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Parasite Abundance-Occupancy Relationships Across Biogeographic Regions: Joint Effects of Niche Breadth, Host Availability and Climate

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ABSTRACT

Aim: Changing biodiversity and environmental conditions may allow multi-host pathogens to spread among host species and affect prevalence. There are several widely acknowledged theories about mechanisms that may influence variation in pathogen prevalence, including the controversially debated dilution effect and abundance-occupancy relationship hypotheses. Here, we explore such abundance-occupancy relationships for unique lineages of three vector-borne avian blood parasite genera (the avian malaria parasite *Plasmodium* and the related haemosporidian parasites *Parahaemoproteus* and *Leucocytozoon*) across biogeographical regions.

Location: Nearctic-Neotropical and Palearctic-Afrotropical regions.

Methods: We compiled a cross-continental dataset of 17,116 bird individuals surveyed from 46 bird assemblages across the Nearctic-Neotropical and Palearctic-Afrotropical regions and explored relationships between local parasite lineage prevalence and host assemblage metrics in a Bayesian random regression framework.

Results: Most lineages from these three genera infected ≥5 host species and exhibited clear phylogenetic or functional host specificity. Lineage prevalence from all three genera increased with host range, but also with higher degrees of specialisation to phylogenetically or functionally related host species. Local avian community features were also found to be important drivers of prevalence. For example, bird species richness was positively correlated with lineage prevalence for *Plasmodium* and *Leucocytozoon*, whereas higher relative abundances of the main host species were associated with lower prevalence for *Plasmodium* and *Parahaemoproteus* but higher prevalence for *Leucocytozoon*.

Conclusions: Our results broadly support several of the leading hypotheses about mechanisms that influence pathogen prevalence, including the niche breadth hypothesis in that higher avian host species diversity and broader host range amplify prevalence through increasing ecological opportunities and the trade-off hypotheses in that specialisation among subsets of available host species may increase prevalence. Furthermore, the three studied avian haemosporidian genera exhibited different abundance-occupancy relationships across the major global climate gradients and in relation to host availability, emphasising that these relationships do not strictly follow common rules for vector-borne parasites with different life histories.

1 | Introduction

Uncovering mechanisms that enable pathogens to spread among multiple host species and maintain high prevalences is a goal that attracts considerable interest to mitigate the impact of infectious diseases. There have been a number of detrimental infectious disease outbreaks in humans and animals following pathogen 'spillover' events, where pathogens have successfully jumped from one host species to another (Jones et al. 2008; Plowright et al. 2021; Smith et al. 2014). There is widespread concern in the scientific community that both spillover events and high levels of pathogen prevalence will become increasingly more frequent. Habitat conversion, climate change and species invasions have dramatically changed the composition of animal communities throughout natural environments (Díaz et al. 2019). The resulting biotic homogenisation and novel contact opportunities are widely expected to increase transmission of pathogens within and among species (Carlson et al. 2022; Gibb et al. 2020; Mora et al. 2022; Wells and Clark 2019). Hence, if changing host community assemblages and dynamic host ranges sets the scene for multi-host pathogen spread, it is crucial to understand how community assembly and environmental conditions (i.e., the local pools of hosts and vectors enabling a multi-host pathogen to spread) and host specificity (i.e., the capacity of a parasite to infect a certain range of hosts from a given host assemblage) synergistically impact a pathogen's capacity to persist and proliferate in dynamic host species communities.

Empirical and theoretical studies suggest that changing biodiversity may be linked to either lower or higher parasite prevalence, especially for parasites infecting multiple hosts and/or being transmitted by vectors. The widely discussed dilution effect hypothesis, for example, posits that because competent vertebrate hosts may be relatively less abundant in species-rich communities, opportunities for vectors to successfully locate a particular host species and transmit pathogens to it are reduced, leading to reduced pathogen prevalence in communities with higher host biodiversity (Keesing et al. 2010). For ectoparasitic fleas infecting mammals, it has been also suggested that lower parasite abundance on auxiliary hosts than the main host species could mean that overall parasite fitness and prevalence decreases with increasing host species diversity (Khokhlova et al. 2012; Krasnov et al. 2004).

But alternative models suggest the opposite, that is, that higher host biodiversity will amplify infection risk due to increasing opportunity (Ferraguti et al. 2021; Roche et al. 2012; Wood et al. 2014). This includes the abundance-occupancy hypothesis, which suggests that locally abundant species tend to occupy greater proportions of available ecological niche space (Gaston et al. 2000). For parasites, whose niches are defined by the spectrum of hosts that they can infect, this could mean an amplifying effect of host biodiversity on infection risk due to increasing ecological opportunity and access to a broader spectrum of host species. For example, the prevalence of vector-transmitted haemosporidian parasites and West Nile virus in birds studied in Spain was not negatively associated with either host species richness or evenness; rather, a positive relationship between *Leucocytozoon* prevalence and host species richness was found (Ferraguti et al. 2021).

These two hypotheses about potential impacts of host biodiversity on parasite prevalence are not necessarily mutually exclusive. Rather, they can be harmonised by considering the host-specificity strategy of the parasites being studied. Presumably, broader host-specificity can involve ecological trade-offs if hosts provide distinct environments for the pathogen and broadening host range results in less optimal adaptation to the main host species (i.e., the single host species with the largest number of infections in a local host assemblage, which is often assumed to be of high competence). For example, parasites that specialise on a small number of host species are thought to be proficient at evading a host's immune defence because of continual selection pressures, leading to an evolutionarily stable strategy in situations where the focal host species comprises an abundant and stable source over time (Devictor, Julliard, and Jiguet 2008; Garamszegi 2006). In contrast, infecting a wider range of host species can increase the chance that a parasite will persist in unstable environments (Hellgren, Pérez-Tris, and Bensch 2009), as generalist species (i.e., those interacting with more diverse ecological partners in biotic interactions) are less likely to vanish from interaction networks in strongly variable communities (Chichorro, Juslén, and Cardoso 2019; Kaiser-Bunbury et al. 2010). This is because strong adaptation to one host may result in maladaptation to a broader range of species with varying immune responses (Elena, Agudelo-Romero, and Lalić 2009). However, empirical evidence to support these predictions is mixed.

Exploring these relationships in more depth is further complicated by the fact that host specificity can be considered in multiple ways. Various definitions have been proposed to incorporate both the ecological and phylogenetic relationships of potential host species (Poulin, Krasnov, and Mouillot 2011), whereas other work has argued that true specificity strategies are likely unobservable given the plasticity in locally realised host spectra arising from host species availability in variable environments (Wells and Clark 2019). It is therefore not surprising that various studies exploring abundance-occupancy relationships for avian haemosporidian parasites in different regions report mixed results in favour of either niche breadth or trade-off hypotheses

(Drovetski et al. 2014; Ellis et al. 2020; Ferraguti et al. 2021; Hellgren, Pérez-Tris, and Bensch 2009; Huang et al. 2018; Medeiros, Ellis, and Ricklefs 2014).

Avian haemosporidian parasites are a diverse group of vector-transmitted parasites (Clark, Clegg, and Lima 2014), which commonly infect blood cells of a wide range of avian hosts throughout temperate and tropical ecoregions (Fecchio et al. 2021). A variety of sympatric genera are transmitted by different dipteran vectors (i.e., *Haemoproteus* ~ louse flies, Hippoboscidae; *Parahaemoproteus* ~ biting midges, Ceratopogonidae; *Plasmodium* ~ mosquitos, Culicidae; *Leucocytozoon* ~ black flies, Simulidae) (Santiago-Alarcon, Palinauskas, and Schaefer 2012; Valkiūnas 2005). The development of these vectors depends on climate and on the presence of either running or standing water (Santiago-Alarcon, Palinauskas, and Schaefer 2012; Valkiūnas 2005). Therefore, the prevalence of these parasites is likely driven by climate as well as changes in habitat that alter host and vector community assembly and host-vector encounter rates (Ellis, Fecchio, and Ricklefs 2020; Fecchio et al. 2021).

In this study, we investigated whether the prevalence of haemosporidian parasites infecting wild birds varies in response to changing local host species richness, relative abundance of host species, measures of host specificity, and climate at macroecological scale.

Using an updated dataset of 17,116 bird individuals surveyed from 46 bird assemblages across the Nearctic-Neotropical and Palearctic-Afrotropical flyways, we build on previous research that reported positive associations of host range and bird species richness with haemosporidian infection risk at local to regional scales (Drovetski et al. 2014; Ellis et al. 2015, 2020; Ferraguti et al. 2021; Hellgren, Pérez-Tris, and Bensch 2009; Huang et al. 2018; Medeiros, Ellis, and Ricklefs 2014). We specifically aim to explore how the prevalence of unique lineages of haemosporidian parasites relates to attributes of local host species assemblages and species pools.

2 | Materials and Methods

2.1 | Host–Parasite Data

To examine the prevalence-host specificity relationships of unique haemosporidian lineages in bird assemblages, we systematically compiled field and molecular screening data from studies that reported individual-level haemosporidian infection status and parasite cytochrome-*b* (cyt-*b*) sequences in bird assemblages with reasonably large sample sizes (≥30 individuals and more than five host species surveyed at a single location) based on a dataset updated from our previous study (Fecchio et al. 2021). The assembled dataset included 36,896 individual birds with recorded presence-absence of infection with the haemosporidian genera *Plasmodium*, *Parahaemoproteus* and *Leucocytozoon* and all infections confirmed by molecular sequencing of a 477 bp nucleotide cyt-*b* fragment (Bensch et al. 2004). Sequence identities were verified with a local BLAST against the MalAvi database (Bensch, Hellgren, and Perez-Tris 2009). We then matched nucleotide sequences to respective amino acid sequences using the R package Biostrings (Pagès et al. 2024), reducing the number of 2070 unique nucleotide lineages to 1983 'functional lineages' based on amino acid sequences. We acknowledge that because we only have data for a fragment of the cyt-*b* sequence, these lineage assignments may not necessarily represent the true functional lineage or species diversity, but are assumed to be the best possible representation of data currently available, amid the recent onset of genomic sequencing of haemosporidians (Videvall 2019).

We obtained data on bird species' phylogenetic relationships from the open-source Birdtree.org phylogenetic supertree (Jetz et al. 2012), using a consensus tree from a random selection of 100 possible tree topologies from the supertree's 'Ericsson All Species' Bayesian posterior distribution (available at Birdtree.org/subsets/). Bird species names from field data were revised according to the taxonomy used in these trees. Phylogenetic distances among pairs of bird species were calculated as mean pairwise distance across the selected trees.

For all bird species, we obtained data on their body mass and the proportional use of 10 diet categories and seven foraging habitats from the EltonTraits v1.0 database (Wilman et al. 2014). We quantified pairwise functional distances using Gower's distance matrix (Gower 1971; Pavoine et al. 2009). For analysis, phylogenetic and functional distance matrices were scaled (dividing by the maximum for each matrix).

To analyse the prevalence of parasite lineages within local assemblages in context of host specificity, we focused on sufficiently well-sampled lineages that allowed reasonable estimates of prevalence and host specificity in a given local context. For this, we filtered the cleaned data and selected only those data for lineages that have been reported infecting ≥8 host individuals in local assemblages with a total ≥10 host individuals and ≥5 host species sampled (a sample size of 10 translates to an ~80% probability of detecting a parasite with a true prevalence of 15%, and we assume a record of eight infections within a community of ≥5 host species to provide reasonable insights into the variation in host specificity of different lineages). This resulted in a dataset of 144 unique lineage-location records from 46 different locations and 17,116 sampled bird individuals, of which 2830 individuals were recorded as infected. Locations were in the zoogeographical regions of the Nearctic, Palearctic, Neotropics and Afrotropics (a single lineage from the Saudi Arabian region was included in the Afrotropics group for analysis) (Tables S1, S2, Figure S1). The number of bird species sampled at the different locations ranged from 6 to 115 (mean 51 ± SD 22), and the number of locally recorded and infected host species for the different lineages ranged from 1 to 21 (mean 5 ± SD 4) (Figure S2), comprising 1% to 69% of the locally sampled bird species. According to host range estimates (Chao-1 species richness estimates based on the frequency different bird species were recorded as host), the true local host ranges were likely larger than the number of recorded host species (species recorded to be infected by a lineage) (Figure S3), whereas the number of recorded host species was not correlated with the respective sample sizes (Spearman's $r = 0.05$) and the proportion of host individuals in a sample was only weakly correlated with sample sizes (Spearman's $r = 0.31$); we therefore assumed that sample sizes were sufficient for inference.

2.2 | Host Assemblage and Environmental Metrics

Within a local context, each haemosporidian lineage was recorded from a number of infected individuals that comprised a subset of the sampled bird individuals, which, in turn, can be considered a random sample of the local bird assemblage. To summarise key aspects of the infected and sampled species assemblage as proxies of aspects of host specificity and host availability, we computed the following metrics:

(1) *Phylogenetic host specificity* (*B.phyl*) – host specificity calculated as a model-based estimate of the relative difference in phylogenetic distances among all pairs of infected versus sampled bird individuals. We regressed all possible pairwise phylogenetic distances δ against the binary categorical classifier X of whether such distance was computed for any pair of infected individuals versus any pair of sampled and uninfected individuals (i.e., a binary indicator variable, where '1' indicates the pair of sampled bird individuals that is infected; '0' indicates that they are uninfected) in a linear model, such that:

$$\delta \sim \mathcal{N}\left(\mu + \beta_{\text{phyl}} X, \sigma^2\right) \quad (1)$$

$\mathcal{N}(\mu, \sigma 2)$ represents the Gaussian distributions with mean μ and variance σ^2 of the linear model, and the coefficient estimate β_{phyl} represents the difference between observed and potential host distances. Values of $\beta_{\text{phyl}} < 0$ indicate smaller distances between infected individuals than those in the entire sample and therefore stronger host specificity, a value of > 0 suggests that a lineage infects more distantly related hosts than expected (Wells, Gibson, and Clark 2019). Model-based β_{phyl} estimates of means and SDs computed with the glm() function in R (R Core Team 2023) independently for each lineage are considered for defining the uncertainty and priors in our Bayesian random regression to compute the possible relationship between lineage prevalence and specificity (refer to statistical analysis). Host diversity calculated as Rao's quadratic entropy (a measure of within and among community diversity of infected versus all sampled individuals from different bird species that takes phylogenetic relationships into account) correlated with *B.phyl* (Spearman $r < 0.7$) and was therefore not considered in analyses.

(2) *Functional host specificity* (*B.func*) – host specificity calculated as a model-based estimate of the relative difference in functional distances among all pairs of infected versus sampled bird individuals, using the same concept as for computing phylogenetic specificity described above.

(3) *Main host availability* ($mainH_{avail}$) – the availability of known suitable main host individuals within a local assemblage. This metric is a probabilistic estimate of the proportion of main host individuals based on the number of individuals from the main host species (i.e., the single host species for which the largest number of infected birds were recorded within a local assemblage) and the total number of individuals sampled from a local assemblage. We used a multinomial model linked to a Dirichlet prior to model the proportion of available host individuals belonging to the main host as described below.

(4) *Host range* (*HR.Chao*) – we computed host range as the Chao species richness estimate based on the locally sampled number of infected bird individuals from different species; host range estimates were computed with the package iNEXT (Hsieh, Ma, and Chao 2016).

(5) *Bird species richness* (*SpRich*)–We measured local bird species richness of terrestrial birds based on a map that summarises species distributions from BirdLife International range maps (https://biodiversitymapping.org/; refer also to Jenkins, Pimm, and Joppa 2013). This measure counts all terrestrial birds (potentially available as host) regardless of whether they have been sampled or not.

To account for key climatic differences across locations that are likely to affect many aspects of host (and vector) species, we selected six climate variables from the WorldClim database of gridded climate data at a 0.01° resolution (Fick and Hijmans 2017; http://world clim.org/version2) (bio1: annual mean temperature, bio4: temperature seasonality, bio7: temperature annual range, bio12: annual precipitation, bio14: precipitation of driest month, bio15: precipitation seasonality based on coefficient of variation). We used principal component analysis (PCA) to generate two principal components from the climate variables. The first component ('climate-PC1') represented mainly higher and seasonally more stable temperatures and more rain with increasing factor values. The second ('climate-PC2') represented mainly stronger seasonality in rain and more extreme dry months with increasing factor values. PC1 explained 51% and PC2 explained 35% of the variation in climate variables (Figure S4).

2.3 | Statistical Analysis

With the aim to explore possible variation in the prevalence of different haemosporidian lineages in context of the realised host specificity and local species richness, we used a Bayesian random regression framework that allowed us to accommodate possible uncertainty in infection and host assemblage metrics arising from incomplete and heterogeneous sampling effort.

We modelled the local overall prevalence $\psi_{all}(i)$ of each unique lineage-location combination (indexed as i) as the proportion of host individuals infected y versus the total number of individuals sampled from known host species w in a local assemblage (here, we assumed the known range of host species to better represent the suitable host community, that is, the fundamental niche, than all sampled birds, since very few lineages are known to spread among a large spectra of bird species (Fecchio et al. 2019)):

$$y(i) \sim Binomial\left[w(i)\, \psi_{all}(i)\right] \quad (2)$$

We modelled variation in $\psi_{all}(i)$ on a logit-scale to explore possible relationships with host assemblage metrics as:

$$logit[\psi(i)] = \pi + \Lambda Z \quad (3)$$

where π is the intercept, Z is a matrix of the five host assemblage and two PCA climate metrics described above for each lineage i, and Λ is a vector of coefficient estimates for each covariate denoted in the matrix Z.

Fitting this model as a Bayesian hierarchical and random linear model, we took advantage of the iterative Markov Chain Monte Carlo (MCMC) sampling for posterior estimation in that for each iteration, we sampled host specificity metrics (*B.phyl*, *B.func*) as random covariates based on the mean and SD (η, υ) of their computed β values for each lineage-assemblage combination j (refer to metric description above) such as:

$$\beta(\mathrm{j}) \sim Normal\left(\eta_{\beta}(j), \upsilon_{\beta}(j)\right) \quad (4)$$

Likewise, main host availability (*mainH.avail*) was iteratively estimated as a random covariate based on the proportions of sampled individuals that belonged to the main host species within a local assemblage. For this, we used a multinomial model linked to a Dirichlet prior to account for the fact that the estimated proportion of individuals θ_x in the three groups x of 'main host', 'marginal host' (any other host species than the main host species) and 'other' (species not recorded as host) should sum to 1. The local counts of individuals Y_x in each of these groups were thus modelled as:

$$Y(x) \sim Multinomial\left(\theta_x\right) \quad (5)$$

and

$$\theta_x \sim Dirichlet\left(\mu_x\right) \quad (6)$$

The scaled vectors of covariates (i.e., Z) were then used in the linear predictor of equation 3. We completed the hierarchical model with Gaussian prior specifications for the Λ coefficient estimates as

$$\mathrm{mu}_{\Lambda} \sim Normal(0, 1) \quad (7)$$

that were deemed suitable following prior predictive checks as part of a Bayesian workflow (iterative processes of model construction, simulation of prior fake data and model/prior adjustment, model fit and posterior predictive checks, checking for alternatives). We also tested alternative *Student.t* ($\nu = 3$, $\mu = 0$, $\sigma = 1$), and regularised horseshoe (RHS) priors (Piironen and Vehtari 2017), which performed less well in terms of model convergence and were thus not considered in the final analysis. We estimated the Brier score as $\mathrm{BS} = \frac{1}{N}\sum_{i=1}^{N}(\mathrm{y(i)} - \varphi(i))^2$ as a measure accuracy of probabilistic predictions of the observed infection status of birds (Gneiting and Raftery 2007), which we computed separately for lineage-location combinations from the three different haemosporidian genera. Parameters were estimated using the Hamiltonian Monte Carlo sampler in the Stan software (Carpenter et al. 2017), using the default sampling option of drawing 1000 posterior after an equal amount of burn-in iterations. Visual checks confirmed that posterior chains converged for the majority of parameters. All data processing and analyses were conducted in R version 4.2 (R Core Team 2023).

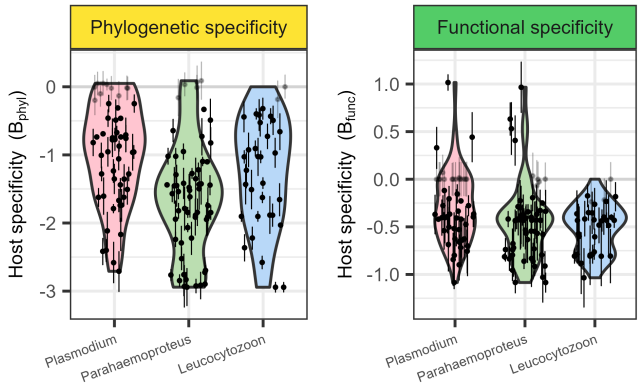

FIGURE 1 | Variation in phylogenetic (*B.phyl*, left panel) and functional (*B.func*, right panel) host specificity metrics for haemosporidian lineages from the three different genera *Plasmodium*, *Parahaemoproteus* and *Leucocytozoon*. Points and error bars represent posterior mean and 90% credible interval estimates for each unique lineage-assemblage combination (with those overlapping zero in transparent colour), and violin illustrate the distribution of the mean values.

3 | Results

3.1 | Strong Phylogenetic and Functional Host Specificity Amid Large Host Ranges

Our dataset included 144 lineage-assemblage combinations, namely 52 for *Plasmodium*, 59 for *Parahaemoproteus* and 33 for *Leucocytozoon*.

Most haemosporidian lineages ($n = 127$ out of 144 lineage-assemblage combinations) from the three genera (*Plasmodium*, *Parahaemoproteus* and *Leucocytozoon*) exhibited clear phylogenetic host specificity (i.e., upper CI estimates of *B.phyl* < 0) and also high functional specificity (for $n = 110$, upper CI estimates of *B.func* < 0; Figure 1), supporting the trade-off hypotheses in that specialisation among subsets of available host species may increase prevalence. The extent of phylogenetic and functional host specificity varied among lineages (as evidenced by non-overlapping CIs, Figure 1), but there was no evidence that the range or distribution of host specificity measures differed among the three genera, with the exception of only a few lineages of *Plasmodium* ($n = 3$) and *Parahaemoproteus* ($n = 4$), which were found on functionally more distinct host species than expected by chance (i.e., *B.func* > 0; Figure 1). Despite clear patterns of phylogenetic and functional host specificity, multi-host relationships were the rule rather than the exception, with local host ranges of ≥ 5 species reported for 40 out of 143 lineage-assemblage combinations and only 29 with a single host species observed.

3.2 | Host Range, Host Specificity, Bird Species Richness and Climate May Synergistically Drive Haemosporidian Prevalence

For all three haemosporidian genera, lineage prevalence increased with increasing host range ($\Lambda_{HR.Chao} > 0$) and also

either increasing phylogenetic ($\Lambda_{B.phyl} < 0$, *Plasmodium* and *Leucocytozoon*) or functional host specificity ($\Lambda_{B.func} < 0$, *Plasmodium* and *Parahaemoproteus*) (Figure 2). Within avian host communities, larger proportions of individuals of the main host species in local assemblages correlated with lower prevalence of *Plasmodium* and *Parahaemoproteus* lineages ($\Lambda_{mainH.avail} < 0$) but with higher prevalence of *Leucocytozoon* lineages ($\Lambda_{mainH.avail} > 0$; Figures 2 and 3). For *Plasmodium* and *Leucocytozoon*, the prevalence increased further with higher local bird species richness ($\Lambda_{SpRich} > 0$; Figures 2 and 4), lending additional support to the niche breadth hypothesis in that higher avian host species diversity and broader host range amplifies prevalence through increasing ecological opportunities.

The prevalence of *Plasmodium* and *Parahaemoproteus* lineages increased with higher and less fluctuating temperatures and more rain ($\Lambda_{climate\text{-}PC1} > 0$; Figure 2), whereas the prevalence of *Leucocytozoon* decreased across this climate gradient ($\Lambda_{climate\text{-}PC1} < 0$). The prevalence of *Parahaemoproteus* and *Leucocytozoon* lineages increased with stronger seasonality in rain and more extreme dry months ($\Lambda_{climate\text{-}PC2} > 0$).

For *Plasmodium*, the average local prevalence of lineages was 9% (CI: 8%–9%) with local prevalences > 30% recorded in the Neotropical and Afrotropical regions (8 out of 51 lineage-location combinations according to lower CI of estimates) at locations with moderate to high bird species richness (Figure 4). For *Parahaemoproteus*, the average local prevalence of lineages was 5% (CI: 5%–6%) with local prevalences > 30% recorded in the Nearctic and Neotropical regions (7 out of 59 lineage-location combinations according to lower CI of estimates), comprising sites with relatively low to moderate bird species richness (Figure 4). For *Leucocytozoon*, the average local prevalence of lineages was 7% (CI: 2%–20%) with local prevalences > 20% from three locations in the Nearctic, Palearctic and Afrotropic regions.

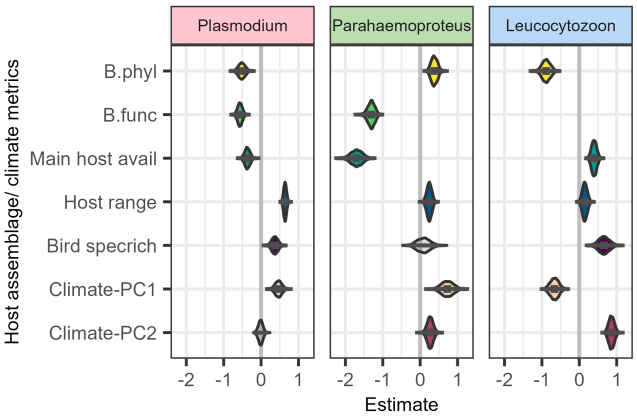

FIGURE 2 | Coefficient estimates for the relative effects of different host assemblage metrics on the prevalence of haemosporidian lineages of the three genera *Plasmodium*, *Parahaemoproteus* and *Leucocytozoon*. The host assemblage metrics are *B.phyl*: Phylogenetic specificity, *B.func*: Functional specificity (not included as covariate for *Leucocytozoon* due to poor convergence), *Main host avail*: Main host availability, *Host range*—host range based on Chao species richness estimate, Bird *specrich*: Bird species richness. Violins represent the posterior sample distribution, posterior means are shown as black squares. Posterior estimates that overlap zero within the 90% confidence interval (interpreted as no evidence of any effect) are plotted in transparent colour.

4 | Discussion

Our results lend support to both the niche breadth hypothesis and the trade-off hypothesis to explain abundance-occupancy relationships for multi-host parasites across biogeographical regions. Higher avian host species diversity and broader host range amplify prevalence through increasing ecological opportunities, whereas specialisation among subsets of available host species may increase prevalence.

At the same time, the three different haemosporidian genera exhibited different relationships to major global climate gradients and host availability, emphasising that abundance-occupancy relationships across biogeographical regions do not strictly follow common rules for parasites with different life histories. Collectively, our findings echo those studies previously suggesting that multi-host–parasite interactions are driven by ecological opportunities arising from host assembly and environmental conditions and the life history strategies of parasites (e.g., Clark et al. 2018; Ellis et al. 2020; Ferraguti et al. 2021; Hellgren, Pérez-Tris, and Bensch 2009).

4.1 | Diverse Host Assemblages and Wider Niche Increase Infection Rates

The local prevalences of lineages for all three genera of avian haemosporidian parasites increased with host range at the studied macroecological scale. We also found a clear increase in the local lineage prevalence of *Plasmodium* and *Leucocytozoon* with increasing bird species richness across bioregions. Together, these findings offer strong support that avian haemosporidian parasites benefit from more diverse avian host assemblages that appear to amplify rather than dilute infection risk. Although these patterns clearly contradict the dilution effect hypothesis (Keesing, Holt, and Ostfeld 2006; LoGiudice et al. 2003), they reinforce regional-scale studies that have suggested that increasing host species richness amplifies infection risk with *Leucocytozoon* (Ferraguti et al. 2021). The positive role of wider niche breadth on increased infection risk is also supported by the increasing prevalence of *Plasmodium* and *Parahaemoproteus* with lower relative densities of the main host species, suggesting that a more balanced mixture of different host species with sufficient levels of competence to maintain transmission chains appears to increase infection risk. This supports findings of previous studies that increasing host species richness may increase pathogen prevalence (Searle et al. 2016), especially if the addition of species with lower competence does not dilute but adds to the overall transmission rate due to an overall increase in the density of host individuals capable of maintaining transmission chains (Johnson et al. 2024).

4.2 | Host Specificity and Selection of Hosts Translates Into Higher Prevalence

We found that higher host specificity (the specialisation of a lineage to subsets of phylogenetically or functionally more closely

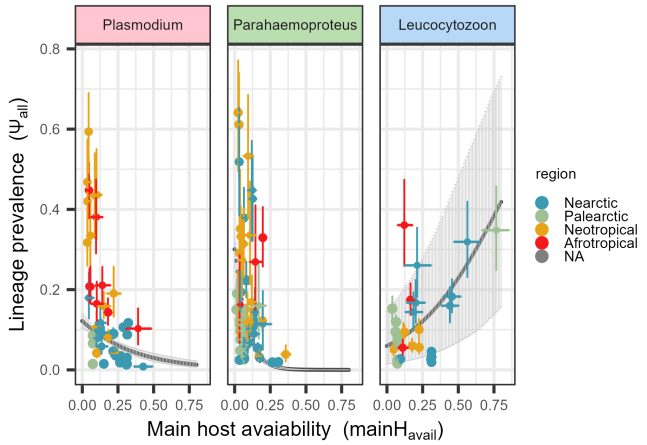

FIGURE 3 | Relationship between the estimated lineage prevalence within all locally recorded host species and main host availability (mainH.avail) for the three different haemosporidian genera *Plasmodium*, *Parahaemoproteus* and *Leucocytozoon*. Coloured points are posterior estimates and error bars are 95% CIs, coloured according to the four zoogeographical regions in which data were collected. Grey points and lines are the derived posterior predictions from the effect of main host availability on lineage prevalence within the model framework of the study.

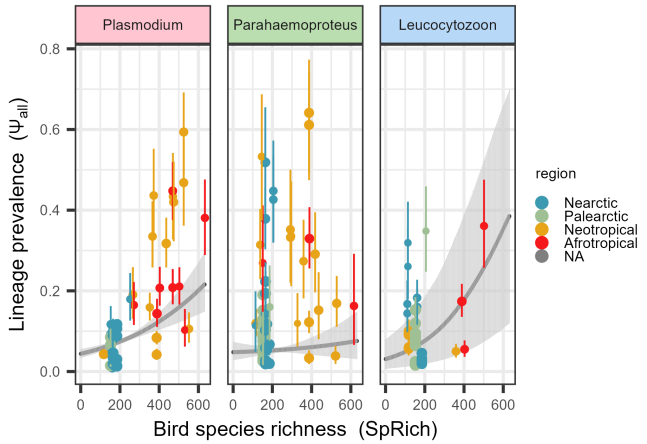

FIGURE 4 | Relationship between the estimated lineage prevalence within all locally recorded host species and regional bird species richness for the three different haemosporidian genera *Plasmodium*, *Parahaemoproteus* and *Leucocytozoon*. Coloured points are posterior estimates and error bars are 95% CIs, coloured according to the four zoogeographical regions in which data were collected. Grey points and lines are the derived posterior predictions from the effect of species richness on lineage prevalence within the model framework of the study.

related host species than expected by chance) was mostly positively associated with higher haemosporidian lineage prevalence in local assemblages in addition to the positive effect of niche breadth.

Our results therefore support previous findings that some common parasites are those better adapted to specific subsets of potential host species pools, possibly those host species that have been more frequently encountered during a parasite's evolutionary history (Huang et al. 2018). Given that host switches (rather than co-speciation) have played an important role in the radiation of haemosporidian parasites (Alcala et al. 2017; Ricklefs et al. 2014), we assume that strong signals of phylogenetic host specificity can be linked to host switches happening mostly among phylogenetically related bird species (Ellis et al. 2020).

The strong phylogenetic signals in host specificity together with increasing prevalence of phylogenetically or functionally specialised lineages suggest that some constraints in avian host species selection may optimise transmission rates and increase prevalence, amid the prominent role that has been suggested for blood-feeding arthropod vectors (that serve as definite hosts for haemosporidians) to play in the distribution of haemosporidian parasites (Ishtiaq et al. 2010). The immunological system of the vertebrate avian hosts is considered more complex compared to those of the invertebrate vectors, likely encompassing a greater diversity of organs, genes, cells and proteins involved in the defensive response to parasite invasion and proliferations (Iwama and Moran 2023). One could therefore expect avian host defence mechanisms to play a prominent role in shaping the host specificity of parasites. Such a hypothesis is for example supported by studies that report similar feeding patterns of the parasite-transmitting vectors on different host species amid signals of phylogenetic host specificity in the distribution of haemosporidians among avian species (Medeiros, Hamer, and Ricklefs 2013). However, vector-parasite interactions in avian haemosporidian systems remain to the best of our knowledge too insufficiently studied to understand the constraining mechanism underlying haemosporidian niche breadth in terms of vertebrate versus arthropod host adaptations and the possible outcome of the interplay of vectors and hosts in supporting high parasite prevalence in regional assemblages.

Nevertheless, our results of increased parasite prevalence with higher phylogenetic or functional host specificity suggest that specialisation to a subset of host species with similar traits is likely beneficial to the parasites in terms of transmission and infection rates, whether or not specialisation results from any selective constraints on host adaptations.

However, an opposing relationship (higher prevalence of lineages infecting more distantly related host species than expected by chance) was observed between the phylogenetic host specificity and the prevalence of *Parahaemoproteus*, for which a plausible explanation awaits, future research.

Overall, the strong relationship of parasite prevalence with features of community assemblages and the host specificity of parasites highlights the importance of considering host abundance and community composition when assessing or forecasting the infection risk of hosts parasitised by multi-host parasites.

4.3 | Climate Gradients Correlate With Lineage Prevalence

Changing environmental conditions can variably affect the distribution and interactions of parasites and their hosts, whereby different parasites are expected to uniquely respond to global change (Fecchio et al. 2021; Mordecai et al. 2020; Ortega-Guzmán et al. 2022; Wood et al. 2023), while at the

same time, this alters features of entire host–parasite interaction networks (de Angeli Dutra and Poulin 2024). To account for such environmental effects in addition to features of the host assemblage that unique parasite lineages encounter, we considered climate gradients across study sites as two principal component variables in our study as potential drivers of infection risk.

We found an increase in lineage prevalence of *Plasmodium* and *Parahaemoproteus* with higher and seasonally more stable temperatures (positive association with climate-PC1) but an opposing trend for *Leucocytozoon* (Figure 2), supporting the notion that these parasites respond differently to climate or biogeographical differences, with *Plasmodium* and *Parahaemoproteus* thriving mostly in warmer climates and *Leucocytozoon* thriving in colder conditions and at higher latitudes (Fecchio et al. 2020, 2023). These relationships could be also linked to the ecology of the different dipteran vectors; the larval development of black flies (transmitting *Leucocytozoon*), for example, appears to be less constrained by low temperatures than those of mosquitos (transmitting *Plasmodium*) (Beck-Johnson et al. 2013; Bernotiene and Bartkeviciene 2013).

Although we found a positive association between the local prevalence of unique *Leucocytozoon* lineages and the seasonality in rainfall and more extreme dry months (i.e., positive correlation with our climate-PC2 variable, Figure 2) we previously found a negative relationship with the overall regional prevalence of *Leucocytozoon* and rainfall seasonality (Fecchio et al. 2021). Possibly, these contradicting associations highlight that the overall local prevalence (i.e., the overall prevalence of a parasite genus as an aggregated measure regardless of lineage/species identity), which may strongly depend on the local diversity of parasite lineages, is not necessarily a good representation of the local prevalence of unique haemosporidian lineages, each of which may have adapted to different subsets of host species. Presumably, the larger the variation in the local prevalence of different lineages due to lineage-specific variation in the suitability of underlying conditions, the weaker the link between lineage specificity and overall prevalence. The niche overlap (i.e., the sharing of host species) of different haemosporidian lineages may vary across regions (de Angeli Dutra and Poulin 2024), and therefore, we expect the strong impact of host assemblage metrics on the prevalence of different lineages to overshadow the joint response to regional drivers such as climate conditions.

4.4 | Study Implications and Limitations

The synergistic effects of lineage-specific host assemblage metrics and regional environmental conditions have important implications for predicting the future spread of avian haemosporidian parasites in a time of global change, given that environmental conditions alone appear to be insufficient in predicting infection risks if the underlying abundance-occupancy relationships for local lineages are not understood. The 'winner and loser' concept implies that changes in the availability of host species may alter the population size and stability of multi-host parasites, depending on the continued availability of suitable hosts that might themselves be sensitive to global change (Lafferty 2012). Our findings underscore that for haemosporidian parasites, lineage-specific features such as niche breadth, key host availability, and host specificity may facilitate the prediction of infection risk, while evaluation of the forecasting capacity or the actual impact of these parasites on host communities awaits future research.

Although our study provides quantitative evidence for the synergistic effects of niche breadth, host availability and host specificity on parasite prevalence, the currently available data are limited in that the large lineage diversity of haemosporidian parasites reported to date is based on a short sequence of haemosporidian mitochondrial cytochrome-*b* gene with uncertainty as to how this diversity translates into distinct species (Pacheco and Escalante 2023). Furthermore, although the statistical models used in our study attempt to account for sampling bias in terms of unequal sample size and the associated uncertainty in parameter estimates (as part of the random regression approach, refer to Materials and Methods section), these models are not able to account for sample bias arising from the data collection process such as unequal chances of capturing different avian host species.

Finally, the strongly idiosyncratic abundance-occupancy relationships observed for different haemosporidian parasite genera require future research to elucidate whether these haemosporidian genera differ fundamentally in their interactions with their host or whether their different vector species are an important missing link in understanding haemosporidian abundance-occupancy relationships. Diverse vertebrate communities may sustain higher vector abundance through more feeding opportunities and could increase pathogen transmission rates (Randolph and Dobson 2012), whereas mosquito densities and feeding patterns are not solely limited by host availability but, rather, other environmental features such as climate and habitat features (Ferraguti et al. 2023; O'Rorke et al. 2024; Roche et al. 2013). Such plasticity in feeding patterns of vectors might fundamentally impact the exposure of different host species to different haemosporidian lineages, but there is to date a lack of understanding of the roles of vector diversity, feeding patterns and host competence for the distribution of haemosporidian parasites infecting birds. We therefore anticipate that our study provides insights into abundance-occupancy patterns, while we acknowledge that understanding the underlying mechanism in more detail and the role of vertebrate hosts versus arthropod vectors in driving host specificity and the prevalence of these parasites requires more empirical evidence.

5 | Conclusion

In conclusion, our work shows that abundance-occupancy relationships of the studied haemosporidian parasites are jointly driven by non-mutually exclusive mechanisms of niche breadth, host availability and diversity along with climate conditions. We therefore suggest that benefiting from ecological opportunity and generalist strategies does not necessarily contradict trade-off principles that may benefit parasites that have specialised to subsets of host species from regional species pools. Finding idiosyncratic patterns in the abundance-occupancy relationships of different haemosporidian parasites with limited knowledge about the underlying vectors, we anticipate that a better

understanding of these relationships requires future research on the interplay of the diversity and competence of all species involved in the underlying host-vector-parasite networks.

Author Contributions

Konstans Wells: Conceptualisation (lead); data curation (supporting); formal analysis (lead); writing – original draft (lead); writing – review and editing (equal). **Alan Fecchio**: Data curation (equal); review and editing (equal). **Jeffrey A. Bell**: Data curation (equal); review and editing (equal). **Nicholas J. Clark**: Formal analysis (supporting); data curation (supporting); writing – review and editing (equal). **All other authors**: Avian tissue collection, parasite screening, funding reagents and field expeditions (equal); writing – review and editing (equal).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and computer code used for data compilation/manipulation and analysis are openly available from the Dryad database (https://doi.org/10.5061/dryad.gmsbcc2xg), and the GitHub repository https://github.com/konswells1/Haemosporidian-abundance-occupancy-relationships/tree/main, https://github.com/konswells1/Haemosporidian-abundance-occupancy-relationships.

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Supporting Information

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