

# Host phylogeny and seasonality shapes avian haemosporidian prevalence in a Brazilian biodiverse and dry forest: the Caatinga

## Research Article

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### Abstract

The relationships between host phylogenetics, functional traits and parasites in wildlife remain poorly understood in the Neotropics, especially in habitats with marked seasonal variation. Here, we examined the effect of seasonality and host functional traits on the prevalence of avian haemosporidians (*Plasmodium* and *Haemoproteus*) in the Brazilian Caatinga, a seasonally dry tropical forest. 933 birds were evaluated for haemosporidian infections. We found a high parasitism prevalence (51.2%), which was correlated with phylogenetic relatedness among avian species. Prevalence varied drastically among the 20 well-sampled species, ranging from 0 to 70%. Seasonality was the main factor associated with infections, but how this abiotic condition influenced parasite prevalence varied according to the host-parasite system. *Plasmodium* prevalence increased during the rainy season and, after excluding the large sample size of Columbiformes ( $n = 462/933$ ), *Plasmodium* infection rate was maintained high in the wet season and showed a negative association with host body mass. No association was found between non-Columbiform bird prevalence and seasonality or body mass when evaluating both *Plasmodium* and *Haemoproteus* or only *Haemoproteus* infections. Parasite community was composed of 32 lineages including 7 new lineages. We evidenced that even dry domains can harbour a high prevalence and diversity of vector-borne parasites and pointed out seasonality as a ruling factor.

### Introduction

Seasonality is an important determinant of vector-borne diseases (Fecchio *et al.*, 2019). Vectors, pathogens and hosts are dependent on abiotic conditions for reproduction and survival, and changes in these conditions may affect the transmission of many distinct diseases (Kelly-Hope *et al.*, 2009; Gonzalez-Quevedo *et al.*, 2014; Ferraguti *et al.*, 2018). For instance, higher temperatures increase vector abundance and often accelerate parasite development in their vectors (Valkiūnas, 2005; Lapointe *et al.*, 2010), thus likely increasing parasite prevalence in vertebrate hosts (Zamora-Vilchis *et al.*, 2012). Similarly, heavy rain periods and severe droughts can increase or decrease the prevalence of diseases transmitted by vectors dependent on water collections for breeding sites (Hoshen and Morse, 2004; Landesman *et al.*, 2007). Changes in the pattern of seasonality may become a challenge to future ecological studies due to global climate change (IPCC, 2021), thus it is important to understand the impact of seasonality on vector-borne pathogens distribution.

Avian haemosporidians are a diverse group of protozoan parasites, including the genera *Plasmodium* and *Haemoproteus* that use a variety of Diptera species as vectors. *Plasmodium* parasites are transmitted by mosquitoes (Culicidae) whereas *Haemoproteus* (*Parahaemoproteus*) and *Haemoproteus* (*Haemoproteus*) are transmitted by either biting midges (Ceratopogonidae) or louse flies (Hippoboscidae), respectively, hence, environmental conditions could affect their transmission differently (Ferreira *et al.*, 2020). There are more than 200 species already described for these parasites, which can develop in a variety of bird and vector species (Marzal, 2012; Clark *et al.*, 2014). Furthermore, avian haemosporidians are associated with mortality episodes in wild birds (Ricklefs, 2017) and can reduce longevity and reproductive fitness of chronically infected hosts (Marzal *et al.*, 2005; Asghar *et al.*, 2015).

Host biological and ecological traits also influence haemosporidian prevalence, diversity and distribution (Pulgarín-R *et al.*, 2018; Fecchio *et al.*, 2021; de Angeli Dutra *et al.*, 2021a). Individual traits such as plumage colour and body mass are associated with differences in parasite prevalence (De La Torre *et al.*, 2020; Filion *et al.*, 2020). For example, a negative effect of haemosporidian parasites on body condition was detected among passerine species (Palinauskas *et al.*, 2016; Schoenle *et al.*, 2017). Species functional traits, such as habitat

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selection, plumage colouration, nest type, migratory behaviour and flocking, have all been implied as predictors in the variation of haemosporidian prevalence (Gonzalez-Quevedo *et al.*, 2014; Ganser *et al.*, 2020; de La Torre and Campião, 2021; de Angeli Dutra *et al.*, 2021b; Aguiar de Souza Penha *et al.*, 2022). For instance, *Haemoproteus* prevalence reaches higher rates among avian species inhabiting mid-high and canopy strata and haemosporidian infections are more common among strictly migratory species (de La Torre and Campião, 2021; de Angeli Dutra *et al.*, 2021b). Moreover, species that are phylogenetically closely related tend to exhibit greater similarity in functional traits as compared to distantly related species, which may be correlated with parasite exposure and likelihood of infection (Barrow *et al.*, 2019).

How seasonality affects avian haemosporidian parasites in tropical seasonally dry environments is still uncertain. Ferreira *et al.* (2017) found seasonal changes in parasite prevalence, while no variation was detected by Fecchio *et al.* (2015). These contrasting results indicate the need for further investigations of avian haemosporidian distributions across different periods in tropical areas with marked seasonality. The Caatinga is a seasonally dry tropical forest (SDTF) in Brazil. This domain is located exclusively in northeastern Brazil, covering an area of approximately 845 000 km<sup>2</sup> which represents about 11% of the national territory (Bucher, 1982). The region's climate is classified as hot semi-arid (type 'BSh') according to Köppen's classification (Alvares *et al.*, 2013), characterized by a long dry season between July and January with irregular distribution of rainfall in the rest of the year. This domain, which had been considered inappropriately associated with low diversity regions in terms of endemism and species richness (Vanzolini *et al.*, 1980; Leal *et al.*, 2005), actually harbours high biodiversity. Caatinga is home to more than 200 bird species with 22 considered endemic (Tabarelli and Silva, 2003).

Due to the high biodiversity in the Caatinga and the lack of knowledge of the distribution and diversity of avian haemosporidians in this region and in seasonally dry environments, we aimed to investigate the effect of seasonality and host functional traits on avian haemosporidian prevalence and diversity in the Caatinga ecosystem.

## Methods

### Study area

We conducted this study in Seridó Ecological Station – ESEC Seridó – (06° 34'36.2" S and 37°15'20.7" W), encompassing an area of 1163 ha and located in the municipality of Serra Negra do Norte, state of Rio Grande do Norte (Brazil) (Fig. 1). The region has a semiarid climate, with dry season reaching up to 10 dry months with irregular rainfall distribution. Mean annual precipitation varies between 500 and 800 mm year<sup>-1</sup> and mean annual temperature varies between 28°C and 30°C, with lowest and highest temperatures ranging between 17°C and 40°C (Bucher, 1982). Local vegetation is composed of grass-covered soil and arboreal-shrub Caatinga with sparse small trees (<7 m) (Duque, 1953). The region has a high bird richness, with approximately 200 species, including some threatened and near-threatened species (Pichorim *et al.*, 2016a, 2016b).

### Sample collection and DNA extraction

We captured wild birds in 4 field campaigns, each consisting of 7 days in 4 different sampling seasons (June 2013: 'first rainy', which had 45.8 mm of accumulated precipitation, January 2014: 'second rainy', with 95.4 mm of accumulated precipitation, July 2014: 'first dry' 7.0 mm of accumulated precipitation, and

December 2014 'second dry', no precipitation). Birds were captured using mist nets (Ecotone®; 18 m × 3 m, mesh 19 mm) set in a 12-ha quadrant (400 × 300 m). This large quadrant was divided into 48 cells measuring 50 × 50 m, with the capture site (i.e. where the mist net was placed) located at the centre of each cell. We sampled 24 cells per day between 5h00 and 10h00 in each field campaign, resulting in an effort of 181 440 m<sup>2</sup> h (54 m<sup>2</sup> of per net × 5 h per day × 24 nets per day × 7 days per campaign × 4 campaigns; Straube and Bianconi, 2002). Captured birds were identified, banded (with metal rings provided by CEMAVE/ICMBio (Centro Nacional de Pesquisa e Conservação de Aves Silvestres), weighed, and examined for the presence of ectoparasites (ticks, mites and lice) and brood patches. We collected blood samples from the brachial vein using insulin needles and stored the samples on filter paper. Captured birds were subsequently released near the capture sites. We extracted the genomic DNA from the blood samples using phenol-and Russellchloroform protocol followed by precipitation with isopropanol, as described by Sambrook and Russell (2001). We quantified the extracted DNA using NanoDrop™ Lite Spectrophotometer (Thermo Scientific®), according to the manufacturer's instructions.

### Molecular detection and characterization of haemosporidian parasites

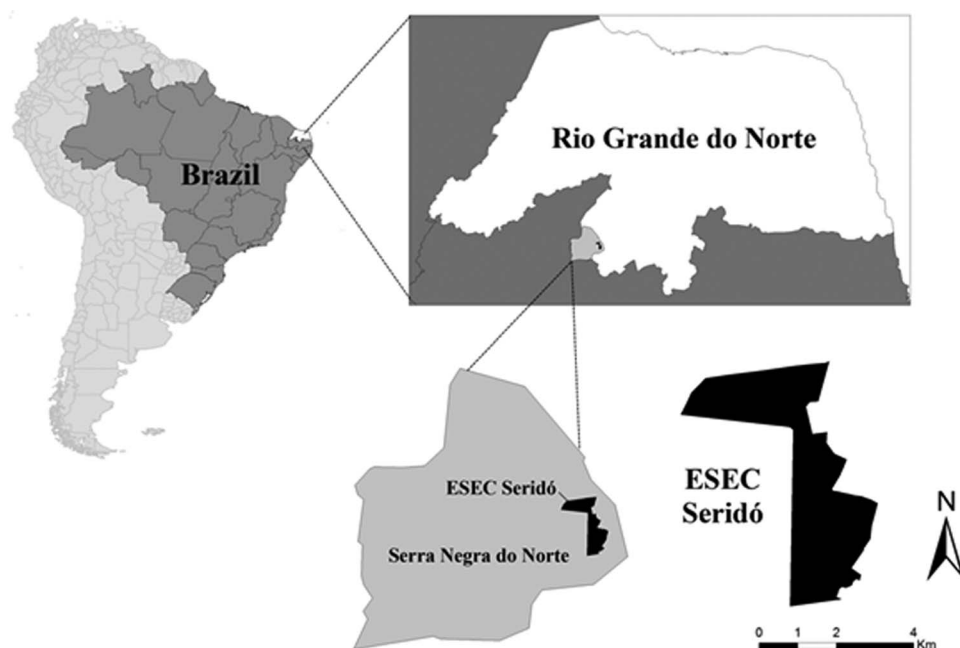
We performed a screening PCR using primers designed by Fallon *et al.* (2003). To amplify both *Plasmodium* and *Haemoproteus* genera. All positive samples at the screening PCR were subjected to a Nested-PCR, described by Hellgren *et al.* (2004), which amplifies a 478 bp fragment of the mitochondrial cytochrome b gene (cyt-b) of *Plasmodium* and *Haemoproteus*. We did not perform the nested assay that amplifies *Leucocytozoon* parasites because of their low prevalence in Brazil (Fecchio *et al.*, 2020). We used *Plasmodium gallinaceum* derived from experimentally infected chicks as a positive control. Sterile ultrapure water was used as a negative control. We performed all PCR and electrophoresis methods according to (Roos *et al.*, 2015).

We purified the positive Nested-PCR products following (Green and Sambrook, 2012). The purified DNA was bidirectionally sequenced by the dideoxynucleotide method in ABI 3100® capillary automated sequencer (Applied Biosystems, USA) using the Big Dye Terminator Mix kit (Applied Biosystems, USA) following reaction and reading conditions indicated by the manufacturer.

We edited obtained sequences using Chromas Pro (Technelysium Pty Ltd, Helensvale, Australia) checking for the presence of mixed infections (presence of double peaks in the electrochromatograms). We compared our assembled sequences to those deposited in public databases, such as GenBank (<http://www4.ncbi.nlm.nih.gov>) and MalAvi (Bensch *et al.*, 2009). Sequences with a minimum of one base difference were considered unique cytochrome b lineages, and those with no database record were considered novel lineages. We deposited novel lineages in GenBank (acc. num. MK981615–MK981622). New records of previously described sequences were also deposited in GenBank (acc. num. MK981623–MK981646).

### Host functional traits data

We obtained avian functional trait data for each host from AVONET (Tobias *et al.*, 2022). We included the variables and categories as follows: (1) migratory behaviour: resident, partially migratory and strictly migratory; (2) primary lifestyle: insessorial, terrestrial and generalist; (3) body mass; (4) host distribution range (i.e. geographical distribution of a bird species).



**Figure 1.** Map of Seridó Ecological Station (ESEC Seridó), Rio Grande do Norte, Brazil.

## Statistical analysis

### Phylogenetic signal

All analyses were conducted in R version 4.0 (R Core Team, 2017). Firstly, we filtered all bird species that were sampled 4 or fewer times, this filtered dataset ( $N=880$ ) was used in all following analyses. To evaluate if the phylogenetic relationship among bird species is correlated with parasite prevalence in our dataset, we downloaded a full avian phylogeny file from the AllBirdsHackett1.tre website (<https://birdtree.org/>) which contain 10 thousand trees (Hackett *et al.*, 2008; Jetz *et al.*, 2012). Later, we applied the 'treeman' package (Bennett *et al.*, 2017) to create a treeman file containing all trees from the original file. Then, we randomly selected a phylogenetic tree to avoid selection bias. We excluded all bird species from the tree which were not present in our dataset. Then, we calculated  $K$  (i.e. a measure that allows comparisons of the amount of phylogenetic signal across a specific trait (Blomberg *et al.*, 2003)) to evaluate the phylogenetic signal for haemosporidian prevalence among bird species in our dataset. Values of  $K$  can range between 0 and 1, equalling 1 when the trait has evolved consistently with a Brownian motion and trait values are similar among related species, or 0 when trait values are phylogenetically unrelated among species. To estimate  $K$ , we applied the 'phylosig' function from the 'phytools' package (Revell, 2012).

### Bayesian analyses

We constructed 4 Bayesian models using the 'brms' package (Bürkner, 2017) to evaluate whether bird functional traits and seasonality influence haemosporidian prevalence. In all models, we created a matrix with phylogenetic distances among all avian species to account for influence of host phylogenetic relationships on haemosporidian prevalence, which was included as a random variable. Since we observed strong phylogenetic signals in our dataset (see Results), adding phylogenetic relatedness among species in our models was important to take into consideration when evaluating the effect of the other variables included in the models. The explanatory variable effects included in each model are represented in Table 1. The 4 models were weighted using the function 'loo\_model\_weights' and the one with the highest weight value

was selected. In all models, we used the infection status of individual birds as our dependent variable (binary response: 0 for uninfected, 1 for infected). We ran all models using the Bernoulli distribution family and 4 chains with 4000 total iterations per chain (2000 for warmup, 2000 for sampling). Priors were chosen using 'get\_prior' function and the models' results were plotted using the 'conditional\_effects' function to visualize the predictions of the population-level effects. The selected model was repeated 6 times using haemosporidians of both genera, *Plasmodium* only and *Haemoproteus* (both subgenera) only parasites (whenever the parasite ID was achieved through sequencing) and using the entire dataset ( $N=880$ ) or the dataset excluding Columbiformes ( $N=483$ ), which represented most of the birds sampled. It is imperative to rerun analyses excluding Columbiformes due to the minor influence of environmental conditions on *H. (Haemoproteus)* vectors, as those mostly reside on their hosts' skin and Columbiformes are the main hosts of *H. (Haemoproteus)*.

## Results

### *Plasmodium* and *haemoproteus* diversity

We detected 481 positive samples (prevalence equal to 51.2%) in the screening PCR. Haemosporidian prevalence varied drastically among the 20 best sampled host species, ranging from 0 to 70%

**Table 1.** Model averaging weights for the 4 models tested using pseudo-BMA (where higher values indicate better model fit) with Bayesian bootstrap method

Models	Pseudo-BMA
<i>Infection status</i> ~ <i>Primary.Lifestyle</i> + <i>Incubation</i> + <i>Ectoparasites</i> + <i>Season</i> + <i>Mass</i> + <i>Migration</i> + <i>Range.Size</i>	0.0083
<i>Infection status</i> ~ <i>Primary.Lifestyle</i> + <i>Incubation</i> + <i>Ectoparasites</i> + <i>Season</i> + <i>Mass</i> + <i>Migration</i>	0.103
<i>Infection status</i> ~ <i>Incubation</i> + <i>Ectoparasites</i> + <i>Season</i> + <i>Mass</i> + <i>Migration</i>	0.246
<i>Infection status</i> ~ <i>Incubation</i> + <i>Ectoparasites</i> + <i>Season</i> + <i>Mass</i>	0.563

**Table 2.** Summary information of the sampling seasons, including infection data

Sampling/Season	Positive	Negative	Total	Prevalence
First rainy	109	129	238	45.79%
Second rainy	99	114	213	46.47%
First dry	197	127	324	60.80%
Second dry	76	82	158	45.79%
Total	481	528	933	51.5%

(Supplementary Table 2). All of those were subjected to *cyt-b* PCR and gene sequencing. However, we were able to obtain high-quality sequences for 191 individuals, which revealed 68 *Plasmodium* infections in 22 bird species (38.41%), 90 subgenus *Haemoproteus* (*Haemoproteus*) infections in 4 bird species (50.84%), and 19 subgenus *Haemoproteus* (*Parahaemoproteus*) infections in 10 bird species (10.83%). We were able to separate out haplotypes in 14 mixed infections in 10 bird species (3.92%), revealing *Plasmodium/Plasmodium* ( $n = 5$ ), *H. (Haemoproteus)/H. (Haemoproteus)* ( $n = 7$ ) and *H. (Parahaemoproteus)/H. (Parahaemoproteus)* ( $n = 2$ ) infections. The parasite community was composed of 32 distinct lineages (*Plasmodium* = 17; *H. (Haemoproteus)* = 05 and *H. (Parahaemoproteus)* = 10); 7 haemosporidian lineages were obtained for the first time.

We observed a difference in host range among distinct parasite taxa. *Haemoproteus (Haemoproteus)* mainly infected Columbiformes (88/90; 04 species), with 2 lineages detected in passerines; SocH3 infected *Pachyramphus polychropterus* (Tityridae) and SocH2 *Myiarchus tyrannulus* (Tyrannidae). This

parasite subgenus was represented by 5 genetic lineages: SocH3 ( $n = 69$ ), COPIC01 ( $n = 16$ ), SocH2 ( $n = 3$ ) and by 2 new lineages ZENAU01 ( $n = 1$ ) and ZENAU02 ( $n = 2$ ). We obtained 68 sequences of genus *Plasmodium* representing 17 lineages, including three novel one (POLPLU01, PHAMUR01 and NYSMAC05), that mainly infected Passeriformes. The most common lineages were PADOM11 (detected 15 times in 6 bird species), PHPAT01 (13 times in 9 species) and PADOM09 (10 times in 8 species). *Haemoproteus (Parahaemoproteus)* parasites were found 19 times, and the most common lineage, PAPOL03, was observed 8 times in 4 bird species. All haemosporidian-host links are available in Supplementary Table 3.

### Factors influencing haemosporidian prevalence

We observed that the haemosporidian prevalence was influenced by seasonality and body mass (Tables 2–4). However, the way that the seasonality influenced parasite prevalence varied according to the haemosporidian genus. When examining the entire dataset, we observed higher haemosporidian prevalence during the dry season (Fig. 2), whereas for *Plasmodium* we found higher prevalence in the rainy season (Fig. 3) and found no difference among seasons when looking at *Haemoproteus* parasites separately (Table 3). Likewise, when evaluating only non-Columbiform birds, we still observed higher *Plasmodium* prevalence in the rainy season. Nonetheless, seasonality did not influence overall haemosporidians prevalence and when *Haemoproteus* was analysed separately (Table 4). We also observed that Columbiform species were more common in the dry season, when they represented 66% of the sampled birds, compared to only 31% of the sampled birds during the rainy season. Further, haemosporidian prevalence varied between Columbiform and non-Columbiform

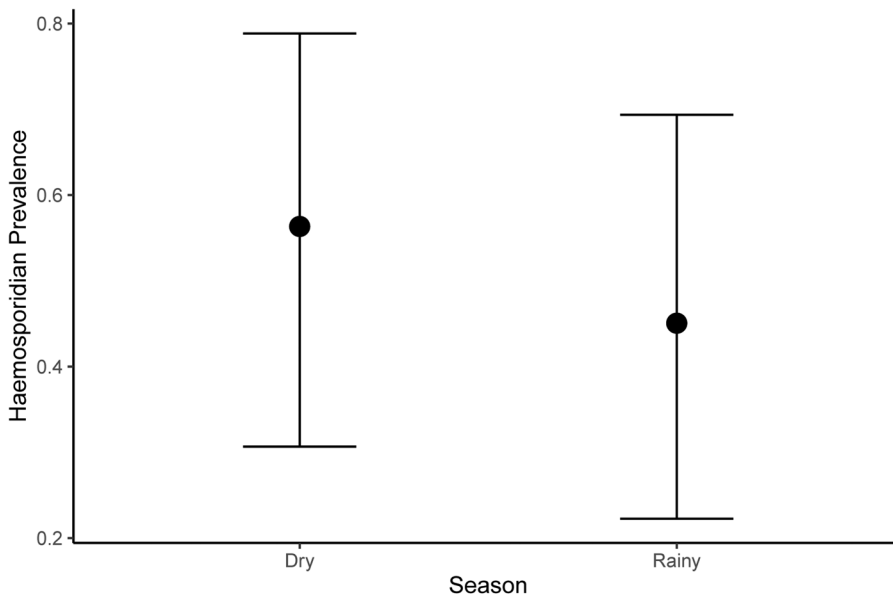
**Table 3.** Estimate, standard error and credible intervals for A-haemosporidians, B- *Plasmodium* and C - *Haemoproteus* prevalence and host functional traits and seasonality

A - All infections	Estimate	Error	Credible intervals	
Intercept	0.26	0.53	-0.81	1.32
Incubation stage 1	0.26	0.47	-0.67	1.18
Incubation stage 2	1.23	0.45	-0.19	2.78
Ectoparasites	-0.12	0.20	-0.50	0.28
Season (Rainy)	-0.46	0.22	-0.89	-0.04
Mass	-0.10	0.16	-0.41	0.21
B - Plasmodium	Estimate	Error	Credible intervals	
Intercept	-3.66	1.08	-5.79	-1.45
Incubation stage 1	-0.39	0.80	-2.07	1.05
Incubation stage 2	0.79	0.86	-1.01	2.41
Ectoparasites	-0.14	0.36	-0.84	0.56
Season (Rainy)	1.09	0.46	0.21	2.04
Mass	0.18	0.26	-0.72	0.30
C - Haemoproteus	Estimate	Error	Credible intervals	
Intercept	-3.44	1.08	-5.79	-1.45
Incubation stage 1	0.89	0.84	-0.81	2.50
Incubation stage 2	1.48	1.13	-0.81	3.59
Ectoparasites	-0.15	0.31	-0.77	0.46
Season (Rainy)	0.23	0.33	-0.41	0.88
Mass	0.09	0.32	-0.58	0.71

**Table 4.** Estimate, standard error and credible intervals for A-haemosporidians, B- *Plasmodium* and C - *Haemoproteus* prevalence and host functional traits and seasonality excluding Columbiformes hosts.

A - All infections	Estimate	Error	Credible intervals	
Intercept	0.00	0.74	-1.47	1.47
Incubation stage 1	0.23	0.49	-0.72	1.19
Incubation stage 2	1.23	0.78	-0.28	2.84
Ectoparasites	-0.03	0.25	-0.51	0.47
Season (Rainy)	-0.37	0.32	-1.00	0.24
Mass	-0.18	0.23	-0.65	0.28
B - Plasmodium	Estimate	Error	Credible intervals	
Intercept	-3.61	0.82	-5.34	-2.14
Incubation stage 1	-0.38	0.77	-2.00	1.04
Incubation stage 2	0.68	0.85	-1.07	2.27
Ectoparasites	-0.09	0.38	-0.82	0.65
Season (Rainy)	0.95	0.48	0.04	1.91
Mass	-1.38	0.54	-2.52	-0.41
C - Haemoproteus	Estimate	Error	Credible intervals	
Intercept	-4.89	1.49	-8.07	-2.15
Incubation stage 1	0.43	1.00	-1.67	2.27
Incubation stage 2	1.21	1.15	-1.14	3.36
Ectoparasites	0.42	0.55	-0.64	1.55
Season (Rainy)	0.93	0.92	-0.69	2.92
Mass	-0.14	0.57	-1.40	0.83





**Figure 2.** Mean ( $\pm$ credible intervals) haemosporidian prevalence according to season birds were collected.

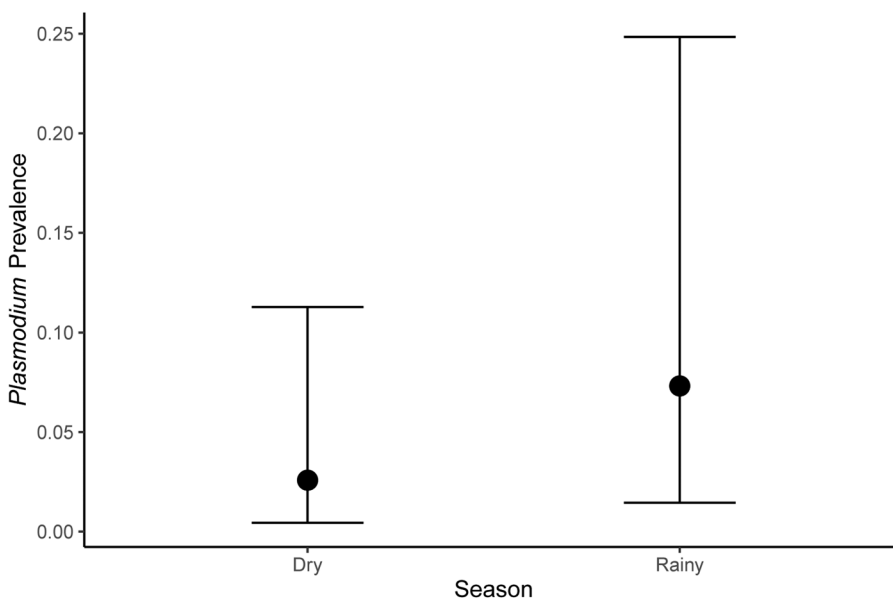
species, being 61% for Columbiformes and 42% for other birds. Among non-Columbiformes birds, body mass was negatively associated with infection when evaluating *Plasmodium* prevalence among different species (Table 4B). We did not observe correlation between most bird functional traits and haemosporidian prevalence in our dataset, but overall prevalence varied according to phylogenetic relatedness among avian species ( $K = 0.67$ , Fig. 4).

### Discussion

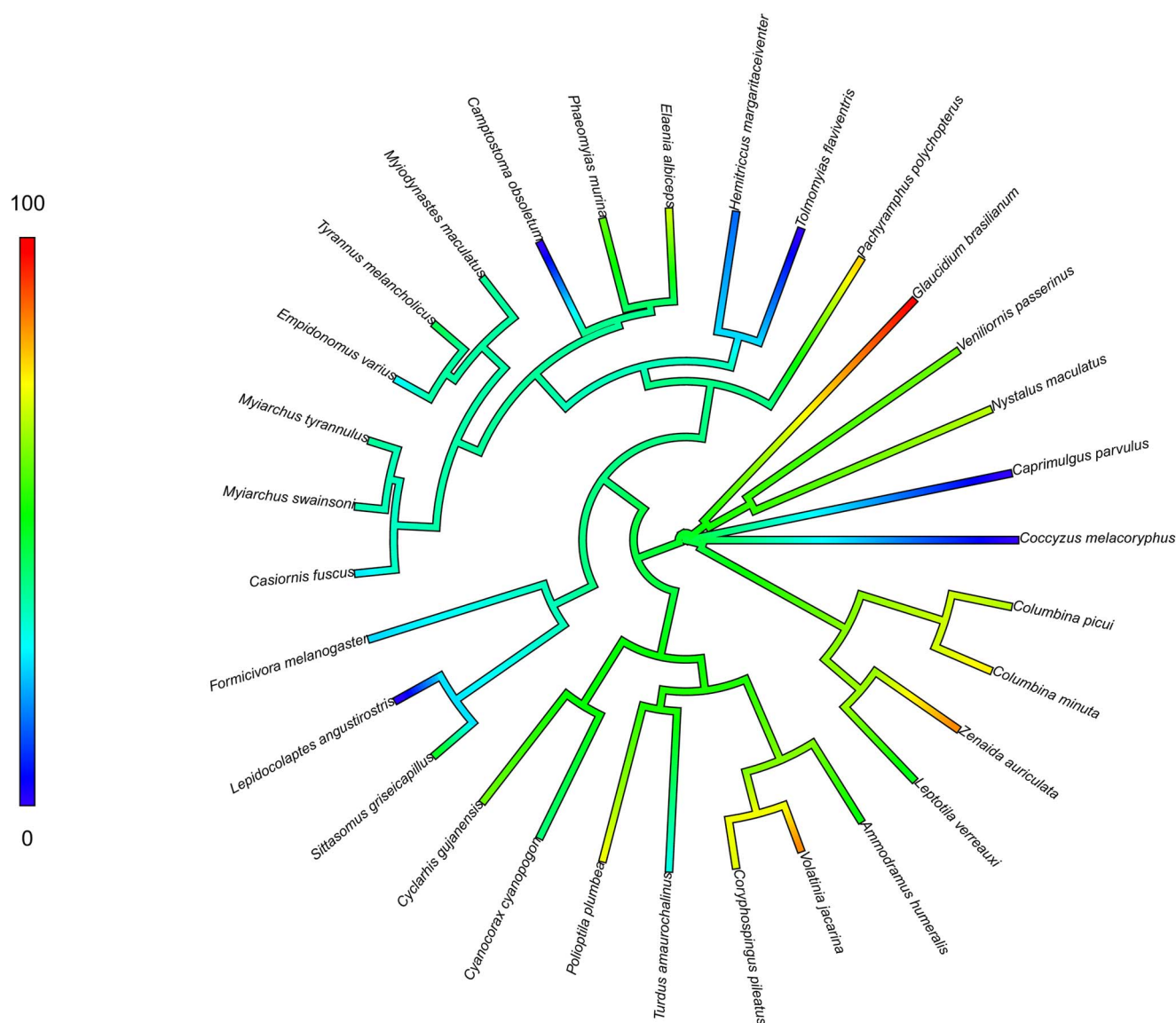
Investigating patterns and functional traits associated with infection is primordial to understand parasite infection dynamics and to determine main target species for conservation programs. Here, we reported that haemosporidian prevalence follows a seasonal pattern and varies distinctively among parasite taxa. Interestingly, we observed that body mass was negatively associated with *Plasmodium* prevalence among non-Columbiform birds, which contradicts a global analysis showing that infection probability for *Plasmodium* is higher in hosts with larger body (Gutiérrez-López *et al.*, 2019; Fillion *et al.*, 2020). Moreover, we also evidenced a

very high-level of phylogenetic association between haemosporidian prevalence and birds from the Brazilian Caatinga.

Phylogenetic relationships among hosts often reflect their association with parasites (Clark *et al.*, 2018; Pacheco *et al.*, 2018; Park *et al.*, 2020; de Angeli Dutra *et al.*, 2022). For this reason, parasite prevalence might vary following phylogenetic relationships among hosts (i.e. closely related hosts present more similar infection rates than distantly related ones), was also observed in this study. Parasites often perform well (i.e. are more successful in completing their life cycle to then be detected in the blood stream) among closely related hosts (Pinheiro *et al.*, 2016), hence, similarity in prevalence among related species should reflect a tendency of those species to support the development of similar parasites lineages. Consequently, our results reinforce the fact that closely related hosts harbour similar prevalence patterns within a community. Most importantly, our results also evidence that the high abundance of Columbiformes species observed in the Caatinga could explain the uncommonly high prevalence of *Haemoproteus* parasites observed in this study in comparison to previous studies showing that *Plasmodium* is the most prevalent haemosporidian



**Figure 3.** Mean ( $\pm$ credible intervals) *Plasmodium* prevalence according to season birds was collected.



**Figure 4.** Mean prevalence according to the phylogenetic relationships across all bird species with more than 10 individuals sampled ( $n = 32$ ).

genus in Brazil (Lacorte *et al.*, 2013; Ferreira *et al.*, 2017; Rodrigues *et al.*, 2021) and in the Neotropics (Fecchio *et al.*, 2021).

Climatic conditions often affect the transmission of vector-borne pathogens due to direct effects on their vectors' abundance and diversity (Consoli and Oliveira, 1994). For this reason, regions presenting high seasonality might be subject to seasonal changes in parasite prevalence and incidence (Lalubin *et al.*, 2013; Ferreira *et al.*, 2017). It occurs due to seasonal changes in vector composition and abundance related to precipitation and temperature that are positively associated with vector abundance (Lalubin *et al.*, 2013; Ferreira *et al.*, 2016). Indeed, the rainy season harbours higher abundance of haemosporidian vectors in the Caatinga (Vasconcellos *et al.*, 2010) and greater prevalence of *Plasmodium*. Nonetheless, when analysing haemosporidians in general we observed higher prevalence during the dry season in Caatinga, which could be due to the higher proportion of Columbiform birds in the dry season and *H. (Haemoproteus)* infections in those hosts.

We found a high haemosporidian prevalence in Caatinga (51%) compared to other Brazilian domains, such as 27–42% in the Brazilian savannah (Lacorte *et al.*, 2013; Ferreira *et al.*, 2017), 25–33% in the Atlantic rainforest (Lacorte *et al.*, 2013; Rodrigues *et al.*, 2021), and 20% in the Amazon rainforest (Fecchio *et al.*, 2017). *H. (Haemoproteus)* represented most of

the infections (50.9%), followed by *Plasmodium* (38.4%) and *H. (Parahaemoproteus)* (10.8%). In most studies conducted in Brazil, however, *Plasmodium* parasites were the most common. This different scenario in parasite prevalence may be explained by the abundance of *Columbina picui*, which harbours a high prevalence of *H. (Haemoproteus)* parasites. High levels of infection among Columbiformes birds by *H. (Haemoproteus)* might be associated with its vector biology since those flies (Hippoboscidae) spend nearly their entire adult life on their hosts (Valkiūnas, 2005). Changes in bird composition in Caatinga have been associated with low precipitation levels, which can trigger migratory movements among several species, increasing the relative proportion of resident species (Pereira, 2013).

Moreover, a high parasite richness in the Caatinga was observed in this study (*Plasmodium* = 17; *H. (Haemoproteus)* = 5 and *H. (Parahaemoproteus)* = 10) and 7 new parasite lineages were described. Both *Plasmodium* and *H. (Parahaemoproteus)* lineages infected a high number of bird species (22 and 10 species, respectively) while *H. (Haemoproteus)* only infected 4 bird species. This high parasite diversity and endemism (21% of all parasite lineages) in the Caatinga reveals the importance of studies in areas with a high degree of host endemism. Moreover, we detected *H. (Haemoproteus)* infecting Passeriform birds (SoCh2 from *M.*

*tyrannulus* and SocH3 from *P. polychopterus*). This parasite group is known to only infect a few seabird species and birds from the order Columbiformes (Levin *et al.*, 2012). Parasite lineages from this subgenus have also been found infecting passerine birds in 2 other studies conducted in Brazil (Lacorte *et al.*, 2013; Ferreira *et al.*, 2017). These findings highlight that non-Columbiformes are exposed to parasites belonging to the subgenus *H.* (*Haemoproteus*) this SDTF. However, this likely represents abortive infections, i.e. infections in which the parasite cannot complete its lifecycle (Valkiūnas *et al.*, 2009). Overall, we found high diversity of haemosporidian parasites in the Caatinga, which infections are mostly represented by *H.* (*Haemoproteus*) parasites, unlike most other regions from Brazil and South America.

To conclude, haemosporidian prevalence in the Caatinga seems to be higher than in other Brazilian biomes. Prevalence varied between dry and rainy seasons depicting higher prevalence during the dry season. *Plasmodium* relative frequency was higher in the rainy season while *H.* (*Haemoproteus*) was more frequent during the dry season. Our models showed that seasonality was the main factor associated with haemosporidian infections, however, it affected distinct parasite genera differently. This is one of the first studies conducted in a SDTF in South America, the Caatinga, which harbours a high diversity and a considerable prevalence of haemosporidian parasites. However, it is important to note that this study comprises only 1 locality in the Caatinga and that several haemosporidian infections lacked parasite identification. For this reason, further studies with diverse host species comprising multiple locations may reveal the uncovered diversity and possible endemicity of haemosporidian lineages in Caatinga.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0031182023000549>

**Data availability.** Data used to perform this research is available as supplementary information or can be shared by Prof. Érika Martins Braga upon reasonable request.

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**Authors' contribution.** AUK, FCF, PAM, MP and EMB conceived and designed the experiments; AUK, FCF and PAM performed the experiments; DdAD, MVB and PAM analysed the data; MP and EMB contributed reagents/materials/analysis tools; DdAD, PAM and EMB wrote the paper. All authors read and approved the final article.

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**Conflict of interest.** NA.

**Ethical standards.** The use of mist-nets and banding at the fieldwork was approved by the Brazilian biodiversity monitoring agency (Institute Chico Mendes for Biodiversity Conservation -ICMbio, (Brazilian National Centre for Bird Conservation – CEMAVE, permission 3239 and, and Sistema de Autorização e Informação em Biodiversidade -SISBIO, 38647-2 and 33206-1). This study was approved by the Ethics Committee in Animal Experimentation (CETEA), Universidade Federal de Minas Gerais, Brazil (Protocol #254/2011).

## References

- Aguiar de Souza Penha V, Maia Chaves Bicalho Domingos F, Fecchio A, Bell JA, Weckstein JD, Ricklefs RE, Braga EM, de Abreu Moreira P, Soares L, Latta S, Tolesano-Pascoli G, Alquezar RD, Del-Claro K and Manica LT (2022) Host life-history traits predict haemosporidian parasite prevalence in tanagers (Aves: Thraupidae). *Parasitology* **150**, 32–41. doi: 10.1017/S0031182022001469
- Alvares CA, Stape JL, Sentelhas PC, de Moraes Gonçalves JL and Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* **22**, 711–728.
- Asghar M, Hasselquist D, Zehndindjiev P, Westerdahl H and Bensch S (2015) Hidden costs of infection: chronic malaria accelerates telomere degradation and senescence in wild birds. *Science (New York, N.Y.)* **347**, 436–438.
- Barrow LN, McNew SM, Mitchell N, Galen SC, Lutz HL, Skeen H, Valqui T, Weckstein JD and Witt CC (2019) Deeply conserved susceptibility in a multi-host, multi-parasite system. *Ecology Letters* **22**, 987–998.
- Bennett DJ, Sutton MD and Turvey ST (2017) Treeman: an R package for efficient and intuitive manipulation of phylogenetic trees. *BMC Research Notes* **10**, 1–10.
- Bensch S, Hellgren O and Pérez-Tris J (2009) MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Molecular Ecology Resources* **9**, 1353–1358.
- Blomberg SP, Garland T and Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioural traits are more labile. *Evolution* **57**, 717–745.
- Bucher EH (1982) Chaco and Caatinga – South American Arid Savannas, Woodlands and Thickets. In Huntley BJ and Walker BH (eds), *Ecology of Tropical Savannas*. Ecological Studies, Vol. **42**. Berlin, Heidelberg: Springer, pp. 48–79. [https://doi.org/10.1007/978-3-642-68786-0\\_4](https://doi.org/10.1007/978-3-642-68786-0_4)
- Bürkner PC (2017) brms: an R package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **80**, 27239.
- Clark NJ, Clegg SM and Lima MR (2014) A review of global diversity in avian haemosporidians (Plasmodium and Haemoproteus: Haemosporida): new insights from molecular data. *International Journal for Parasitology* **44**, 329–338.
- Clark NJ, Clegg SM, Sam K, Goulding W, Koane B and Wells K (2018) Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Diversity and Distributions* **24**, 13–23.
- Consoli RAGB and Oliveira RL (1994) *Principais mosquitos de importância sanitária no Brasil*. Rio de Janeiro: Editora Fiocruz. doi:10.1590/S0102-311X1995000100027.
- de Angeli Dutra D, Filion A, Fecchio A, Braga EM and Poulin R (2021a) Migrant birds disperse haemosporidian parasites and affect their transmission in avian communities. *Oikos* **130**, 979–988.
- de Angeli Dutra D, Fecchio A, Martins Braga É and Poulin R (2021b) Migratory birds have higher prevalence and richness of avian haemosporidian parasites than residents. *International Journal for Parasitology* **51**, 877–882.
- de Angeli Dutra D, Fecchio A, Braga EM and Poulin R (2022) Migratory behaviour does not alter cophylogenetic congruence between avian hosts and their haemosporidian parasites. *Parasitology* **149**, 905–912.
- De La Torre GM and Campião KM (2021) Bird habitat preferences drive hemoparasite infection in the Neotropical region. *Integrative Zoology* **16**, 755–768.
- De La Torre GM, Freitas FF, Fratoni RDO, Guaraldo ADC, Dutra DDA, Braga EM and Manica LT (2020) Hemoparasites and their relation to body condition and plumage coloration of the white-necked thrush (*Turdus albicollis*). *Ethology Ecology and Evolution* **00**, 1–18.
- Duque JG (1953) *Solo e água no polígono das secas*. Fortaleza, Ceará: Tipografia Minerva, Brazil.
- Fallon SM, Ricklefs RE, Swanson BL and Bermingham E (2003) Detecting avian malaria: an improved polymerase chain reaction diagnostic. *Journal of Parasitology* **89**, 1044–1047. doi: 10.1645/GE-3157
- Fecchio A, Lima M, Silveira P, Ribas A, Caparroz R and Marini M (2015) Age, but not sex and seasonality, influence Haemosporida prevalence in white-banded tanagers (*Neothraupis fasciata*) from central Brazil. *Canadian Journal of Zoology* **93**, 71–77.
- Fecchio A, Ellis VA, Bell JA, Andretti CB, D'horta FM, Silva AM, Tkach VV and Weckstein JD (2017) Avian malaria, ecological host traits and mosquito abundance in southeastern Amazonia. *Parasitology* **144**, 1117–1132.
- Fecchio A, Wells K, Bell JA, Tkach VV, Lutz HL, Weckstein JD, Clegg SM and Clark NJ (2019) Climate variation influences host specificity in avian malaria parasites. *Ecology Letters* **22**, 547–557.
- Fecchio A, Bell JA, Bosholm M, Vaughan JA, Tkach VV, Lutz HL, Cueto VR, Gorosito CA, González-Acuña D, Stromlund C, Kvasager D, Comiche KJM, Kirchgatter K, Pinho JB, Berv J, Anciães M, Fontana



- CS, Zyskowski K, Sampaio S, Dispoto JH, Galen SC, Weckstein JD and Clark NJ (2020) An inverse latitudinal gradient in infection probability and phylogenetic diversity for Leucocytozoon blood parasites in New World birds. *Journal of Animal Ecology* **89**, 423–435.
- Fecchio A, Clark NJ, Bell JA, Skeen HR, Lutz HL, De La Torre GM, Vaughan JA, Tkach VV, Schunck F, Ferreira FC, Braga EM, Lugarini C, Wamiti W, Dispoto JH, Galen SC, Kirchgatter K, Sagario MC, Cueto VR, González-Acuña D, Inumaru M, Sato Y, Schumm YR, Quillfeldt P, Pellegrino I, Dharmarajan G, Gupta P, Robin VV, Ciloglu A, Yildirim A, Huang X, Chapa-Vargas L, Álvarez-Mendizábal P, Santiago-Alarcon D, Drovetski SV, Hellgren O, Voelker G, Ricklefs RE, Hackett SJ, Collins MD, Weckstein JD, Wells K and Kamath P (2021) Global drivers of avian haemosporidian infections vary across zoogeographical regions. *Global Ecology and Biogeography* **30**, 2393–2406.
- Ferraguti M, Martínez-de la Puente J, Bensch S, Roiz D, Ruiz S, Viana DS, Soriguer RC and Figuerola J (2018) Ecological determinants of avian malaria infections: an integrative analysis at landscape, mosquito and vertebrate community levels. *Journal of Animal Ecology* **87**, 727–740.
- Ferreira FC, Rodrigues RA, Sato Y, Borges MAZ and Braga EM (2016) Searching for putative avian malaria vectors in a Seasonally Dry Tropical Forest in Brazil. *Parasites and Vectors* **9**. doi: 10.1186/s13071-016-1865-y
- Ferreira FC, Rodrigues RA, Ellis VA, Leite IO, Borges MAZ and Braga EM (2017) Habitat modification and seasonality influence avian haemosporidian parasite distributions in southeastern Brazil. *PLoS ONE* **12**, 0178791.
- Ferreira FC, Santiago-Alarcon D and Braga EM (2020) Diptera vectors of avian haemosporidians: with emphasis on tropical regions. In Santiago-Alarcon D and Marzal A (eds), *Avian Malaria and Related Parasites in the Tropics*. Cham: Springer International Publishing, pp. 185–250. doi: 10.1007/978-3-030-51633-8\_6
- Filion A, Eriksson A, Jorge F, Niebuhr CN and Poulin R (2020) Large-scale disease patterns explained by climatic seasonality and host traits. *Oecologia* **194**, 723–733.
- Ganser C, Monadjem A, McCleery RA, Ndlela T and Samantha M (2020) Is it best on the nest? Effects of avian life-history on haemosporidian parasitism. *International Journal for Parasitology: Parasites and Wildlife* **13**, 62–71. doi: 10.1016/j.ijppaw.2020.07.014
- Gonzalez-Quevedo C, Davies RG and Richardson DS (2014) Predictors of malaria infection in a wild bird population: landscape-level analyses reveal climatic and anthropogenic factors. *Journal of Animal Ecology* **83**, 1091–1102.
- Green M and Sambrook J (2012) *Molecular Cloning: A Laboratory Manual*, 4th Edn. New York: Cold Spring Harbor Laboratory Press.
- Gutiérrez-López R, Martínez-De La Puente J, Gangoso L, Soriguer R and Figuerola J (2019) Effects of host sex, body mass and infection by avian Plasmodium on the biting rate of two mosquito species with different feeding preferences. *Parasites and Vectors* **12**, 1–10.
- Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han K-L, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC and Yuri T (2008) A phylogenomic study of birds reveals their evolutionary history. *Science (New York, N.Y.)* **320**, 1763–1768.
- Hellgren O, Waldenstro J and Bensch S (2004) A new PCR assay for simultaneous studies of *Leucocytozoon*, *Plasmodium*, and *Haemoproteus* from avian blood. *Journal of Parasitology* **90**, 797–802.
- Hoshen MB and Morse AP (2004) A weather-driven model of malaria transmission. *Malaria Journal* **3**, 32.
- IPCC (2021) *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. United Kingdom and New York, NY, USA.
- Jetz W, Thomas GH, Joy JB, Hartmann K and Mooers AO (2012) The global diversity of birds in space and time. *Nature* **491**, 444–448.
- Kelly-Hope LA, Hemingway J and McKenzie FE (2009) Environmental factors associated with the malaria vectors *Anopheles gambiae* and *Anopheles funestus* in Kenya. *Malaria Journal* **8**, 1–8.
- Lacorte GA, Flix GMF, Pinheiro RRB, Chaves AV, Almeida-Neto G, Neves FS, Leite LO, Santos FR and Braga EM (2013) Exploring the diversity and distribution of neotropical avian malaria parasites – A molecular survey from southeast Brazil. *PLoS ONE* **8**, 1–9.
- Lalubin F, Delévant A, Glazot O and Christe P (2013) Temporal changes in mosquito abundance (*Culex pipiens*), avian malaria prevalence and lineage composition. *Parasites and Vectors* **6**, 1–8.
- Landesman WJ, Allan BF, Langerhans RB, Knight TM and Chase JM (2007) Inter-annual associations between precipitation and human incidence of West Nile Virus in the United States. *Vector-Borne and Zoonotic Diseases* **7**, 337–343.
- Lapointe DA, Goff ML and Atkinson CT (2010) Thermal constraints to the sporogonic development and altitudinal distribution of avian malaria plasmodium relictum in Hawai'i. *Journal of Parasitology* **96**, 318–324.
- Leal IR, da Silva JMC, Tabarelli M and Lacher TE (2005) Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. *Conservation Biology* **19**, 701–706.
- Levin II, Valkiūnas G, Iezhova TA, O'Brien SL and Parker PG (2012) Novel haemoproteus species (Haemosporida: Haemoproteidae) from the Swallow-Tailed Gull (Lariidae), with remarks on the host range of hippoboscids-transmitted avian hemoproteids. *Journal of Parasitology* **98**, 847–854.
- Marzal A (2012) Recent Advances in Studies on Avian Malarial Parasites. In Omolade O. (eds). InTech, pp. 135–158. doi: 10.5772/33730
- Marzal A, De Lope F, Navarro C and Møller AP (2005) Malarial parasites decrease reproductive success: an experimental study in a passerine bird. *Oecologia* **142**, 541–545.
- Pacheco MA, Matta NE, Valkiūnas G, Parker PG, Mello B, Stanley CE, Lentino M, Garcia-Amado MA, Cranfield M, Kosakovsky Pond SL and Escalante AA (2018) Mode and rate of evolution of haemosporidian mitochondrial genomes: timing the radiation of avian parasites. *Molecular Biology and Evolution* **35**, 383–403.
- Palinauskas V, Platonova E, Žiegyte R and Mukhin A (2016) Dynamics of blood and sporozoite induced malarial infections in experimentally infected passerines. *International Journal of Parasitology* **50**, 1057–1065.
- Park E, Jorge F and Poulin R (2020) Shared geographic histories and dispersal contribute to congruent phylogenies between amphipods and their microsporidian parasites at regional and global scales. *Molecular Ecology* **29**, 3330–3345.
- Pereira G (2013) Variação sazonal de aves em uma área de caatinga no Nordeste do Brasil. *Ornitologia Neotropical* **24**, 387.
- Pichorim M, Damasceno JP, Toledo-Lima G, de Araújo RD and Ferreira PV (2016a) *Guia de Aves da Estação Ecológica do Seridó*. Natal: Editora Caula de Papiro.
- Pichorim M, Valdenor de Oliveira D, de Oliveira Júnior TM, Câmara TPF and Galvão do Nascimento EP (2016b) Pristine semi-arid areas in northeastern Brazil remain mainly on slopes of mountain ranges: a case study based on bird community of Serra de Santana. *Tropical Zoology* **29**, 189–204.
- Pinheiro RBP, Félix GMF, Chaves AV, Lacorte GA, Santos FR, Braga EM and Mello MAR (2016) Trade-offs and resource breadth processes as drivers of performance and specificity in a host-parasite system: a new integrative hypothesis. *International Journal for Parasitology* **46**, 115–121.
- Pulgarin-R PC, Gómez JP, Robinson S, Ricklefs RE and Cadena CD (2018) Host species, and not environment, predicts variation in blood parasite prevalence, distribution, and diversity along a humidity gradient in northern South America. *Ecology and Evolution* **8**, 3800–3814.
- R Core Team (2017) *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Revell L (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223.
- Ricklefs RE (2017) Historical biogeography and extinction in the Hawaiian honeycreepers. *The American Naturalist* **190**, E000–E000.
- Rodrigues RA, Felix GMF, Pichorim M, Moreira PA and Braga EM (2021) Host migration and environmental temperature influence avian haemosporidians prevalence: a molecular survey in a Brazilian Atlantic rainforest. *PeerJ* **9**, e11555.
- Roos FL, Belo NO, Silveira P and Braga EM (2015) Prevalence and diversity of avian malaria parasites in migratory black skimmers (*Rynchops niger*, Laridae, Charadriiformes) from the Brazilian Amazon Basin. *Parasitology Research* **114**, 3903–3911.
- Sambrook J and Russell DW (2001) *Molecular Cloning: A Laboratory Manual*, Vol. 1, 3rd Edition, New York: Cold Spring Harbor Laboratory Press.
- Schoenle LA, Kernbach M, Haussmann MF, Bonier F and Moore IT (2017) An experimental test of the physiological consequences of avian malaria infection. *Journal of Animal Ecology* **86**, 1483–1496.
- Straube FC and Bianconi GV (2002) Sobre a grandeza e a unidade utilizada para estimar esforço de captura com utilização de redes-de-neblina. *Chiroptera Neotropical* **8**, 150–152.
- Tabarelli M and Silva J (2003) Áreas e ações prioritárias para a conservação da biodiversidade da caatinga. In Leal I, Tabarelli M and Silva J (eds),



- Ecologia E Conservação da Caatinga*. Recife: Universidade Federal de Pernambuco, pp. 349–374.
- Tobias JA, Sheard C, Pigot AL, Devenish AJM, Yang J, Sayol F, Neate-Clegg MHC, Alioravainen N, Weeks TL, Barber RA, Walkden PA, MacGregor HEA, Jones SEI, Vincent C, Phillips AG, Marples NM, Montaña-Centellas FA, Leandro-Silva V, Claramunt S, Darski B, Freeman BG, Bregman TP, Cooney CR, Hughes EC, Capp EJR, Varley ZK, Friedman NR, Korntheuer H, Corrales-Vargas A, Trisos CH, Weeks BC, Hanz DM, Töpfer T, Bravo GA, Remeš V, Nowak L, Carneiro LS, Moncada RAJ, Matysioková B, Baldassarre DT, Martínez-Salinas A, Wolfe JD, Chapman PM, Daly BG, Sorensen MC, Neu A, Ford MA, Mayhew RJ, Fabio Silveira L, Kelly DJ, Annorbah NND, Pollock HS, Grabowska-Zhang AM, McEntee JP, Carlos T, Gonzalez J, Meneses CG, Muñoz MC, Powell LL, Jamie GA, Matthews TJ, Johnson O, Brito GRR, Zyskowski K, Crates R, Harvey MG, Jurado Zevallos M, Hosner PA, Bradfer-Lawrence T, Maley JM, Stiles FG, Lima HS, Provost KL, Chibesa M, Mashao M, Howard JT, Mlamba E, Chua MAH, Li B, Gómez MI, García NC, Päckert M, Fuchs J, Ali JR, Derryberry EP, Carlson ML, Urriza RC, Brzeski KE, Prawiradilaga DM, Rayner MJ, Miller ET, Bowie RCK, Lafontaine R, Scofield RP, Lou Y, Somarathna L, Lepage D, Illif M, Neuschulz EL, Templin M, Dehling DM, Cooper JC, Pauwels OSG, Analuddin K, Fjeldså J, Seddon N, Sweet PR, DeClerck FAJ, Naka LN, Brawn JD, Aleixo A, Böhning-Gaese K, Rahbek C, Fritz SA, Thomas GH and Schleuning M (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecology Letters* 25, 581–597.
- Valkiūnas G (2005) *Avian Malaria Parasites and Other Haemosporidia*. Boca Raton: CRC Press. doi: 10.1201/9780203643792.fmatt
- Valkiūnas G, Iezhova TA, Loiseau C and Sehgal RNM (2009) Nested cytochrome B polymerase chain reaction diagnostics detect sporozoites of hemosporidian parasites in peripheral blood of naturally infected birds. *Journal of Parasitology* 95, 1512–1515.
- Vanzolini PE, Ramos-Costa AMM and Vitt LJ (1980) *Répteis das caatingas*. Academia Brasileira de Ciências, Rio de Janeiro. doi: 10.5962/bhl.title.109659
- Vasconcellos A, Andreazze R, Almeida AM, Araujo HFP, Oliveira ES and Oliveira U (2010) Seasonality of insects in the semi-arid Caatinga of north-eastern Brazil. *Revista Brasileira de Entomologia* 54, 471–476.
- Zamora-Vilchis I, Williams SE and Johnson CN (2012) Environmental temperature affects prevalence of blood parasites of birds on an elevation gradient: implications for disease in a warming climate. *PLoS ONE* 7. doi: 10.1371/journal.pone.0039208