

Contrasting effects of host or local specialization: Widespread haemosporidians are host generalist, whereas local specialists are locally abundant

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Funding information

Daniela Dutra was supported by a doctoral scholarship from the University of Otago, New Zealand. Gabriel Félix was supported by a doctoral scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil.

Editor: Pauline Kamath

Abstract

Aim: Despite the wide distribution of many parasites around the globe, the range of individual species varies significantly, even among phylogenetically related taxa. Given that parasites need suitable hosts to complete their development, parasite geographical and environmental ranges should be limited to communities where their hosts are found. Parasites might also suffer from a trade-off between being locally abundant or widely dispersed. We hypothesize that the geographical and environmental ranges of parasites are negatively associated with their host specificity and their local abundance.

Location: World-wide.

Time period: 2009–2021.

Major taxa studied: Avian haemosporidian parasites.

Methods: We tested these hypotheses using a global database that comprises data on avian haemosporidian parasites from across the world. For each parasite lineage, we computed five metrics, namely phylogenetic host range, environmental range, geographical range and the mean local and total number of observations in the database. Phylogenetic generalized least squares models were run to evaluate the influence of phylogenetic host range and the total and local abundances on geographical and environmental ranges. In addition, we analysed separately the two regions with the largest amount of available data: Europe and South America.

Results: We evaluated 401 lineages from 757 localities and observed that generalism (i.e., phylogenetic host range) was associated positively with both the geographical and environmental ranges of the parasites at global and European scales. For South America, generalism was associated only with geographical range. Finally, mean local abundance (mean local number of parasite occurrences) was negatively related to geographical and environmental ranges. This pattern was detected world-wide and in South America, but not in Europe.

Main conclusions: We demonstrate that parasite specificity is linked to both their geographical and environmental ranges. The fact that locally abundant parasites present restricted ranges indicates a trade-off between these two traits. This trade-off, however, becomes evident only when sufficient heterogeneous host communities are considered.

KEYWORDS

avian haemosporidians, community assembly, geographical range, host specificity, niche breadth, parasite ecology

1 | INTRODUCTION

Organisms present variable distribution patterns across the globe. Local communities are organized by the addition of new species via speciation and dispersal, and their relative abundances are shaped by local stochastic dynamics, niche processes and ongoing dispersal (Ricklefs & Jenkins, 2011; Vellend, 2010; Weiher et al., 2011). In order to persist in a locality, organisms must tolerate its abiotic conditions (e.g., temperature and precipitation) and the interactions with other species already established (e.g., competitors, predators and parasites) (Weiher et al., 2011). Thus, apart from dispersal, environmental and biological filters determine species colonization into new regions. These requirements underpin the widespread relationship between niche breadth and geographical range size, with species that are generalists in terms of resource needs and environmental tolerance achieving larger ranges (Brown, 1984; Slatyer et al., 2013). For parasites, establishment into new communities should be directly dependent upon the range of host taxa they currently exploit and/or their capacity to develop fully in novel hosts, which may constrain their niche and spatial dynamics (Mestre et al., 2020). This occurs because parasites must go through an additional biological filter, which is the presence of suitable hosts. Importantly, distribution and dispersal patterns can be scale dependent because the relative importance of different processes can change between scales (Ricklefs, 2008; Ricklefs & Jenkins, 2011; Vellend, 2010). Furthermore, particular regions present unique assemblages of hosts and environmental conditions, thereby modifying the selective pressures acting on parasite dispersal and colonization.

Parasites are one of the most important groups of organisms and represent one of the most widespread life-history strategies in nature, playing a fundamental role in shaping trophic interaction in communities (Dunne et al., 2013; Kuris et al., 2008; Lafferty et al., 2008; Mouritsen & Poulin, 2005). Parasites also present variable levels of specificity for their hosts, which could lead to differences in their ability to switch to novel hosts, thereby impacting their likelihood of colonizing new communities. In addition, the phylogenetic ancestry of parasites and their hosts determines the host specificity of parasites and community assembly (Clark & Clegg, 2017). Concomitantly, studying parasite range patterns is fundamental to understand their dispersal in nature and, potentially, to predict their colonization of new regions. Past studies have observed contrasting outcomes regarding the influence of host specificity of parasites on their distribution. Drovetski et al. (2014) observed that both specialist and generalist avian haemosporidian parasites were widely distributed in Europe and North Africa, with parasite abundance (e.g., the number of times a parasite was observed) as the main factor explaining parasite range. Earlier, however, host specificity has been shown to

relate to the spatial spread of localities in which a parasite is found (Krasnov et al., 2005).

Specialization can limit species distributions to a restricted range of favourable environments (Tuomisto et al., 2003). Previous research suggests that specialized species may perform well in certain homogeneous conditions but achieve low performance across a range of conditions (Pinheiro et al., 2019). Thus, parasites inhabiting multiple and heterogeneous environments might achieve lower local performance when compared with parasites residing in few homogeneous localities. Concomitantly, community similarity in both fauna and flora decreases with distance (Nekola & White, 1999; Qian & Ricklefs, 2012; Tuomisto et al., 2003). Therefore, the larger the geographical range of a parasite, the more diverse must be the assemblage of potential hosts and environmental conditions it confronts. Consequently, to explore dissimilar sets of hosts and environments successfully, widespread parasites might present generic, locally suboptimal adaptations (Futuyma & Moreno, 1988). For instance, Clark et al. (2018) showed that host phylogeny and climate shape haemosporidian parasite assemblages and limit parasite distribution, respectively. Furthermore, specialized haemosporidian lineages colonizing new sites with diverse host communities may be less prone to find suitable hosts and persist in this new community (Pérez-Tris & Lima, 2020). Hence, parasites must balance generalism and performance within a set of regions and environments, because a trade-off between being widespread and having high performance is expected in heterogeneous conditions (Pinheiro et al., 2019).

Avian haemosporidian parasites are vector-borne protozoan parasites and are among the most prevalent, diverse and well-studied avian parasites, being globally distributed and able to infect many avian clades (Fecchio et al., 2020; Valkiūnas, 2005). These parasites have been widely used in the last decade as models for the study of host-parasite interaction. To date, c. 4,000 distinct lineages have been detected and c. 250 species described (Bensch et al., 2009; Valkiūnas, 2005; Valkiūnas & Iezhova, 2018). Avian haemosporidians also possess distinct levels of host specificity (i.e., their ability to infect few vs. multiple host species) and geographical range, with some lineages able to infect multiple avian species and found on all continents, except Antarctica (Valkiūnas, 2005). Furthermore, host specificity varies greatly among genera, with *Plasmodium* parasites generally presenting lower host specificity (Hellgren et al., 2009; Moens & Pérez-Tris, 2016; Ricklefs & Fallon, 2002). Some *Plasmodium* lineages have been found in ≥ 50 different bird species, and the *Plasmodium relictum* lineage SGS1 has been recorded in > 110 bird species world-wide (Rivero & Gandon, 2018). Thus, owing to their high prevalence, diversity, geographical range and variable levels of host specificity, avian haemosporidians represent an ideal host-parasite system in which to investigate the putative impact of parasite specificity and abundance patterns on their distributional range.

Here, we evaluate the widely studied relationship between niche breadth and range size. We hypothesize that the geographical range of parasites is linked to their ability to infect multiple hosts (generalism). Given that haemosporidian development can be constrained by environmental factors during their life cycle within vectors (Lapointe et al., 2010) and vector populations are also affected by environmental conditions (Kelly-Hope et al., 2009), parasites may achieve wide geographical ranges but be restricted to regions with similar environmental conditions. Thus, besides geographical ranges, here we also test whether parasites infecting a wider range of hosts can also colonize more environmentally distinct regions, hypothesizing that host-generalist parasites should exploit wider environmental ranges (i.e., the range of climatic conditions across which a parasite occurs). In addition, we test the hypothesis that there is a trade-off (measured as a negative interspecific relationship) between local parasite performance (measured as local mean parasite abundance) and geographical and environmental ranges, possibly owing to local community (habitat) specialization. To address these hypotheses, we calculate the host, environmental and geographical ranges of haemosporidian parasites and, thereafter, test whether parasite phylogenetic host range and mean local parasite abundance (e.g., the mean local number of times a parasite was observed) are related to parasite geographical and environmental range. Our study therefore addresses some aspects of the area-occupancy relationship (Gaston et al., 2000), but goes beyond, to test the influence of environmental conditions explicitly. Furthermore, aiming to compare results between distinct scales and regions with different degrees of host and environmental diversity, we also test our hypothesis separately for the South American and European continents (Girardello et al., 2019; Jetz et al., 2012).

2 | METHODS

2.1 | Dataset

We compiled data on haemosporidian lineages from the MalAvi database (<http://130.235.244.92/Malavi/>; Bensch et al., 2009), including all the data available from the “Grand Lineage Summary” representing *Plasmodium* and *Haemoproteus* genera from wild birds and that contained information regarding location. After checking for duplicated sequences, this dataset comprised a total of c. 6,200 sequenced parasites representing 1,602 distinct lineages (775 *Plasmodium* and 827 *Haemoproteus*) collected from 1,139 different host species and 757 localities from all continents except Antarctica (Supporting Information Figure S1; Table S1). The parasite lineages deposited in MalAvi are based on a *Cytb* fragment of 478 bp. This dataset was used to calculate the geographical, environmental and phylogenetic ranges of the parasites.

2.2 | Geographical range

All analyses in this study were performed using R v.4.0.2. In order to estimate the geographical range of each parasite lineage, we applied

the R package “GeoRange” (Boyle, 2017) and chose the variable minimum spanning tree distance (i.e., shortest total distance of all lines connecting each locality where a particular lineage has been found). Using the function “create.matrix” from the “fossil” package, we created a matrix of lineages and coordinates and used the function “GeoRange_MultiTaxa” to calculate the minimum spanning tree distance for each parasite lineage distance (i.e., shortest total distance, in kilometres, of all lines connecting each locality). Therefore, given that at least two distinct sites are necessary to calculate this distance, parasites observed in a single locality could not have their geographical range estimated. For this reason, only parasites observed in two or more localities were considered in our phylogenetically controlled least squares (PGLS) models.

2.3 | Host and environmental diversity

Traditionally, ecologists use Shannon entropy to measure diversity in ecological assemblages (Pielou, 1966). The Shannon entropy of a set of elements is related to the degree of uncertainty someone would have about the identity of a random selected element of that set (Jost, 2006). Thus, Shannon entropy matches our intuitive notion of biodiversity, because the more diverse an assemblage is, the more uncertainty regarding the species to which a randomly selected individual belongs. Shannon diversity increases with both the assemblage richness (e.g., the number of species) and evenness (e.g., uniformity in abundance among species).

To compare the diversity of assemblages that vary in richness and evenness in a more intuitive manner, we can normalize diversities by Hill numbers (Chao, Gotelli, et al., 2014). The Hill number of an assemblage represents the effective number of species in the assemblage (i.e., the number of equally abundant species that are needed to give the same value of the diversity metric in that assemblage). Hill numbers can be extended to incorporate phylogenetic information. In such cases, instead of species, we are measuring the effective number of phylogenetic entities in the assemblage.

Here, we computed the phylogenetic host range as the phylogenetic Hill number associated with the assemblage of hosts found infected by a given parasite. Analyses were performed using the function “hill_phylo” from the “hillr” package (Chao, Chiu, et al., 2014). Hill numbers are parameterized by a parameter, q , that determines the sensitivity of the metric to relative species abundance. Different values of q produce Hill numbers associated with different diversity metrics. We set $q = 1$ to compute the Hill number associated with Shannon diversity. Here, a low Hill number indicates specialization on a narrow phylogenetic range of hosts, whereas a higher Hill number indicates generalism across a broader phylogenetic spectrum of hosts.

We also used Hill numbers to compute the environmental range of sites occupied by each parasite lineage. Firstly, we collected the 19 bioclimatic variables from WorldClim v.2 (<http://www.worldclim.com/version2>) for all sites used in this study ($n = 713$). Then, we standardized the 19 variables by centring and scaling them by their respective mean and standard deviation. Thereafter, we computed

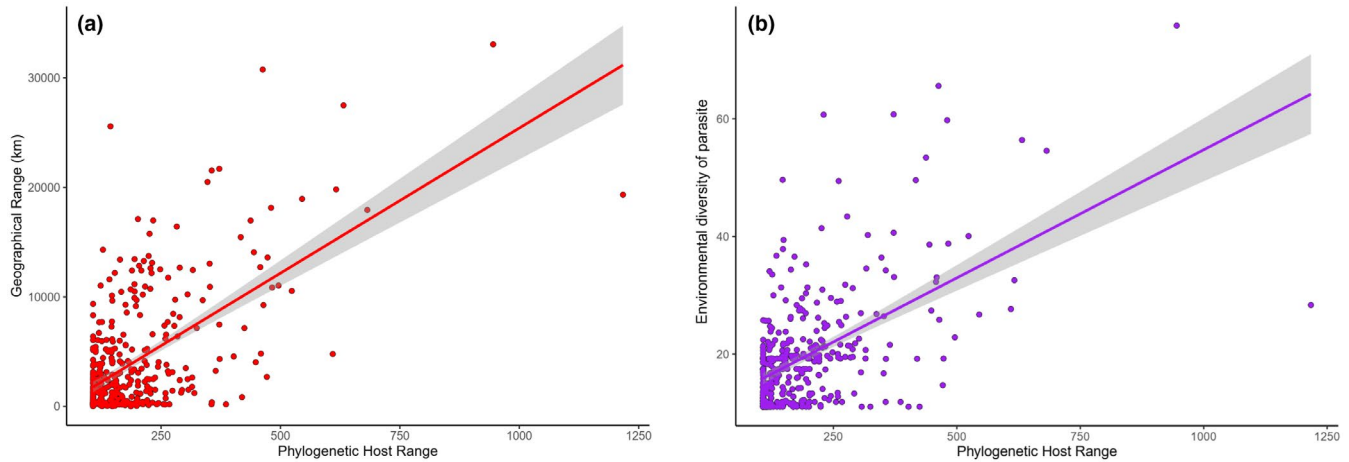


FIGURE 1 (a) Relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range (in kilometres). (b) Relationship between the host phylogenetic range of haemosporidians and their environmental range

the pairwise Euclidian environmental distance among all sites and used this distance to compute a dissimilarity cluster. Finally, as for the phylogenetic Hill number, we used this dissimilarity cluster to compute the environmental Hill number of the assemblage of sites occupied by each parasite lineage. The environmental Hill number for each parasite can be interpreted as the effective number of environmental conditions in which a parasite lineage occurs. Thus, the higher the environmental Hill number, the more generalist the parasite is regarding the environmental conditions in which it can occur.

2.4 | Parasite phylogenetic tree

A Bayesian phylogenetic reconstruction was performed. We built a tree for all parasite sequences for which we were able to estimate the geographical, environmental and phylogenetic ranges of the parasite (see geographical range section); this represented 401 distinct parasite lineages. This inference was produced using MRBAYES v.3.2.2 (Ronquist & Huelsenbeck, 2003), with the GTR+I+G model of nucleotide evolution, as recommended by MODELTEST (Posada & Crandall, 1998), which selects the best-fitting nucleotide substitution model for a set of genetic sequences. We ran four Markov chains simultaneously for a total of 7.5 million generations that were sampled every 1,000 generations. The first 1,250 million trees (25%) were discarded as burn-in, and the remaining trees were used to calculate the posterior probabilities of each estimated node in the final consensus tree. Our final tree obtained a cumulative posterior probability of .999. *Leucocytozoon caulleryi* was used as the outgroup to root the phylogenetic tree, because *Leucocytozoon* spp. represent a basal group within avian haemosporidians (Pacheco et al., 2020).

2.5 | Statistical analyses

Two PGLS models were made to estimate whether more generalist parasites achieve greater geographical and environmental ranges,

using only data on lineages for which we were able to estimate geographical, environmental and phylogenetic ranges (see geographical range section). We used the minimum spanning tree distance (i.e., geographical range) and environmental Hill numbers (i.e., environmental range) as the dependent variable, each in a separate model, and the phylogenetic Hill number (i.e., host phylogenetic range) and mean local abundance (mean number of observations) as our independent variables in both models. Total abundance (total number of times a parasite was observed, as recorded in the MalAvi database) was added as a population-level effect and parasite phylogeny as a random effect. Only lineages observed in two or more localities were included in our analyses because others returned missing values when calculating the geographical range. Likewise, we discarded all lineages that did not possess an available complete *Cytb* fragment in MalAvi or phylogenetic information for their hosts. We ran the PGLS models by applying the “pgls” function from the “caper” package (Orme, 2013).

We repeated the analyses above at smaller spatial scales for the two best-sampled regions in our dataset, Europe and South America. With these additional analyses, we aimed to compare the results between two regions with different degrees of environmental and host diversity. Therefore, a principal components analysis (PCA) was performed using WorldClim data for all localities in Europe and South America to confirm that there were differences regarding the environmental heterogeneity between the two continents. Both global PGLS analyses were also performed for the *Plasmodium* and *Haemoproteus* genera separately, but not at the regional scale owing to the reduced number of distinct lineages.

3 | RESULTS

Out of the c. 6,200 sequences of parasites representing 1,602 distinct lineages, c. 4,900 sequences from 401 distinct lineages were retained and analysed in the PGLS models. From the 401 parasite lineages evaluated, 212 lineages represented *Plasmodium* parasites

and 189 were *Haemoproteus* parasites. The analysis included data from 757 localities world-wide, with 207 in South America and 209 in Europe. Principal components analyses confirmed that there was greater environmental heterogeneity among South American than European localities (Supporting Information Figure S2).

World-wide, host phylogenetic range (generalism) of parasites was positively associated with both their geographical (Figure 1a; Table 1) and environmental ranges (Figure 1b; Table 2). This result remained when evaluating *Plasmodium* and *Haemoproteus* parasites separately (Supporting Information Tables S2–S5). In addition, the total and mean local number of occurrences of parasites were positively and negatively associated, respectively, with their geographical and environmental global ranges (Tables 1 and 2). However, when evaluating *Haemoproteus* lineages only, no relationship between geographical range and mean local and total abundance was observed (Supporting Information Table S4). Moreover, no association was found between total abundance of *Plasmodium* spp. and parasite geographical range (Supporting Information Table S2). For all other models, we again observed negative associations between the mean local abundance of parasites and their geographical and environmental ranges (Supporting Information Tables S2, S3 and S5).

On the continental scale, the results were slightly different. First, although the host phylogenetic range (generalism) of the parasites was still positively associated with their geographical range in both Europe and South America, it related to only environmental range in Europe (Figure 2a–d; Tables 3–6). Second, although the mean number of local occurrences of a parasite remained negatively associated with its geographical range in South America, this relationship was absent in Europe (Tables 3 and 5). At the global scale and on both continents, the mean number of local occurrences was negatively associated with environmental ranges (Tables 4 and 6). Finally, the occupancy–abundance relationship (i.e., the positive relationship between the total number of occurrences of a parasite and its geographical range) was still found in Europe but disappeared in South America (Tables 3 and 5). Nonetheless, we still observed a positive relationship between the total number of occurrences and environmental range in both continental models (Table 4 and 6).

4 | DISCUSSION

Parasite specificity and the individual characteristics of the hosts they are able to infect can shape parasite life history, including their global range by altering their putative ability to find suitable hosts or be carried to and colonize new communities through migrants

(Mestre et al., 2020; Poulin & de Angeli Dutra, 2021). Here, we demonstrate that host phylogenetic range is linked to geographical and environmental ranges of parasites. This supports the relationship between niche breadth and geographical range size postulated for free-living taxa (Brown, 1984; Slatyer et al., 2013). At the same time, being able to colonize multiple regions also seems to come at a cost, because high local abundance of parasites is associated with reduced geographical and environmental ranges, indicating a trade-off between being locally abundant or widely dispersed. In addition, we demonstrate that these processes operate differently among geographical scales and can vary depending on the properties of different continents. Our findings suggest that parasite geographical ranges are constrained for locally abundant parasites only in highly diversified environments with high host diversity, such as South America, whereas in less diversified regions, such as Europe, parasite mean local abundance is unrelated to their geographical distribution.

Parasites must face both environmental and biotic pressures, which are exerted by the physiological and immunological traits of their hosts and the abiotic conditions external to their hosts (Mestre et al., 2020). Furthermore, host switching and dispersal seem to be the two major drivers for haemosporidian diversification (Fecchio et al., 2018), and these processes could be correlated intrinsically. As we observed in the present study, generalist parasites achieve a higher geographical and environmental range; concomitantly, these parasites are more likely to switch hosts (Beadell et al., 2004). Host switching facilitates parasite dispersal because it provides opportunities to infect hosts that inhabit regions unoccupied by the original hosts. Hosts and vectors play a fundamental role in parasite spread, defining the Hutchinsonian niche of parasites and determining their biotic, environmental or dispersal barriers during the processes of range expansion (Mestre et al., 2020). In addition, de Angeli Dutra et al. (2021) demonstrated that infecting and being transported by migratory hosts enhance haemosporidian geographical ranges. Likewise, haemosporidians rely on competent vectors to complete their life cycle, to reproduce sexually and be transmitted to a new host (Fecchio et al., 2020; Valkiūnas, 2005). Therefore, being able to infect both residents and migratory hosts and to develop fully in a wide range of vectors also favour parasite dispersal and might be one of the factors explaining the role of host specificity in shaping parasite range.

Although parasite spread seems to be restricted by host specificity at both global and continental scales, the relationship between local abundance and geographical range depends on both the geographical scale and the continent analysed. Local abundance of parasites, at least as measured by records in MalAvi, is negatively related

TABLE 1 Parameter estimates, standard errors, *t* and *p*-values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range

Parameter	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	−0.12	1.33	0.09	.92
Host phylogenetic range	0.67	0.04	14.47	< .001
Occurrences per area	−0.24	0.05	−5.34	< .001
Total occurrences	0.09	0.03	2.64	.008

Parameter	Estimate	SE	t-value	p-value
Intercept	0.22	1.17	0.02	.98
Host phylogenetic range	0.57	0.04	14.02	< .001
Occurrences per area	-0.37	0.04	-9.19	< .001
Total occurrences	0.34	0.03	10.74	< .001

TABLE 2 Parameter estimates, standard errors, *t* and *p*-values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range

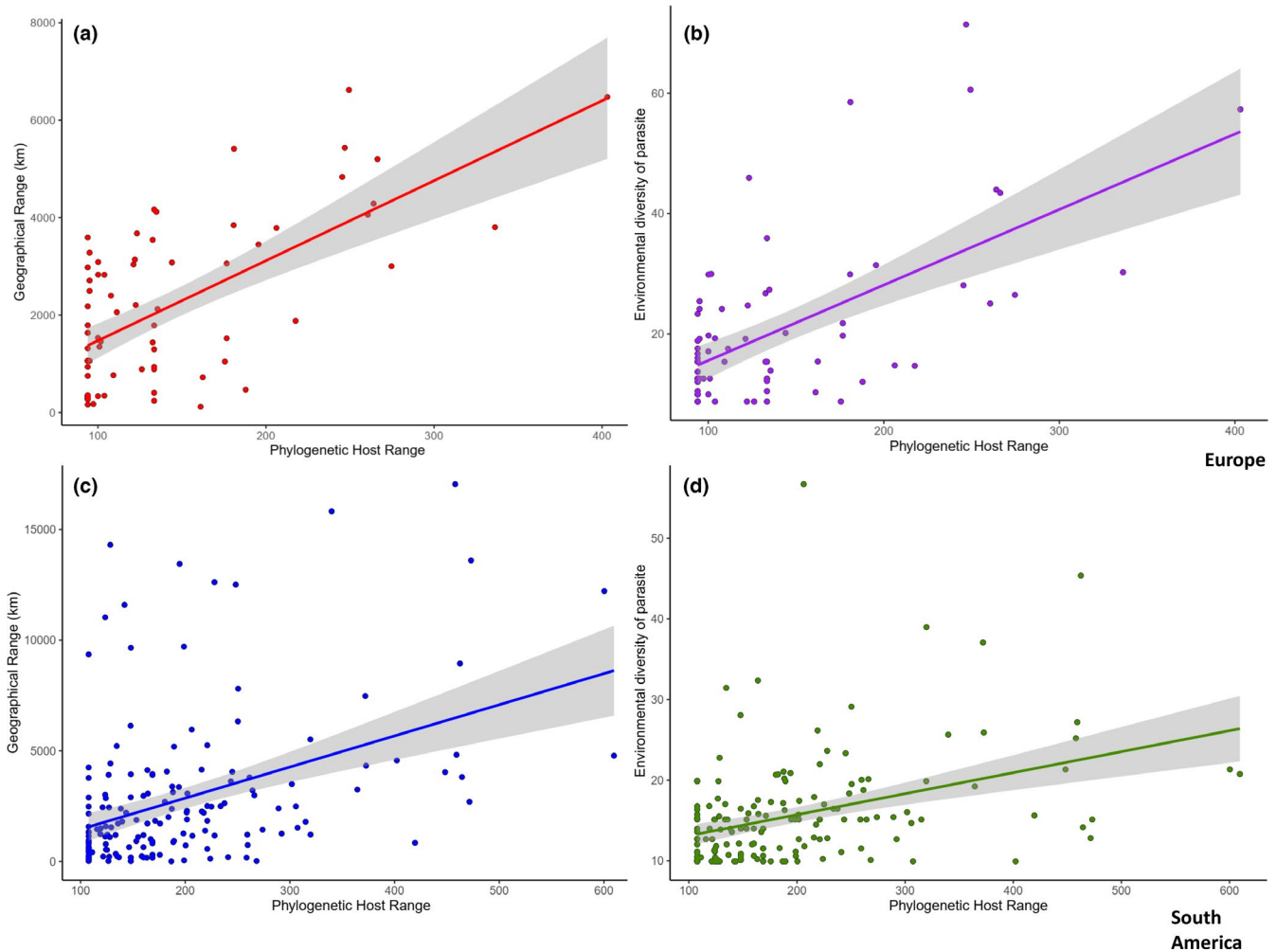


FIGURE 2 (a) Relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range (in kilometres) in Europe. (b) Relationship between the host phylogenetic range of haemosporidians and their environmental range in Europe. (c) Relationship between the host phylogenetic range of haemosporidians and their geographical range (in kilometres) in South America. (d) Relationship between the host phylogenetic range of haemosporidians and their environmental range in South America

Parameter	Estimate	SE	t-value	p-value
Intercept	0.02	1.21	0.01	.98
Host phylogenetic range	0.37	0.11	3.17	.002
Occurrences per area	-0.11	0.08	-1.29	.20
Total occurrences	0.42	0.12	3.21	.002

TABLE 3 Parameter estimates, standard errors, *t* and *p*-values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range in Europe

to their geographical range, both at a world scale and in South America. In contrast, this relationship is not detected in Europe. These seemingly contradictory results can be explained by the fact that Europe and South America present highly different degrees

of host and vector diversity (Jetz et al., 2012; Santiago-Alarcon et al., 2012). Europe is a much more environmentally homogeneous continent than South America, which comprises > 10 distinct biomes and multiple phytophysiognomies (Turchetto-Zolet et al., 2013). As

TABLE 4 Parameter estimates, standard errors, t and p -values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range in Europe

Parameter	Estimate	SE	t-value	p-value
Intercept	-0.04	0.76	-0.05	.95
Host phylogenetic range	0.28	0.07	3.77	< .001
Occurrences per area	-0.19	0.05	-3.67	< .001
Total occurrences	0.59	0.08	7.08	< .001

TABLE 5 Parameter estimates, standard errors, t and p -values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range in South America

Parameter	Estimate	SE	t-value	p-value
Intercept	0.12	1.67	0.07	.94
Host phylogenetic range	0.55	0.11	4.83	< .001
Occurrences per area	-0.29	0.09	-3.06	.002
Total occurrences	0.12	0.10	1.27	.20

TABLE 6 Parameter estimates, standard errors, t and p -values for the phylogenetically controlled least squares model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range in South America

Parameter	Estimate	SE	t-value	p-value
Intercept	0.27	1.01	0.25	.80
Host phylogenetic range	-0.05	0.07	-0.65	.51
Occurrences per area	-0.37	0.06	-5.88	< .001
Total occurrences	0.75	0.06	11.25	< .001

pointed out by Pinheiro et al. (2016), adaptations that enhance the local fitness of parasites, by increasing either their performance in the local host community or their tolerance to the local environment, are also expected to have adaptive value in similar sites, but to be maladaptations in dissimilar ones. Therefore, a trade-off among parasite lineages between local abundance and geographical range is expected to emerge only if sufficiently heterogeneous regions are considered (Pinheiro et al., 2019). This is the case for South America, in which different localities expose parasites to wider sets of resources (e.g. avian hosts and vectors) and abiotic conditions, but not for Europe. Interestingly, when considering the environmental range of parasites directly, its relationship to the local abundance of parasites is negative in both continents.

Overall, our results suggest that locally abundant parasites are also geographically and environmentally restricted; conversely, we also demonstrate that parasite abundance is an important factor determining haemosporidian range, with more abundant parasites (e.g., parasites presenting a higher total number of observations) also more widely spread. Restricted assemblages of hosts and environmental conditions could benefit parasites by allowing them to allocate more resources to reproduction instead of investing in mechanisms to combat and adapt to multiple environmental features. In addition, being locally restricted also enables haemosporidian parasites to complete their life cycles at the optimal temperature for their development while in the vector. It is known, for example, that the development of *Plasmodium relictum* in its vector is constrained below 13°C (Lapointe et al., 2010). Hence, local community adaptation could enhance the performance of local specialist parasites, thereby increasing

their abundance. We also observed that host phylogenetic range is positively associated with the environmental range of parasites only at a global scale and in Europe, whereas it seems to have no impact on the environmental range of parasites in South America. Thus, it is possible that environmental range in highly diversified habitats is associated mainly with the presence of abiotic conditions adequate for parasite development and/or competent vector availability.

Identifying the determinants of parasite geographical and environmental ranges can contribute to predictions of the lineages most likely to spread into new regions. Haemosporidian invasions into new areas have been linked to extinctions and outbreaks in susceptible bird populations world-wide (Schoener et al., 2014; Van Riper III et al., 1982, 1986; Vanstreels et al., 2014, 2019). Thus, recognizing and forecasting future haemosporidian spillover into new regions and naïve populations is fundamental for successful management of endangered species. Naturally, the geographical range and prevalence of haemosporidian lineages are expected to change owing to the effects of climate change (Garamszegi, 2011; Loiseau et al., 2013). Haemosporidians could increase or decrease their ranges, because changes in climatic conditions are expected to modify their potential distribution (Pérez-Rodríguez et al., 2014). It is important to note, however, that symbionts require suitable hosts to establish in new communities (Mestre et al., 2020); therefore, parasites ranging into warmer regions in the future will be subject to the constraints of their phylogenetic host range or their propensity to switch hosts. Nevertheless, no research on haemosporidians has evaluated the impact of vector specificity on the geographical or environmental range of the parasites.

5 | CONCLUSION

In summary, here we demonstrate that the geographical and environmental ranges of haemosporidian parasites are strongly linked to the ability of the parasites to infect multiple hosts. In other words, we observed that there is a substational relationship between the niche breadth of parasites and their geographical and environmental range size. At the same time, our findings also reveal that geographically and environmentally constrained parasites achieve higher local abundances in nature, indicating the existence of a trade-off between being widespread and being locally abundant. In addition, we confirm that host specificity is linked to parasite range at both global and regional levels. However, we observed no relationship between mean parasite local abundance and parasite geographical range in Europe, which might indicate that in regions with limited host or environmental diversity, there is no advantage to being a habitat-specialist parasite. To achieve a more complete picture of the factors associated with geographical or environmental ranges in haemosporidians, future research should investigate the role of the vector specificity and vectorial capacity of parasites, which are factors that have received extremely little attention to date.

ACKNOWLEDGMENTS

We thank the MalAvi curators for maintaining the database and for making all data available, and all the researchers who shared their data. We are also grateful to Dr Ludovic Dutoit for supportive assistance with our analyses.

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

All authors conceived the idea and designed the study. D.A.D. and G.M.F. performed the data analyses. D.A.D. wrote the manuscript with input from both other authors. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in MalAvi at: <http://130.235.244.92/Malavi/> (Bensch et al., 2009). The R code and all files necessary to perform our analyses are available as Supporting Information.

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BIOSKETCHES

Daniela de Angeli Dutra is currently interested in the dispersal patterns of parasites/pathogens (and their consequences). This research is part of her PhD project at the University of Otago.

Gabriel Moreira Félix is currently interested in ecological specialization and its consequences for the structure of ecological networks.

Robert Poulin is a professor of Zoology at the University Otago whose research extends to all ecological and evolutionary aspects of host–parasite interactions, across all taxa and biomes.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article at the publisher's website.

How to cite this article: de Angeli Dutra, D., Moreira Félix G., & Poulin R. (2021). Contrasting effects of host or local specialization: Widespread haemosporidians are host generalist, whereas local specialists are locally abundant. *Global Ecology and Biogeography*, *30*, 2467–2476. <https://doi.org/10.1111/geb.13403>