**Abstract:**

**Aim:** Despite the wide distribution of many parasites around the globe, the range of individual species varies significantly even among phylogenetically related taxa. Since parasites need suitable hosts to complete their development, parasite geographical and environmental ranges should be limited to communities where their hosts are found. Parasites may 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 to their host specificity and their local abundance.

**Location:** Worldwide

**Time period:** 2009 to 2021

**Major taxa studied:** Avian haemosporidian parasites

**Methods:** We tested these hypotheses using a global database which comprises data on avian haemosporidian parasites from across the world. For each parasite lineage, we computed five metrics: phylogenetic host-range, environmental range, geographical range, and their mean local and total number of observations in the database. Phylogenetic generalized least squares models were ran to evaluate the influence of phylogenetic host-range and total and local abundances on geographical and environmental range. 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) associates positively to both the parasites’ geographical and environmental ranges at global and Europe scales. For South America, generalism only associates with geographical range. Finally, mean local abundance (mean local number of parasite occurrences) was negatively related to geographical and environmental range. This pattern was detected worldwide 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, only becomes evident when sufficient heterogeneous host communities are considered.

**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 (Vellend, 2010; Ricklefs & Jenkins, 2011; Weiher *et al.*, 2011). Indeed, 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 fully develop 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 as the relative importance of different processes can change between scales (Ricklefs, 2008; Vellend, 2010; Ricklefs & Jenkins, 2011). Further, 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 into shaping trophic interaction in communities (Mouritsen & Poulin, 2005; Kuris *et al.*, 2008; Lafferty *et al.*, 2008; Dunne *et al.*, 2013). 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 to colonize new communities. In addition, phylogenetic ancestry of parasites and their hosts determines parasites’ host specificity and community assembly (Clark & Clegg, 2017). Concomitantly, studying parasite range patterns is fundamental to understand their dispersal in nature and potentially predict their colonization of new regions. Past studies have observed contrasting outcomes regarding the influence of parasites’ host specificity 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., number of times a parasite was observed) as the main factor explaining parasite range. However, host specificity has earlier 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 favorable environments (Tuomisto *et al.*, 2003). Indeed, previous research suggests specialized species may perform well in certain homogenous 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 to parasites residing in few homogenous localities. Concomitantly, community similarity in both fauna and flora decreases with distance (Nekola & White, 1999; Tuomisto *et al.*, 2003; Qian & Ricklefs, 2012). Therefore, the higher the geographical range of a parasite, the more diverse must be the assemblage of potential hosts and environmental conditions it confronts. Consequently, to successfully explore dissimilar sets of hosts and environments, widespread parasites may present generic, locally sub-optimal adaptations (Futuyma & Moreno, 1988). Indeed, Clark *et al.*, (2018) showed that host phylogeny and climate shape haemosporidian parasite assemblages and limit parasite distribution, respectively. Further, 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 since a trade-off between being widespread and 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 (Valkiūnas, 2005; Fecchio *et al.*, 2020). These parasites have been widely used as models for the study of host-parasite interaction in the last decade. To date, ~4000 distinct lineages have been detected and about 250 species have been described (Valkiūnas, 2005; Bensch *et al.*, 2009; Valkiūnas & Iezhova, 2018). Avian haemosporidians also possess distinct levels of host specificity (i.e. their ability to infect few versus multiple host species) and geographical range, with some lineages able to infect multiple avian species and found on all continents, except Antarctica (Valkiūnas, 2005). Further, host specificity varies greatly among genera, with *Plasmodium* parasites generally presenting lower host specificity (Ricklefs & Fallon, 2002; Hellgren *et al.*, 2009; Moens & Pérez-Tris, 2016). Some *Plasmodium* lineages have been found in at least 50 different bird species, and the *Plasmodium relictum* lineage SGS1 has been recorded in over 110 bird species worldwide (Rivero & Gandon, 2018). Thus, due 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). Since haemosporidian development can be constrained by environmental factors during their lifecycle 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 tested as well whether parasites infecting wider range of hosts can also colonize more environmentally distinct regions, hypothesizing that host generalist parasites should exploit wider environmental ranges (i.e. range of climatic conditions across which a parasite occurs). In addition, we also tested 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 due to local community (habitat) specialization. To address these hypotheses, we calculated the host, environmental and geographical ranges of haemosporidian parasites and, thereafter, tested whether parasite phylogenetic host-range and mean local parasite abundance (e.g., mean local number of times a parasite was observed) were 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 explicitly test the influence of environmental conditions. Further, aiming to compare results between distinct scales and regions with different degrees of host and environmental diversity, we also tested our hypothesis separately for the South American and European continents (Jetz *et al.*, 2012; Girardello *et al.*, 2019).

**Methods**

*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 ~6200 sequenced parasites representing 1602 distinct lineages (775 *Plasmodium* and 827 *Haemoproteus*) collected from 1139 different host species and 757 localities from all continents except Antarctica (Supplementary figure 1, Supplementary Table 1). The parasite lineages deposited in MalAvi are based on a cyt b fragment of 478 bp. This dataset was used to calculate the parasites’ geographical, environmental and phylogenetic ranges.

*Geographical range*

All analyses in this study were performed using R version 4.02. 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 employed the function “GeoRange\_MultiTaxa” to calculate the minimum spanning tree distance for each parasite lineage distance (i.e. shortest total distance in kilometers of all lines connecting each locality). Therefore, as 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.

*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, as the more diverse an assemblage is, the more uncertainty regarding to which species 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 *et al.*, 2014b). 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 case, instead of species, we are measuring the effective number of phylogenetic entities in the assemblage.

Here, we computed 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 *et al.*, 2014a). Hill numbers are parameterized by a parameter “q” that determines the sensitivity of the metric to relative species abundance. Different “q” values produce Hill numbers associated with different diversity metrics. We set q = 1 to compute the Hill number associated with Shannon diversity. Here, low Hill numbers indicate 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 version 2 (http://www.worldclim.com/version2) for all sites used in this study (N = 713). Then, we standardized the 19 variables by centering and scaling them by their respective mean and standard deviation. Thereafter, we computed 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.

*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 parasite’s geographical, environmental and phylogenetic ranges (see above); this represented 401 distinct parasite lineages. This inference was produced using MrBayes 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-fit 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 1000 generations. The first 1250 million trees (25%) were discarded as a burn-in step 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 0.999. *Leucocytozoon caulleryi* was used as the outgroup to root the phylogenetic tree as *Leucocytozoon* spp. represents a basal group within avian haemosporidians (Pacheco *et al.*, 2020).

*Statistical analyses*

Two phylogenetically controlled least squares models (PGLS) were performed 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 above). We used 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 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 population-level effects and parasite phylogeny was included as a random effect. Only lineages observed in two or more localities were included in our analyses since others returned missing values when calculating geographical range. Likewise, we discarded all lineages that did not possess an available complete cyt b fragment in MalAvi or phylogenetic information for their hosts. We ran the PGLS models applying the “pgls” function from the “caper” package (Orme, 2013). In addition, 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 component analyses (PCA) was performed using WorldClim data for all localities in Europe and South America to confirm there are 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 due to the reduced number of distinct lineages.

**Results**

Out of the ~6200 sequences of parasites representing 1602 distinct lineages, ~4900 sequences from 401 distinct lineages were retained in the and analysed in the PGLS models. From the 401 parasite lineages evaluated, 212 lineages represented *Plasmodium* parasites while 189 were *Haemoproteus* parasites. The analysis included data from 757 localities worldwide, with 207 in South America and 209 in Europe. Principal component analyses confirmed there is greater environmental heterogeneity among South American than European localities (Supplementary Figure 2).

Worldwide, parasites’ host phylogenetic range (generalism) was positively associated with both their geographical (Figure 1A, Table 1) and environmental ranges (Figure 1B, Table 2). This result remains when evaluating *Plasmodium* and *Haemoproteus* parasites separately (Supplementary Tables 2-5). In addition, total and mean local number of occurrences of parasites were positively and negatively, respectively, associated 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 (Supplementary Table 4). Moreover, no association was found between total abundance of *Plasmodium* spp. and parasite geographical range (Supplementary Table 2). For all other models, we again observed negative associations between the parasites’ mean local abundance and their geographical and environmental ranges (Supplementary Tables 2-3,5).

On the continental scale, the results were slightly different. First, although the parasite’s host phylogenetic range (generalism) was still positively associated with their geographical range in both Europe and South America, it only related to environmental range in Europe (Figure 2A-D, Tables 3-6). Second, while 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). As well as on the global scale, the mean number of local occurrences was negatively associated with environmental ranges on both continents (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 total number of occurrences and environmental range in both continental models (Table 4 and 6).

**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 since 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 geographic 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, while 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 host (Mestre *et al.*, 2020). Further, host switching and dispersal seem the two major drivers for haemosporidian diversification (Fecchio *et al.*, 2018), processes which could be intrinsically correlated. As we observed in this study, generalist parasites achieve a higher geographical and environmental range, concomitantly, these parasites are more likely to host switch (Beadell *et al.*, 2004). Host switching facilitates parasite dispersal as it provides opportunities to infect hosts that inhabit regions unoccupied by the original hosts. Hosts and vectors play a fundamental role for parasite spread, defining the Hutchinsonian niche of parasites and determining their biotic, environmental or dispersal barriers during the range expansion processes (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, sexually reproduce and be transmitted to a new host (Valkiūnas, 2005; Fecchio *et al.*, 2020). Therefore, being able to infect both residents and migratory hosts and fully develop in a wide range of vectors also favor parasite dispersal and may be one of the factors explaining the role of host specificity in shaping parasite range.

While 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 to their geographical range on both 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 more than ten distinct biomes and multiple phytophysiognomies (Turchetto-Zolet *et al.*, 2013). As pointed out by Pinheiro *et al.* (2016), adaptations that enhance the local fitness of parasites – either by increasing their performance in the local host community or their tolerance to the local enviroment – are also expected to have adaptive value in similar sites, but 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 enviromental range of parasites directly, its relationship to parasite’s local abundance is negative in both continents.

Together, our results suggest that locally abundant parasites are also geographically and environmentally restricted; conversely we also demonstrate that parasite abundance is an important factor determing haemosporidian range, with more abundant parasites (e.g., parasites presenting 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 cycle 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 13ºC (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 only positively associated with the parasites’ environmental range at a global scale and in Europe, whereas it seems to have no impact on parasites’ environmental range in South America. Thus, it is possible that environmental range in highly diversified habitats is mainly associated with the presence of abiotic conditions adequate to parasite development and/or competent vector availablility.

Identifying the determinants of parasite geographical and environmental ranges can contribute to predictions of the lineages most likely to spread into new regions. Indeed, haemosporidian invasions into new areas have been linked to extictions and outbreaks in susceptible bird populations worldwide (Van Riper III *et al.*, 1982, 1986; Schoener *et al.*, 2014; Vanstreels *et al.*, 2014, 2019). Thus, recognising 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 due to the effects of climate change (Garamszegi, 2011; Loiseau *et al.*, 2013). Haemosporidians could, then, increase or decrease their range as 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 estabilish into 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 propensity to host switch. Nevertheless, no research on haemosporidians has evaluated the impact of vector specificity on the parasites’ geographical or environmental range.

**Conclusion**

In summary, here we demonstrate that the geographical and environmental ranges of haemosporidian parasites are strongly linked to the parasites’ ability to infect multiple hosts. In other words, we observed that there is a substacional relationship between parasites’ niche breadth and their geographical and environmental range size. At the same time, our findings also reveal that geographical 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 may indicate that in regions with limited host or environmental diversity, there is no advantage of 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 parasites’ vector specificity and vectorial capacity, factors that have received extremely little attention to date.

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**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). R code and all files necessary to perform our analyses are available as supplementary material.

Figure 1: A- relationship between the host phylogenetic range of avian haemosporidian parasites, and their geographical range in kilometers. B- relationship between the host phylogenetic range of haemosporidians and their environmental range.

Figure 2: A- relationship between the host phylogenetic range of avian haemosporidian parasites, and their geographical range in kilometers 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 kilometers in South America. D- relationship between the host phylogenetic range of haemosporidians, and their environmental range in South America.

Table 1: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | -0.12 | 1.33 | 0.09 | 0.92 |
| Host phylogenetic range | 0.67 | 0.04 | 14.47 | <0.001 |
| Occurrences per area | -0.24 | 0.05 | -5.34 | <0.001 |
| Total occurrences | 0.09 | 0.03 | 2.64 | 0.008 |

Table 2: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | 0.22 | 1.17 | 0.02 | 0.98 |
| Host phylogenetic range | 0.57 | 0.04 | 14.02 | <0.001 |
| Occurrences per area | -0.37 | 0.04 | -9.19 | <0.001 |
| Total occurrences | 0.34 | 0.03 | 10.74 | <0.001 |

Table 3: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range in Europe.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | 0.02 | 1.21 | 0.01 | 0.98 |
| Host phylogenetic range | 0.37 | 0.11 | 3.17 | 0.002 |
| Occurrences per area | -0.11 | 0.08 | -1.29 | 0.20 |
| Total occurrences | 0.42 | 0.12 | 3.21 | 0.002 |

Table 4: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range in Europe.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | -0.04 | 0.76 | -0.05 | 0.95 |
| Host phylogenetic range | 0.28 | 0.07 | 3.77 | <0.001 |
| Occurrences per area | -0.19 | 0.05 | -3.67 | <0.001 |
| Total occurrences | 0.59 | 0.08 | 7.08 | <0.001 |

Table 5: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their geographical range in South America.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | 0.12 | 1.67 | 0.07 | 0.94 |
| Host phylogenetic range | 0.55 | 0.11 | 4.83 | <0.001 |
| Occurrences per area | -0.29 | 0.09 | -3.06 | 0.002 |
| Total occurrences | 0.12 | 0.10 | 1.27 | 0.20 |

Table 6: Parameter estimates, standard errors, and confidence intervals for the PGLS model testing the relationship between the host phylogenetic range of avian haemosporidian parasites and their environmental range in South America.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | Stand. Error | T value | P value |
| Intercept | 0.27 | 1.01 | 0.25 | 0.80 |
| Host phylogenetic range | -0.05 | 0.07 | -0.65 | 0.51 |
| Occurrences per area | -0.37 | 0.06 | -5.88 | <0.001 |
| Total occurrences | 0.75 | 0.06 | 11.25 | <0.001 |