

# Network specificity decreases community stability and competition among avian haemosporidian parasites and their hosts

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## Abstract

**Aim:** Parasites play a fundamental role in shaping ecological communities and influencing trophic interactions. Understanding the factors that drive parasite impacts on community structure and stability (i.e. resilience to disturbances) is crucial for predicting disease dynamics and implementing effective conservation strategies. In this study, using avian malaria and malaria-like parasites as a model system, we investigated the relationship between specificity, community stability and parasite vulnerability and their association with host diversity and climate.

**Location:** Global.

**Time period:** 2009–2023.

**Major taxa studied:** Avian malaria and malaria-like parasites.

**Methods:** By compiling occurrence data from a global avian haemosporidian parasite database (MalAvi), we constructed a comprehensive dataset encompassing 60 communities. We utilized a phylogenetic model approach to predict missing host–parasite interactions, enhancing the accuracy of our analyses. Network analyses based on bipartite interactions provided measures of network specificity, stability, modularity, parasite competition and vulnerability to extinction.

**Results:** We found that the high network specificity reduced community stability and decreased competition among parasites. Furthermore, we found that parasite vulnerability decreased with increasing community stability, highlighting the importance of community stability in host–parasite interactions for long-term parasite persistence. When exploring the influence of local host diversity and climate conditions on host–parasite community stability, we demonstrated that increasing host biodiversity and precipitation reduces parasite competition. Conversely, higher temperature raises competition among parasites.

**Conclusion:** These findings provide valuable insights into the mechanisms underlying parasite impacts on communities and the interplay between specificity, community stability and environmental factors. Further, we reveal the role of climate in shaping host–parasite interactions. By unravelling the complexities of parasite-mediated interactions, our research substantially improves the current knowledge of the importance of specificity as a modulator of interactions in bipartite networks.

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## KEYWORDS

community stability, modularity, network structure, parasite competition, parasite extinction, specificity

## 1 | INTRODUCTION

The association between parasites and their hosts impacts community dynamics and shapes ecosystems' trophic structure and energy flow, affecting local biodiversity and overall stability (Dunne et al., 2013; Lafferty et al., 2008). For this reason, ecologists have directed much effort at the effects of parasites on species interactions among several host–parasite systems worldwide (Friesen et al., 2019; Harvey et al., 2011; Médoc & Beisel, 2011; Poulin, 1999). For instance, parasites are known to increase predation rates (Hasik et al., 2022), reduce fitness (Hasik & Siepielski, 2022) and modulate intra and interspecific competition (Hudson & Greeman, 1998; Schall, 1992). Nonetheless, specific parasites can have different effects in a community depending on several factors, such as their prevalence and life cycle. Tropically transmitted parasites, for example, have the greatest influence on host predation when compared to other parasites (Hasik et al., 2022). Despite the wide variety of effects parasites may exert on biodiversity, little is known about the driving factors behind their impact on different ecological communities.

Host specificity (i.e. the spectrum of host species in which a parasite can fully develop) is a key property of parasites: it determines their ability to switch to novel hosts and, consequently, their odds of colonizing new communities and expanding their geographical distribution (de Angeli Dutra et al., 2021; Krasnov et al., 2005). For this reason, the cascading effects of parasites can be modulated by their host specificity to determine how they impact community structure and the complexity of networks of interactions among species (Dunne et al., 2013; Lafferty et al., 2008). Distinct parasite species have variable levels of prevalence, pathogenicity and ecological significance within a community (Lipsitch & Moxon, 1997; Valkiūnas et al., 2022). For instance, among disease-causing haemosporidian parasites, the generalist parasite *Plasmodium relictum* is the main agent of avian malaria infections worldwide and has been associated with the decline and extinction of several bird populations and species globally (Schoener et al., 2014; Van Riper III et al., 1986). On the other hand, specialist parasites benefit from host-specific adaptations that increase their performance within a single or a small subset of hosts (Pinheiro et al., 2019), enabling these parasites to reach higher local abundance (de Angeli Dutra et al., 2021).

Although resource specialization benefits parasites by increasing their performance among their small set of hosts, highly specialized parasites are subject to multiple trade-offs (Pinheiro et al., 2019). For instance, narrow host ranges (i.e. high parasite specificity) increase the odds of extinction as parasites become too reliant on a single or few host species (Colwell et al., 2012). Distinct levels of host specificity lead to characteristic interactions among host and parasite species, shaping host–parasite community structure and complexity (Fenton & Brockhurst, 2008; Galen et al., 2022; Pinheiro et al., 2016). The degree of specialization of host–parasite networks is dependent

on, and highly correlated with, the level of specialization of parasites towards their hosts (Blüthgen et al., 2006). Increasing host specificity should lead to increasing network partitioning and reduction in resource utilization. For this reason, network specificity should affect parasite competition, and vulnerability to extinction and shape community stability by affecting network structure (e.g. increase in network modularity) (Figure 1, Box 1).

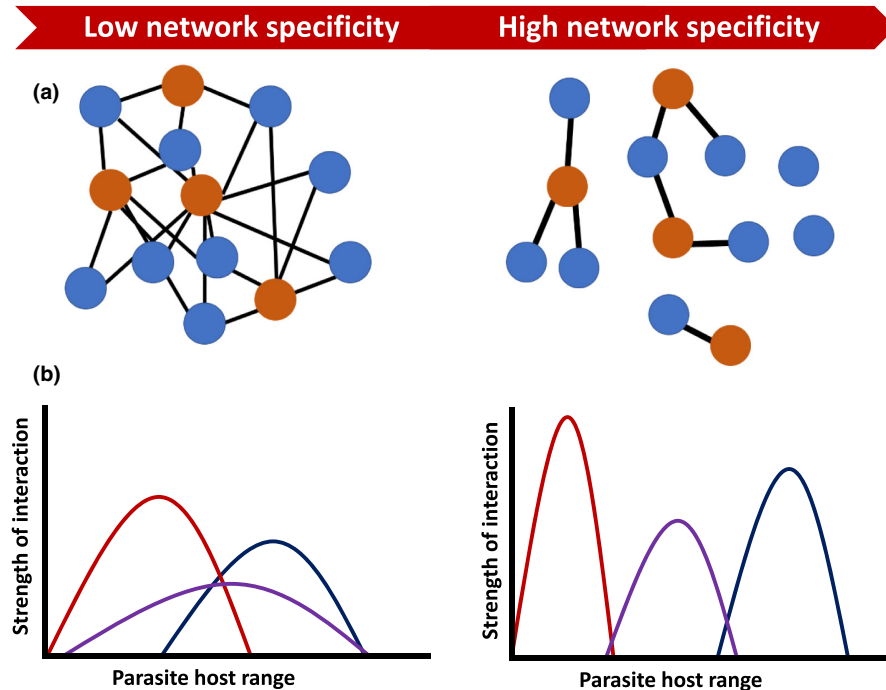
Nested bipartite networks (i.e. where specialists interact with subsets of the species with whom generalists interact) are cohesive, robust and more stable as nested structures favour redundancies, reducing the odds of central species becoming extinct and preserving the overall shape of the network in case of extinctions (Bascompte, 2007, 2010; Grilli et al., 2016). Therefore, a stable community resilient to disturbances such as extinctions is usually a community with a highly nested network of species interactions. On the other hand, in specific circumstances network modularity (i.e. degree of network subdivision into separate subsets of highly interacting species) contributes to higher community stability as disturbances (e.g. extinctions) in one module are less likely to impact species in other modules (Eskuche-Keith et al., 2023; Grilli et al., 2016).

Environmental and host features play a crucial role in shaping the dynamics of host–parasite communities (Runghen et al., 2021). For instance, host diversity is a known driver of parasite diversity. On one hand, parasite diversity tends to mirror the local diversity of hosts (Kamiya et al., 2014). Therefore, higher host diversity might determine network complexity and stability by providing a broader range of ecological niches and facilitating more potential links within the community (Galiana et al., 2022). On the other hand, host functional diversity shapes ecosystem functions (e.g. primary productivity) (Tilman et al., 1997), while certain host traits have been associated with increased parasite infection risk (Filion et al., 2020). Climate, on the other hand, can influence the host specificity of parasites (Fecchio et al., 2019), which could further impacts network properties, affecting ecosystem stability. For instance, aridity has been associated with decreased stability in certain systems (García-Palacios et al., 2018). For these reasons, we explored the interplay among host functional diversity (i.e. the variety of traits hosts possess), taxonomic diversity (i.e. the variety of host species), temperature and precipitation patterns, and their collective influence on community stability (i.e. the community's capacity to maintain its structure and function over time in the face of various environmental changes or disturbances).

Understanding these complex relationships can shed light on the mechanisms that govern the structure and resilience of host–parasite communities in various ecological settings. In this study, we hypothesize (see Box 1) that network specificity (i) decreases parasite competition and (ii) host–parasite community stability while (iii) increasing parasite extinction risk. Additionally, we anticipate that parasite extinction risk will (iv) decrease with an increase in

**BOX 1** Effects of network specificity on community structure and parasite–host range

We expect parasite–host network structure to change as specificity increases. Networks with a low degree of specificity should be more interconnected (Figure 1a) and parasites should share more hosts than in networks composed mainly of specialist parasites (Figure 1b). We predict changes in network dynamics with increasing specificity will affect network stability and parasite competition and extinction risk.



**FIGURE 1** (a) Expected structure of host–parasite networks containing multiple generalist parasites (left) and host–parasite networks containing mainly specialist parasites (right). Parasites: orange, hosts: blue. The thickness of links is proportional to the strength of interaction between a host and a parasite (i.e. prevalence or intensity of parasite infection). (b) Expected host range used by parasites given network specificity. We predict low network specificity (left) leads to high host use overlap among distinct parasites (colours represent different parasite lineages), while high network specificity (right) reduces the overlap of host use between distinct parasites while increasing the strength of interaction between parasites and their hosts.

community stability. We also put forward the following hypotheses regarding the effects of climate and host diversity on host–parasite community stability, parasite competition and extinction risk: (v) host diversity enhances stability and reduces parasite competition and extinction; (vi) climatic factors affect network stability, parasite competition and extinction risk.

To elucidate those questions, we compiled from multiple sources a large dataset on local assemblages of birds and their malaria and malaria-like (haemosporidians) vector-borne parasites. Avian haemosporidians are among the most prevalent and diverse avian parasites, comprising more than 300 species and almost 4000 genetic lineages distributed worldwide (Valkiūnas, 2005). Given their extensive prevalence, diversity, distribution, variable levels of host specificity and long coevolution with their hosts (de Angeli Dutra, Fecchio, et al., 2022; Pacheco et al., 2018) avian haemosporidian parasites represent an ideal model to investigate the role of host specificity in driving host–parasite community stability and parasite competition and extinction risk. Our research explored the dynamics between avian

haemosporidian parasites and their hosts, shedding light on the crucial role of specificity in regulating interactions within bipartite networks.

## 2 | MATERIALS AND METHODS

### 2.1 | Data compilation

To test our hypotheses, in June 2023 we extracted haemosporidian occurrence data from MalAvi. MalAvi (<http://130.235.244.92/Malavi/>) is an online, freely available global database on avian haemosporidian parasites (*Plasmodium*, *Haemoproteus* and *Leucocytozoon*) (Bensch et al., 2009). The database comprises >15,000 entries, each representing a recorded malaria infection in an individual bird, with information on parasite lineage identity, bird species identity and geographical location.

Each entry in our dataset consisted of an individual link of an identified malaria lineage in an identified host species from a given

geographical locality. However, the absence of a parasite lineage from a particular host species may reflect inadequate sampling, rather than a true host–parasite incompatibility. Therefore, to increase the accuracy of our data, missing but likely host–parasite interactions were predicted using a phylogenetic model approach implemented with the package 'HPprediction' in the R computing environment (Farrell et al., 2022). This approach is based on hierarchical Bayesian models that leverage information on network stability and then scale phylogenetic distances among hosts to generate link prediction. Hence, this modelling approach predicts missing links based primarily on the evolutionary relationships among hosts within a community where the parasite occurs. For example, the absence of a link between a given parasite lineage and a host species is more likely to be the result of insufficient sampling if that parasite is found in congeners of that host species than if it is not found in any closely related bird species. Raster files of bird species' geographical ranges were extracted from the BirdLife International database while a bird phylogeny was constructed using the AllBirdsHackett1.tre file from the <https://birdtree.org/> website (Jetz et al., 2012). MalAvi data and both bird distribution and phylogenetic data were used to generate a list of species present in each locality. The predicted links would be integrated into our initial dataset extracted from MalAvi to produce communities more likely to include all existing local host–parasite associations.

## 2.2 | Network analyses and specificity

All analyses were performed in the R environment version 4.3 (R Core Team, 2023). Each community was composed of all parasite lineages and host species occurring within a given geographical locality including the potential missing links. Communities were defined as cell grids of equal ( $5^\circ \times 5^\circ$ , total=2592) dimensions harbouring 20 or more distinct parasite lineages and at least 10 distinct host species. Grids harbouring fewer than 20 distinct parasite lineages, or less than 10 host species were excluded from our analyses. It is important to note that the majority of the grids in our study represent regions with scarce sampling (e.g. Africa and Asia) and/or regions with no haemosporidian parasites (e.g. oceans and Antarctica) as they cover the entire globe. We chose the cell grid size that provides the optimal compromise between the number of cells that met the inclusion criteria mentioned above, and the spatial extent that could reasonably be expected to allow for species interactions. We acknowledge that the area covered by a 5X5 degrees cell encompasses diverse habitats and that not all bird species will occupy the entire cell; thus, it is at the upper end of what may be considered a community. The use of geographical grids to delimit communities is consistent with previous studies on avian haemosporidian parasites (de Angeli Dutra et al., 2023) and well established in ecology (Bousquin, 2021; Rangel et al., 2018).

As detailed below, network specificity ( $H_2'$ ) and stability (measured as nestedness and modularity), parasite inter-specific competition and vulnerability to extinction (measured as niche overlap and extinction slope respectively) were calculated using the package

'bipartite' in R (Dormann et al., 2008). Network modularity was calculated by comparing observed modularity with the partition that maximizes modularity (Beckett, 2016).

Network specificity ( $H_2'$ ) was estimated as the degree of specialization or partitioning among both host and parasite species within a bipartite network based on their interaction patterns (Blüthgen et al., 2006). This metric is useful to compare the degree of specialization across distinct interaction webs as it considers both parties of a bipartite network. Likewise, nestedness is also a network-level index (i.e. considers both parties, hosts and parasites, of a bipartite network). It reflects the degree to which specialist parasites interact with a subset of the hosts used by progressively more generalist parasites. Here, we calculated nestedness based on decreasing fill (or DF) and paired overlap (Almeida-Neto et al., 2008). Since nested networks are cohesive and robust and nestedness is a network-level measurement (Bascompte, 2007), we used this metric to estimate community stability. Additionally, in certain cases, modularity can be associated with higher stability (Grilli et al., 2016), therefore we also evaluated the role of network specificity on modularity. Here, we calculated modularity using label propagation and multi-step agglomeration to attempt to maximize modularity in binary bipartite networks applying the LPAwb+ algorithm (Beckett, 2016).

On the other hand, niche overlap and extinction slope metrics only take into account one party of the bipartite networks: the parasites. Niche overlap measures the similarity in resource utilization between two or more species within a community (Dormann et al., 2008). In our analyses, it measures the degree to which parasites share host species. As a result, communities with low overlap in host utilization by parasites are subject to generally lower levels of interspecific competition. The extinction slope estimates the impact of removing a species from a bipartite network. It measures the coextinction of parasites as a consequence of repeated removals of host species from the network (Dormann et al., 2008). In the selected algorithm, the host species infected by fewer parasites are removed first. The present algorithm was selected since those species are expected to have the weakest impact on community stability and extinction slope is a metric of parasite vulnerability to their hosts' extinction.

All network metric values were standardized among distinct communities using null models and Z-scores (i.e. a numerical measurement that describes the position of a given value according to the mean) to account for the fact that the different community networks differ widely in the number of nodes (diversity of hosts and parasites) and the number of interactions (biases in sampling effort and/or prevalence). This method corrects for those biases as we used null models to create a thousand different and reshuffled networks. Our null models created shuffled binary matrices, assigning interspecific interactions according to species-specific probabilities based on abundance of host species while ensuring that all hosts and parasites still had at least one interaction. This procedure was repeated a thousand times for each host–parasite network. All those new matrices were used to calculate randomized network metrics (e.g. nestedness, niche overlap, extinction

slope and specificity). After we obtained a thousand random values of each network metric for each host–parasite network, we used them to calculate Z-scores. Therefore, the final network metric values obtained and used in the analyses represent how the original value compares to randomly generated values, that is, if the parasites compete as much, are as likely to get extinct or whether our networks are more, less or equally specific and stable, as they would be by chance alone based solely on their number of nodes and interactions.

### 2.3 | Local biodiversity and climate conditions

Local host taxonomic and functional diversity and climatic conditions were calculated for each community evaluated. Host taxonomic diversity was calculated based on avian occurrence data extracted from the BirdLife International database. Host functional traits for each bird species were extracted from the Open Traits Network database (<https://opentraits.org/datasets.html>) (Wilman et al., 2014), migratory status followed classification by Dufour et al. (2020). We used Hill numbers to estimate both diversity metrics using the package hillR in R (Chao et al., 2014). Hill numbers are a common metric of diversity used in community ecology. Taxonomic diversity is measured as Shannon entropy. In our study, it refers to the level of uncertainty in identifying the host species of a randomly selected parasite. On the other hand, functional diversity was calculated as the sum of the pairwise distances (i.e. variety in host functional attributes evaluated: migratory status, territoriality, body weight, diet and habitat) among the host species that parasites infect in each cell grid (Chao et al., 2014).

We extracted climate data obtained from Worldclim (<https://worldclim.org/>) at a resolution of 10km for the whole grid area. To do so, we used the 'getData' function from the 'raster' package in R climate data (Hijmans, 2023). Values obtained across each grid were averaged so that our climatic metrics took into consideration conditions for the entire cell. The Worldclim dataset consists of 19 distinct environmental attributes, encompassing measurements related to temperature and precipitation. To reduce the dimensions of our climatic data, we ran two Principal Component Analysis (PCAs) separating the variables for temperature variables (Bio1–11) and precipitation variables (Bio12–19). PCAs for temperature and precipitation were performed separately to provide a clearer interpretation of the principal components for each variable. This is important in understanding the dominant patterns of variability in temperature and precipitation independently. We added the first axis of both PCAs (which explained 78% and 60% of the variance respectively) as explanatory variables in the Bayesian models.

### 2.4 | Bayesian analyses

Due to their high modelling flexibility, all statistical analyses were performed in R using Bayesian models from the 'brms' package

(Bürkner, 2017; Hobbs & Hooten, 2015). For the first three hypotheses, we ran three models (one for each hypothesis) evaluating the role of network specificity on host–parasite communities. In all three models network specificity was used as the only explanatory variable. Response variables were (i) community stability (nestedness and modularity, first hypothesis), (ii) parasite competition (niche overlap, second hypothesis), (iii) and parasite vulnerability (extinction slope, third hypothesis). A fourth model was performed to test the relationship between parasite vulnerability/extinction slope (response variable) and community stability/nestedness (explanatory variable), our fourth hypothesis.

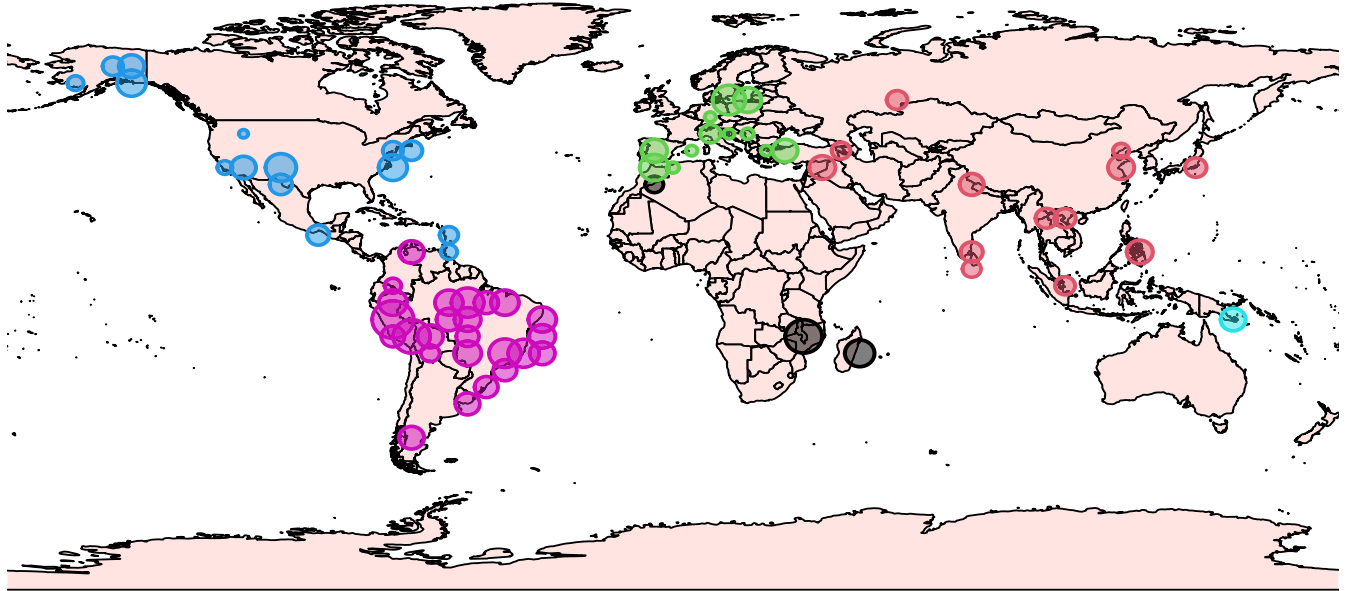
Secondly, to test our fifth and sixth hypotheses, we ran three models evaluating the influence of host taxonomic diversity and climate features on community stability (nestedness and modularity), parasite competition (niche overlap) and parasite vulnerability (extinction slope). Host functional diversity was excluded from our analyses as the correlation between host functional diversity and taxonomic diversity was too high (0.97). In those three models, the explanatory variables were host taxonomic diversity, temperature (first axis of PCA) and precipitation (first axis of PCA). Here, the response variable was one of the following: (i) community stability (nestedness and modularity, first model testing hypotheses v and vi), (ii) parasite competition (niche overlap, second model testing hypotheses v and vi), (iii) and parasite vulnerability (extinction slope, third model testing hypotheses v and vi).

All models were posteriorly subject to model diagnosis and selection by (i) a visual check of model convergence and (ii) cross-validation via Pareto-smoothed importance sampling ('loo' function). This latter method points to data that might be causing problems for Bayesian models and estimates the ability of the implemented models to make predictions. All Bayesian models were run using eight chains with 10,000 total iterations per chain (5000 for warm-up, 5000 for sampling). Data distributions were visually checked and for all models, the Gaussian family was applied. Results were plotted using the function 'conditional\_effects' from 'brms', which allows visualization of the predicted Bayesian outputs. All models were checked for convergence visually and via Pareto-smoothed importance sampling. Both diagnostic methods confirmed the models were well performed and no data point failed to converge.

## 3 | RESULTS

In total, we analysed 60 communities of birds and haemosporidian parasites after selecting localities with 20 or more distinct parasite lineages and at least 10 host species in which network specificity could be estimated (for nine communities network specificity could not be estimated due to small numbers of realized links, as a result, they were excluded from our analyses) (Figure 2). South and North Americas were the two best sampled continents in our analyses with a total of 25 and 15 communities evaluated. A total of 13, 12, 3 and 1 host–parasite communities were included from Asia, Europe, Africa and Oceania respectively (Figure 2). On average,





**FIGURE 2** Haemosporidian-bird communities used in Bayesian models. Colours represent distinct continents; circle diameters depict the size of haemosporidian-bird community matrices in log scale.

haemosporidian-bird occurrence matrices had 2765 possible interactions between parasites and hosts, with a minimum of 20 and a maximum of 73,682 potential links. The number of realized host-parasite interactions per matrix ranged from 11 to 4151 links, with an average of 1301 haemosporidian-bird interactions per community matrix. Bayesian hierarchical models used to predict missing links between hosts and parasites did not add any missing links to our networks.

After running our models, we observed a negative association between network specificity and both nestedness and niche overlap; in other words, high network specificity decreases community stability and competition among distinct parasites (Table 1a,b and Figure 3a,b). At the same time, parasite vulnerability (i.e. extinction slope) decreased with increasing community stability/host-parasite nestedness (Table 2 and Figure 3c). Nonetheless, we observed no association between network specificity and either parasite vulnerability or network modularity (Supplementary Tables S1 and S2). Overall, specificity mediated host-parasite network stability and parasite competition.

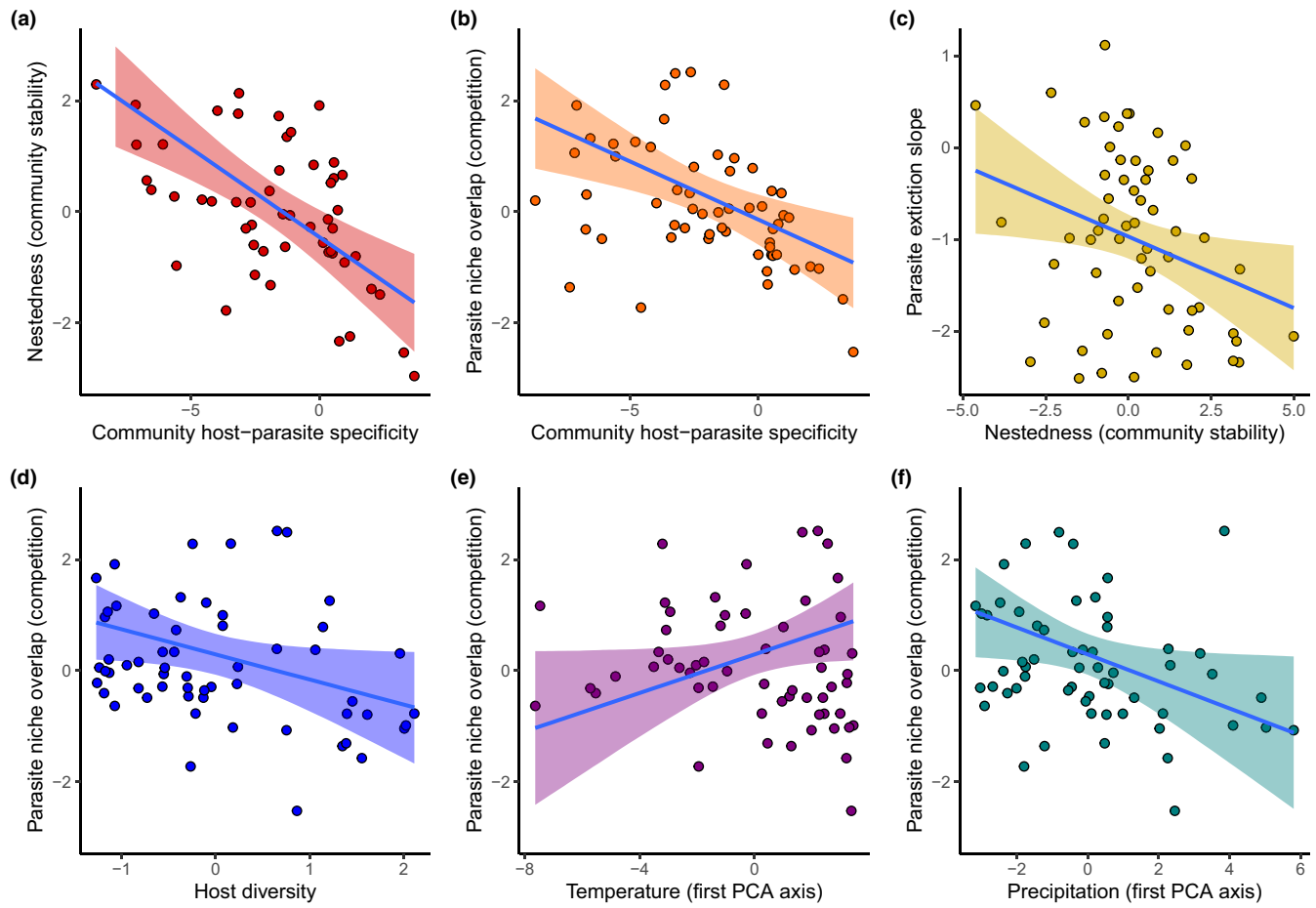
When assessing the influence of host diversity and climate on host-parasite community stability, we observed that only parasite competition (niche overlap) appeared driven by environmental factors (Table 3, Supplementary Tables S3). For network stability (nestedness and modularity) and parasite vulnerability (extinction slope) we observed no effects of host diversity, temperature or precipitation in any model. More specifically, higher host taxonomic diversity and precipitation values decreased parasite competition (i.e. lower niche overlap), whereas temperature was positively associated with increased parasite competition (i.e. greater niche overlap) (Figure 3d-f). We found no association between climatic features or host diversity and either nestedness or parasite extinction slope.

**TABLE 1** (a) Parameter estimates, standard errors and credible intervals for the Bayesian model evaluating the effect of host-parasite specificity on network nestedness. (b) Parameter estimates, standard errors and credible intervals for the Bayesian model evaluating the effect of host-parasite specificity on parasite niche overlap. Estimates whose confidence intervals do not overlap 0 are considered significant.

Response	Population-effects	Estimate	Error	Credible intervals	
a. Nestedness	Intercept	-0.45	0.25	-0.95	0.04
	Specificity	-0.32	0.07	-0.46	-0.18
b. Niche overlap	Intercept	-0.14	0.23	-0.59	0.31
	Specificity	-0.21	0.06	-0.34	-0.08

## 4 | DISCUSSION

The cascading effects of parasites shape community structure, stability and diversity (Dunne et al., 2013); therefore, understanding the mechanisms that determine the stability of host-parasite communities is essential for predicting the role of parasites in distinct environments. Here, we investigated the role of a primary parasite trait shaping host-parasite communities: the parasite's host specificity. Essentially, we show that high values of network specificity impair community stability and reduce the extent of parasite competition. At the same time, we showed that parasite extinction risk decreases with community stability. No effect of host specificity on parasite extinction risk was observed. Interestingly, parasite competition (i.e. niche overlap) was negatively associated with host taxonomic diversity and precipitation levels, and positively associated with temperature values. Both host-parasite community stability (i.e. nestedness, and also modularity) and parasite extinction risk did not appear affected by either host diversity or climatic features. This indicates that



**FIGURE 3** (a) Relationship ( $\pm$ credible intervals) between nestedness (i.e. a measure of community stability) and specificity among bird-haemosporidian interaction networks. (b) Relationship ( $\pm$ credible intervals) between parasite niche overlap (i.e. a measure of parasite competition) and specificity among bird-haemosporidian interaction networks. (c) Relationship ( $\pm$ credible intervals) between parasite extinction slope (i.e. a measure of parasite vulnerability) and nestedness (i.e. a measure of community stability) among bird-haemosporidian interaction networks. (d) Relationship ( $\pm$ credible intervals) between parasite niche overlap (i.e. a measure of parasite competition) and host diversity among bird-haemosporidian interaction networks. (e) Relationship ( $\pm$ credible intervals) between parasite niche overlap (i.e. a measure of parasite competition) and temperature among bird-haemosporidian interaction networks. (f) Relationship ( $\pm$ credible intervals) between parasite niche overlap (i.e. a measure of parasite competition) and precipitation among bird-haemosporidian interaction networks.

**TABLE 2** Parameter estimates, standard errors and credible intervals for the Bayesian model evaluating the effect of network nestedness on parasite extinction slope. Estimates whose confidence intervals do not overlap 0 are considered significant.

Population-effects	Estimate	Error	Credible intervals	
Intercept	-0.97	0.12	-1.21	-0.73
Nestedness	-0.16	0.07	-0.29	-0.02

environmental features alone might not play a role in shaping community stability or parasite extinction risk. Overall, we demonstrate that specificity is an important driver of host-parasite community stability and also mediates parasite competition.

Since host-parasite communities with a high degree of specificity seem less stable, those are more likely to be disrupted by changes in the environment (e.g. global change) or by the introduction of alien parasites. As formally addressed, this tendency is explained by the high levels of specificity facilitating coextinction events (i.e.

**TABLE 3** Parameter estimates, standard errors and credible intervals for the Bayesian model evaluating the effect of host taxonomic diversity and climate on parasite niche overlap. Estimates whose confidence intervals do not overlap 0 are considered significant.

Population-effects	Estimate	Error	Credible intervals	
Intercept	0.29	0.19	-0.07	0.66
Host diversity	-0.45	0.23	-0.90	-0.01
Temperature	0.17	0.09	0.00	0.35
Precipitation	-0.24	0.12	-0.47	-0.02

loss of a species because of the extinction of another species on which the first one depends) among parasites as their primary or only host goes extinct (Dunn et al., 2009). However, two parasites occupying very similar niches are not likely to coexist in evolutionary time (Levin, 1970), thus, specificity might play an important role preventing parasite competitive exclusion by reducing niche overlap.

Likewise, it is important to note that we observed no association between parasite extinction risk and overall network specificity, indicating parasite extinction may not be the main cause of reduced community stability. On one hand, the extinction of a generalist parasite may affect multiple host species. On the other hand, the extinction of a specialist parasite could lead to the higher abundance and greater competitive ability of their only or few former host species (Fenton & Brockhurst, 2008), potentially increasing community disruption. Therefore, the loss of a specialist parasite can have a more unbalanced and disruptive effect on the network structure than the loss of a generalist parasite, possibly leading to increased instability of generalist-dominated host-parasite communities.

At the same time, we observed that host-parasite communities with a high degree of specificity are generally characterized by lower parasite competition (i.e. niche overlap). When a host-parasite community experiences low niche overlap, the host species in this community have limited interaction and are less likely to share parasites (Dunn et al., 2009). We observed that niche overlap decreased with increasing host diversity and precipitation and that it increased with temperature. Higher host diversity broadens the variety of available niches, which could reduce parasite competition. Haemosporidian competition is higher in regions with lower precipitation and higher temperatures, demonstrating the effect of climatic features on haemosporidian-bird interactions. Fecchio et al. (2019) showed that greater seasonality and dryness generally increase haemosporidian specificity. As a result, climate might have important bottom-up effects by driving parasite competition (Albrecht et al., 2018). At the same time, seasonality is also linked to higher turnover and diversity of haemosporidians (de Angeli Dutra, 2023; de Angeli Dutra et al., 2023) and could affect vector diversity and abundance (Gray & Ogden, 2021; Kelly-Hope et al., 2009; Li et al., 2021). This suggests that environmental specialization might occur in regions with high seasonality, a phenomenon that might have emerged as a mechanism to decrease competition in harsher environments. Therefore, high specificity might benefit parasites subject to high interspecific competition pressures and challenging climatic conditions.

Despite the fact no association was found between network specificity and parasite extinction risk, we observed that community stability (i.e. nestedness) decreased haemosporidian vulnerability. Nested community structures are more stable as they make it unlikely that central species may go extinct and create redundancies of interactions because specialists tend to associate mainly with a subset of the species used by generalist species; therefore, the overall structure of the network is preserved in case of extinctions (Bascompte, 2007, 2010). For this reason, parasites from nested communities generally are less subject to extinction risk, as revealed by our analyses. Interestingly, this trend is indirectly mediated by network specificity, as generalist parasites and 'super-hosts' (i.e. hosts infected by several species) should increase the nestedness of the network. At the same time, specialist species rely on a small set of hosts/resources in which they perform better than their generalist counterparts (Felix et al., 2022; Pinheiro et al., 2016, 2019). Since haemosporidians have a tight co-evolutionary history with their hosts (Pacheco et al., 2018), specific

adaptation to and high performance on, particular host species are likely to occur, outweighing extinction risks associated with dependence on a small set of host resources. This feature of highly specialist parasites (i.e. only infect a very limited set of hosts) might explain why haemosporidian-bird communities with a high degree of specialization are not subject to higher risks of parasite extinctions.

Global change can directly affect the distribution and behaviour of both parasites and their hosts (Atkinson et al., 2014; Cable et al., 2017; Carlson et al., 2017; de Angeli Dutra, Poulin, et al., 2022; Ortega-Guzmán et al., 2022). For parasites, rising temperatures and shifts in precipitation patterns can influence their transmission rate, and, as a result, their incidence (Atkinson et al., 2014; Mordecai et al., 2013, 2020; Ryan et al., 2019). Nevertheless, distinct parasites respond differently to global change. For avian haemosporidians, the optimum temperature for transmission varies among distinct parasite species (Fecchio et al., 2020; Lapointe et al., 2010). Furthermore, several host species (~13% of world bird biodiversity) are threatened with extinction (IUCN, 2020). Host extinction is likely to trigger multiple parasite extinction events, particularly among specialist parasites (Dunn et al., 2009). Further, species extinctions are likely to decrease even further regional functional diversity (Fricke et al., 2022). These events might modify the structure of haemosporidian-bird networks, particularly if generalist parasites or central host species succumb to extinction (Bascompte, 2007). However, high network specialization and modularity may have a protective effect against fast global change-driven host extinction. Sonne et al. (2022) have shown that coextinctions are reduced in specialized communities as there are fewer overlapping interactions; therefore, in the future, strongly nested host-parasite communities might be the most susceptible to global change and extinction events.

It is important to note that this study has some limitations. Here, we combined and utilized multiple datasets, assembled by different people, to address the role of host specificity in mediating host-parasite interactions. However, integrating diverse data sources increases the risk of inherent errors, such as typographical mistakes and discrepancies in species names (Nekola & Horsák, 2022). While we made efforts to ensure data accuracy, these intrinsic issues should be taken into consideration when interpreting our findings. Another significant limitation lies in the geographical distribution of haemosporidian samples since our data are biased towards the Americas. Moreover, our phylogenetic hierarchical Bayesian modelling did not predict any missing links between hosts and parasites; thus, future studies may consider using trait-based machine learning approaches (Fricke et al., 2022). Finally, our analysis did not consider spatial variation in the abundance of host and parasite species, as well as vector species, potentially introducing bias into our results.

In conclusion, our study provides valuable insights into the role of specificity in shaping host-parasite communities and their responses to global change. We demonstrate that high levels of network specificity in host-parasite communities can have both positive and negative effects on community stability and parasite competition. While high specificity can lead to decreased stability and increased vulnerability to environmental disruptions, it can also reduce competition among



parasites, benefiting them in harsh and competitive environments. Importantly, our findings suggest that parasite extinction risk is not directly associated with network specificity but is strongly influenced by community stability (i.e. nestedness). Specialist parasites, despite relying on a limited set of hosts, might exhibit greater adaptation and performance on their single or few hosts, thereby decreasing their extinction risk in nested communities. The vulnerability of host–parasite communities varies with their degree of host–parasite specificity and network stability, particularly when assessing the potential impact of parasite coextinctions. This is particularly relevant for conservation as the world faces ongoing environmental challenges, such as climate change and habitat degradation. Overall, network specificity shapes host–parasite interactions, altering community stability, parasite competition and potentially parasite vulnerability to global change.

### AUTHOR CONTRIBUTIONS

Daniela Dutra and Robert Poulin conceived and designed the study. Daniela Dutra performed the data analyses. Daniela Dutra wrote the manuscript with input from Robert Poulin. Both authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

None.

### DATA AVAILABILITY STATEMENT

Data used in this research are available on MalAvi (<http://130.235.244.92/Malavi/>) and Open Traits datasets (<https://opentraits.org/datasets.html>). Species distribution maps can be requested from BirdLife at <http://datazone.birdlife.org/species/requestdis>. The dataset used in our analyses and R code is deposited in Data dryad (<https://doi.org/10.5061/dryad.sf7m0cgdf>).

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## BIOSKETCH

**Daniela de Angeli Dutra** is a disease ecologist whose research focuses on the drivers of parasite community structure, parasite dispersal and the impacts of global change on parasite transmission/spread.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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