplementary material, table S3. The results of the cross-validation procedure indicate a good overall model performance, with root mean square errors (RMSE) mostly below 0.32 (table 1). Across all spatial data subsets (global, Nearctic and Neotropical), pairwise parasite dissimilarity was exceptionally high (see electronic supplementary material, figure S10). Similar patterns are found in the separate subsets of Bufonidae, Hylidae and Ranidae (see electronic supplementary material, figure S11).

At the global scale, spatial distance followed by the minimum temperature of the coldest month and host composition explained approximately 32% of nematode turnover (table 1). In comparison, the first two variables explained around 38% of trematode turnover (table 1). In the Nearctic models, the minimum temperature of the coldest month followed by the mean diurnal temperature range and spatial distance explained around 15% of nematode turnover and around 26% of trematode turnover, although the effect of spatial distance was negligible for the latter (table 1). In the Neotropical

realm, spatial distance and mean diurnal temperature range explained around 12% of nematode turnover (table 1). For Neotropical trematodes, spatial distance and precipitation of the wettest month explained around 23% of parasite turnover, although the latter variable's effect was only marginally significant ($p = 0.06$) (table 1).

In the Nearctic, the fitted I-spline curves showing the turnover rate along the minimum temperature of the coldest month's gradient indicate a clear threshold point where the turnover rate is higher for both parasite groups. Nearctic trematode turnover barely responded to the gradient until approximately -11° (electronic supplementary material, figure S3). Similarly, the turnover rate for Nearctic nematodes is higher for values above roughly zero degrees (electronic supplementary material, figure S4). In contrast with the results in the Nearctic, the primary turnover thresholds for Neotropical parasites are mainly related to spatial distance, though trematode turnover appears to accelerate at higher precipitation of wettest month values (electronic supplementary material, figures S4 and S5).

(a) How do the drivers of parasite turnover vary with spatial scale?

We found evidence confirming our hypothesis that the importance of spatial distance (a proxy for dispersal

Table 1. Sum of the l-spline coefficients for each GDM model, followed by the per cent of deviance explained by that model and its corresponding RMSE. The strongest variable for each model is highlighted in italics, and the asterisk symbol denotes a marginally significant effect ($p = 0.06$). Near, Nearctic; Buf, Bufonidae family; Hyl, Hylidae family; Ran, Ranidae family.

	Nematoda						Trematoda		
	global	Nearctic	Neotropical	Near Buf	Near Hyl	Near Ran	global	Nearctic	Neotropical
spatial distance	5.50	0.60	2.62	1.36	1.5	<0.01	3.82	<0.01	11.95
mean diurnal temperature range	NA	1.12	1.44	NA	NA	2.44	NA	1.58	NA
min. temperature of coldest month	0.64	2.23	NA	NA	NA	NA	2.11	2.71	NA
precipitation of wettest month	NA	NA	NA	NA	4.27	NA	NA	NA	7.78*
host composition	0.63	NA	NA	NA	NA	NA	NA	NA	NA
% explained	31.51	14.76	11.66	13.17	28.89	15.01	38.13	26.15	22.55
RMSE	0.27	0.32	0.32	0.30	0.27	0.3	0.23	0.30	0.38

limitation) on parasite β -diversity decreases from global to regional (realm) scales. While spatial distance was critical at the global scale, its relative importance and strength in relation to climate diminishes at the regional level, especially in the Nearctic models (table 1 and figure 2). For example, at the global scale, spatial distance was around an 8.6 times stronger predictor of nematode turnover than the minimum temperature of the warmest month. By contrast, this climatic variable was an approximately 3.7 times stronger predictor of Nearctic nematode turnover than spatial distance (table 1).

(b) How do the drivers of parasite turnover vary between realms?

We discovered that the key climatic variables, as well as their relative importance and strength, differ between zoogeographical realms (table 1 and figure 2). More specifically, the mean diurnal temperature range and minimum temperature of the coldest month were critical for Nearctic nematodes while only the mean temperature diurnal range affected Neotropical nematodes (table 1 and figure 2). Likewise, Nearctic trematodes responded to minimum temperature of the coldest month while tropical trematodes responded marginally ($p = 0.06$) to precipitation of the wettest month (table 1 and figure 2). Therefore, we confirmed our hypothesis that temperature extremes are more important in the Nearctic than in the Neotropics.

(c) How do the drivers of parasite turnover vary in relation to helminth group?

We found evidence that climatic differences are more critical for trematodes than for nematodes at the global and Nearctic scales. Notably, this is evidenced both in terms of strength of effect (table 1) and variable importance (figure 2). At the global scale, the effect of spatial distance on the nematode model was approximately 8.6 times stronger than the effect of minimum temperature, whereas the effect of spatial

distance on trematodes was only approximately 1.8 times stronger than the effect of the same climatic variable (table 1). Similar results were found in the Nearctic realm, where minimum temperature was around 3.7 times stronger than spatial distance for nematodes, while spatial distance was negligible for Nearctic trematodes (table 1). At the Neotropical scale, we found a different result in terms of strength of effect. Proportionally, spatial distance was slightly stronger for neotropical trematodes than neotropical nematodes (table 1). Variable importance, on the other hand, exhibits the same general pattern as the other models (figure 2).

Furthermore, we discovered evidence that the two groups respond to different climatic variables or to varying degrees when the variables are the same (table 1 and figure 2). For instance, in the Nearctic, nematodes responded to spatial distance, minimum temperature of the coldest month and mean temperature diurnal range, whereas trematodes did not respond to the latter variable (table 1 and figure 2). These differences are even more pronounced in the Neotropics, where nematodes responded to the mean diurnal temperature range while trematodes responded (marginally, $p = 0.06$) to maximum precipitation of the wettest month (table 1 and figure 2).

(d) Did host composition affect parasite β -diversity?

Surprisingly, we only detected an effect of host composition on parasite turnover in the global nematode model (table 1). However, such effect was both weaker and less important than climate and spatial distance (table 1 and figure 2).

(e) Does selecting different host subsets affect general trends in parasite turnover?

We found different trends when we compared Ranidae, Bufonidae and Hylidae hosts in the Nearctic bioregion (table 1 and figure 3). Spatial distance was the only important predictor of nematode turnover in Bufonids, whereas spatial distance and precipitation of the wettest month influenced

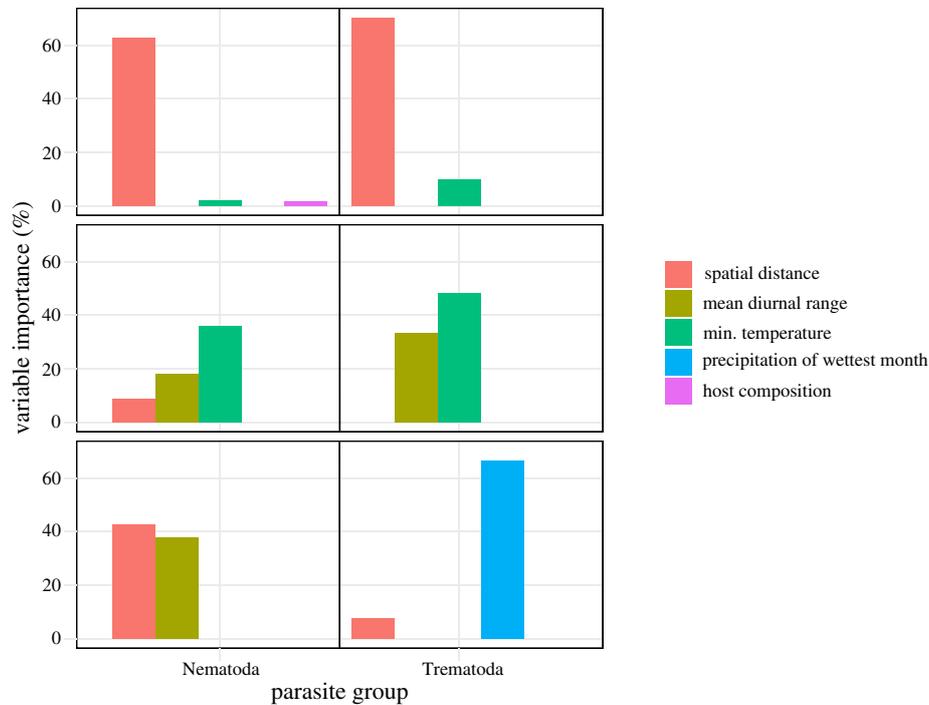


Figure 2. Variable importance for each GDM model according to spatial scale (global, Nearctic and Neotropical) and parasite group (Trematoda and Nematoda). (Online version in colour.)

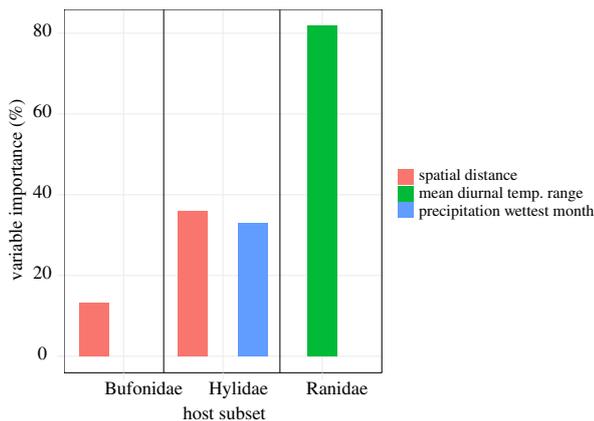


Figure 3. Variable importance for the separate nematode GDM models according to host family (Bufonidae, Hylidae and Ranidae). (Online version in colour.)

nematode turnover in Hylidae (table 1 and figure 3). Nematode turnover in Ranidae was only influenced by the mean diurnal temperature range (table 1 and figure 3). These results were also different from the Nearctic nematode model when all hosts are considered (table 1 and figure 2).

4. Discussion

Although most macroecological studies have investigated processes affecting the global distribution of free-living organisms on Earth, to our knowledge, the processes underlying parasite β -diversity have never been investigated at the global scale. We studied for the first time how spatial scale can be used to tease apart the drivers of parasite β -diversity from regional (zoogeographical realm) to global extents. Overall, spatial distance is a major driver of helminth turnover in anuran hosts. Additionally, we found five primary patterns: (i) for both parasite groups, the effects of climate

on parasite β -diversity increase from the global to the regional scale. (ii) There is a spatially dependent effect of climate on β -diversity linked to the realms. Specifically, minimal temperature of the coldest month is dominant in the Nearctic, while neotropical nematodes and trematodes responded to the mean diurnal temperature range and precipitation of the wettest month, respectively. (iii) Nematodes and trematodes show distinct trends in their response to climate and spatial distance. More specifically, trematodes are generally more sensitive to climatic conditions, while nematodes are more spatially structured. Additionally, the most important variables differed between parasite groups, especially in the Neotropics. (iv) Overall, host turnover was not an important predictor of parasite turnover. (v) We found that drivers of parasite β -diversity vary with host taxonomic subset, even when analysing lower hierarchies such as host families.

The few existing broad-scale studies investigating the effects of climate, spatial distance and host composition on parasite β -diversity reveal some general trends in parasite β -diversity at the macroecological scale. For instance, Eriksson *et al.* [14] studied bat flies across the Neotropical realm (from Mexico to Brazil) and found that host composition and temperature seasonality are the main drivers of parasite β -diversity. Similarly, in another study at the regional scale (about 2500 km in Mongolia), Maestri *et al.* [11] demonstrated air temperature and host β -diversity as the best predictors of rodent flea turnover. The other existing studies (such as [10,12,13]) show high heterogeneity in investigated hosts, parasites, realms and scale (grain and extent). However, these studies indicate parasite β -diversity to be mainly affected by host composition, climate or a combination of both, with a negligible effect of spatial distance. Conversely, we found a major role of spatial distance as a driver of anuran parasite turnover at both the global and Neotropical scales. Although it should be interpreted with caution, the prominence of spatial distance in these models indicates

that dispersal-based processes may be a major determinant of anuran helminth β -diversity.

Parasites rely on hosts to disperse, and there is evidence that spatial connectivity among host assemblages is an essential driver of parasite similarity [18]. As a result, spatial distance can be even more influential in host–parasite systems where both parasites and hosts are dispersal limited. Indeed, due to the nature of the helminth life cycle, these parasites rely on hosts for dispersing, and amphibians are recognized for their poor dispersal abilities. For instance, Buckley & Jetz [41] found spatial turnover to be around four times higher for amphibians than birds, which is consistent with amphibians having many small-ranged species. Besides being dispersal limited, previous studies argued that habitat specialization is a relevant factor determining small range sizes from amphibians compared with birds and mammals [7]. As a result, the marked differences in composition between sites and regions may be explained by the fact that poor dispersers may have higher speciation rates (as gene flow decreases) [42].

We found evidence for increasing the importance of niche-based processes from the global to the regional scale. This result is expected and follows the observed increase in niche-based processes at proportionally smaller scales (e.g. [29], but see [30]). However, we accept that this finding is not surprising, given that distinct realms with distinct parasite and host pools are being compared at the global scale, implying that species composition is likely to vary significantly, and that these variations would increase with distance. This will result in low predictive power for any factor other than distance, as turnover would be extremely high regardless of environmental differences.

Different parasite groups showed distinct trends in terms of how they responded to climate and spatial distance. Besides helminths being ectothermic animals, most species have complex life cycles that involve releasing eggs or larvae into the environment [43]. Consequently, during these environmental stages, parasite persistence can be directly affected by local climatic conditions, given that temperature and precipitation can directly influence their survival and infectivity [15,44,45]. This could explain the relevance of climate as a broad-scale driver of helminth β -diversity. We found that trematodes are generally more sensitive to climate than nematodes. Also, the two groups responded to different climatic variables, especially in the Neotropics. The higher sensitivity of trematodes to climatic differences may be explained by biological characteristics. For instance, most trematodes have aquatic swimming stages, while many parasitic nematodes (despite their enormous variation) produce larvae and eggs resistant to environmental extremes [43]. This may explain why the former is more vulnerable to climate than the latter, as well as why precipitation affected Neotropical trematodes, given that in this region, temperature extremes are not as limiting as they are in the Nearctic.

The prominence of the minimum temperature of the coldest month found in the Nearctic models may be explained by its direct effect on parasites, an indirect effect mediated by hosts or both. Previous studies have demonstrated that ectotherms such as amphibians have a limited capacity to survive at low temperatures [46]. As a result, physiological tolerance of parasites and hosts to low temperatures could be the primary explanation for these findings. Conversely, in the Neotropical models, spatial distance showed the greatest

strength of effect. We also found that the proportional importance of spatial distance in relation to climate increased in the Neotropics when compared with the Nearctic. Perhaps, this can be explained by host species in the Neotropical realm having smaller range sizes in response to low climate variability and high geographical complexity which, in turn, leads to specialization and limits range expansion (see [47]).

We only found an effect of host composition on parasite β -diversity for global nematodes (table 1). This result is hard to interpret and run against the existing theory [10,14] and our predictions. First, host composition may be less important for helminths of amphibians than for other host groups, indicating that perhaps these parasites are more generalists. However, we believe that the most likely explanation is methodological. As shown in electronic supplementary material, table S2, parasite composition was mostly available for two host species per site. This represents only a subset of the available host pool, which can result in low statistical power to detect a host effect. Moreover, this lack of response may need further investigation. Despite the fact that parasite dissimilarity is unusually high even at the regional scale (see electronic supplementary material, figure S10), GDM is quite strong in the face of response data with a large bias towards high dissimilarity values. The nonlinear link function used in GDM is intended to address, at least in part, the issues posed by high dissimilarity values, including total dissimilarity (see [37]). Such high dissimilarity also highlights the need for more studies investigating parasite β -diversity both within and between realms, adding valuable sampling sites and host species.

Another interesting finding is that the separate analyses on Nearctic nematodes of Bufonidae, Hylidae and Ranidae revealed contrasting results both among them and when compared with the model with all hosts. Notably, the habits of these anuran families differ. Hylids, for example, are mostly arboreal, whereas bufonids are mostly terrestrial and ranids are semiaquatic [48]. This may warrant further investigation, given that biological differences between hosts can result in diverging pressures for parasite colonization and persistence, resulting in the differences we observed. The take-home message from this discovery could be the importance of specifically incorporating host life history into parasite β -diversity studies at the macroecological level. The general trends may be disproportionately affected by which host group has the majority of data points, especially in studies based on sparse data. Such contingencies should be further discussed, as they can have significant implications for the quest for universal drivers of parasite diversity at broad scales.

One of the main goals of disease macroecology is to predict disease emergence and outbreaks [49]. In this context, a robust understanding of what drives turnover in pathogen diversity at broad spatial scales and, therefore, limits geographical ranges of parasites, is an essential step to reach this end. The central role of spatial distance in most of our models contrasts most current studies on parasite β -diversity. Such differences in the relevance of predictor variables may highlight current disease macroecology's limited ability to have broad expectations about parasite β -diversity. Compared to free-living organisms, parasites are by far less studied regarding diversity drivers, especially at broad scales. Therefore, it reinforces the need for further investigations, especially on less explored realms, hosts and parasite groups. Amphibians are the most vulnerable group of vertebrate hosts, especially considering the current pace

of climate change [46] and disease transmission [50]. Accordingly, combining abiotic and biotic drivers of both parasites and their hosts in a multiscale approach can improve the predictability of macroecology and disease macroecology [21]. Our study contributes to an essential step in this direction and provides an empirical foundation for disease macroecology's goals to be achieved with amphibians.

Data accessibility. The data are provided in electronic supplementary material [51].

Authors' contributions. P.M.M.: conceptualization, methodology, formal analysis, investigation, data curation, writing—original draft. R.P.: conceptualization, methodology, writing—review and editing. T.G.-S.: conceptualization, methodology, writing—review and editing, supervision.

Competing interests. The authors have no conflicts of interest to disclose.

Funding. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (CAPES)—Finance Code 001.

Acknowledgements. P.M.M. thanks the many authors of the original studies that composed our dataset who provided additional information when required. P.M.M. thanks Alan Eriksson for his valuable help during data analysis. P.M.M. thanks Prof. Simon Ferrier (CSIRO, Australia) for clarifying some aspects related to GDM models. P.M.M. also thanks his colleagues from the Ecological Synthesis and Biodiversity Conservation Lab (ECOFUN/UFRPE) for valuable comments and insights on an early version of this manuscript. P.M.M., R.P. and T.G.-S. thank two anonymous reviewers for useful and constructive comments during the reviewing process.

References

- Gotelli NJ, Colwell RK. 2001 Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **4**, 379–391. (doi:10.1046/j.1461-0248.2001.00230.x)
- Anderson MJ *et al.* 2011 Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* **14**, 19–28. (doi:10.1111/j.1461-0248.2010.01552.x)
- Whittaker RH. 1960 Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* **30**, 279–338. (doi:10.2307/1943563)
- Whittaker RH. 1972 Evolution and measurement of species diversity. *Taxon* **21**, 213–251. (doi:10.2307/1218190)
- Baselga A, Jiménez-Valverde A, Niccolini G. 2007 A multiple-site similarity measure independent of richness. *Biol. Lett.* **3**, 642–645. (doi:10.1098/rsbl.2007.0449)
- Baselga A. 2010 Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **19**, 134–143. (doi:10.1111/j.1466-8238.2009.00490.x)
- Qian H, Ricklefs RE. 2012 Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Glob. Ecol. Biogeogr.* **21**, 341–351. (doi:10.1111/j.1466-8238.2011.00672.x)
- Soininen J, McDonald R, Hillebrand H. 2007 The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12. (doi:10.1111/j.0906-7590.2007.04817.x)
- Fitzpatrick MC, Sanders NJ, Normand S, Svenning J-C, Ferrier S, Gove AD, Dunn RR. 2013 Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. *Proc. R. Soc. B* **280**, 20131201. (doi:10.1098/rspb.2013.1201)
- Berkhout BW, Borregaard MK, Brandl R, Brändle M, Dehling DM, Hof C, Poulin R, Thieltges DW. 2020 Host assemblage and environment shape β -diversity of freshwater parasites across diverse taxa at a continental scale. *Glob. Ecol. Biogeogr.* **29**, 38–49. (doi:10.1111/geb.13005)
- Maestri R, Shenbrot GI, Krasnov BR. 2017 Parasite beta diversity, host beta diversity and environment: application of two approaches to reveal patterns of flea species turnover in Mongolia. *J. Biogeogr.* **44**, 1880–1890. (doi:10.1111/jbi.13025)
- Krasnov BR, Shenbrot GI, Vinarski MM, Korolov-Vinarskaya NP, Khokhlova IS. 2020 Multi-site generalized dissimilarity modelling reveals drivers of species turnover in ectoparasite assemblages of small mammals across the northern and central Palaearctic. *Glob. Ecol. Biogeogr.* **29**, 1579–1594. (doi:10.1111/geb.13143)
- Vinarski MV, Korolov NP, Krasnov BR, Shenbrot GI, Poulin R. 2007 Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: geographic distance, host-species composition or environment. *J. Biogeogr.* **34**, 1691–1700. (doi:10.1111/j.1365-2699.2007.01735.x)
- Eriksson A, Doherty JF, Fischer E, Gracioli G, Poulin R. 2020 Hosts and environment overshadow spatial distance as drivers of bat fly species composition in the Neotropics. *J. Biogeogr.* **47**, 736–747. (doi:10.1111/jbi.13757)
- Pietrock M, Marcogliese DJ. 2003 Free-living endohelminth stages: at the mercy of environmental conditions. *Trends Parasitol.* **19**, 293–299. (doi:10.1016/S1471-4922(03)00117-X)
- Thieltges DW, Rick J. 2006 Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Renicolidae). *Dis. Aquat. Organ.* **73**, 63–68. (doi:10.3354/dao073063)
- Kamiya T, O'Dwyer K, Nakagawa S, Poulin R. 2014 Host diversity drives parasite diversity: meta-analytical insights into patterns and causal mechanisms. *Ecography* **37**, 689–697. (doi:10.1111/j.1600-0587.2013.00571.x)
- Clark NJ, Clegg SM, Sam K, Goulding W, Koane B, Wells K. 2018 Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Divers. Distrib.* **24**, 13–23. (doi:10.1111/ddi.12661)
- Holt BG *et al.* 2013 An update of Wallace's zoogeographic regions of the world. *Science* **339**, 74–78. (doi:10.1126/science.1228282)
- Zuloaga J, Currie DJ, Kerr JT. 2019 The origins and maintenance of global species endemism. *Glob. Ecol. Biogeogr.* **28**, 170–183. (doi:10.1111/geb.12834)
- Gusmão RAF, Hernandez FA, Vancine MH, Naka LN, Doña J, Gonçalves-Souza T. 2021 Host diversity outperforms climate as a global driver of symbiont diversity in the bird-feather mite system. *Divers. Distrib.* **27**, 416–426. (doi:10.1111/ddi.13201)
- Leibold MA, Chase J. 2017 *Metacommunity ecology*. Princeton, NJ: Princeton University Press.
- Vellend M. 2016 *The theory of ecological communities*. Princeton, NJ: Princeton University Press.
- Cottenie K. 2005 Integrating environmental and spatial processes in ecological community dynamics. *Ecol. Lett.* **8**, 1175–1182. (doi:10.1111/j.1461-0248.2005.00820.x)
- Soininen J. 2014 A quantitative analysis of species sorting across organisms and ecosystems. *Ecology* **95**, 3284–3292. (doi:10.1890/13-2228.1)
- Hubbell SP. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
- Barber NA, Marquis RJ. 2011 Leaf quality, predators, and stochastic processes in the assembly of a diverse herbivore community. *Ecology* **92**, 699–708. (doi:10.1890/10-0125.1)
- Tuomisto H, Ruokolainen K, Yli-Halla M. 2003 Dispersal, environment, and floristic variation of Western Amazonian forests. *Science* **299**, 241–244. (doi:10.1126/science.1078037)
- Gonçalves-Souza T, Romero GQ, Cottenie K. 2014 Metacommunity versus biogeography: a case study of two groups of neotropical vegetation-dwelling arthropods. *PLoS ONE* **9**, 1–20. (doi:10.1371/journal.pone.0115137)
- Keck F, Franc A, Kahlert M. 2018 Disentangling the processes driving the biogeography of freshwater diatoms: a multiscale approach. *J. Biogeogr.* **45**, 1582–1592. (doi:10.1111/jbi.13239)

31. Martins PM, Poulin R, Gonçalves-Souza T. 2021 Integrating climate and host richness as drivers of global parasite diversity. *Glob. Ecol. Biogeogr.* **30**, 196–204. (doi:10.1111/geb.13213)
32. Frost DR. 2021 *Amphibian species of the world: an online reference*. See <https://amphibiansoftheworld.amnh.org/index.php>. New York, NY: American Museum of Natural History. (doi:10.5531/db.vz.0001)
33. GBIF Secretariat. 2020 *GBIF backbone taxonomy*. See <https://doi.org/10.15468/39omei>, access via GBIF.org.
34. Fick SE, Hijmans RJ. 2017 WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315. (doi:10.1002/joc.5086)
35. IUNC. 2020 *The IUCN Red List of threatened species Version 2020–3*. See <https://www.iucnredlist.org>.
36. Fitzpatrick MC, Mokany K, Manion G, Lisk M, Ferrier S, Nieto-Lugilde D. 2021 *gdm: generalized dissimilarity modeling* <https://cran.r-project.org/web/packages/gdm/gdm.pdf>.
37. Ferrier S, Manion G, Elith J, Richardson K. 2007 Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* **13**, 252–264. (doi:10.1111/j.1472-4642.2007.00341.x)
38. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
39. James G, Witten D, Hastie T, Tibshirani R. 2013 *An introduction to statistical learning with applications in R*. Berlin, Germany: Springer.
40. Leitão P, Schwieder M, Senf C. 2017 *sgdm: an R package for performing sparse generalized dissimilarity modelling with tools for gdm*. *ISPRS Int. J. Geo-Information* **6**, 23. (doi:10.3390/ijgi6010023)
41. Buckley LB, Jetz W. 2008 Linking global turnover of species and environments. *Proc. Natl Acad. Sci. USA* **105**, 17 836–17 841. (doi:10.1073/pnas.0803524105)
42. Kisel Y, Timothy TG. 2010 Speciation has a spatial scale that depends on levels of gene flow. *Am. Nat.* **175**, 316–334. (doi:10.1086/650369)
43. Goater TM, Goater CP, Esch GW. 2014 *Parasitism: the diversity and ecology of animal parasites*. Cambridge, UK: Cambridge University Press.
44. Morley NJ. 2011 Thermodynamics of cercarial survival and metabolism in a changing climate. *Parasitology* **138**, 1442–1452. (doi:10.1017/S0031182011001272)
45. Morley NJ. 2012 Thermodynamics of miracidial survival and metabolism. *Parasitology* **139**, 1640–1651. (doi:10.1017/S0031182012000960)
46. Araújo MB, Thuiller W, Pearson RG. 2006 Climate warming and the decline of amphibians and reptiles in Europe. *J. Biogeogr.* **33**, 1712–1728. (doi:10.1111/j.1365-2699.2006.01482.x)
47. Whitton FJS, Purvis A, Orme CDL, Olalla-Tárraga MÁ. 2012 Understanding global patterns in amphibian geographic range size: does Rapoport rule? *Glob. Ecol. Biogeogr.* **21**, 179–190. (doi:10.1111/j.1466-8238.2011.00660.x)
48. Wells KD. 2007 *The ecology and behaviour of amphibians*. Chicago, IL: University of Chicago Press.
49. Stephens PR *et al.* 2016 The macroecology of infectious diseases: a new perspective on global-scale drivers of pathogen distributions and impacts. *Ecol. Lett.* **19**, 1159–1171. (doi:10.1111/ele.12644)
50. Cohen JM, Civitello DJ, Venesky MD, McMahon TA, Rohr JR. 2019 An interaction between climate change and infectious disease drove widespread amphibian declines. *Glob. Change Biol.* **25**, 927–937. (doi:10.1111/gcb.14489)
51. Martins PM, Poulin R, Gonçalves-Souza T. 2021 Drivers of parasite β -diversity among anuran hosts depend on scale, realm and parasite group. Figshare.