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RESEARCH ARTICLE

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Global drivers of avian haemosporidian infections vary across zoogeographical regions

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Abstract

Aim: Macroecological analyses provide valuable insights into factors that influence how parasites are distributed across space and among hosts. Amid large uncertainties that arise when generalizing from local and regional findings, hierarchical approaches applied to global datasets are required to determine whether drivers of parasite infection patterns vary across scales. We assessed global patterns of haemosporidian infections across a broad diversity of avian host clades and zoogeographical realms to depict hotspots of prevalence and to identify possible underlying drivers.

Location: Global.

Time period: 1994–2019.

Major taxa studied: Avian haemosporidian parasites (genera *Plasmodium*, *Haemoproteus*, *Leucocytozoon* and *Parahaemoproteus*).

Methods: We amalgamated infection data from 53,669 individual birds representing 2,445 species world-wide. Spatio-phylogenetic hierarchical Bayesian models were built to disentangle potential landscape, climatic and biotic drivers of infection probability while accounting for spatial context and avian host phylogenetic relationships.

Results: Idiosyncratic responses of the three most common haemosporidian genera to climate, habitat, host relatedness and host ecological traits indicated marked variation in host infection rates from local to global scales. Notably, host ecological drivers, such as migration distance for *Plasmodium* and *Parahaemoproteus*, exhibited predominantly varying or even opposite effects on infection rates across regions, whereas climatic effects on infection rates were more consistent across realms. Moreover, infections in some low-prevalence realms were disproportionately concentrated in a few local hotspots, suggesting that regional-scale variation in habitat and microclimate might influence transmission, in addition to global drivers.

Main conclusions: Our hierarchical global analysis supports regional-scale findings showing the synergistic effects of landscape, climate and host ecological traits on parasite transmission for a cosmopolitan and diverse group of avian parasites. Our results underscore the need to account for such interactions, in addition to possible variation in drivers across regions, to produce the robust inference required to predict changes in infection risk under future scenarios.

KEYWORDS
avian malaria, avian migration, disease hotspot, disease macroecology, haemosporidian prevalence, host–parasite interaction, infection probability, parasite macroecology, *Plasmodium*, spatio-phylogenetic models

1 | INTRODUCTION

A growing consensus based on theory and empirical evidence suggests that global change will impact the world-wide distributions and burdens of vector-transmitted pathogens that infect humans (Lafferty, 2009; Mordecai et al., 2020; Ryan et al., 2019). Likewise, climate change and anthropogenic landscape modification are predicted to alter the geographical range of non-human pathogens, such as avian malaria parasites (Benning et al., 2002; Loiseau et al., 2012, 2013; Pérez-Rodríguez et al., 2014), whereby infection patterns of avian hosts in natural environments are often driven by an interplay of regional changes in biotic and abiotic conditions (Fecchio et al., 2019). The anticipation of spatial or temporal shifts in infection risk requires reliable estimates of prevalence across habitats under different anthropogenic disturbance levels and climatic gradients (Stephens et al., 2016; Weiss et al., 2019). The synergistic effects of such drivers on the broadest levels of host taxonomic and community organization are poorly described for the majority of non-human parasites.

Mean temperatures are expected to increase unevenly across the globe in the coming decades (Wehner, 2020). For example, nights are expected to be warmer in continental interiors than in coastal regions (Wehner, 2020), and extreme temperature ranges are expected to decrease at high latitudes and increase within subtropical regions (Fischer et al., 2011). Given that the effects of climate-driven temperature change will not be uniform spatially, average global warming could alter disease transmission rates and shift the geographical ranges of many parasitic organisms with different modes of transmission (Altizer et al., 2013; Loiseau et al., 2013). For example, optimal temperatures for reproduction of *Plasmodium* malaria parasites within invertebrate vectors are a crucial prerequisite for successful transmission to humans (Mordecai et al., 2013). The existence of thermal niches that promote vector activity means that distributions of many vector-borne pathogens might extend into new geographical regions as temperatures change (Ryan et al., 2019). In Africa, for example, where average temperatures are expected to increase between 3 and 4°C by 2100 (*c*. 1.5 times the global mean response; Christensen et al., 2007), hotspots for human malaria risk are predicted to shift toward higher elevations, and the relative burdens of dengue fever over malaria are expected to increase across the Sub-Saharan region (Mordecai et al., 2020). Given that temperature might predominately influence infection risk for vector-transmitted pathogens, future climate warming will be an important force driving the prevalence of many human and wildlife diseases (Benning et al., 2002; Cable et al., 2017; Lafferty, 2009; Loiseau et al., 2013).

For those parasites infecting multiple host species, spatial heterogeneity in infection probability across host communities might change in response not only to climate filters, but also to changing host species distributions (e.g., host richness) that provide new ecological opportunities for a parasite to expand its host range and increase its local prevalence (Canard et al., 2014; Wells & Clark, 2019). Inevitably, transformation of natural habitats for urban development and agriculture is creating widespread change in habitats and microclimates, leading to shifts in host and vector species pools, thereby impacting parasite transmission (Ferraguti et al., 2020). This human-induced habitat modification is occurring unevenly across regions and most rapidly within tropical and subtropical grasslands, savannahs and shrubland ecosystems (Williams et al., 2020).

At the avian host-species level, functional traits, such as preferred foraging habitat or dependence on forested habitats (e.g., higher vegetation density) and foraging height, can influence rates of vector exposure for a given avian host, leading to heterogeneous infection probabilities across avian species (Clark et al., 2020; Garvin & Greiner, 2003). However, assessing the influence of host and parasite traits on infection rates across host communities requires careful consideration of the evolutionary histories of species. Traits that influence avian host immune responses and potentially restrict parasite invasion, such as body size (Ruhs et al., 2020), are often phylogenetically conserved (Minias, 2019). Accordingly, one would expect greater variation in infection rates among rather than within host clades. Furthermore, avian life-history strategy is known to influence haemosporidian prevalence (Barrow et al., 2019; Ellis et al., 2020; Lutz et al., 2015). For example, larger and migratory avian species are more often infected by haemosporidian parasites, owing to their propensity to harbour a broader diversity of parasite lineages or by being exposed to a higher abundance and diversity of vectors and, in turn, to vector-transmitted parasites (de Angeli Dutra et al., 2021; Filion et al., 2020).

Avian haemosporidian parasites of the genera *Plasmodium*, *Haemoproteus*, *Parahaemoproteus* and *Leucocytozoon* are a diverse group of vector-transmitted parasites (Galen et al., 2018; Valkiūnas, 2005). They infect blood cells of a wide range of avian hosts across all zoogeographical regions (Valkiūnas, 2005). The parasite genera *Plasmodium*, *Haemoproteus*, *Parahaemoproteus* and *Leucocytozoon* are predominantly transmitted by mosquitos (Culicidae), hippoboscid flies (Hippoboscidae), biting midges (Ceratopogonidae) and black flies (Simuliidae), respectively (reviewed by Santiago-Alarcon et al., 2012). The life histories of these dipteran vectors depend on temperature and on the presence of either running or standing water (Santiago-Alarcon et al., 2012; Valkiūnas, 2005). Black fly larval development and *Leucocytozoon* sexual reproduction do not appear to be highly constrained by low temperature (Fecchio et al., 2020; Valkiūnas, 2005). In contrast, the expected optimal temperature range of 13–28°C for *Plasmodium* sexual reproduction and mosquito activity suggests some constraint on the transmission of avian malarial parasites along latitudinal or elevational gradients, despite the global distribution of *Plasmodium* (Atkinson et al., 2014; Santiago-Alarcon et al., 2012; Valkiūnas, 2005).

Haemosporidian parasites exhibit broad variation in prevalence, but the drivers of this variation across zoogeographical realms and among avian clades are only partially understood from region-level studies. In recent years, numerous studies have explored haemosporidian infection rates in birds across habitat gradients under different regional land-use or climate conditions, but with no consistent predictor identified across studies (e.g., Ellis et al., 2020;

Gupta et al., 2020; Harvey & Voelker, 2019; Ishtiaq et al., 2017; Lutz et al., 2015; Santiago-Alarcon et al., 2019). Mounting evidence that various landscape and climate conditions, in addition to host and vector species attributes, might drive avian haemosporidian infections calls for global approaches to disentangle abiotic and biotic drivers and anticipate macroecological patterns of parasite spread under current and future conditions.

To explore macroecological patterns of avian haemosporidian prevalence, we compiled global-scale infection data from 53,669 birds sampled from 141 avian families and 48 countries dispersed across 10 zoogeographical realms. First, we used 14 biotic and abiotic factors known to influence infection rates of haemosporidian parasites from multiple regional-scale studies to identify the drivers of infection probability for each parasite genus. Second, we assessed whether estimated effects of these drivers vary across zoogeographical realms. Third, we tested whether parasite prevalence varies among and within avian host clades. Our use of Bayesian hierarchical spatio-phylogenetic modelling to estimate prevalence at the broadest levels of host taxonomic and community organization across 10 zoogeographical realms, coupled with information on host species traits, allowed us to assess empirically how recent anthropogenic landscape transformations and climatic gradients synergistically drive the prevalence of a multi-host vector-transmitted group of parasites world-wide.

2 | MATERIALS AND METHODS

2.1 | Host–parasite data

To compile a representative global dataset, we amalgamated field data from an international network of collaborators. We screened the available literature iteratively for studies reporting haemosporidian parasite prevalence. We screened the MalAvi database, the dominant public repository for avian malaria and related parasites (Bensch et al., 2009), for studies reporting haemosporidian infection and parasite sequences in bird assemblages with reasonably large sample sizes (> 100 individuals and more than five host species). The raw capture data, including presence–absence records of infections and geographical coordinates of surveyed birds, were then requested from the authors of relevant studies (for further details, see Supporting Information Appendix S1). The compiled infection data can be accessed in the Supporting Information (Table S1).

Any compiled dataset is a finite and biased sample, given that study locations are chosen by researchers according to interest and logistic constraints rather than comprising a truly random sample. Nonetheless, we believe that our dataset provides a reasonable sample for exploring global patterns of haemosporidian infection in birds because it covers all major geographical regions (for an overview of sample sizes from different zoogeographical regions, see Supporting Information Table S2). Moreover, our dataset includes *c*. 24% of all known bird species (2,445 out of *c*. 10,000 species recognized by Jetz et al., 2012) and, to the best of our knowledge, covers the majority of areas surveyed for haemosporidian parasites in birds to date (Supporting Information Figure S1).

Bird species names from field data were revised and assigned to families according to the taxonomy used by Birdtree.org (Jetz et al., 2012). To generate a family-level phylogenetic tree, we randomly selected five species-level fossil-calibrated trees from a phylogenetic posterior distribution estimated from multiple genetic loci for the majority of extant bird species (Jetz et al., 2012). We calculated the pairwise mean Euclidean distance from all combinations of species for each pair of bird families and then converted the resulting distance matrix into a phylogenetic dendrogram using functions in the *ape* and *phylogram* R packages (Paradis et al., 2004).

2.2 | Parasite detection and identification

Blood or tissue samples (liver or muscle) from all individuals were screened for haemosporidian infection by polymerase chain reaction, following standard protocols for amplifying a fragment of the parasite cytochrome-*b* gene (cyt-*b*). For a detailed description of the molecular detection of parasites, see the Supporting Information (Appendix S1).

Detected haemosporidian parasites were classified as *Haemoproteus*, *Leucocytozoon*, *Parahaemoproteus* or *Plasmodium* following the lineage identification protocol from the MalAvi database (Bensch et al., 2009). We characterized each individual bird with respect to each parasite genus as infected, not infected (screened with relevant primers but no lineage detected) or missing (when the sample was not screened for the genus *Leucocytozoon* or when separation of parasites of the genera *Haemoproteus* and *Plasmodium* was not achieved via sequencing).

2.3 | Host traits and climatic and environmental data

Relevant climatic variables at sample locations were obtained from the WorldClim database of gridded climate data at a resolution of .01° (Fick & Hijmans, 2017; http://worldclim.org/version2). We used annual mean temperature (bio1), annual rainfall (bio12), rainfall of the driest month (bio14) and rainfall seasonality (coefficient of variation in rainfall over the year; bio15) to characterize aspects of climate previously shown to be associated with haemosporidian occurrence (Clark et al., 2020; Fecchio et al., 2019). Elevation for all locations was quantified using Shuttle Radar Topography Mission (SRTM) data, accessible through the *raster* package in R. We classified the proportion of cover with forest and wetland in buffers of 10 km radius around sample locations based on Copernicus landcover data from 2010 (map v.2.07; https://cds.climate.copernicus.eu). We downloaded the normalized difference vegetation index (NDVI) for the year 2010 in buffers of 10 km radius around all sampling locations from the Terra Moderate Resolution Imaging Spectroradiometer (MODIS, MOD13Q1 v.6; https://lpdaac.usgs.gov/products/mod13q1v006/)

and calculated the mean and one standard deviation of NDVI as measures of the vegetation density and its annual fluctuation.

We defined local species richness of terrestrial birds based on a published map that summarizes bird species richness from BirdLife International range maps (https://biodiversitymapping.org/). Zoogeographical realm characterization followed Holt et al. (2013), who delineated realms for birds by integrating the distributions and phylogenetic relationships of 10,074 bird species.

We obtained species-level host traits from the EltonTraits v.1.0 database (Wilman et al., 2014). In particular, we considered host body mass and the proportion of time that individuals spend foraging in the upper canopy, following previous trait-based analyses (Clark et al., 2020; Fecchio et al., 2020; Filion et al., 2020). For species with missing attributes in this database, values for the closest relative were used instead. We also included migration distance, extracted from the study by Dufour et al. (2020), as a covariate. The migration distances of species were estimated from distribution maps (distance between midpoints of breeding and wintering ranges). Given that ages of individual birds were not available for all datasets, we did not include this trait in our model. We tested the 14 covariates for collinearity and found no strong correlation between predictor variables (all pairwise Spearman's $|r| < .7$).

2.4 | Spatio-phylogenetic statistical modelling of multi-host infection patterns

To identify key drivers of infection of birds by haemosporidian parasites, while accounting for possible spatio-temporal and phylogenetic patterns underpinning the global dataset, we used a Bayesian statistical model to jointly estimate the posterior distributions of fixed parameters (host traits and environmental data as described above) and random effect parameters. This approach enabled us to reduce possible bias of modelled random effects in our multiple-species system, including the spatial clustering of samples (i.e., multiple host individuals captured in the same climate and habitat conditions), phylogenetic relationships of multiple species (i.e., bird species belonging to different families, which vary in sampling intensity and are unevenly clustered among sampling locations), temporal bias (i.e., samples collected in different years), and possible statistical interactions between these factors and zoogeographical region (i.e., when the effect of a factor differs across regions).

We assumed that infection Y of any sampled bird individual x with one of the haemosporidian genera p was a random draw from the true underlying parasite prevalence φ conditional on location l and host species identity h:

$$Y_x = \text{Bernoulli}\left(\varphi_{l,h}\right) \quad (1)$$

Within our generalized linear mixed-effect model (GLMM) framework, $\varphi_{l,h}$ was modelled further with a suitable link function (e.g., logit-link) and regressed against a range of location- and host-specific covariates (X_i and X_j; see descriptions in paragraph above), which we considered as fixed effects. In multispecies models, phylogenetic relationships are likely to influence conclusions on infection patterns, because closely related species often exhibit similar infection rates. We considered phylogenetic relationship of host species at the family level as a random effect. We considered four different model structures of increasing complexity to model logit($\varphi_{i,l,h}$) (see Equations 2–5).

First, in addition to the fixed effects, we considered sampling year, sampling source (τ_S, with the three categories: blood, muscle and liver) and phylogenetic position as additional random effects, resulting in a phylogenetic GLMM (phyl-cov-GLMM), given as:

$$\text{logit}\left(\varphi_{l,h}\right) = \beta_i X_{i,l} + \beta_j X_{j,h} + \gamma_y + \tau_S + v_F \quad (2)$$

Here, β_i and β_j are the respective coefficient estimates for fixed effects, and γ_y is a random effect estimate based on sampling year. The random effect for phylogenetic relationships of different host species (v_F) is based on an inverse phylogenetic variance–covariance matrix derived from the pairwise distance relationships (i.e., each sampled bird individual is characterized by its distance relationship in terms of its family to that of any other sampled bird individual), which can be expressed as latent Gaussian Markov random fields in Bayesian frameworks (we used the default "generic0" option in the INLA package in R, which set the log-Gamma hyperparameter prior to a shape parameter of one and a rate of .00005). This option is equivalent to assuming that parameter estimates are derived from multivariate Gaussian distributions with (zero) means as hyperparameters and spatially structured covariance matrices based on the underpinning dependence structure of distance/similarity relationships.

Given that our dataset included samples from different zoogeographical realms with distinct host species assemblages, we tested a second model by including the zoogeographical realm as a random effect (π_r), extending our basic phylogenetic GLMM (regional phyl-GLMM):

$$\text{logit}\left(\varphi_{l,h}\right) = \beta_i X_{i,l} + \beta_j X_{j,h} + \gamma_y + \tau_S + \pi_r + v_F \quad (3)$$

Given that captures of multiple host individuals at the same sampling locations in field surveillance leads to spatial pseudo-replication, we included a spatial random effect (u_l) in a third model, resulting in a spatio-phylogenetic GLMM (spatio-phyl-GLMM) given as:

$$\text{logit}\left(\varphi_{l,h}\right) = \beta_i X_{i,l} + \beta_j X_{j,h} + \gamma_y + \tau_S + \pi_r + v_F + u_l \quad (4)$$

As an additional extension of the model, the fourth structure we explored included possible varying coefficient estimates for the fixed effects, assuming that because of the global scale of the study, drivers of infection probabilities (denoted as fixed effects) might vary across zoogeographical realms. Without loss of generality of the GLMM concept, we can assume that the fixed effect coefficient estimates β_i and β_j are not constant across zoogeographical realms,

and they allow for possible deviation by modelling coefficients for each zoogeographical realm based on baseline values β_{0i} and β_{0j}, respectively. Moreover, random deviation from these values across samples from different zoogeographical realms *r* result in a spatio-phylogenetic varying coefficient GLMM (spatio-phyl-varcoef-GLMM) given as:

$$\text{logit}\left(\varphi_{l,h}\right) = \left(\beta_{0i} + \xi_{i,r}\right) X_{i,l} + \left(\beta_{0j} + \xi_{j,r}\right) X_{j,h} + \gamma_y + \tau_S + \pi_r + v_F + u_l \quad (5)$$

where $\xi_{i,r}$ and $\xi_{j,r}$ are vectors of random effects ($r = 1, \ldots, R$) defining a stochastic process with a specified Gaussian model over the $R = 10$ zoogeographical realms covered in this study.

In addition to the models described above, we fitted an intercept-only model to derive estimates of overall infection probability. We also fitted GLMMs with either realm or location as a random effect to derive location- and region-specific estimates of infection probabilities. We did so to identify possible regional/local hotspots (average high infection probabilities). For model fitting and inference, we used the integrated nested Laplace approximation (INLA) as a computationally efficient way to solve such latent Gaussian spatial models (Lindgren et al., 2011; Rue et al., 2009). The INLA program models covariance for a random effect using a precision matrix (the inverse of a covariance matrix), taking advantage of sparse structures for efficient computation (Rue et al., 2009). For all random effects based on groupings (i.e., year, region and region-level varying coefficients), we fitted first-order random walk models (Gaussian Markov random field, specified by a zero mean multivariate Gaussian probability density function).

For fitting the spatial random effect, u_l, we used the stochastic partial differential equation (SPDE) approach, as implemented in INLA, to model spatial effects using a Gaussian field based on a Matérn correlation function and a spatial triangulate mesh around sampling locations (Bakka et al., 2018). Setting the minimum allowed distance between points (cut-off) to .1° of latitude and the largest allowed triangle edge length (max edge) to three resulted in a mesh of 38,305 triangles, with the smallest edge lengths and finest mesh resolution adjacent to sampling locations (Supporting Information Figure S2).

Continuous predictor variables were standardized to unit variance before analysis. For fixed effects, we used penalized complexity priors (using the "pc.prec" option in the INLA settings), which penalize any departure from the base model and constrain coefficients to zero if there is insufficient support in the data otherwise. Such priors are commonly used for regularization of regression coefficients in multiple regression models (Simpson et al., 2017).

For model comparison and validation, we computed deviance information criteria (DIC) for each candidate model (Spiegelhalter et al., 2002). We also computed conditional predictive ordinates (CPO) as cross-validation criteria, which estimate, for each observation, a probability of obtaining the observed value when the model is fitted using all data apart from the left-out observation; larger values indicate a better model fit to the data, whereas small values indicate a poorer model fit.

We present results as posterior means and 95% credible intervals (CIs) and considered CIs that did not overlap with zero or with each other in pairwise comparisons as "significantly different". Despite the overall large sample size, group-specific estimates can be burdened by substantial uncertainty (i.e., when few individuals for a certain location or host clade have been sampled). We considered group-level estimates to be meaningful only if the width of the respective CI was < 10%.

3 | RESULTS

3.1 | Strong spatial variation in haemosporidian infection probability coincides with strong phylogenetic variation among host clades

The estimated global average infection probability of birds with haemosporidian parasites differed among parasite genera: *Leucocytozoon* (13.2%, CI: 12.8–13.7%, *n* = 26,635 screened birds, intercept-only model), *Plasmodium* (12.8%, CI: 12.5–13.1%, *n* = 53,669), *Parahaemoproteus* (13.8%, CI: 13.5–14.1%, *n* = 53,669) and *Haemoproteus* (.7%, CI: .6–.8%, *n* = 53,669). The low overall infection probability for *Haemoproteus* can be explained by this genus being mostly restricted to Columbidae (doves and pigeons) and Fregatidae (frigatebirds), whereas the similar infection probabilities for the other three haemosporidian genera might reflect their ability to infect a broad spectrum of avian clades (Supporting Information Figure S3). Among the 141 avian host families surveyed, those with the highest average infection probabilities were all songbirds (Passeriformes): Paridae, Corvidae and Oriolidae for *Leucocytozoon*; Zosteropidae and Melanocharitidae for *Parahaemoproteus*; and Parulidae, Turdidae and Conopophagidae for *Plasmodium*, according to the lower CI estimates of phylogenetic effects (Supporting Information Figure S3).

Infection probabilities differed considerably among zoogeographical realms (Figure 1; Supporting Information Table S2). For the three most common haemosporidian genera (*Leucocytozoon*, *Parahaemoproteus* and *Plasmodium*), infection probabilities were highest in the Saharo-Arabian realm, with lower CI estimates ≥ 24%. *Leucocytozoon* infection probabilities were lowest in the Oceanian, Oriental and Panamanian realms. *Parahaemoproteus* infection was lowest in the Australian, Neotropical and Sino-Japanese realms. *Plasmodium* infection was lowest in the Australian, Oceanian, Oriental and Sino-Japanese realms (all respective upper CIs < 10% from GLMMs with region as random effects; Figure 1). Given its restriction to doves and frigatebirds, the prevalence of *Haemoproteus* was < 5% (respective upper CIs) in all realms except for Oceanian and estimated to be highest in the Palearctic and Oceanian realms (both lower CIs ≥ 2.3%).

We found considerable spatial variation in average infection probabilities across locations within regions (GLMM with locations as random effects), although estimates with acceptable uncertainty (CIs ≤ 10%) occurred in only 45–104 of the 1,630 sampling

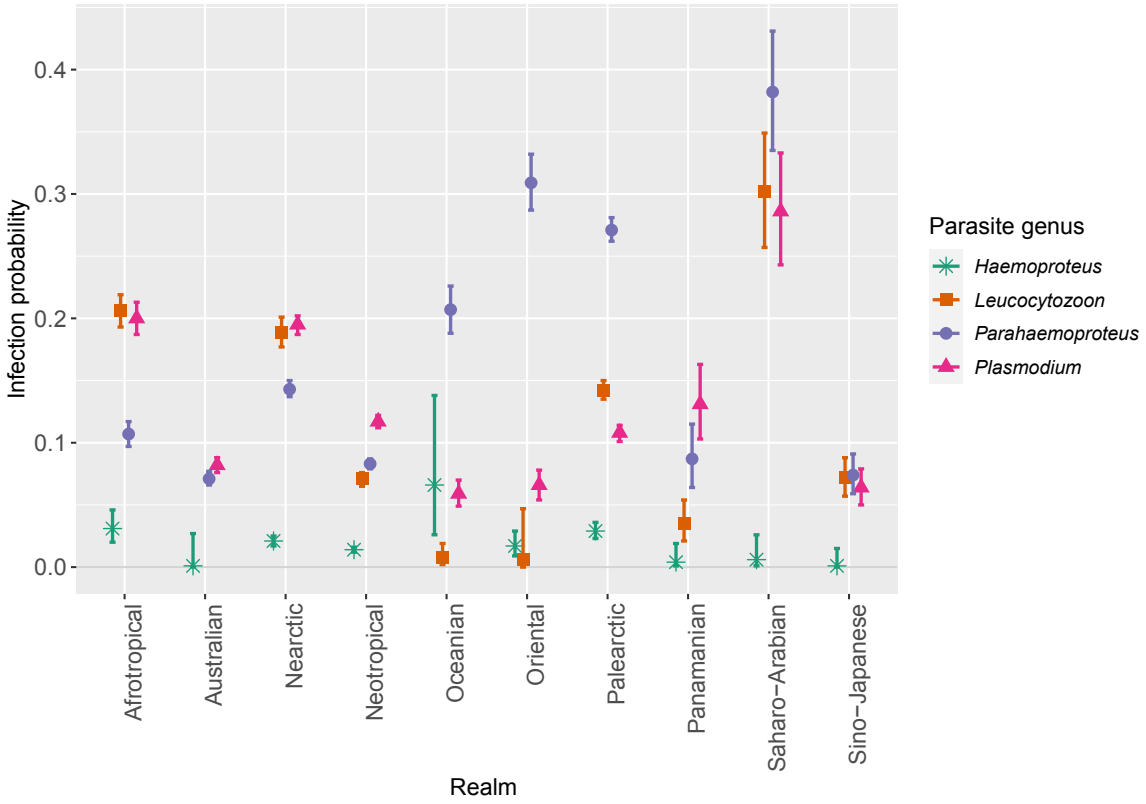

FIGURE 1 Region-specific estimates of average infection probabilities of birds for four haemosporidian genera, based on 53,669 sampled bird individuals [estimates from generalized linear mixed-effect model (GLMM), with region as a random effect]. Error bars depict 95% credible intervals, reflecting uncertainty related to sample sizes in different regions

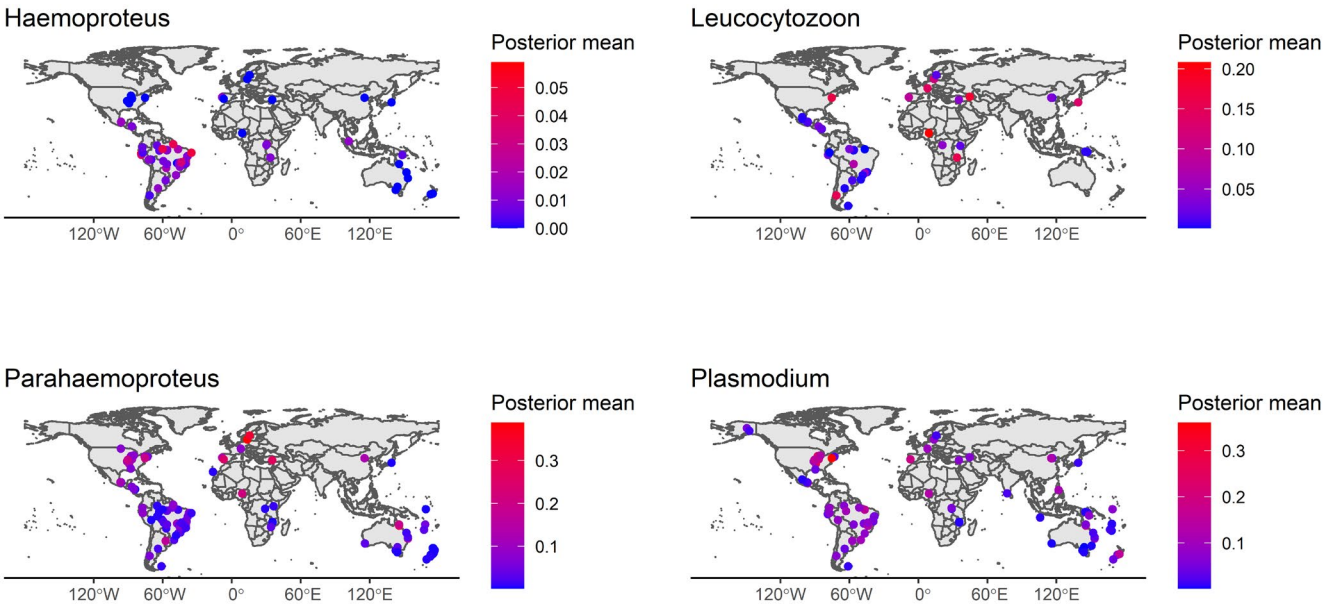

FIGURE 2 Estimated average parasite prevalence at different locations, shown only for locations with ≤ 10% uncertainty in estimates according to the size of 95% credible intervals

locations (Figure 2). Using these location-based estimates, four currently recognizable local hotspots of *Haemoproteus* infection were identified in the Neotropical realm, with infection rates > 2% (respective lower CIs ≥ 2%). Hotspots (locations with highest lower CIs) for *Leucocytozoon* and *Parahaemoproteus* were dispersed across different zoogeographical realms: *Parahaemoproteus* in the Palearctic and Australian realms with lower CIs ≥ 25%, and *Leucocytozoon* in Afrotropical, Nearctic and Palearctic with lower CIs ≥ 13%). Hotspots

of *Plasmodium* occurred in the Nearctic realm (three locations with lower CIs ≥ 21%).

3.2 | Drivers of global infection probability

Models that included phylogenetic and spatial effects and accounted for varying fixed-effect coefficients (spatio-phyl-varcoef-GLMM; Equation 5) provided the best fit to the observed data and the strongest predictive power according to both the DIC and CPO criteria (Supporting Information Table S3). We therefore report results from this model unless stated otherwise. We note, however, that phylogenetic effects were burdened by high uncertainties, indicating the challenges of disentangling phylogenetic effects from spatial and climatic covariates (Supporting Information Figure S3).

Infection probabilities exhibited idiosyncratic associations with host traits, landscape variables and climate conditions at the global scale. Among the 14 covariates used in the analyses, 11 exhibited "global average" coefficient estimates for which CIs did not overlap with zero (Figure 3; Supporting Information Table S4). Given that overall *Haemoproteus* prevalence was extremely low (370 infections in 53,669 screened birds) and constrained to two host families (Columbidae and Fregatidae), this parasite genus was not considered in the following analysis.

Local bird species richness showed a positive effect on infection probability for *Leucocytozoon* [odds ratio (OR) 1.83, CI 1.26–2.56] and *Parahaemoproteus* (OR 1.32, CI 1.09–1.59). Infection probability increased with increasing host body mass for *Leucocytozoon* (OR 1.25, CI 1.11–1.41), *Parahaemoproteus* (OR 1.62, CI 1.47–1.79) and *Plasmodium* (OR 1.36, CI 1.24–1.48). Infection probability increased among bird species spending more time foraging in the canopy for *Leucocytozoon* (OR 1.13, CI 1.05–1.22) and *Parahaemoproteus* (OR 1.26, CI 1.18–1.35), but decreased for *Plasmodium* (OR .88, CI .81–.95). *Leucocytozoon* infection probability increased with host migration distance (OR 1.19, CI 1.07–1.32). Higher proportions of wetland cover at different sites increased infection probability for *Plasmodium* (OR 1.35, CI 1.03–1.79), but decreased infection probability for *Parahaemoproteus* (OR .53, CI .37–.78) and *Leucocytozoon* (OR .52, CI .29– .95). Elevation increased infection probability for *Leucocytozoon* (OR 1.47, CI 1.14–1.9), but decreased infection probability for *Plasmodium* (OR .65, CI .53–.80). Infection probability for *Leucocytozoon* (OR .33, CI .20–.53) was considerably lower at sites with higher rainfall during the driest month and decreased with increasing rainfall seasonality (OR .59, CI .43– .80). At locations with higher annual rainfall, infection probability increased for

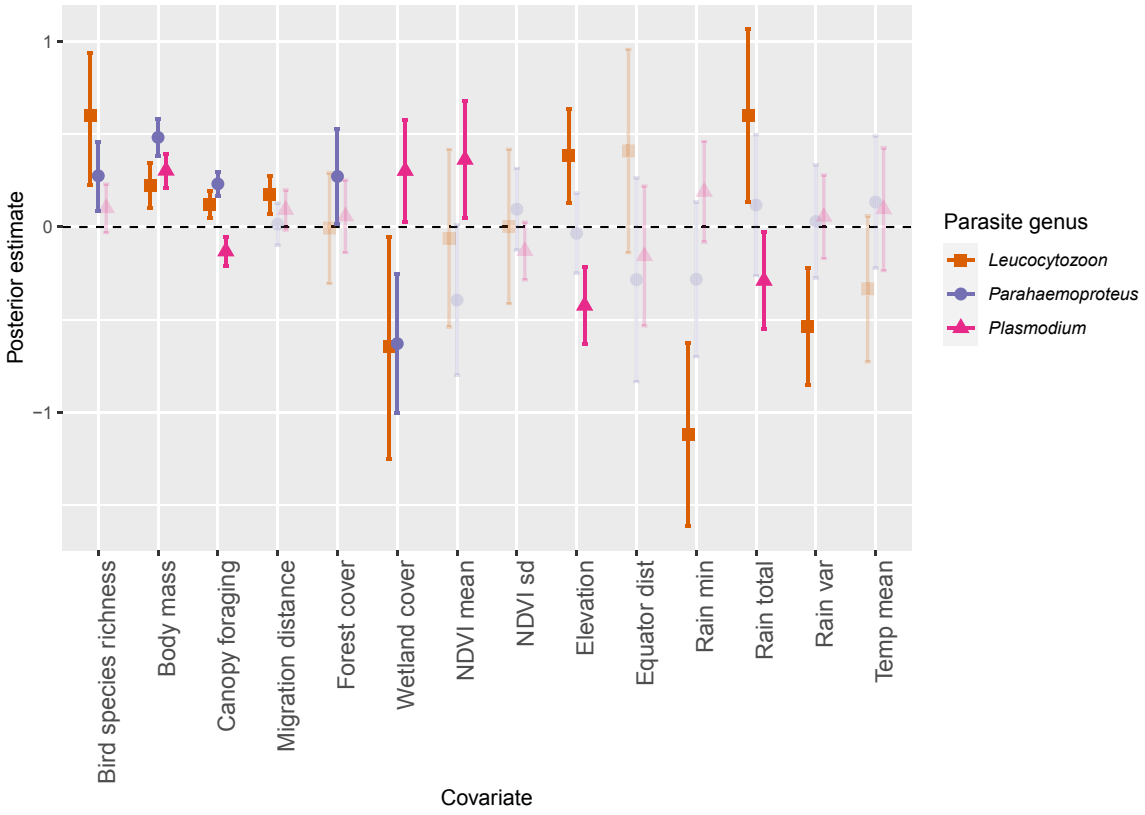

FIGURE 3 Estimates of the "global average" effects of different drivers on variation in the infection probability of the three most common avian haemosporidian genera (based on scaled covariates). Points depict posterior means of the fixed effect estimates from a spatio-phylogenetic varying coefficient model, and vertical lines indicate 95% credible intervals. For each parasite genus, the covariates that overlap with zero are shown in light bars. Abbreviation: NDVI = normalized difference vegetation index

Leucocytozoon (OR 1.83, CI 1.15– 2.91), but decreased for *Plasmodium* (OR .75, CI .58–.97). Sites with higher proportions of forest cover and vegetation density exhibited increased probability of infection by *Parahaemoproteus* (OR 1.31, CI 1.02–1.70) and *Plasmodium* (OR 1.44, CI 1.05–1.97), respectively. Annual mean temperature, annual fluctuation in vegetation density and distance to the equator showed no evident covariation with infection probability (i.e., CIs overlapped with zero) for any of the three parasite genera (Figure 3).

Varying coefficient estimates revealed that several covariate effects, notably mostly host ecological traits rather than environmental predictors, differed across zoogeographical realms (for variance estimates in coefficients, see Supporting Information Table S5). Two host traits and one environmental driver exhibited opposing effects on the probability of parasite infection across zoogeographical realms: Local bird species richness had a positive effect on infection probability for *Parahaemoproteus* in the Afrotropical, Palearctic and Sino-Japanese realms and a negative effect in the Saharo-Arabian realm (Figure 4). Migration distance was associated with increased *Parahaemoproteus* infection probability in the Neotropical, Saharo-Arabian and Sino-Japanese realms, but with decreased infection probability in the Nearctic and Oriental realms (Figure 4). Likewise, migration distance was associated with increased *Plasmodium* infection in the Neotropical, Oceanian and Oriental realms, but with decreased infection probability in the Nearctic realm (Figure 4). Annual fluctuation in vegetation density was associated with increased infection with *Leucocytozoon* in the Nearctic realm, but with decreased infection in the Palearctic realm (Figure 4). In addition, host body mass (infection with *Leucocytozoon* and *Parahaemoproteus*), canopy foraging frequency (infection with *Parahaemoproteus* and *Plasmodium*) and proportion of wetland cover (infection with *Leucocytozoon*) all varied across realms according to variance in coefficient estimates (Figure 4; Supporting Information Table S5).

4 | DISCUSSION

Understanding large-scale variation in parasite prevalence and spread is of increasing importance in a changing world, where counteracting disease emergence and outbreaks poses a global challenge. Using a global database of infections by four genera of a cosmopolitan group of vector-transmitted blood parasites of birds, we show that infection probabilities for each parasite genus vary considerably across zoogeographical realms and avian host families. Our hierarchical global analysis identified key drivers of infection probability that differed in their magnitudes and directions among parasite genera. In particular, we found that bird richness and host attributes might have rather different impacts on infection risk in different zoogeographical realms, whereas climate and habitat conditions are more likely to influence infection risk consistently across zoogeographical realms. Multiple global hotspots of avian haemosporidian infection emerge from our results, with strong variation in infection probabilities within realms, indicating that prevalence in avian hosts responds to regional factors in addition to broad-scale global drivers, such as latitudinal ecological/climatic gradients. Accounting for environmental context in synergy with biotic drivers, such as species ecological traits and host species assembly patterns, is crucial for understanding variation in infection probability and conditions that enable parasites to spread.

4.1 | Hotspots of haemosporidian infection probability

Disease hotspots are not necessarily stable over time and can result from a high frequency of local spillover events from alternative hosts species. A key challenge in disease ecology is to identify the traits of alternative host species (phylogenetically related or not) that might make them competent reservoirs of pathogens and increase local prevalence (Jones et al., 2008). Here, we identified locations with the greatest infection risk of a vector-transmitted parasite and host traits that potentially increase local prevalence. Notably, our macroecological analyses of infection probability identified hotspots for haemosporidian parasites dispersed across different zoogeographical regions, some well outside the known biodiversity hotspots for most free-living organisms in the tropics. Unlike the pantropical distribution of human malaria hotspots, our map on global infection risk depicts hotspots for avian malaria in the Nearctic region and for *Parahaemoproteus*, a related avian malaria parasite, in the Palearctic region.

The longstanding and much-debated hypothesis that infection risk increases toward the equator (Allen et al., 2017; Jones et al., 2008; Stephens et al., 2016) was not supported in our synthesis for vector-transmitted parasites. Tropical regions support higher bird diversity in comparison to temperate regions (Duchêne & Cardillo, 2015); hence, haemosporidian parasites from tropical regions might have a higher diversity of available "niches" to exploit. Furthermore, the greater diversity of both avian and vector host species in the tropics could lead to increased diversity within individual hosts through lineage sharing and host shifting (Ricklefs et al., 2014). Although surprising, the observed absence of a latitudinal gradient in infection probability for the three most prevalent haemosporidian parasites matches what was found for lineage diversity at a global scale (Clark, 2018). Clark (2018) demonstrated that more diverse communities of haemosporidian parasites do not necessarily occur in tropical regions and suggested that macroevolutionary factors, such as a propensity of parasites to shift hosts locally or timing of diversification, are more important drivers of local parasite diversity. Whether haemosporidian prevalence is correlated with lineage diversity and the propensity of these parasites to shift among hosts at different rates across latitude has yet to be investigated.

Our findings suggests that haemosporidian infection probabilities emerge not only from general global drivers, such as climate, avian host richness and, possibly, migratory flyways that determine macroecological patterns of community assembly, but also from region-scale habitat and climate variation.

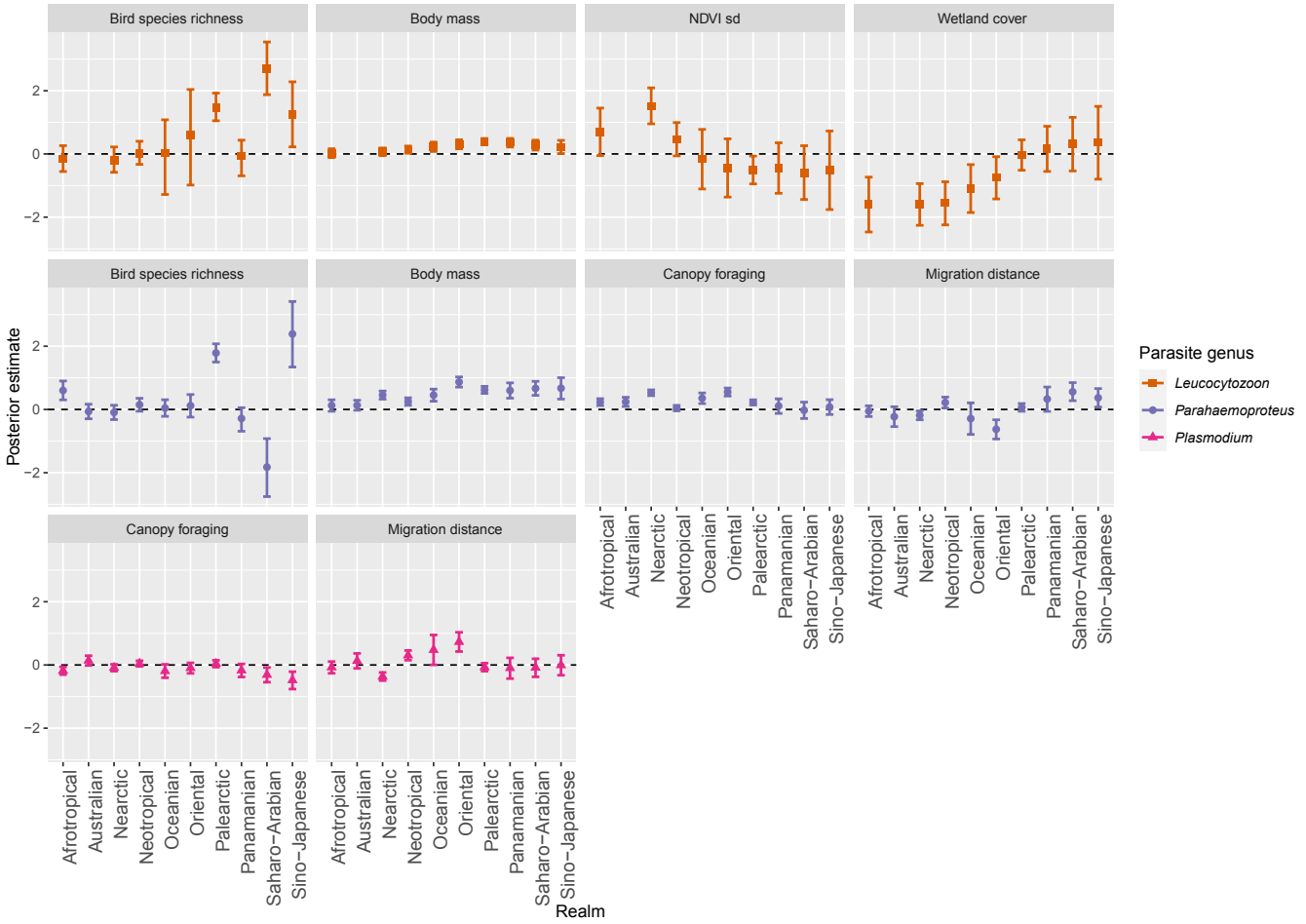

FIGURE 4 Varying coefficient estimates for variables with distinct effects across zoogeographical realms. The points depict the posterior mean of the regional-level effect estimates from a spatio-phylogenetic varying coefficient model, and vertical lines indicate 95% credible intervals. Abbreviation: NDVI = normalized difference vegetation index

4.2 | Spatial distribution of avian hosts overshadows phylogenetic signal in infection probability

Host phylogenetic position has been associated with variation in haemosporidian prevalence in avian communities and host clades (Barrow et al., 2019; Clark et al., 2020). Our study confirms these previous findings in terms of a strong phylogenetic signal in bird infection patterns with haemosporidian parasites. However, after accounting for both phylogeny and the location of the collected samples, we found considerable uncertainty in the phylogenetic signal at a global scale, indicating that strong phylogenetic signal inferred from a pooled sample (i.e., without taking spatial context/covariance into account) can be misleading. This uncertainty in phylogenetic signal can be especially pronounced at a large scale, in which distinct local host assemblages and samples are likely to include closely related individuals/species, which in turn might generate phylogenetic "pseudoreplicates" at the same locations.

Recognizing that avian haemosporidian prevalence is highly variable within and among host clades, and that it is spatially clustered, as we have shown here, provides a new framework for outlining region-specific predictions of infection risk by multi-host vector-transmitted parasites. This is particularly true for areas undergoing rapid climate change, anthropogenic landscape transformation and shifting host species assemblages. We believe that these patterns point to strong synergistic effects of host traits, landscape features and climatic filters driving infection patterns.

4.3 | Idiosyncratic drivers influence differences in global infection risk among haemosporidian genera

A central finding of our analysis was not only the identification of host traits driving infection probability for the three most prevalent haemosporidian genera, but also how their effects vary across zoogeographical realms. We showed that bird species which migrate longer distances are more likely to be infected by *Leucocytozoon* world-wide. Given that most long-distance migrants spend part of their annual cycle breeding in temperate regions, where black fly vectors are more diverse and abundant (Currie & Adler, 2008), there would be much higher potential for *Leucocytozoon* transmission in long-distance migrants than in resident tropical species. Migration distance influenced infection probability in opposing

directions across zoogeographical realms for the genera *Plasmodium* and *Parahaemoproteus* (see Results and Figure 4). These inverse trends in infection risk for vector-transmitted parasites in response to migration patterns warrant future research into the underlying mechanisms. Perhaps one of the interesting aspects to consider (if relevant data become available) could be the spatial context of parasite transmission, given the possibility that transmission in migratory birds might take place either in the wintering area or in the breeding area, but not necessarily in both. This is especially relevant given the multifaceted environmental changes that are likely to amplify the anticipated changes in bird migration and community assembly (Howard et al., 2020; Visser et al., 2009), hence the future infection risk with haemosporidian parasites.

Avian hosts inhabiting sites with a higher proportion of wetland cover and denser vegetation are at greater risk of *Plasmodium* infection. The probability of a bird being infected with *Parahaemoproteus* consistently increased with the proportion of forest cover, whereas it decreased in sites with higher proportions of wetland cover. When anthropogenic landscape changes create structures capable of collecting rainwater (e.g., artificial lakes, mining pits and rice fields) or change the course or flooding regime of rivers (e.g., dams and irrigation systems), such changes in water availability might increase avian malaria prevalence. Conversely, reduction in forest cover might diminish the local transmission of *Plasmodium* and *Parahaemoproteus* among avian hosts, but whether tree cover removal has a direct effect on vector capacity or parasite capacity to shift between hosts at large spatial scales has yet to be investigated.

We found that higher annual rainfall is associated with decreased prevalence of *Plasmodium* but increased prevalence of *Leucocytozoon*. Furthermore, *Leucocytozoon* infection risk decreases at sites with substantial rainfall during the driest months and sites with pronounced variation in rainfall throughout the year. The relationship between rainfall and prevalence suggests that the expected disruption of precipitation patterns owing to anthropogenic impacts on global climate (Wehner, 2020) might affect the prevalence of avian haemosporidian genera differentially in the future. The magnitude of this impact might vary by region owing to biogeographical structure in realized host specialization of haemosporidian lineages (Fecchio et al., 2019).

Elevation emerged as a predictor of *Plasmodium* and *Leucocytozoon* infection probability at a global scale, although with an opposite effect for each parasite genus. Our global dataset allowed us to determine the probability of a bird being infected across an elevation gradient ranging from sea level to *c*. 4,700 m a.s.l. across 10 zoogeographical realms, while simultaneously controlling for other climatic characteristics known to constrain vector development, activity and abundance (e.g., temperature and moisture level), in addition to parasite reproduction (temperature). This approach consistently demonstrated that the probability of an individual bird being infected with *Plasmodium* decreases with elevation across the globe, presumably because of constraints in parasite development and transmission by mosquito vectors at higher-elevation sites (Atkinson et al., 2014). Although we showed that *Leucocytozoon* infection probability increased with elevation, presumably owing to the affinity of black fly vectors for colder sites at high elevations, hotspots of *Leucocytozoon* prevalence were also scattered across lowland bird assemblages.

Generally, with the currently available empirical evidence being constrained mostly to vertebrate host infections, correlative approaches, as taken in the present study, allow limited insights into which species and interactions in the vertebrate–host–pathogen transmission cycle are most sensitive to environmental change, warranting future research into specific host–vector associations and host preferences. This is especially relevant for ectothermic arthropod vectors, for which host preferences and biting rates are sensitive to changes in climate and land use (Rose et al., 2020).

4.4 | Conclusions

Our spatio-phylogenetic analysis revealed that infection probability of haemosporidian parasites varies across zoogeographical realms and avian host clades owing to broad-scale and, possibly, also regional-scale variation in environmental conditions and host assemblages. A novel aspect of our study was to determine the drivers and hotspots of infection probability for each haemosporidian genus on a global scale rather than at population or community levels. Importantly, we found that infections in some low-prevalence realms were disproportionately concentrated in local hotspots, suggesting that regional-scale modifications in habitat and microclimate (and perhaps also the way host species assemble in response to strong habitat modification) might increase transmission at a regional scale. However, the synergistic effect of environmental drivers, such as precipitation, vegetation density and the proportion of forest and wetland cover, along with host community and assembly attributes on the prevalence of multi-host pathogens across realms underscores the importance of considering biogeographical patterns in host–parasite systems. At the same time, we suggest that the scattered distribution of local infection hotspots demonstrates that local processes, such as strong habitat modification and the resulting shifts in host species assemblages, can produce unexpected increases in parasite prevalence, emphasizing that disease outbreaks might be difficult to predict from generalizable large-scale patterns, such as climate, alone.

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AUTHOR CONTRIBUTIONS

A.F., K.W. and N.J.C. conceived the idea, designed the research, analysed the data and wrote the manuscript; the remaining authors contributed with avian tissue collection, sample screening, data curation, and funding reagents and field expeditions. All authors contributed critically to the manuscript drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The bird infection data used in this study are available as Supporting Information (Table S1). All data and R code are also deposited in the Zenodo repository at: https://zenodo.org/record/5182472

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BIOSKETCH

We have worked as a team to characterize local and regional datasets of avian haemosporidian assemblages for a global synthesis. This study represents the efforts of a broad range of researchers from different disciplines: Ecologists, entomologists, molecular biologists, ornithologists and parasitologists interested in factors that shape the prevalence and distribution of parasitic organisms in avian hosts world-wide.

SUPPORTING INFORMATION

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

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