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Do latitudinal and bioclimatic gradients drive parasitism in Odonata?

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ABSTRACT

Prevalence of parasites in wild animals may follow ecogeographic patterns, under the influence of climatic factors and macroecological features. One of the largest scale biological patterns on Earth is the latitudinal diversity gradient; however, latitudinal gradients may also exist regarding the frequency of interspecific interactions such as the prevalence of parasitism in host populations. Dragonflies and damselflies (order Odonata) are hosts of a wide range of ecto- and endoparasites, interactions that can be affected by environmental factors that shape their occurrence and distribution, such as climatic variation, ultraviolet radiation and vegetation structure. Here, we retrieved data from the literature on parasites of Odonata, represented by 90 populations infected by ectoparasites (water mites) and 117 populations infected by endoparasites (intestinal gregarines). To test whether there is a latitudinal and bioclimatic gradient in the prevalence of water mites and gregarines parasitizing Odonata, we applied Bayesian phylogenetic comparative models. We found that prevalence of ectoparasites was partially associated with latitude, showing the opposite pattern from our expectations – prevalence was reduced at lower latitudes. Prevalence of endoparasites was not affected by latitude. While prevalence of water mites was also positively associated with vegetation biomass and climatic stability, we found no evidence of the effect of bioclimatic variables on the prevalence of gregarines. Our study suggests that infection by ectoparasites of dragonflies and damselflies is driven by latitudinal and bioclimatic variables. We add evidence of the role of global-scale biological patterns in shaping biodiversity, suggesting that parasitic organisms may prove reliable sources of information about climate change and its impact on ecological interactions.

1. Introduction

Recent advances in the study of host–parasite interactions have unravelled spatial and environmental gradients (Stephens et al., 2016). Parasites are notable elements of ecosystems, since up to half of all animal species evolved such a lifestyle (Poulin and Morand, 2000). These organisms act as connectors between communities by linking food webs, providing stability to ecosystems, and structuring multiple levels of biodiversity through their use of trophic transmission during complex life cycles (Lafferty et al., 2006). A large number of studies addressed how environmental factors may determine the presence or absence of parasites in free-living organisms and their diversity and prevalence in natural populations (Kamiya et al., 2014; Morand, 2015; Clark, 2018).

A myriad of factors may affect parasitism (Amaral et al., 2017), including climatic and other macroecological patterns (Fecchio et al., 2020). One of the largest scale biological patterns on Earth is the latitudinal diversity gradient (LDG). Over the past decades, it has been shown that species diversity increases from the poles towards the tropics and the equator (Pianka, 1966; Rohde, 1992; Willig et al., 2003; Jablonski et al., 2017). Although several hypotheses have been proposed to explain this pattern, most remain inconclusive (see Pontarp et al., 2019) for an extensive review of these hypotheses). For instance, most hypotheses deal with rates of diversification and biogeographic rules that shape diversity (Mittelbach et al., 2007); the increasing diversity as a function of productivity, since high resource availability potentially supports a wider set of lineages (Janzen, 1970; Connell, 1971); or the decreasing diversity with environmental temperature which mediates biological processes (Allen et al., 2002; Brown et al., 2004).

Studies on coevolutionary processes and interspecific interactions have helped address some of these hypotheses that attempt to unravel the main selective forces driving the evolution of LDG patterns (Schemske et al., 2009). For instance, host–parasite interactions have become good models to test for the mechanisms behind LDG patterns – diversity of parasites per host tends to be

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higher towards the tropics, including for protozoan parasites of birds (Svensson-Coelho et al., 2014), helminths of cricetid rodents (Preisser, 2019) and ectoparasites of marine fish (Rohde and Heap, 1998). Similarly, early predictions suggested that there should also be a higher prevalence of parasites in the tropics, due to the more stable environment and stronger coevolution between parasites and hosts (Janzen, 1970; Connell, 1971). Recent evidence supports these claims for blood parasites, showing that their prevalence increases with lower latitudes in birds (Merino et al., 2008) and parasite loads tend to be higher in tropical populations of lizards (Salkeld et al. 2008, but see Cuevas et al., 2020). This tendency may be related to the increasing abundance and diversity of vectors and/or the response of parasite reproduction and transmission rates to climate at lower latitudes, and a way to test this hypothesis would be a comparison of parasitism rates in the same host species across a latitudinal range (Schemske et al., 2009).

Although LDG patterns may also affect parasite occurrence and prevalence, these organisms seem to be affected differentially by latitudinal variations due to their dependence on host biology and distribution, since parasites depend on their hosts for survival (Kamiya et al., 2014). Evidence in support of the LDG pattern was found for ectoparasites (e.g., Krasnov et al., 2007), however, several other studies have shown that diverse factors affect parasite diversity (Kamiya et al., 2014; Clark, 2018; Eriksson et al., 2020; Fecchio et al., 2020), which may explain why endoparasites respond differently compared with ectoparasites, and tend not to follow latitudinal gradients (Poulin, 1995). Therefore, here we focused on addressing the hypothesis that parasite prevalence exhibits a latitudinal gradient, with higher infection rates at lower latitudes due to climatic stability (Janzen, 1970; Connell, 1971). Moreover, we addressed whether this pattern is observable only for ectoparasites, but not for endoparasites, which may suffer less direct effects of environmental temperature and humidity (Poulin, 1995).

For this, we tested whether there is a latitudinal and bioclimatic gradient in the prevalence of water mites and gregarines parasitizing dragonflies and damselflies (order Odonata). We hypothesized that the prevalence of water mites and gregarines across distinct host populations would respond differently to latitudinal gradients: (i) prevalence of water mites should increase towards lower latitudes and warmer climates, since water mite distribution and abundance are highly dependent on host availability (Pozojević et al., 2018), which is higher at lower latitudes and warmer climates (Kalkman et al., 2008); (ii) prevalence of gregarines should show no response to climatic/latitudinal gradients, since gregarines are endoparasites with trophic transmission from insect prey (Åbro, 1976), a transmission mode unlikely to be affected by climate. We test these hypotheses with a comparative approach, accounting for the influence of host phylogeny, using a global dataset compiled from published results extracted from the literature.

Dragonflies and damselflies, similar to many other aquatic insects, are ubiquitously parasitized by a diversity of ecto- and endoparasites (Mendes et al., 2019). For instance, biting midges *Forcipomyia* spp. (Diptera: Ceratopogonidae) are ectoparasites that feed on the haemolymph by piercing the odonate host on the wings or thorax (Wildermuth and Martens, 2007; Guillermo-Ferreira and Vilela, 2013; Cordero-Rivera et al., 2019). Water mites *Arrenurus* spp. (Acari: Hydrachnidia) adopt a similar strategy. Mite larvae attach to the insect host thorax or abdomen to feed on digested tissue and haemolymph (Rolff and Martens, 1997). Gregarines (Apicomplexa: Eugregarinorida) also have high prevalence in some odonate groups. These are endoparasites that infect the gut of arthropods and, in some cases, an individual odonate may be parasitized by a horde of these parasites (Ilvonen et al., 2018), while there may be a negative covariance between gregarines and water mites in other cases (Kaunisto et al., 2018). It is noteworthy that most studies on odonate parasites were carried out in temperate regions, resulting in gaps in knowledge for most regions, mainly the tropics.

Dragonfly and damselfly hosts – and consequently their parasites – are affected by several environmental features that shape their distribution, mainly climate (Hassall and Thompson, 2008), solar radiation (De Marco et al., 2015), and vegetation structure (Guillermo-Ferreira and Del-Claro, 2011a; da Silva Monteiro Júnior et al., 2013). Latitude is a convenient proxy for environmental factors, however testing for the direct effect of these factors themselves allows us to better understand why various ecto- and endoparasites may respond differently to latitude. For instance, water mites are expected to be affected by environmental factors in such a way that temperature may affect egg hatching (Zawal et al., 2018a) and the degree of melanization of mite feeding tubes by the host immunological system (Robb and Forbes, 2005). Moreover, mite distribution may be related to warmer riparian springs (Więcek et al., 2013), specific vegetation characteristics (Cyr and Downing, 1988) and flood regimes (Zawal et al., 2018b). Similarly, insect susceptibility to gregarine parasites may also be reduced by high temperatures (Åbro, 1976; Jancarova et al., 2016) and humidity (Clopton and Janovy, 1993). Host occurrence and distribution in the habitat may also affect parasite prevalence. Hence, bioclimatic factors and vegetation biomass surrogates, such as net primary productivity and plant height, are usually considered good predictors of odonate richness and spatial patterns (Rodrigues et al., 2016; Brasil et al., 2019). Vegetation provides resources for odonates, such as substrates for larval emergence (Tavares et al., 2017) and reproduction sites and perches for adults (Guillermo-Ferreira and Del-Claro, 2011a, 2011b), which may constrain their occurrence, distribution and abundance (as well as prey availability) (Hykel et al., 2020) at sites where parasite incidence/transmission is facilitated (Zawal and Buczyński, 2013; Hupało et al., 2014).

2. Materials and methods

2.1. Data compilation

To determine whether there is a relationship between latitude and prevalence of water mites and gregarines parasitizing Odonata, we built models based on data retrieved from the literature. Studies were obtained by extensively searching for articles containing the keywords "odonata" or "damselfl*" or "dragonfl*" and "parasit*" and "latitud*" or "prevalen*" or "water mite" or "gregarin*". We searched the academic database Web of Science, with some articles retrieved by other means such as cited references or additional searches of studies indexed in Google Scholar. For inclusion in the dataset, studies had to report not only data on prevalence of parasites in dragonflies or damselflies, but also information on the site of sampling (allowing latitude to be obtained), the number of sampled host individuals, and the species identity of the sampled hosts. Several studies had to be excluded due to missing information; for example, some studies did not report essential data such as geographic coordinates or species identification, the latter necessary to conduct phylogenetic analysis. Our initial search retrieved 111 articles on parasitism by water mites and/or gregarines, of which 71 were omitted due to lacking species identification, bioclimatic variables or geographic coordinates. We extracted data for prevalence, host species identity, sampling effort (number of collected individuals) and coordinates of the sampling locality from the remaining articles ($n = 40$) to build a matrix comprising all available data for these parasitic interactions. When populations were sampled repeatedly within the same year, we used mean values of prevalence, and if the sampling occurred in different years, we used separate annual values as repeated measures. We then considered as valid entries only those in which parasite prevalence was higher than zero. We had to exclude species that did not appear in the Odonata supertree we used in the Phylogenetic Comparative Models and sites where there were missing data for some environmental envelopes. After this further pruning of the data in the matrix, we ended up with information for 28 different species of Odonata parasitized by water mites and 32 species parasitized by gregarines retrieved from 27 articles, considering that there were multiple valid data entries for the same host species. A dataset with the data included in the analysis and tables with the lists of full-text articles used and those that were excluded following the literature review are provided as Supplementary Tables S1–S4, as well as a PRISMA (Moher et al., 2009) flow chart (Supplementary Fig. S1). The geographic distribution of sampling localities included in the data set is shown in Fig. 1. All entries retained in the data set are from the Northern Hemisphere. Histograms of frequency of samples as a function of latitude are provided as Supplementary Figs. S2 and S3.

2.2. Tree construction

The phylogenetic trees used in this study were obtained from the Odonata Super Tree available through the Odonate Phenotypic DataBase (OPDB) Project (Waller and Svensson, 2017). At the time of the analysis, this supertree consisted of 809 species of Odonata, with node distances based on molecular data from GenBank and calibrated with fossil data. To manipulate the tree, we used the software R, version 3.5.3 (R Core Team, 2019. R: A language and environment for statistical computing.) with the “ape” package (Paradis and Schliep, 2019). We cut out from the final trees the species that did not feature in the dataset. This procedure was necessary since the analysis requires a perfect match of species names in the dataset and at the “tips” of the tree. In the process, using the 28 host species in the tree for water mite parasitism, and the 32 species in the tree for gregarine parasitism from our final data matrix, we built a secondary tree containing only species that matched those in the matrix and that were included in the

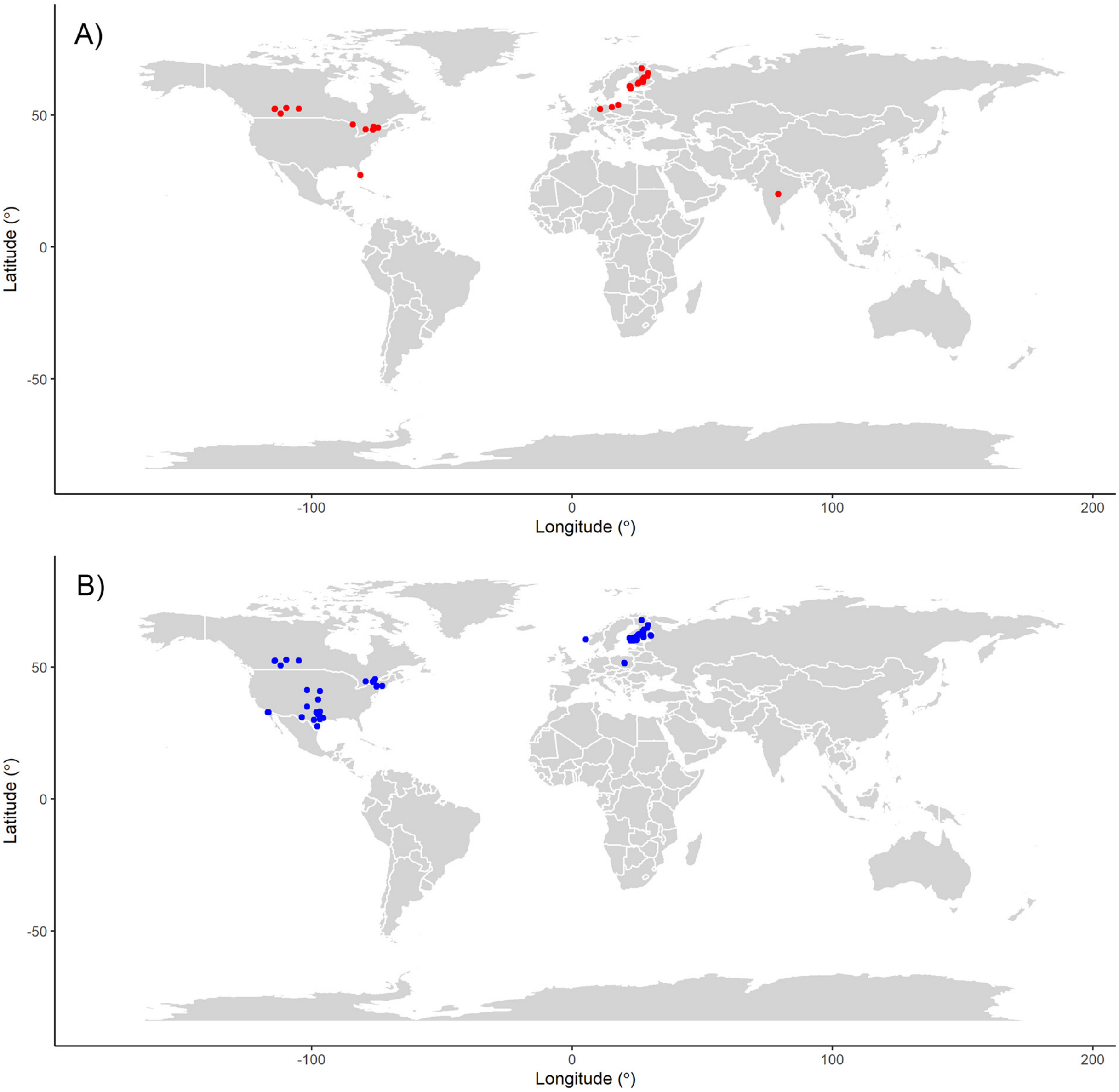

Fig. 1. Locations of the host-parasite samples retrieved from the literature and included in the dataset on parasitized Odonata, representing occurrences of water mites (A) and gregarines (B).

supertree, while maintaining the original node distances. We also tested the tree for ultrametricity and checked if it was fully bifurcated, as required by phylogenetic comparative methods (Garamszegi, 2014), using "ape" R package functions. The resultant trees are available at https://doi.org/10.17632/d7ttdszxyw.1.

2.3. Latitude and bioclimatic variables

Our predictors initially consisted of 24 variables including bioclimatic and vegetation-related variables. The bioclimatic predictors were extracted from the WorldClim database (Hijmans, 2005; O'Donnell and Ignizio, 2012) for each of the sampled locations (see https://www.worldclim.org/data/bioclim.html for the description of each bioclimatic variable). We also used other continuous variables such as latitude, and annual mean UV-B radiation (measured as spectral surface UV-B irradiance and erythemal dose product at 15 arc-minute resolution, available at https://www.ufz.de/gluv/index.php?en=32367, Beckmann et al., 2014), plant height (crown-area-weighted mean height estimates derived from Geoscience Laser Altimeter System (GLAS) shots of approximately 70/230 meters of resolution, available at https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1271, Healey, S.P., Hernandez, M.W., Edwards, D.P., Lefsky, M.A., Freeman, E., Patterson, P.L., Lindquist, E.J., 2015. CMS: GLAS LiDAR-derived Global Estimates of Forest Canopy Height, 2004–2008. ORNL DAAC. https://doi.org/10.3334/ORNLDAAC/1271), and global patterns of Net Primary Production (NPP); obtained through a terrestrial carbon model applied to the global normalized difference vegetation index (NDVI) derived from the Advanced Very High Resolution Radiometer (AVHRR) Global Inventory Modelling and Mapping Studies (GIMMS), available in a grid of 0.25 × 0.25 degrees of resolution in a pattern of millions of grams of carbon per grid cell at https://sedac.ciesin.columbia.edu/data/set/hanpp-net-primary-productivity, Imhoff and Bounoua, 2006).

We used a principal component analysis (PCA) to reduce the BioClim variables to be used in future analysis due to high collinearity between the 19 climatic envelopes, UV-B and latitude. These PCA analyses, run separately for water mites and gregarines, resulted in three major axes for each parasite (considering a minimum cumulative axis contribution threshold of 85%). We extracted the scores for each axis and used them as predictor variables in our analyses. Since riparian vegetation is considered a predictor of odonate hosts, we considered the predictors NPP and plant height in our models as proxies for plant biomass, besides PCA scores.

2.4. Phylogenetic models with repeated measures

We built phylogenetic generalized linear models using the package "MCMCglmm" (Hadfield, 2010), which is capable of handling phylogenetic information in multilevel models and used Markov chain Monte Carlo (MCMC) sampling to obtain values from posterior distributions. We modelled water mite prevalence and gregarine prevalence in populations of Odonata (90 samples for water mites and 117 samples for gregarine parasitism). For each model, predictor variables included standardized (to a mean of zero and standard deviation of one) species means and within-species predictors. Our predictors consisted of the bioclimatic and environmental variables represented as PCA scores (see above) that may encompass potential drivers of the relationships between parasite prevalence variation, sample size and plant biomass proxies (NPP and plant height). We built one model for each parasite group, using host species and study ID as random effects. We ran four chains for each model in MCMCglmm using the *MCMCglmm ()* function with 'gaussian' family and default priors. Each chain consisted of 200,000 iterations with a burn-in period of 100,000, thinned every 100 steps, for a total of 4,000 samples. The code was adapted from another study that used a similar approach (Barrow et al., 2019). Predictor variables were rescaled before analyses (range: 0–1).

2.5. Phylogenetic signal estimates

Phylogenetic signal was estimated from the superior distributions of the models, similar to the phylogenetic heritability described by Lynch (1991). Similar to heritability in quantitative genetics, we can estimate the phylogenetic signal in parasite prevalence as the proportion of the total variance that is attributed to phylogenetic variance. We estimated the phylogenetic signal using the models where species, sample size and study ID were used as random effects. In the package "MCMCglmm", the mean and the 95% highest posterior density (HPD) of the phylogenetic signal (λ) is computed for each MCMC chain by dividing the phylogenetic variance–covariance (VCV) matrix by the sum of the phylogenetic, species and residual VCV matrices (Hadfield and Nakagawa, 2010).

3. Results

Across 90 populations of 28 host species (27 Zygoptera, one Anisoptera), prevalence of water mites ranged from 1.6% to 100% (mean = 44%). Among the 117 populations of 32 host species (29 Zygoptera, three Anisoptera), prevalence of gregarines ranged from 1.1% to 100% (mean = 45.2%). Mean prevalence per region is shown in Fig. 2.

The PCAs showed a strong relationship between latitude and bioclimatic variables and UV-B (Table 1). The PCA for water mites resulted in three major axes, with 45–69–87% cumulative variance explained. The PCA for gregarines also resulted in three axes with 40–73–86% cumulative variance explained.

3.1. Phylogenetic models with repeated measurements

The model built for water mite prevalence in Odonata with species and study ID as random effects indicates a negative effect of the third axis of the PCA and a positive effect of NPP (Fig. 3A). Results also suggest a positive effect of latitude and a negative effect of UV-B on the prevalence of these parasites (captured by the third axis of the PCA). The third axis of the PCA also showed a strong relationship with Bio2 (diurnal temperature amplitude) and Bio7 (annual temperature amplitude). For gregarines, latitude, climate and vegetation had no association with prevalence (Fig. 3B).

3.2. Phylogenetic signal estimates

The phylogenetic signal was stronger in the model built for prevalence of gregarines (λ = 0.35, 95% confidence interval (CI) = 0.08–0.68) in Odonata than in the model for water mite prevalence (λ = 0.37, 95% CI = 0.08–0.74).

4. Discussion

Our results suggest an association between latitudinal and bioclimatic variations with the prevalence of parasitism in odonate populations. Results showed that the third axis of the PCA analysis was responsible for explaining the geographic variation in the prevalence of water mites prasitizing dragonflies and damselflies. However, no pattern was found for gregarines. Hence, we found that the prevalence of ectoparasites, but not endoparasites, increases with increasing latitude, opposite to our initial hypothe-

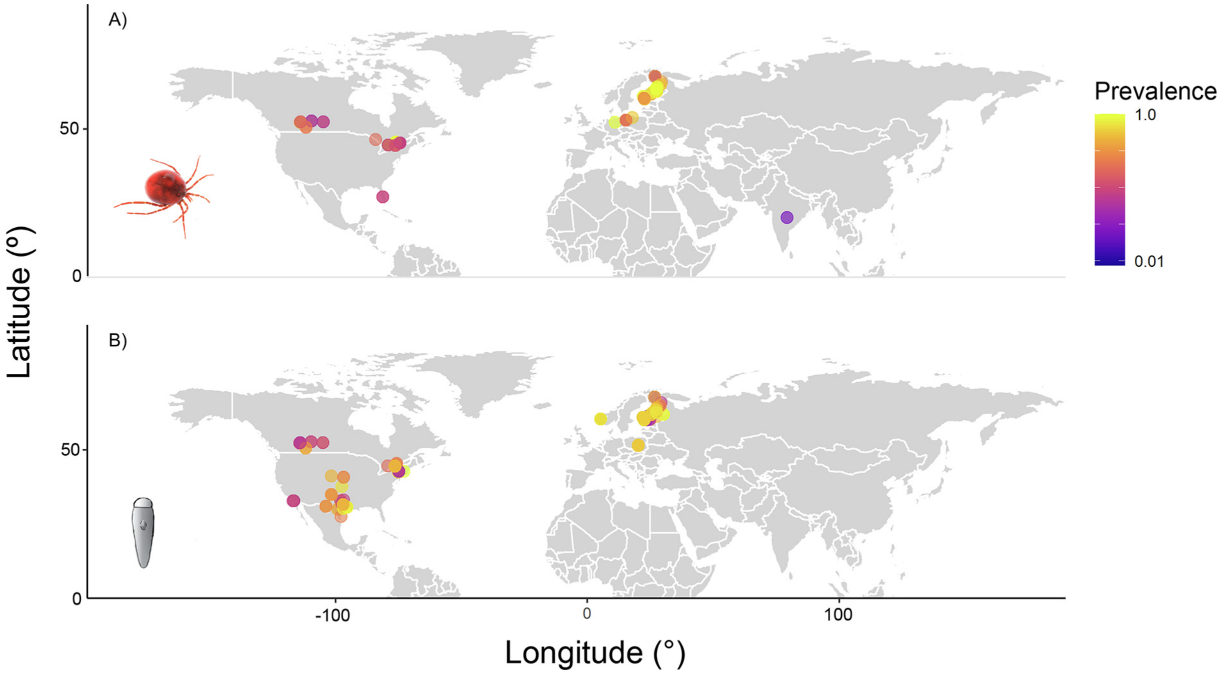

Fig. 2. The distribution of prevalence of water mites (A) and gregarines (B) in populations of Odonata across studies in the Northern Hemisphere. The heat scale bar represents the gradient of prevalence, from low (close to 0.01) to maximum (1.0). Note: when more than one population was sampled from the same location, the mean prevalence was computed across samples for illustrative purposes only.

Table 1
Parameters describing the bioclimatic variables, UV-B radiation and latitude of sampled sites. The correlations of these parameters are shown on the first axis of the principal component analysis. The scores of the three axes were used in further analyses as predictor variables.

Variables	Water mites			Gregarines		
	PCA1	PCA2	PCA3	PCA1	PCA2	PCA3
Bio1	0.935	−0.119	−0.131	0.981	−0.046	0.084
Bio2	0.383	0.249	0.828	0.566	−0.697	0.336
Bio3	0.750	−0.384	0.334	0.903	−0.276	−0.074
Bio4	−0.543	0.746	0.344	−0.615	−0.467	0.604
Bio5	0.867	0.184	0.365	0.823	−0.422	0.357
Bio6	0.630	−0.419	−0.637	0.836	0.317	−0.246
Bio7	−0.251	0.688	0.658	−0.238	−0.733	0.618
Bio8	0.248	−0.373	0.308	0.354	−0.358	−0.259
Bio9	0.486	−0.686	−0.354	0.838	0.155	−0.377
Bio10	0.925	0.136	0.165	0.881	−0.268	0.327
Bio11	0.793	−0.436	−0.395	0.954	0.142	−0.156
Bio12	0.805	0.442	−0.275	0.283	0.918	0.213
Bio13	0.846	−0.251	0.197	0.468	0.771	−0.106
Bio14	0.432	0.809	−0.384	−0.047	0.838	0.458
Bio15	−0.025	−0.779	0.593	0.099	−0.533	−0.730
Bio16	0.885	−0.116	0.169	0.353	0.820	−0.084
Bio17	0.426	0.800	−0.406	0.093	0.865	0.448
Bio18	0.724	0.174	0.102	−0.206	0.630	0.281
Bio19	0.378	0.720	−0.559	0.195	0.872	0.105
UV-B	0.841	0.259	0.415	−0.848	0.267	−0.380
Latitude	−0.861	−0.309	−0.342	0.863	−0.357	0.325

sis. Furthermore, climatic variables mostly affected parasitism by water mites, especially NPP and Mean Temperature Diurnal Range (Bio2, which had higher relationship with the third axis of the PCA). Nevertheless, considering that this PCA axis only explained 18% of the variance, the effect of latitude and temperature may not be substantial. The strength of the phylogenetic signals detected by our models did not indicate a major influence of host phylogeny on prevalence. The phylogenetic signal index we used varies from 0 to 1, with λ = 1 representing a strong signal and λ = 0 representing the absence of any phylogenetic signal (Garamszegi, 2014).

The biodiversity of most free-living organisms responds positively to the latitudinal gradient, i.e., it increases toward the tropics, however, the diversity of parasites may respond differently (Kamiya et al., 2014). While there is evidence that parasite richness and diversity are not driven by latitudinal variation (Kamiya et al., 2014; Clark, 2018), and even present an inverse tendency to increase with latitude in some cases (Fecchio et al., 2020), parasite prevalence has been shown to respond more consistently to latitudinal gradients, with prevalence of many parasites increasing towards the equator (Merino et al., 2008; Cuevas et al., 2020; Fecchio et al., 2020). Our results suggest that the prevalence of

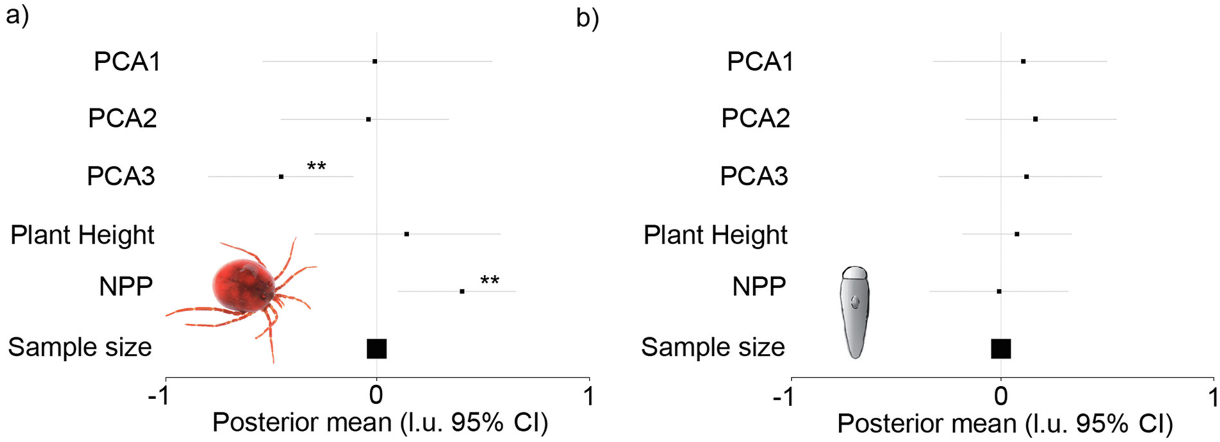

Fig. 3. Forest plot for the results of the Generalised Linear Mixed Models using Markov chain Monte Carlo built with prevalence of water mites (A) and gregarines (B) as response variables and host species and study ID as random effects, showing posterior mean estimates and lower and upper (l.u.) 95% credible intervals of predictors. Significance values of pMCMC: ** <0.01.

water mites increases towards higher latitudes, which is the inverse pattern of the predictions by Janzen (1970) and Connell (1971) that higher parasitic loads should be expected at lower latitudes due to climatic stability. These results go against the general rule for latitudinal gradients that expects an increase in species interactions toward the equator (Schemske et al., 2009; Cuevas et al., 2020; Fecchio et al., 2020). The pattern found in our study may be a consequence of host biology and occurrence, both of which also follow a latitudinal gradient (Møller, 1998; Raffel et al., 2008; Salkeld et al., 2008; Pearson and Boyero, 2009), but may also show that endoparasites of insects exhibit similar prevalences regardless of environmental conditions.

Factors other than the latitudinal gradient may also influence parasitism, such as host-related determinants – behavior, taxonomic group and body size (Morand, 2015) and other climatic variables (Guernier et al., 2004). Here, some of the climatic or environmental factors considered showed an effect on prevalence of water mites, especially Net Primary Production. The observable effect of NPP (an indicator of vegetation density and plant biomass) may suggest that forested environments influence the prevalence of water mites in odonate hosts. Considering that conservation areas may exhibit a higher host richness and abundance, reduced prevalence may be an outcome of a dilution effect due to higher host availability. The prevalence of gregarines showed no response towards lower latitudes, nor did it show a relationship with any bioclimatic dimension. These results are contrary to those found for other endoparasites, such as haematozoans of birds and lizards (Merino et al., 2008; Salkeld et al., 2008). These studies highlight the role of climate, especially temperature, in determining prevalence and other ecological processes that influence parasite biodiversity. In our study, gregarine prevalence might have been influenced by host dependence, since endoparasites are in a relatively stable environment inside their hosts (Rohde and Heap, 1998).

Higher parasite prevalence may be related to host activity patterns that could be driven by temperature seasonality and could shape host exposure to parasites (Salkeld et al., 2008). Indeed, since mites and gregarines show seasonal patterns, the period when sampling occurs may also influence estimates of prevalence of parasites, especially in temperate regions (Forbes et al., 2012; Mlynarek et al., 2015). The results obtained here also suggest a role of climatic stability and seasonality on water mite prevalence. For instance, water mite prevalence was lower in sites where diurnal and annual temperature amplitude were higher (Bio2 and Bio7, respectively), probably affecting the stability of mite and host populations. Another explanation could be the effect of temperature variation across seasons on immunity parameters of the hosts (Raffel et al., 2008). A role of temperature in immunity was observed for odonates, in which higher temperatures may cause an increase in immune response and resistance to *Arrenurus* water mites (Robb and Forbes, 2005). Hence, higher latitudes may result in higher prevalence due to lower host resistance to water mites. Nevertheless, more evidence is needed to identify macroecological factors driving parasitism in insects, since most available data are related to vertebrate hosts (Morand, 2015; Stephens et al., 2016) and the available data regarding arthropod hosts is limited by sampling effort bias (Kamiya et al., 2014) or restricted to higher latitudes in the case of the Odonata database studied here. The limitation of this database is mostly biased by the sampling gaps in tropical regions, mainly in the southern hemisphere. All collection sites were located in the Northern Hemisphere, and the samples were obtained across a time span of several decades (see dataset in Supplementary Tables S1–S4). Nevertheless, the collection sites cover a broad latitudinal range, and any year-to-year variation in local bioclimatic conditions is likely insignificant compared with large scale geographic variation.

In conclusion, only the prevalence of water mites parasitizing Odonata responds to latitudinal and bioclimatic gradients, tending to be highest at lower latitudes. Our study adds evidence that supports the notion that endoparasites remain unaffected inside their hosts. The role of bioclimatic variables in determining prevalence indicates that parasitic organisms may prove reliable sources of information about climate change and its impact on ecological interactions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ijpara.2020.11.008.

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