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“ECOLOGICAL RELATIONSHIPS BETWEEN BIRDS AND HAEMOSPORIDIAN PARASITES IN PRESENT AND FUTURE CLIMATE CHANGE SCENARIOS”

Tesis que presenta

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Haemosporida

On the wing of mosquitos

To the blood of birds

Larissa Ortega

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ABBREVIATIONS

BIO	(Climate change) Bioclimatic variable
CMIP	(Climate change) Coupled Model Intercomparison Project
IPCC	(Climate change) Intergovernmental Panel on Climate Change
OCU	(Climate change) Operational climate unit
RCP	(Climate change) Representative Concentration Pathways
SSP	(Climate change) Shared Socioeconomic Pathways
DNA	(Molecular biology) Deoxyribonucleic acid
PCR	(Molecular biology) Polymerase chain reaction
AUC	(Statistics) Area under the curve
CI	(Statistics) Confidence interval
MPD	(Statistics) Mean Pairwise Distance
Ntaxa	(Statistics) Number of taxa in our avian host community
mpd.obs	(Statistics) Observed mean pairwise distance in null host communities
pROC	(Statistics) Predictive receiver operatic characteristic curve
mpd.obs.p	(Statistics) P-value (quantile) of observed mpd vs. null host communities
ROC	(Statistics) Receiver operatic characteristic curve
SEM	(Statistics) Standard error of the mean
SES	(Statistics) Standarized effect sizes
MSd	(Vegetation) Degraded Mesquite-dominated Shrub
MSd	(Vegetation) Degraded Mesquite-dominated Shrub
PERd	(Vegetation) Degraded Perennial Forest
LSA	(Vegetation) Livestock Area
MSm	(Vegetation) Mature Mesquite-dominated Shrub
PERm	(Vegetation) Mature Perennial Forest
MPF	(Vegetation) Mexican Pinyon Forest
MDS	(Vegetation) Microphyllous Desert Shrubland
MCF	(Vegetation) Montane Cloud Forest
OPF	(Vegetation) Oak-pine Forest
PL	(Vegetation) Pastureland
PF	(Vegetation) Pine Forest
POF	(Vegetation) Pine-oak Forest
RDS	(Vegetation) Rosethophyllous Desert Shrubland
TDF	(Vegetation) Tropical Deciduous Forest
TSD	(Vegetation) Tropical Sub-deciduous Forest
YS	(Vegetation) Yucca Shrubland

GLOSSARY

From Chapter I:

Apoptosis. Cellular death.

Co-infection. Simultaneous infection of a host by multiple pathogen strains, lineages, or species.

Denaturalization. Also known as denaturation, it's the process in which proteins or nucleic acids lose their original folded structure by the application of external stressors.

Ecological niche. Multivolume space occupied by a species, often defined as the specific role a species plays in an ecosystem, its interactions with other organisms and its environment.

Ecotone. Transitional area between two biological communities.

Erythrocyte. Red blood cell.

Host. Any living organism that knowingly or unknowingly harbours another organism(s) on or within its own body.

Merozoite. Invasive stage of the malarian parasites that infects red blood cells and causes the disease.

Parasitemia. Quantitative content of parasites in the blood.

Prevalence. Proportion of infected individuals in a population that have a disease at a particular time.

Protozoan. Single-celled eukaryotic organisms. They can be either free-living or form symbiotic relationships with orther organisms (as in parasitism).

Sporogony. Asexual reproductive phase of a parasite that occurs outside the host

Vector. Living organism that carries a disease-inducing agent from an infected individual to a non-infected individual, its food, or environment.

From Chapter II:

Bioclimatic space. The multidimensional environmental space occupied by a species.

Generalist. A parasitic lineage capable of infecting an array of taxonomically distant hosts.

Specialist. A parasitic lineage that infects taxonomically related hosts.

Suitability. Assessment of the environmental space where a species reaches its maximum fitness

ABSTRACT

Avian haemosporidian parasites, including *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*, are among the most common parasitic infections in wild birds in the Americas. Parasites within each genus exhibit a wide array of environmental tolerance and host specificity, and their distributions are influenced by various environmental factors, the most important being temperature and humidity. Transmitted by dipteran vectors (such as mosquitoes and biting midges), haemosporidian infections can cause significant health issues in wild bird populations, including reduced reproductive success and increased mortality rates. Despite extensive studies on the environmental drivers of distribution and prevalence of these parasites, the potential impacts of climate change on parasite-host dynamics remain difficult to assess due to the complex interactions between the haemosporidians, their hosts, and the environment. In this study, we examined the bioclimatic variables influencing haemosporidian prevalence in avian communities across central to eastern Mexico and continental North America, with a focus on how climate change might affect the distribution trends of haemosporidians in the future. Using spatial modeling, we assessed how the bioclimatic variables, such as temperature and humidity, shape the distribution of haemosporidians across an altitudinal gradient, and in relation to their host specificity. We forecast that in contrasting climate change scenarios, the temperature increases, and precipitation declines might lead to shifts in prevalence trends following the altitudinal gradient, with a potential rise of haemosporidian prevalence at higher elevations, particularly in temperate climates. However, the bioclimatic space associated with haemosporidian prevalence located in arid and semi-arid habitats might become heavily compromised as climate change becomes more severe. In relation to their host specificity, climate change projections suggest a northward latitudinal migration of the bioclimatic variables related to the presence of certain haemosporidian lineages. For specialist lineages, this shift may be more pronounced, given their geographic and host specificity limitations.

Under both approaches (altitudinal and latitudinal analysis), our projections suggest that anthropogenic climate change may disrupt the life cycles of both haemosporidians and their vectors, altering infection dynamics and potentially introducing new risks for avian populations. These findings highlight the importance of incorporating climate change projections and analysis into the study of wildlife diseases and underscore the need for further research in relation to the environmental tolerances and host specificity of haemosporidian parasites.

Keywords: avian haemosporidians, avian malaria, *Plasmodium*, *Haemoproteus*, *Leucocytozoon*, disease ecology, climate change models, bioclimatic space, specificity, landscape parasitology

RESUMEN

Los parásitos hemosporidios como Plasmodium, Haemoproteus y Leucocytozoon constituyen algunos de los principales agentes infecciosos en aves silvestres en el continente americano. Los parásitos dentro de cada uno de estos géneros exhiben una amplia gama de tolerancia ambiental y especificidad de hospedero, por lo que sus distribuciones se ven influenciadas por diversos factores medioambientales, de los cuales los más importantes son la temperatura y humedad. Estas infecciones son transmitidas por vectores del orden Diptera (mosquitos y moscas hematófagas) y pueden ocasionar trastornos de salud significativos en las poblaciones de aves silvestres, tales como reducciones en su éxito reproductivo e incrementos en las tasas de mortalidad. No obstante, a pesar de la existencia de diversos estudios acerca de los factores que influyen en la distribución y prevalencia de estos parásitos, aun es difícil evaluar los efectos del cambio climático a largo plazo sobre las dinámicas parásito-hospedero debido a la complejidad de las interacciones entre los hemosporidios, sus hospederos y el medioambiente. En el presente estudio, examinamos las variables bioclimáticas detrás de la prevalencia y presencia de los parásitos hemosporidios en comunidades aviares en el centro-este de México y sobre linajes hemosporidios registrados en América del Norte, con un enfoque especial sobre la manera en que el cambio climático podría afectar las tendencias de distribución de estos parásitos en el futuro. Mediante el uso de modelaje espacial, evaluamos las tendencias de distribución de los hemosporidios a lo largo de un gradiente altitudinal en México y con relación a su especificidad de hospedero bajo una escala continental. Nuestras proyecciones sugieren que, bajo escenarios contrastantes de cambio climático, los incrementos de temperatura y reducción en las tasas de precipitación en el país podrían ocasionar cambios en la expresión de las tasas de prevalencia de los hemosporidios a lo largo de un gradiente altitudinal, con incrementos potenciales de prevalencia en las regiones altas (especialmente en áreas de clima templado). Sin embargo, el espacio bioclimático asociado con la prevalencia de hemosporidios que se encuentra en regiones áridas y semiáridas podría encontrarse fuertemente comprometido conforme el cambio climático se vuelve más severo. Al tomar en consideración los grados de especificidad de hospedero que presentan estos parásitos, las proyecciones de cambio climático sugieren la existencia de una migración latitudinal de las condiciones bioclimáticas relacionadas con la presencia de ciertos linajes hemosporidios hacia el norte del continente, además de una pérdida de espacio bioclimático. Bajo ambos enfoques (análisis altitudinal y latitudinal), nuestras proyecciones sugieren que el cambio climático antropogénico podría alterar las dinámicas de infección y distribución de estos organismos y podría introducir riesgos imprevistos a las poblaciones aviares. Los resultados obtenidos sólo recalcan la importancia de incorporar las proyecciones de cambio climático en el estudio de las enfermedades de vida silvestre y enfatizan la necesidad de realizar mayores investigaciones en relación con la tolerancia ambiental de los parásitos hemosporidios bajo distintos enfoques.

Palabras clave: hemosporidios aviares, malaria aviar, *Plasmodium, Haemoproteus, Leucocytozoon*, ecología de enfermedades, modelos de cambio climático, espacio bioclimático, especificidad, parasitología del paisaje

PROLOGUE

Avian malaria (*Plasmodium*) and related infections produced by *Haemoproteus* and *Leucocytozoon* protozoans (Phylum Apicomplexa, order Haemosporida) represent one of the most common parasitic infections occurring in birds. Infection is carried over from host to host by insects of the order Diptera (mosquitoes and biting midges), and once infected, bird hosts become reservoirs of the disease, furthering the appearance of infectious outbreaks within populations if the environmental conditions are favorable (Valkiūnas 2005). These diseases are quite common on resident and migratory bird populations but have become an issue of concern for conservation efforts due to the unforeseen effects that climate change might have on the equilibrium between parasite and host relationships (Huijben*, et al.* 2007), particularly in island ecosystems but also in other vulnerable avian populations (Samuel*, et al.* 2011; Atkinson*, et al.* 2014; Miranda-Paez*, et al.* 2022).

The populations dynamics, distribution, and bite frequency of the dipteran vectors responsible for the dispersal of haemosporidian parasites get favored by temperature increases (Stresman 2010; Garamszegi 2011), and there is substantial evidence that supports the existence of an optimal threshold for the development and spread of malaria infections (Benning*, et al.* 2002), involving both the parasite and its hosts. For example, in the case of *Plasmodium* infections propagated by anopheline mosquitoes, the 16° C isotherm marks the limit for their reproduction and maintenance, and the optimal temperature for the development of haemosporidian parasites is located at 26° C. Transmission cannot occur under 16° C or above 33° C, but climate change could situate local average temperatures within this infection threshold, particularly along an elevation gradient (Benning*, et al.* 2002; Khasnis & Nettleman 2005; Zamora-Vilchis*, et al.* 2012).

For the birds, these climatic changes mean they are at a higher risk of becoming more susceptible to acquiring haemosporidian infections (Garamszegi 2011; Miranda-Paez*, et al.* 2022). With this in consideration, the development of spatial projections that integrate the environmental conditions behind the proliferation, transmission, and range of infection of avian haemosporidians are a critical tool for conservation efforts and for the mitigation of parasitic vector-borne diseases on wild bird populations (Sehgal*, et al.* 2011).

Haemosporidian parasites. Avian haemosporidians are a group of protozoan organisms that have been closely studied in tropical habitats since the 19th century, serving as research models for malaria and other protozoan infections in humans (Danilewsky 1889; Valkiūnas*, et al.* 2009). The order includes over 500 known species of obligated parasites of vertebrate hosts distributed within 15 distinct genera, from which the most representative in the Americas are *Plasmodium*, *Haemoproteus* and *Leucocytozoon* (Valkiūnas 2005; Borner*, et al.* 2016). Haemosporidians are found in a wide variety of ecosystems, and their prevalence, range, and distribution are directly linked to the ecology, habitat preferences, and climatic niche of their hosts and vectors (Friend & Franson 1999).

When birds are infected by haemosporidians (Fig. I), the parasites first invade the tissues, where they reproduce asexually into the merozoite stage that later invades the erythrocytes of their host. Symptoms of the disease develop when the merozoites enter and mature inside the cell, causing apoptosis of the erythrocytes.

After apoptosis occurs, the infective form of the parasite releases into the bird's bloodstream where a new vector can ingest it and begin the cycle anew (Fig. 2). It's at this stage that infected avian hosts present the acute form of the disease, having symptoms such as: anemia, loss of appetite, weight loss, respiratory complications, general body weakness, apathy, and even death (Valkiūnas 2005). Surviving individuals develop a certain degree of immunity to reinfection but continue to carry the disease in a dormant stage that "activates" during periods of stress (relapse) (Atkinson 1999; Valkiūnas 2005). Stressors can be physiological (i.e., like the hormonal changes that occur during the reproductive season) or ecological (i.e., changes in the environment, like temperature increases and drought periods associated with climate change) (Cornet*, et al.* 2014).

Vectors. The main vectors behind the transmission of avian malaria, haemoproteosis and leucocytozoonosis are dipteran insects, such as mosquitoes from the genera *Culex*, *Aedes*, *Culiseta*, *Anopheles*, *Mansonia* and *Aedeomya* (Valkiūnas 2005), and biting midges (Simulidae, Ceratopogonidae, and Hippoboscidae) (Atkinson 1999). Reproduction, development, and geographic distribution for these insects are strongly dependent on environmental conditions, particularly temperature and humidity. Therefore, human-induced climate change may alter the dynamics behind their proliferation and haemosporidian infections (Garamszegi 2011). The critical transmission window of haemosporidian parasites typically occurs during the reproductive season of its vectors and avian hosts (spring-summer), but any temperature increases or land use modifications has the potential to facilitate local population changes on dipteran vectors (such as alterations on their abundances, feeding habits and distribution), and cause a relapse of the disease in previously infected birds or even promote host switching of the haemosporidian parasites they carry (Brooks & Hoberg 2007; Møller 2010). Such modifications to the parasite-host complex could have disastrous effects on bird populations, particularly those that historically had never or scarcely been into contact with the parasites (Benning*, et al.* 2002; Zamora-Vilchis*, et al.* 2012; Abella-Medrano*, et al.* 2015).

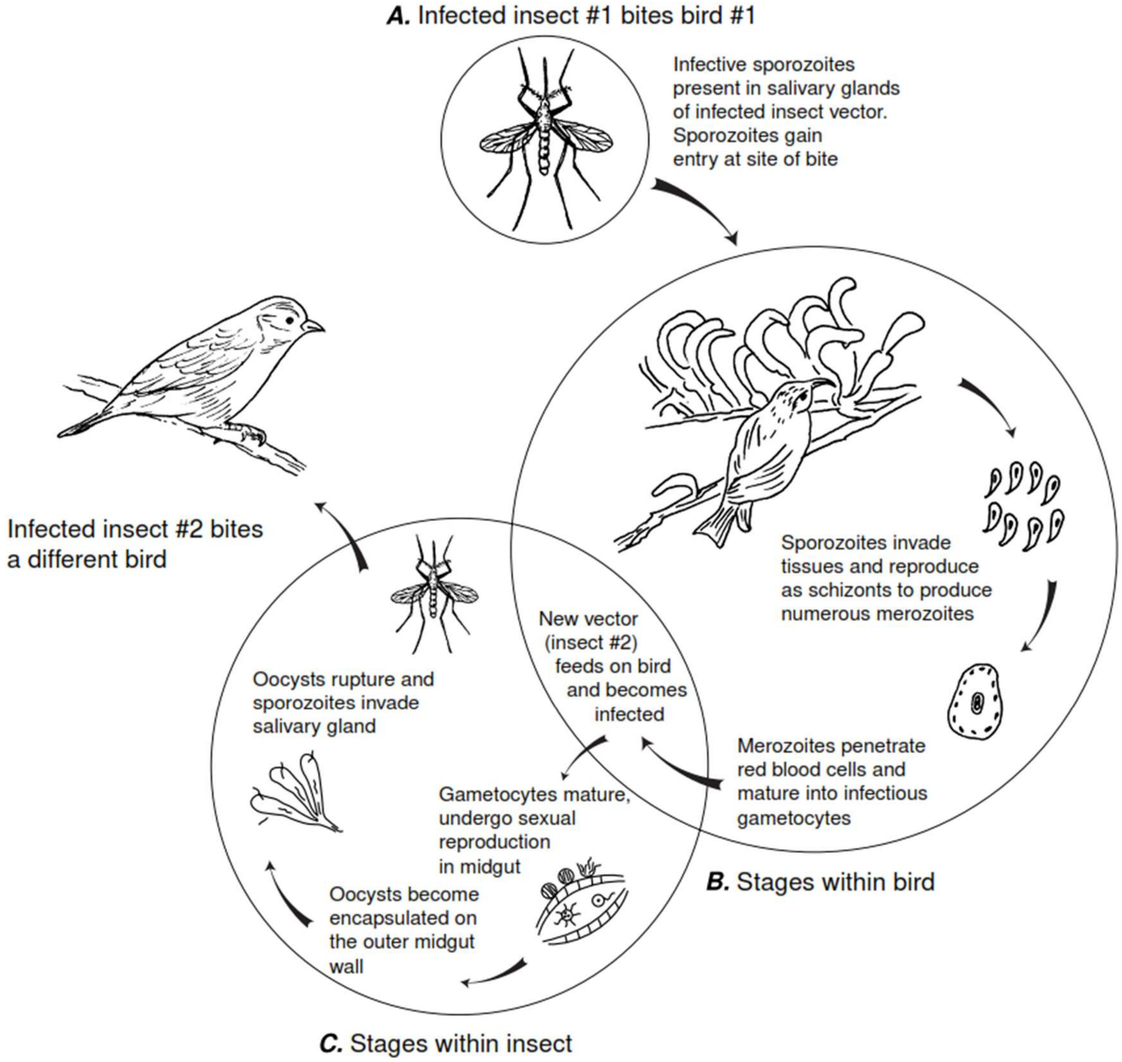

Figure 1. General life cycle of haemosporidian parasites. Infection starts with (**A**) an infected dipteran insect that feeds upon the blood of a susceptible bird host, where (**B**) the first stage of development of several intermediate forms takes place, until a new insect feeds upon the bird, acquiring the infection. The last stage of

development occurs (**C**) inside the new dipteran vector, who carries over the parasite until it bites a new host, completing the cycle (**D**) (Taken from Atkinson 1999).

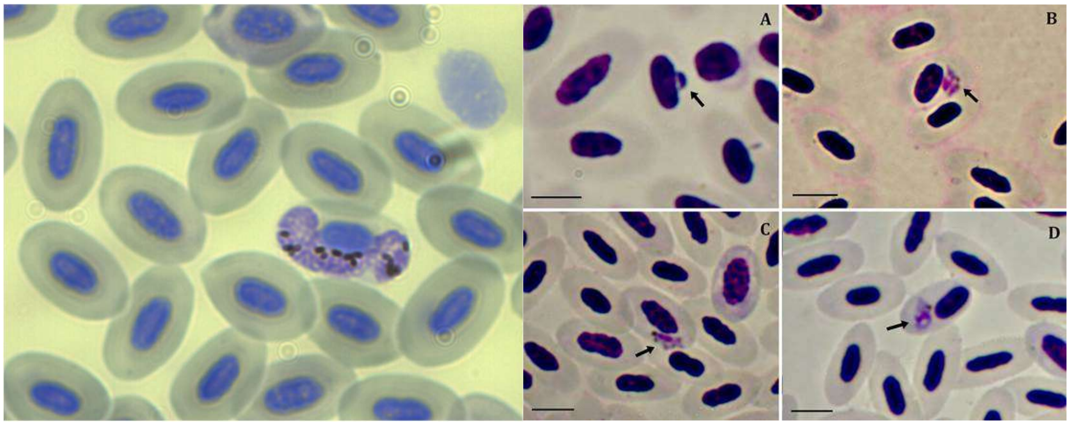

Figure 2. Left: Gametocyte of *Haemoproteus* sp. (Ewing 2015). Right: Merozoites of Plasmodium sp. infecting erythrocytes of infected birds (Tostes*, et al.* 2015).

Spatial distribution and environmental niche modelling. Environmental models are an important tool for faunal studies since they can be used to predict allocation changes and dispersal movements, among other ecological features. With the recent advancements of satellite imagery, computer modelling and molecular analysis, we are now capable of studying infectious diseases and their impact on human and wildlife systems at different spatial scales (Brooks & Hoberg 2007; Kurane 2010; Goedknegt*, et al.* 2015). Because the geographical distribution of the host-haemoparasite complex is strongly dependent on environmental conditions (mainly temperature and humidity), environmental models can be used to gauge the climate drivers and model the potential environmental niche behind haemosporidian prevalence, as well as making projections under different climate change scenarios (Benning*, et al.* 2002; Samuel*, et al.* 2011; Sehgal*, et al.* 2011). This approach is being used to provide information on potential changes to the spatial distribution occupied by the host-parasite complex and, if sufficient information is available, it could be used to assess infection risks i.e., which species of birds can be the most vulnerable to haemosporidian potential distribution changes, exposure to new vector-parasite interactions, assess vector-parasite mobility and predict host switching phenomena correlated to climate change (Benning*, et al.* 2002; Brooks & Hoberg 2007; Martins-Braga*, et al.* 2011; Rooyen*, et al.* 2013; Clark*, et al.* 2016).

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HYPOTHESIS AND OBJECTIVES

MAIN HYPOTHESES

Climate change will affect the regimes of humidity and temperature that determine local haemosporidian prevalences in the avian communities of central to eastern Mexico. Under contrasting climate change scenarios, the projected temperature increases, and rainfall decreases will cause a statistically significant spatial turnover of haemosporidian infections across an altitudinal gradient, amplifying haemosporidian prevalence at higher elevations and reducing prevalences in the lowlands.

At continental scales, haemosporidian specificity plays an important role in how haemosporidian lineages adapt to climate change scenarios. Generalist lineages infecting a wide range of avian hosts will show a higher environmental tolerance than specialist lineages with a more limited range of avian host infectivity. There will be a noticeable trend of northward environmental shift under contrasting climate change scenarios and the suitability of the niche space of haemosporidians will become compromised, with specialist lineages being the most susceptible to suffer an important loss of suitable climate space.

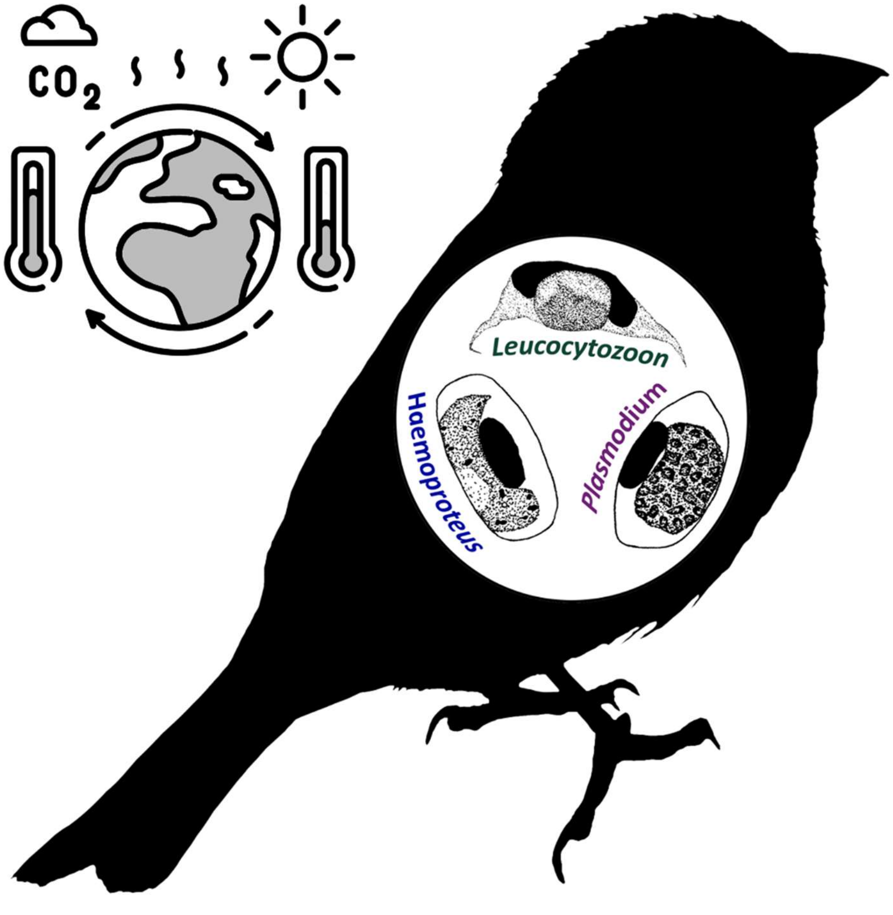
MAIN OBJECTIVES

Model current environmental niche conditions and distribution trends for avian hosts, vectors and haemosporidian parasites within an elevation gradient, and project potential distribution changes under future climate change scenarios in central to eastern Mexico to assess vulnerability to species replacement and/or the formation of new parasite-host relationships in the region.

Identify the infection strategies of haemosporidian lineages found in continental North America and assess the environmental tolerance of generalist vs specialist haemosporidians by identifying the most influential bioclimatic predictor variables that drive their potential climate range and suitable niche space under contrasting climate change scenarios

CHAPTER I

CLIMATE PREDICTORS AND CLIMATE CHANGE PROJECTIONS FOR AVIAN HAEMOSPORIDIAN PREVALENCE IN CENTRAL TO EASTERN MEXICO[1]



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ABSTRACT

It is well known that long-term inter-annual and seasonal trends in temperature and precipitation influence prevalence, host specificity, and distribution of haemosporidian (intraerythrocytic) parasites. To better understand the climate drivers and potential climate distribution behind haemosporidian prevalence in central to eastern Mexico, we characterized the climatic niche behind global haemosporidian prevalence and projected the influence of climate change over said prevalence in the region. Using the MaxENT modelling algorithm, we assessed the relative contributions of bioclimatic predictor variables to identify those most influential to the haemosporidian prevalence documented in different avian communities in central to eastern Mexico. Two contrasting climate change scenarios over the next 50 years were used, to create distribution models that explain variation in the overall prevalence of the three main haemosporidian genera (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*) infecting future avian communities. We assigned our study sites into polygonal units (Operational Climatic Units, or OCUs). We used the general haemosporidian prevalence for each OCU as an indirect measure of environmental suitability for these parasites. The highest prevalence currently occurred in three semi-arid habitats, while the lowest prevalence was found at three of the most humid habitat types. Among bioclimatic variables, the association of mean diurnal temperature range and annual temperature range showed high statistical significance with the total observed prevalence. Climate change model projections for the decade of 2070 showed a significant modification of the current distribution of suitable climate areas for haemosporidians in the study region. On a local scale, the studied parasite-vector-host system could face a significant spatial turnover in prevalence caused by climate change.

Keywords: avian haemosporidian, avian malaria, infection, prevalence, climate change models, disease ecology, landscape parasitology

INTRODUCTION

The geographical distribution of host-parasite systems is strongly dependent on environmental conditions (Morand & Krasnov 2010; Prieto-Torres*, et al.* 2020). Spatial modelling of environmental responses to climate change (Peterson*, et al.* 2002; Sehgal*, et al.* 2011; Ponce-Reyes*, et al.* 2012; Ponce-Reyes*, et al.* 2017) can be used to describe the current distribution of climatic variables most relevant to observed haemosporidian prevalence in present day conditions (Benning*, et al.* 2002; Samuel*, et al.* 2011; Sehgal*, et al.* 2011). Then, this information is used to create spatial projections of those variables under climate change scenarios to predict potential changes of prevalence or infection rate in years to come. This approach has been used for studying vector-borne human diseases, such as dengue and malaria (Lindsay & Martens 1998; Patz & Reisen 2001; Massad*, et al.* 2011; Ojogba*, et al.* 2012; Robles-Fernández*, et al.* 2021) and could provide insightful information when applied to the study of wildlife infectious diseases (Prieto-Torres*, et al.* 2020).

Avian malaria and related parasites are protozoans belonging to the genera *Plasmodium*, *Haemoproteus*, *Leucocytozoon*, and *Fallisia* (Phylum Apicomplexa, order Haemosporida), which are distributed worldwide except for Antarctica (Valkiūnas 2005). Different dipteran species from the families Culicidae, Hippoboscidae, Ceratopogonidae and Simuliidae transmit these parasites (Atkinson 1999; Valkiūnas 2005; Santiago-Alarcon*, et al.* 2012; Ferreira*, et al.* 2020). Currently, there is little information available regarding how climate fluctuations may affect ecological dynamics involving haemosporidians, but likely functional responses include the following: 1) range expansion of haemosporidian parasites to higher altitudes, (Benning*, et al.* 2002; Peterson*, et al.* 2002; Samuel*, et al.* 2011; Atkinson*, et al.* 2014; McClure 2017; Martina Ferraguti*, et al.* 2020; Rodríguez-Hernández*, et al.* 2021); 2) shifts in geographic range and colonization patterns towards areas were the presence of certain haemosporidian lineages or avian hosts are uncommon or absent (Lindsay & Martens 1998; Khasnis & Nettleman 2005; Brooks & Hoberg 2007; Kurane 2010; Coon & Martin 2013; McClure 2017; Martina Ferraguti*, et al.* 2020); and 3) the reduction and eventual disappearance of ecotones and contact zones that limits the dispersal of haemosporidian parasites (Odum & Barrett 2004; Brooks & Hoberg 2007; Atkinson*, et al.* 2014).

Latitudinal shifts in the distribution of avian haemosporidian are hard to assess, mainly because different parasite groups present different distribution patterns in response to latitude and local climate trends (Kamiya*, et al.* 2014). Preliminary —albeit fragmentary— information indicates a lack of a latitudinal pattern in avian haemosporidians (Clark 2018) or a reverse latitudinal pattern (higher prevalence the higher the latitude, instead of the opposite) in the case of *Leucocytozoon* spp. (Fecchio*, et al.* 2019b). Hence, further investigations on how haemosporidians respond to climate change at different spatial scales are necessary. In regions with sharp seasonal changes, climate regulates haemosporidian infections at crucial life-cycle stages – from the development of haemosporidian parasites within the dipteran vectors to the transmission to their final avian hosts –, and the seasonality of disease is marked by temperature increases (Valkiūnas 2005; Schröder & Schmidt 2008; Garamszegi 2011; Santiago-Alarcon*, et al.* 2012). For this reason, temperature and humidity are considered strong predictors of haemosporidian prevalence (Stresman 2010; Garamszegi 2011; Sehgal*, et al.* 2011; Fecchio*, et al.* 2019a; Chapa-Vargas*, et al.* 2020).

Critical transmission windows typically occur when climate variation or land use modifications facilitate the development and dispersion of haemosporidian parasites within avian communities (Hoberg*, et al.* 1997; Møller 2010; Clark*, et al.* 2016; Clark*, et al.* 2018). Recent studies demonstrate that long-term inter-annual and seasonal trends in temperature and precipitation (called *bioclimatic variables*) influence haemosporidian prevalence, host specificity, and distribution within a geographical region (Sehgal*, et al.* 2011; Clark*, et al.* 2016; Ferraguti*, et al.* 2018; Fecchio*, et al.* 2019a). Though common in wild bird communities, haemosporidian infections may represent a potential conservation issue due to unforeseen effects of climate change on parasite-host interactions (Khasnis & Nettleman 2005; Stresman 2010). Several factors could potentially influence how haemosporidian infection trends are expressed within avian communities (Benning*, et al.* 2002), including potential changes on transmission risk (Huijben*, et al.* 2007; Garamszegi 2011), changes in prevalence and coinfection rates (Zamora-Vilchis*, et al.* 2012; Clark*, et al.* 2016), species turnover (Clark 2018; Álvarez-Mendizábal*, et al.* 2021), and changes in distribution and development thresholds (Marcogliese 2008; Paaijmans & Thomas 2013). For instance, avian malaria (i.e., *Plasmodium* spp.) prevalence correlates positively with temperature and humidity (Lindsay & Martens 1998; Benning*, et al.* 2002; Valkiūnas 2005; Stresman 2010; Garamszegi 2011; Atkinson*, et al.* 2014). Temperature increases stimulate the reproduction of parasites and vectors (Garamszegi 2011), while proximity to freshwater sources fosters the reproduction of anopheline mosquitoes (Culicidae) responsible for *Plasmodium* transmission (Krama*, et al.* 2015; Ferraguti*, et al.* 2018). Although there is limited information on the temperature thresholds for most of the species of this genus, the distribution and abundance of its vectors are directly associated with temperature. Upper limits may reduce vector and parasite developmental rates and even eliminate them from some geographical areas where extreme (+2° C) increases in temperature are predicted, whereas the opposite might be true for areas with current temperate climates (Loiseau*, et al.* 2013; Atkinson*, et al.* 2014; Liao*, et al.* 2017). Similarly, *Haemoproteus* prevalence correlates positively with temperature (Valkiūnas 2005; Zamora-Vilchis*, et al.* 2012), as the distribution and abundance of its vectors (ceratopogonids and hippoboscids) is directly associated with temperature increases and agricultural development (Friend & Franson 1999; Rooyen*, et al.* 2013). In comparison, *Leucocytozoon* is better adapted to colder climates and its prevalence increases at higher latitudes (Valkiūnas 2005; Ramey*, et al.* 2014; Smith*, et al.* 2016), and with increasing altitude (over 2200 masl) (Galen & Witt 2014; Lotta*, et al.* 2016; Fecchio*, et al.* 2019b). These conditions usually have high humidity, precipitation, and coincide with lower temperatures which limit *Haemoproteus* and *Plasmodium* infections but provide suitable habitat for the larvae of the black fly (Simulidae) vectors of Leucozoonoid infections in birds (Forrester & Greiner 2008; Harrigan*, et al.* 2014; Illera*, et al.* 2017; Ferreira*, et al.* 2020). These parasites undergo sporogony (the asexual reproduction stage where the bird-infective forms of haemosporidian parasites are formed) in temperatures between 15° C to 20° C, meaning Leucozoonoid parasites have the lowest temperature threshold for transmission of the three haemosporidian genera (Valkiūnas 2005).

Climate change projections for Mexico by 2100 estimate temperature increases of 2.5 to 3.5° C and precipitation decreases of 5 to 10% all over the country (Gosling*, et al.* 2011; Cavazos*, et al.* 2013). These trends have already had substantial impacts on mountain habitats across the Trans-Mexican Volcanic Belt forcing their migration by several hundred meters to higher elevations (Jiménez-García*, et al.* 2021). Nationwide, the average temperature has risen by 0.85°C since the 1960s (IPCC 2014). Governmental mitigation strategies work under two essential assumptions: 1) Mexico commits to reduce greenhouse gas emissions and to contribute to maintaining global average temperature increase under 2.4° C; 2) no reductions of emissions occur and average global temperature shoots over 4.9° C (SEMARNAT-INECC 2016). Following the Representative Concentration Pathways (RCP) adopted by the Intergovernmental Panel for Climate Change (Wayne 2013; IPCC 2014), these assumptions correspond to two specific climate change scenarios: scenario RCP 4.5, referred to as an "optimistic" climate change scenario, where greenhouse emissions are stabilized under 650ppm shortly after 2100 and a global temperature increase up to 2° to 3° C (Smith & Wigley 2006; Clarke*, et al.* 2007; Thomson*, et al.* 2010; IPCC 2014); and RCP 8.5, labeled as the "business as usual, worst case scenario", where global failure to curb warming by greenhouse emissions by 2100 will lead to a global temperature increase of 4.5° C by 2100 (Riahi*, et al.* 2007; Riahi*, et al.* 2011; IPCC 2014).

The objective of this study was to identify the bioclimatic predictor variables that are the most influential on the haemosporidian prevalence documented in different avian communities in central to eastern Mexico and the likely trends of their effects on said prevalence over the next 50 years under two contrasting climate change scenarios. Specifically, we associated the recorded haemosporidian prevalence in our study sites to their temperature and humidity conditions and projected them 50 years into the future under the two contrasting climate change scenarios described above. Since haemosporidian prevalence is mainly driven by temperature and humidity, projection models might provide potential shifts in distributional trends of infections in response to climate change (particularly across an altitudinal gradient), comparable to what has been reported in Hawaii, Europe, and Africa (Garamszegi 2011; Atkinson*, et al.* 2014). Additionally, climate change projections could show potential distributional shifts of the climate currently occupied by avian haemosporidians in the study region, representing potential new areas of the occurrence of these parasites. We predicted increasing prevalence at higher elevations, and decreasing prevalence at lowlands, where increases in temperature of already hot environments along with lower humidity are likely to interrupt the life cycle of both Diptera vectors and haemosporidians.

METHODS

Study region and sampling sites. The study region includes the states of San Luis Potosí and Veracruz, in central to eastern Mexico, where three physiographic regions converge: the Mexican Plateau (MP), the Sierra Madre Oriental (SMO) and the Gulf of Mexico's Coastal Plain (GCP). Altitude, average annual temperatures, and mean annual precipitation range from sea level to 3700 masl, 32° to 8° C, and 2000 to 50mm (CONABIO 2008; INEGI 2008). In this region, we captured and obtained blood samples from 1273 birds across 19 geographical locations. The sampling design was focused on covering the climate variation present in the region based on temperature and precipitation (Fig. 1).

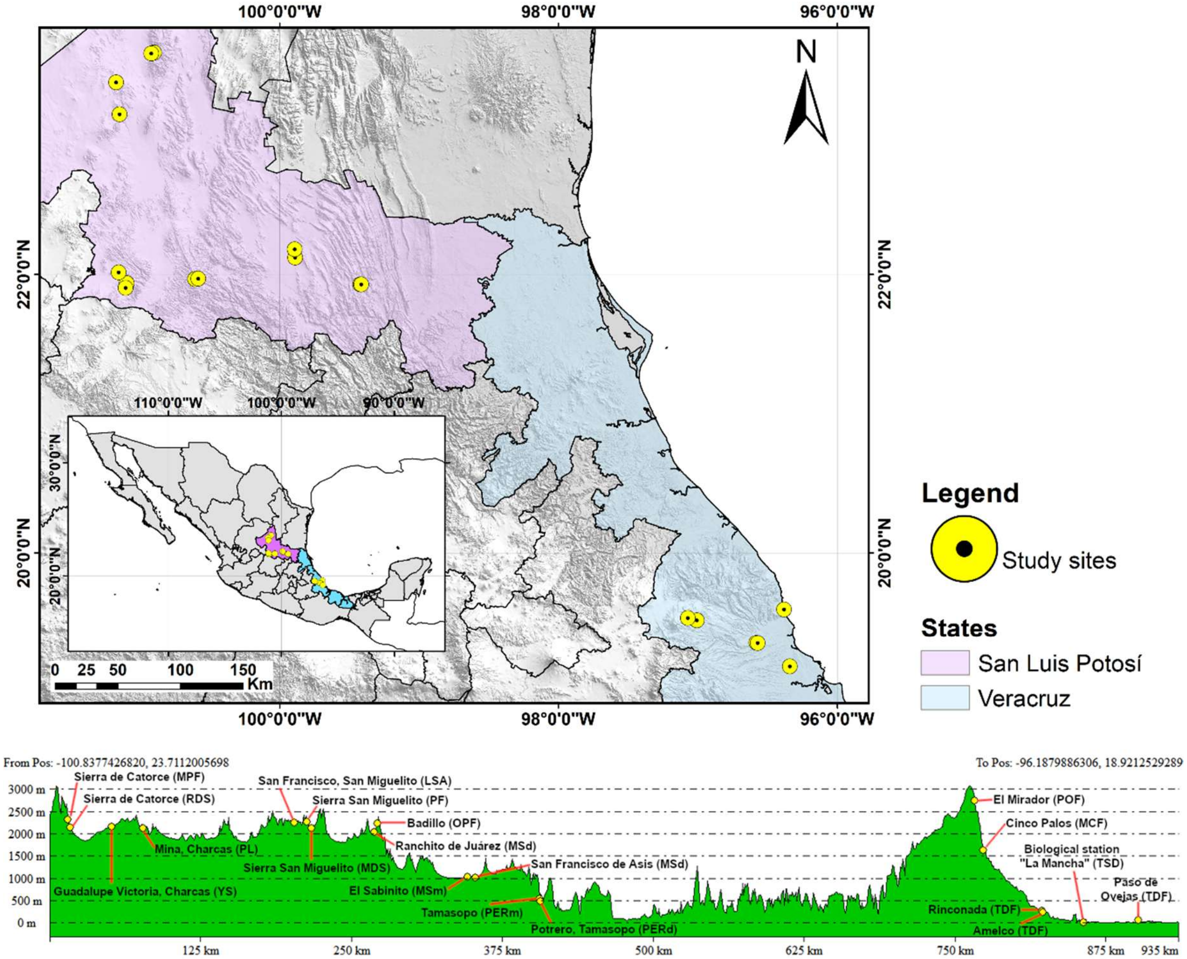

Figure 1. Extent of the study region and altitudinal spread of the sampling sites.

Sampling considered the major vegetation habitat types in the region, including *Rosetophyllous* desert shrubland (RDS), *Microphyllous* desert shrubland (MDS), *Yucca* shrubland (known as *izotal*) (YS), Pasturelands (PL) and Livestock areas (LSA), Mesquite shrubland (MS), Mexican pinyon forest (MPF), Pine Forest (PF), Pine-Oak Forest (POF), Oak-Pine Forest (OPF), Perennial Forest (PER), Tropical sub-deciduous forest (TSD), Tropical deciduous forest (TDF), and Montane cloud forest (MCF) (Rzedowski 1961) (Fig. 2).

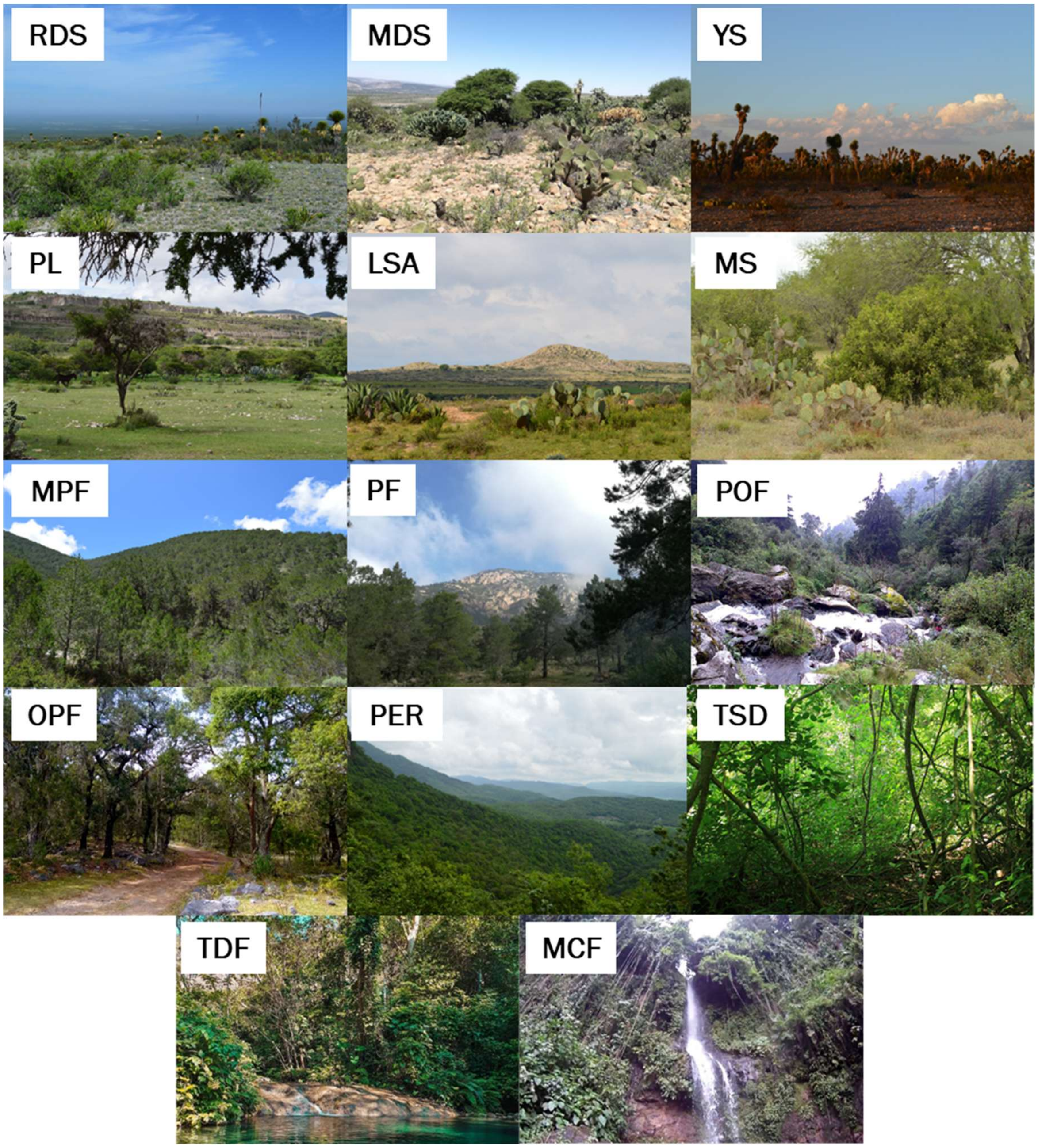

Figure 2. Vegetation types covered in this study.

Birds were captured via mist-netting from May to September of 2017 and 2018. These are the warmest and most humid months, and thus coincide with the reproductive season of resident bird populations and the peak of infection prevalence associated with increased vector activity (Ham-Dueñas*, et al.* 2017; Hernández-Lara*, et al.* 2017; Rodríguez-Hernández*, et al.* 2021). Every captured bird was ringed, measured, weighed, and released according to guidelines described in the Bird Ringing Station Manual (Busse & Meissner 2015). 10-30 µl of blood were obtained by brachial venipuncture. In the case of hummingbirds and other small species blood was collected by nail clipping. Blood smears were prepared with approximately 1-2 µl of the collected blood samples and fixed *in situ* using absolute methanol for five minutes to preserve the samples from degradation. The rest of the blood was stored in 1.5ml plastic tubes for subsequent use of molecular analysis (Santiago-Alarcon & Carbó-Ramírez 2015) (Fig. 3).

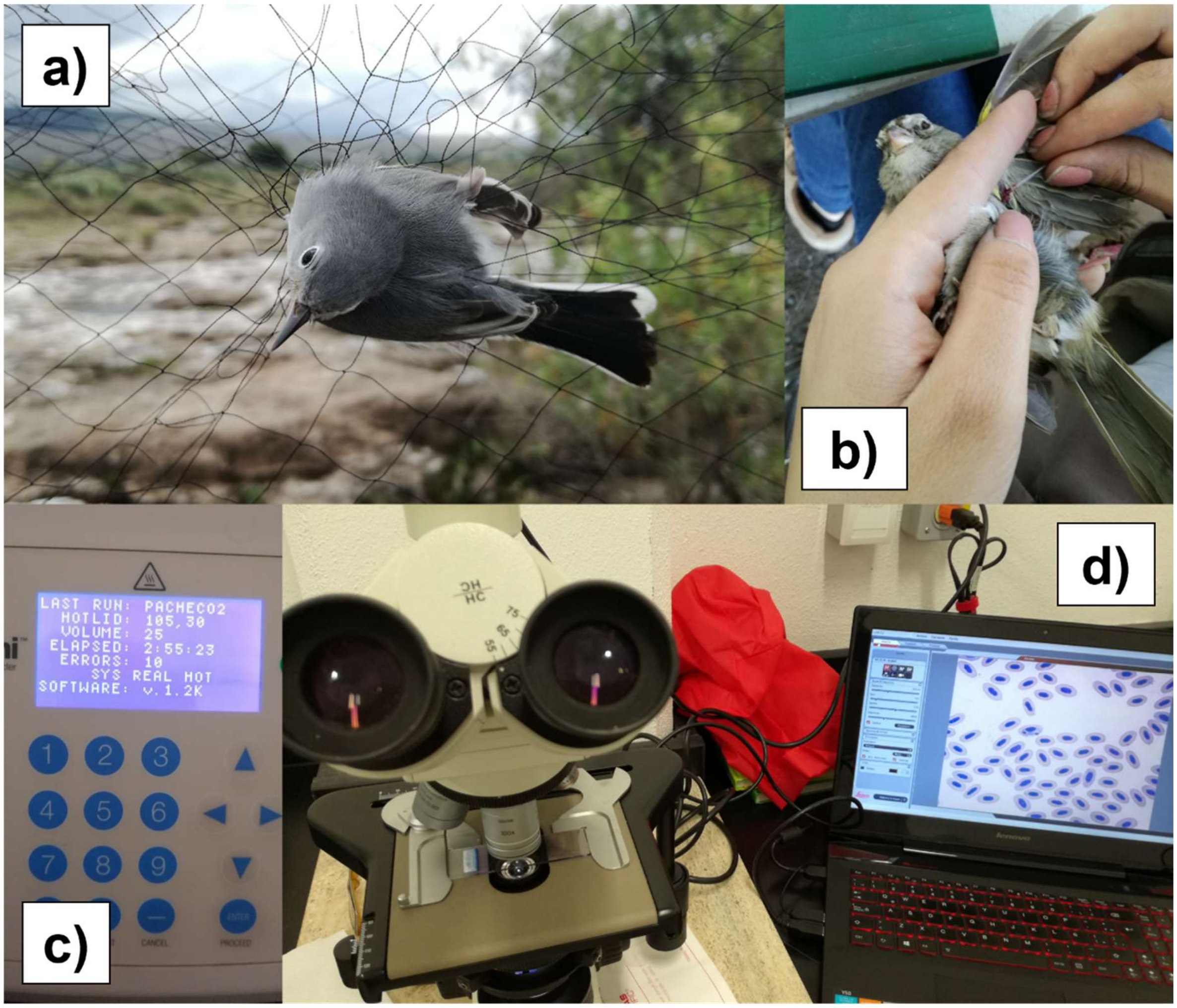

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Figure 3. a) Bird netting, b) Blood sampling by brachial venipuncture technique, c) Molecular analysis and d) Microscopic analysis.

Microscopy and molecular analyses. Blood samples were examined for haemosporidian parasites with microscopy and three different PCR molecular protocols that amplify fragments of the mtDNA cytochrome *b* gene of different sizes (Beadell *et al.,* 2004; Hellgren *et al.,* 2004; Bell *et al.,* 2015; Pacheco *et al.,* 2018), to increase the probability of recovering all potential infections. This way we obtained information on the genetic diversity of the haemosporidian species present in the samples and detected parasitic infections with lower parasitemia or that might have passed undetected by microscopic analysis and by different molecular protocols (Santiago-Alarcon & Carbó-Ramírez 2015; Rodríguez-Hernández*, et al.* 2021).

DNA samples were processed first using the PCR protocol proposed by Pacheco *et al*. (2018); this protocol produces the longest mtDNA cyt *b* fragment. Each reaction contained a total volume of 25µl, consisting of 5µl sample DNA at 30-50 ng/µl, 6.5µl injectable water, 12.5µl PCR Buffer (Invitrogen Platinum ™ Green Hot Start PCR Master Mix, Thermo Fisher Scientific) and 0.5µl of each primer. In the first run we used primers AE974-EF and AE299-ER to amplify a 1773bp fragment under the following conditions: initial denaturalization at 94° C for 5 min, 40 cycles of denaturalization at 94° C for 30 s, annealing at 45° C for 2 min and extension at 72° C for 2 min, and a final extension step at 72° C for 10 min. The first run product was used for a second run to amplify a 1109bp fragment, adding to the reaction mix 1.6µl of primer AE064-IF and 0.2µl of the AE066-IR primer, running the reaction for 35 cycles and an annealing temperature of 56° C for 30 s. Negative samples from the first protocol were tested again for haemosporidian infection with the PCR protocol proposed by Beadell *et al*. (2004) to amplify a 533bp fragment of cyt *b* using primers 3760F and 4292Rw2. Reactions were run using a denaturalization temperature of 94° C for 5 min, and 35 cycles of denaturalization at 94° C for 45 s, annealing at 54° C for 45 s, and extension at 72° C for 45 s, with a final extension step at a temperature of 72° C for 10 min. Again, the resulting negatives were tested for haemosporidian infection using the Hellgren *et al*. (2004) PCR protocol. Primers used were HaemNFI and HaemNR3 to obtain a 580bp on the first run. For the following nested PCR, corresponding primers HaemF and HaemR2 amplify a fragment of approximately 524 nucleotides for *Plasmodium* spp. and *Haemoproteus* spp. Reactions were run using a denaturalization temperature of 94° C for 3 min, with 20 cycles of denaturalization at 94° C for 30 s, annealing at 50° C for 30 s, extension 72° C for 45 s for the first run and 35 cycles for the second, with a final extension period of 72° C for 10 min. To test for *Leucocytozoon* infections we used primers HaemFL and HaemR2L on 2µl of the products obtained from the second Pacheco PCR run, the products of the first Beadell PCR run, and the products from the first Hellgren PCR run as templates. Temperature conditions for the *Leucocytozoon* runs were those previously described for the first Hellgren PCR run. Combining these three methods allowed us to reduce false negatives (Beadell*, et al.* 2004; Hellgren*, et al.* 2004; Pacheco*, et al.* 2018). The amplified cytochrome *b* fragments obtained with these analyses were sent to Macrogen Korea for sequencing. Sequence data has been approved by the NCBI and deposited into GenBank (accession numbers MZ604564, MZ604565, MZ604566, MZ604567, MZ604568, MZ604569, MZ604570, MZ604571, MZ604572, MZ604573, MZ604574, MZ604575, MZ604576, MZ604577, MZ604578, MZ604579 and MZ604580).

Haemosporidian prevalence estimates. We were unable to obtain appropriate sample sizes for environmental modelling for each lineage or genera; most of these lineages were present only once in the sample (Table 1). Therefore, we report a general haemosporidian prevalence rate, without making a distinction among haemosporidian genus. To assess the variability of haemosporidian prevalence with habitat type, we ran a generalized linear mixed model (GLMM) analysis, using the function "glmer" implemented in the statistical package "lme4" (Bates*, et al.* 2015) in R software v.4.0.3 (Core-Team 2013). The model was constructed using the binomial distribution (logit link), with habitat type (vegetation) as the fixed predictor for haemosporidian prevalence and the avian host species as a random variable.

Table 1. List of sequenced haemosporidian lineages and respective sample size per host species, study site and corresponding habitat type.

Haemosporidian lineage	Sample size	Host species	Study site	Habitat type
ARRRUF02	1	*Arremonops rufivirgatus*	El Sabinito	MSm
BAEBIC02	6	*Arremonops rufivirgatus*	Tamasopo – Perennial forest	PERm
	2	*Basileuterus culicivorus*		
	3	*Basileuterus lachrymosus*		
	1	*Xiphorhynchus flavigaster*		
	1	*Basileuterus culicivorus*	Tamasopo – Pastureland	PERd
	1	*Basileuterus rufifrons*		
	1	*Dives dives*		
BASCUL02	1	*Basileuterus culicivorus*	Tamasopo – Perennial forest	PERm
CARCAR02	1	*Eugenes fulgens*	Badillo	OPF
	1	*Hylocharis leucotis*		
	1	*Amphispiza bilineata*	Guadalupe Victoria, Charcas	YS
	1	*Empidonax minimus*	Matorral, Sierra de Catorce	RDS
	2	*Empidonax occidentalis*		
	1	*Passerina versicolor*		
	1	*Haemorhous mexicanus*	Sierra San Miguelito – Shrubland	MDS

	7	*Cardinalis cardinalis*	El Sabinito	MSm
	1	*Thryomanes bewickii*		
	1	*Chondestes grammacus*	San Francisco de Asis	MSd
	1	*Columbina passerina*		
	1	*Empidonax sp.*		
	1	*Melanerpes aurifrons*		
	2	*Henicorhina leucophrys*	Tamasopo – Perennial forest	PERm
	2	*Sittasomus griseicapillus*		
	1	*Basileuterus rufifrons*	Tamasopo – Pastureland	PERd
	1	*Dives dives*		
	1	*Melanerpes aurifrons*		
	1	*Saltator atriceps*		
	4	*Turdus grayi*		
CARCAR29	7	*Cardinalis cardinalis*	El Sabinito	MSm
	1	*Columbina inca*		
	1	*Melanerpes aurifrons*		
	1	*Passerina versicolor*		
	1	*Thryomanes bewickii*		
	1	*Vireo griseus*		
	1	*Cardinalis cardinalis*	San Francisco de Asis	MSd
	1	*Dives dives*	Tamasopo – Pastureland	PERd
COLINC03	1	*Columbina inca*	Mine, Charcas	PL
COLPAS03	3	*Columbina passerina*	San Francisco de Asis	MSd
COLPAS09	1	*Columbina passerina*	San Francisco de Asis	MSd
GEOTRI01	1	*Basileuterus lachrymosus*	Tamasopo – Perennial forest	PERm
GEOTRI02	2	*Passerina versicolor*	El Sabinito	MSm
	1	*Passerina versicolor*	San Francisco de Asis	MSd
HENLEU01	1	*Henicorhina leucophrys*	Tamasopo – Perennial forest	PERm
ICTCAY01	1	*Basileuterus culicivorus*	Tamasopo – Pastureland	PERd
ICTLEU01	1	*Icterus parisorum*	Guadalupe Victoria, Charcas	YS
	1	*Icterus parisorum*	Sierra San Miguelito – Pine	PF
	2	*Icterus parisorum*	Ranchito de Juarez	MSd
	1	*Basileuterus culicivorus*	Tamasopo – Perennial forest	PERm
	1	*Henicorhina leucophrys*		
ICTPUS01	1	*Icterus pustulatus*	Tamasopo – Pastureland	PERd
ICTPUS02	1	*Icterus pustulatus*	Tamasopo – Pastureland	PERd
LAIRI01	3	*Toxostoma curvirostre*	Guadalupe Victoria, Charcas	YS

	1	*Toxostoma curvirostre*	Mine, Charcas	PL
	1	*Cardinalis cardinalis*	El Sabinito	MSm
	3	*Thryomanes bewickii*		
	1	*Turdus grayi*		
	1	*Baeolophus atricristatus*	San Francisco de Asis	MSd
	1	*Passerina versicolor*		
	1	*Quiscalus mexicanus*		
	1	*Thryomanes bewickii*		
	1	*Henicorhina leucophrys*	Tamasopo – Perennial forest	PERm
	1	*Arremonops rufivirgatus*	Tamasopo – Pastureland	PERd
LANLUD01	1	*Lanius ludovicianus*	Guadalupe Victoria, Charcas	YS
MELAUR01	1	*Melanerpes aurifrons*	Tamasopo – Pastureland	PERd
MELAUR02	1	*Melanerpes aurifrons*	Guadalupe Victoria, Charcas	YS
MELFUS01	1	*Melozone fusca*	Ranchito de Juarez	MSd
MIMGIL01	1	*Mimus polyglottos*	San Francisco de Asis	MSd
	1	*Dives dives*	Tamasopo – Pastureland	PERd
MOLATE01	1	*Haemorhous mexicanus*	Guadalupe Victoria, Charcas	YS
MONNIG01	1	*Coccyzus americanus*	El Sabinito	MSm
PADOM09	1	*Arremonops rufivirgatus*	El Sabinito	MSm
	1	*Basileuterus lachrymosus*	Tamasopo – Perennial forest	PERm
	3	*Pheugopedius maculipectus*		
	1	*Turdus grayi*		
	1	*Basileuterus lachrymosus*	Tamasopo – Pastureland	PERd
	4	*Dives dives*		
PADOM11	7	*Passerina versicolor*	El Sabinito	MSm
	1	*Passerina versicolor*	San Francisco de Asis	MSd
	1	*Pheugopedius maculipectus*	Tamasopo – Perennial forest	PERm
	1	*Dives dives*	Tamasopo – Pastureland	PERd
SEIAUR01	1	*Arremonops rufivirgatus*	El Sabinito	MSm
	2	*Quiscalus mexicanus*	San Francisco de Asis	MSd
	1	*Dives dives*	Tamasopo – Pastureland	PERd
SIAMEX01	1	*Dives dives*	Tamasopo – Pastureland	PERd
SISKIN1	2	*Haemorhous mexicanus*	Guadalupe Victoria, Charcas	YS
	1	*Haemorhous mexicanus*	El Sabinito	MSm
	1	*Melanerpes aurifrons*		

	1	*Arremonops rufivirgatus*	Tamasopo – Perennial forest	PERm
	2	*Euphonia hirundinacea*		
	2	*Henicorhina leucophrys*		
	1	*Momotus coeruliceps*		
	1	*Pheugopedius maculipectus*		
SPMAG06	1	*Turdus grayi*	El Sabinito	MSm
	1	*Turdus grayi*	Tamasopo – Pastureland	PERd
TACRUB04	1	*Cyanerpes cyaneus*	Tamasopo – Perennial forest	PERm
TOXCUR01	1	*Toxostoma curvirostre*	El Sabinito	MSm
TOXLON01	1	*Toxostoma longirostre*	El Sabinito	MSm
TURGRA01	1	*Turdus grayi*	El Sabinito	MSm
TURGRA02	1	*Turdus grayi*	Tamasopo – Pastureland	PERd
VIGIL07	2	*Vireo griseus*	El Sabinito	MSm
	1	*Vireo griseus*	Tamasopo – Pastureland	PERd
VIGRI04	1	*Baeolophus atricristatus*	El Sabinito	MSm
	1	*Passerina versicolor*		
	2	*Vireo griseus*		
VIGRI04	1	*Vireo griseus*	El Sabinito	MSm
VIRGRI01	1	*Vireo griseus*	El Sabinito	MSm
VIRHUT04	1	*Vireo huttoni*	Sierra San Miguelito – Pine	PF
ZEMAC01	1	*Melanerpes aurifrons*	San Francisco de Asis	MSd
ZEMAC17	1	*Campylorhynchus brunneicapillus*	San Francisco de Asis	MSd
ZOCAP01	1	*Melanerpes aurifrons*	San Francisco de Asis	MSd
ZOCAP08	3	*Junco phaeonotus*	Badillo	OPF
	1	*Passerina caerulea*	Ranchito de Juarez	MSd
	1	*Pipilo maculatus*		
	1	*Passerina amoena*	El Sabinito	MSm
	2	*Passerina versicolor*		
	1	*Passerina versicolor*	San Francisco de Asis	MSd
ZOCAP17	1	*Icterus parisorum*	Sierra San Miguelito – Pine	PF

Operational Climatic Units. To increase our sampling area and obtain the best possible climate characterization for the observed haemosporidian prevalence rates, we devised a method based on previous modelling approaches, where sampling locations are used to train the MaxENT modelling algorithm to identify the relationship between vegetation communities where the haemosporidians are present and bioclimatic predictor variables (Sehgal*, et al.* 2011; Ponce-Reyes*, et al.* 2012; Ponce-Reyes*, et al.* 2017). For each of our 19 sampling locations, we calculated haemosporidian prevalence and extracted the associated bioclimatic data from WorldClim environmental layers (see below) at a spatial resolution of 30” of arc (~1km^2) with ArcMap 10.3. Then, we assigned the study sites into polygons concerning site proximity and vegetation type. These units were labeled as Operational Climatic Units (OCUs). The demarcation of each OCU rests on the following assumptions: 1) each vegetation type relates to well-defined climatic trends; 2) climate does not change drastically within a 15km radius around the original sampling sites (averaged climate values determined around each sample site to define each OCU plus vegetation polygons), and 3) haemosporidian prevalence remain relatively constant within OCUs and would be comparable due to climate similarity. Each resulting polygon was converted into a 1km^2 point grid using environmental data from the WorldClim bioclimatic layers and the average prevalence obtained from our haemosporidian sampling sites. We randomly selected 5% data points from each polygon (see Ponce-Reyes*, et al.* (2012)) as experimental haemosporidian presence data to run the models in MaxENT (Hijmans*, et al.* 2005) (Fig. 4). Given that there is limited information on environmental thresholds for *Haemoproteus, Plasmodium* and *Leucocytozoon* morphospecies and the environmental requirements of most lineages are largely unknown, we grouped them and associated the general haemosporidian prevalence data for each OCU as an indirect response of environmental suitability for these parasites.

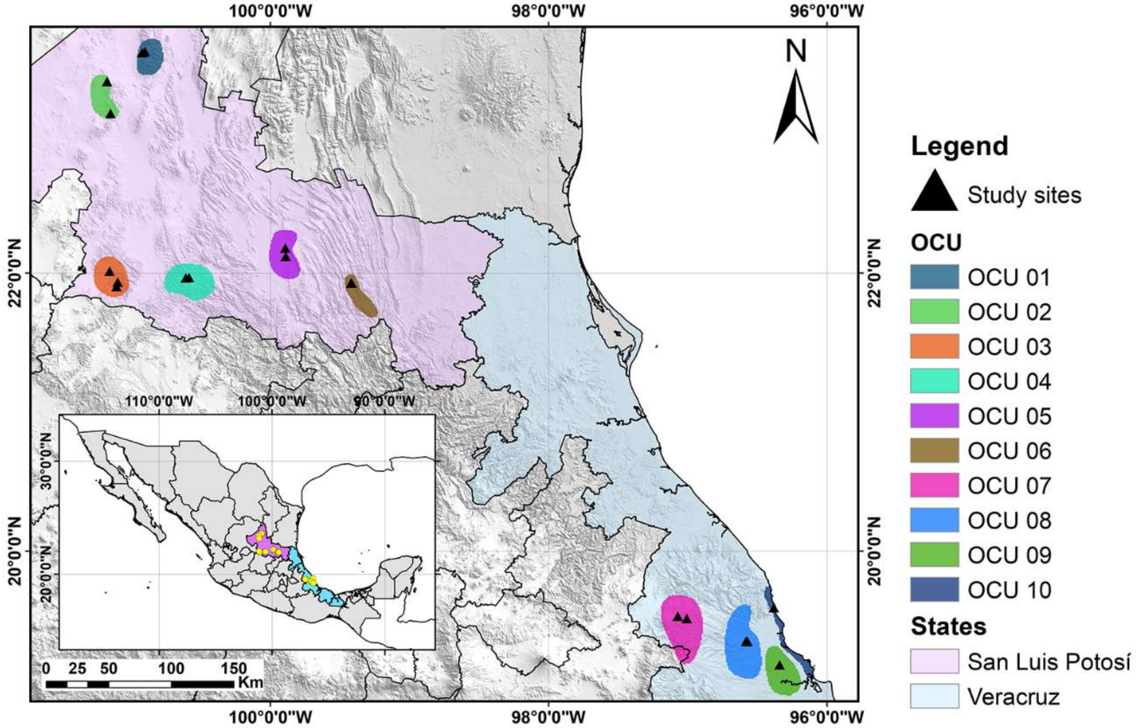

Figure 4. Study sites are scattered across the states of San Luis Potosí and Veracruz, Mexico, and occur under a variety of climate conditions. To homogenize our sample data and increase the number of sampling locations, we grouped our localities into Operational Climate Units (OCU) which facilitated the analysis and extraction of associated environmental data for each area.

Climatic variables. To characterize the climate associated with the prevalence of each study site, we used 19 bioclimatic variables (Table 2) derived from an interpolation of average monthly temperature and rainfall values obtained from weather stations and representing annual trends (Hijmans*, et al.* 2005). We clipped each environmental grid using the OCU polygon. As an exploratory analysis to relate the potential effect of bioclimatic variables on the prevalence recorded at each location, we extracted from the clipped grids the climatic information from the precise localities where the prevalence was recorded. Then we ran a regression analysis with the MiniTab 17.1.0 Statistical Software (Ryan*, et al.* 2013) to explore the potential effect of bioclimatic variables on the prevalence recorded in each location.

Table 2. Worldclim's bioclimatic variables list. The environmental variables in bold correspond to the ones used to run the final models. Variables marked with an asterisk were those variables omitted to avoid overfitting of the models.

Code	**Bioclimatic variable**
BIO1	Annual Mean Temperature
BIO2	**Mean Diurnal Range (Mean of monthly (max temp - min temp))**
BIO3	**Isothermality (BIO2/BIO7) (×100)**
BIO4	**Temperature Seasonality (standard deviation ×100)**
BIO5	Max Temperature of Warmest Month
BIO6	**Min Temperature of Coldest Month**
BIO7	**Temperature Annual Range (BIO5-BIO6)**
BIO8*	Mean Temperature of Wettest Quarter
BIO9*	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	**Mean Temperature of Coldest Quarter**
BIO12	**Annual Precipitation**
BIO13	**Precipitation of Wettest Month**
BIO14	Precipitation of Driest Month
BIO15	**Precipitation Seasonality (Coefficient of Variation)**
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18*	Precipitation of Warmest Quarter
BIO19*	Precipitation of Coldest Quarter

Next, to select the set of climatic variables for the next analysis based on Ecological Niche Modeling, we used the same set of 19 bioclimatic variables from the Worldclim project (Hijmans*, et al.* 2005). We first excluded the four layers that combine precipitation and temperature information into the same layer (Mean Temperature of Wettest Quarter, Mean Temperature of Driest Quarter, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter), since these present spatial anomalies in the form of odd discontinuities between neighboring pixels

(Escobar *et al.,* 2014). Then we applied a Jackknife test (Cobos*, et al.* 2019) automatically generated in preliminary modeling procedures in MaxENT (see next section for details). For this preliminary modeling, we used 5% random points previously defined from the OCU point grids (see above) and the remaining 15 variables. Then, we selected those variables that contributed the most to each model. Nine were the predictor variables with the highest gain (highest contribution to the model when used in isolation) from the preliminary models for each OCU (Table 2), which were used to run the final models.

Climate characterization modelling. For the final modeling we used MaxENT (Phillips *et al.,* 2006) ver. 3.4.1, a presence-only distribution-modelling algorithm to characterize the climatic conditions present in the OCUs. Please note that we moved from the traditional "niche" modeling to "climate" modeling in MaxENT following Ponce-Reyes*, et al.* (2012) and Ponce-Reyes*, et al.* (2017). To validate the models, we used a tenfold cross-validation –a technique to evaluate predictive models by partitioning the original sample into a training set to train the model, and a test set to evaluate it—, and calculated the mean area under the receiver operating characteristic curve (AUC) (Peterson*, et al.* 2008; Mandrekar 2010). MaxENT's model performance is automatically assessed using the ROC curve (Phillips*, et al.* 2006). However, several problems are associated with this test (Lobo*, et al.* 2007; Peterson*, et al.* 2008); therefore, we used the partial ROC test as an alternative, a modification proposed by Peterson*, et al.* (2008) allocating different weight to commission and omission errors. Partial ROCs were calculated using the NicheToolbox software package (Osorio-Olvera*, et al.* 2020). A presence/absence map of haemosporidian prevalence climate suitability was obtained by applying a binary threshold (10 percentile training presence) to the projection of probability distribution. Climate change projection models for the haemosporidian probability distributions were based on RCP scenarios 4.5 and 8.5 and projected to 50 years into the future (2070) to contrast potential changes in the distribution of present-day haemosporidian prevalence between a moderate scenario (+2-3° C temperature increase) and a worst-case scenario (+4.5° C temperature increase).

Projections were categorized into three classes: 1) *climate gain*, where the models predict newly suitable areas for haemosporidian parasites, 2) *climate deficit*, no longer suitable areas for haemosporidians under climate change scenarios; and 3) *climate continuity*, suitable areas for haemosporidian parasites that are expected to remain suitable under climate change scenarios. These classes represent the areas where the models predict the climatic conditions associated with our original haemosporidian prevalence under climate change scenarios (RCP 4.5 and RCP 8.5) for 2070.

RESULTS

Haemosporidian prevalence. Avian haemosporidian infection was confirmed in all 19 sampling locations. Overall haemosporidian prevalence was 58.6% (CI=55.8-61.3, n=1266). By state, prevalence was 82.9% (CI=79.8-85.7, n=659) in San Luis Potosí and 32.3% (CI=28.6-36.2, n=607) in Veracruz. *Haemoproteus* was the most common infection recorded in the study region, with a total prevalence of 19.5% (CI=17.4-21.8, n=247), followed by *Plasmodium* infections with a prevalence of 15.6% (CI=13.6-17.7, n=197). *Leucocytozoon* and coinfections were found mostly in

Veracruz, with an estimated prevalence of 5.1% (CI=3.9-6.4, n=64) and 2.6% (CI=1.8-3.6, n=33), respectively. Out of the total infected individuals, a prevalence of 21.1% (CI=18.9-23.4, n=267) detected by PCR analysis belonged to unidentified haemosporidian infections; the haemosporidian DNA recovered from these samples was too degraded for sequencing, which resulted in our inability to identify the genera behind these infections.

Within San Luis Potosí, infections caused by *Haemoproteus* represented a prevalence of 24.6% (CI=21.3-28.1, n=162), while estimated *Plasmodium* prevalence was 17.3% (CI=14.5-20.4, n=114), and only three samples tested positive for *Leucocytozoon* (0.5%, CI=0.1-1.3). In addition, 267 infected samples from San Luis Potosí (40.5% prevalence, CI=36.7-44.4) could not be identified to genus level by molecular analysis. These samples tested positive for the haemosporidian cytochrome *b* gene, but not enough DNA was recovered for sequencing despite several attempts (either the blood sample was too small or degraded naturally). For Veracruz, *Plasmodium* infections were the most common, with 12.5% (CI=10.0-15.4, n=76). *Haemoproteus* had a prevalence of 9.7% (CI=7.5-12.4, n=59), and *Leucocytozoon* 4.6% (CI=3.1-6.6, n=28). In contrast to San Luis Potosí, a small percentage of Veracruz' samples matched to coinfections, where a 4.9% prevalence corresponded to *Haemoproteus/Leucocytozoon* (CI=3.2-7.1, n=26) co-infections, and 1.2% prevalence (CI=0.5-2.4, n=7) belonged to *Plasmodium/Leucocytozoon* co-infections. Lastly, only one infected sample (0.7% prevalence) from Veracruz was not identified to the genus level for the same reason mentioned above.

Haemosporidian prevalence varied among study sites (Fig. 5, Table 3). The highest prevalence occurred in three of the semi-arid habitats (LSA, MDS, and RDS). In contrast the lowest prevalences were found at three of the most humid habitat types (MCF, TDF, TSD), and at the arid habitats (PL and YS) we surveyed. Above-average prevalence occurred at PERm and MSm sites (Fig. 5, Table 3). GLMM results (Table 4) show that haemosporidian prevalence concerning habitat type varies significantly from one vegetation community to another (residual variance = 1.408). Part of this variability can be explained by the effects of the avian hosts (variance of random variable = 1.564). The model did not present overdispersion ($\phi = 0.7369$).

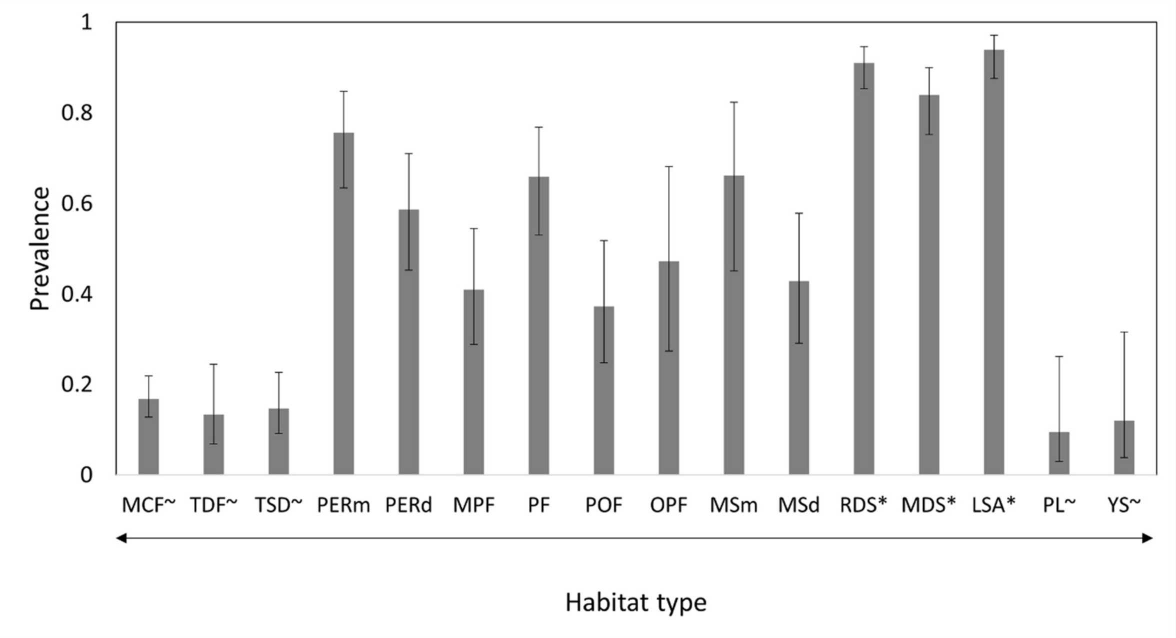

Figure 5. Haemosporidian prevalence per representative habitat type, from the most humid to the most arid vegetation communities, estimated by an additive generalized linear model using binomial distribution and logistic link function. Habitat types are as follow: MCF (Montane cloud forest), TDF (Tropical deciduous forest), TSD (Tropical sub-deciduous forest), PERm (Mature perennial forest), PERd (Degraded perennial forest), MPF (Mexican pinyon forest), PF (Pine forest), POF (Pine-Oak forest), OPF (Oak-Pine forest), MSm (Mature mesquite-dominated shrub), MSd (Degraded mesquite-dominated shrub), RDS (Rosetophyllous desert shrubland), MDS (Microphyllous desert shrub), LSA (Livestock area), PL (Pastureland), YS

(Yucca shrubland). Error bars represent ± 1 SEM. Highest prevalence trends are indicated with an asterisk while lowest prevalence trends are indicated with a tilde.

Table 3. Haemosporidian prevalences by study site.

State	OCU	Study site	Vegetation type	# of bird species	Total tested	Total positives	Haemosporidian prevalence (%)	Lower CL (95%)	Upper CL (95%)
San Luis Potosí	1	Sierra de Catorce - Pine	MPF	9	12	8	66.7	34.9	90.1
		Sierra de Catorce - Shrubland	RDS	21	50	47	94	83.5	98.7
	2	Guadalupe Victoria, Charcas	YS	20	84	62	73.8	63.1	82.8
		Mine, Charcas	PL	11	38	26	68.4	51.3	82.5
	3	Sierra San Miguelito - Shrubland	MDS	10	28	25	89.3	71.8	97.7
		Sierra San Miguelito - Pine	PF	21	62	37	87.9	76.7	95
		San Francisco, Sierra San Miguelito	LSA	5	10	10	100	69.2	100
	4	Ranchito de Juarez	MSd	15	23	18	78.3	56.3	92.5
		Badillo	OPF	14	33	24	72.7	54.5	86.7
Veracruz	5	El Sabinito	MSm	24	101	85	84.2	75.6	90.7
		San Francisco de Asis	MSd	20	63	55	87.3	76.5	94.4
	6	Tamasopo	PERm	17	76	67	88.2	78.7	94.4
		Tamasopo - Pastureland	PERd	30	83	68	81.9	72	89.5
	7	El Mirador	POF	23	118	61	51.7	42.3	61
		Cinco Palos	MCF	35	196	38	19.4	14.1	25.6
	8	Rinconada	TDF	12	14	4	28.6	8.4	58.1
		Amelco	TDF	19	62	19	30.6	19.6	43.7
	9	Paso de Ovejas	TDF	24	129	55	42.6	34	51.6
	10	Biologic Station “La Mancha”	TSD	23	88	19	21.6	13.5	31.6

Table 4. Generalized linear mixed model (GLMM) parameter estimates for haemosporidian prevalence prediction in relation to habitat type. Significant p-values are highlighted in bold. SE = Standard error, OR = Odd ratio, CI = Confidence intervals.

Response variable	Estimate	SE	OR	95% CI	p-value
Montane Cloud Forest (MCF)	-1.596	0.325	0.203	0.107-0.383	**0.000**
Tropical Subdeciduous Forest (TSD)	-0.165	0.485	0.848	0.328-2.195	0.734
Pastureland (PL)	-0.660	0.662	0.517	0.141-1.892	0.319
Tropical Deciduous Forest (TDF)	-0.270	0.425	0.763	0.332-1.755	0.525
Mature Perennial Forest (PERm)	2.729	0.482	15.313	5.955-39.379	**0.000**
Degraded Perennial Forest (PERd)	1.950	0.433	7.031	3.010-16.426	**0.000**
Oak-pine Forest (OPF)	1.489	0.524	4.431	1.588-12.368	**0.004**
Pine-oak Forest (POF)	1.080	0.431	2.943	1.266-6.843	**0.012**
Pine Forest (PF)	2.257	0.495	9.552	3.618-25.216	**0.000**
Mexican Pinyon Forest (MPF)	1.235	0.805	3.439	0.711-16.648	0.125
Yucca Shrubland (YS)	-0.398	0.511	0.672	0.247-1.830	0.437
Mature Mesquite-dominated Shrub (MSm)	2.269	0.452	9.670	3.985-23.465	**0.000**
Degraded Mesquite-dominated Shrub (MSd)	1.310	0.437	3.705	1.573-8.731	**0.003**
Microphyllous Desert Shrub (MDS)	3.252	0.712	25.834	6.394-104.376	**0.000**
Rosetophyllous Desert Shrubland (RDS)	3.916	0.677	50.204	13.316-189.278	**0.000**
Livestock Area (LSA)	4.337	1.176	76.440	7.623-766.513	**0.000**

Climate correlation and potential distribution models. Among all variables, the association of temperature annual range (p = 0.049) with the observed total prevalence showed a positive statistical significance, and there was a negative non-significant trend of mean temperature diurnal range (p = 0.090) on total prevalence. We also recorded positive significant associations between local haemosporidian prevalence and mean temperature diurnal range (p=0.019), and temperature annual range (p=0.027), and negative non-significant trends for minimum temperature of coldest month (p=0.076), annual precipitation (p=0.091), and precipitation of wettest month (p=0.092). The Jackknife analysis yielded trends suggesting similar associations among the bioclimatic variables and haemosporidian prevalence as those recorded through the regression analysis but added isothermality (variation quotient between the diurnal temperature range and annual temperature range), temperature seasonality, mean temperature of coldest quarter, and precipitation seasonality. Therefore, nine bioclimatic variables were considered for climate modelling. Models created a projection for the optimal climate conditions in which haemosporidian prevalence could be inferred within 50km of each OCU. Our resulting mean partial ROC values for all models ranked between 0.913 and 1.999 for RCP 4.5 and between 1.036 and 1.999 for RCP 8.5, indicating an excellent prediction capability within our OCUs and confirming the utility of these models for making projections under climate change scenarios (Table 5).

Table 5. Model validation, geographical zones, and number of study sites contained per Operational Climate Units. We used a random test percentage of 20% in MaxENT to train the models. The Area Under the Curve (AUC) analysis shows the training data test data values provided by MaxENT at the end of the run. These values show the 'goodness of fit' (predictive power) of the model. Additionally, we ran an independent Receiver Operating Characteristics (ROC) analysis to assess the predictive power for the climate change projection scenarios. For AUC, a mean value above 0.70 indicates a very good model, while for pROC analysis, values closer to 2 indicate good sensitivity of the models.

State	OCU	# of study sites	Geographical zone name	Training points	AUC		Partial ROC	
					Training data	Test data	4.5-50y	8.5-50y
San Luis Potosí	1	2	Sierra de Catorce	57	0.895	0.859	1.903	1.614
	2	2	Charcas	107	0.89	0.903	1.873	1.726
	3	3	San Miguelito	82	0.892	0.85	1.788	1.111
	4	2	Sierra de Alvarez	96	0.822	0.883	1.461	1.524
	5	2	Rioverde	103	0.951	0.932	0.913	1.999
	6	2	Tamasopo	61	0.856	0.839	1.713	1.496
Veracruz	7	2	Mirador-Cinco Palos	112	0.926	0.931	1.918	1.913
	8	2	Riconada-Amelco	89	0.955	0.95	1.217	1.036
	9	1	Paso de Ovejas	70	0.907	0.928	1.999	1.999
	10	1	La Mancha	14	0.975	0.966	1.999	1.999

Table 6. Climate categorization of the Operational Climate Units (OCU), descriptive climate type and Köppen climate group key

OCU	**Climate category**	**Climate type**	**Köppen climate group**
1	Semi-arid	Cold semi-arid climate	BSk
2		Hot semi-arid climate	BSh
3		Steppe climate	BS1kw
4		Steppe climate	BS1kw
5		Semi-arid steppe climate	BShw
6	Temperate	Monsoon-influenced humid subtropical climate	Cwa
7		Monsoon-influenced humid subtropical climate	Cwa
8	Tropical	Humid subtropical climate	Cfa
9		Tropical savanna, wet	Aw
10		Tropical sub-humid and hot climate	Awg

The OCUs can be grouped into three climate categories: semi-arid climate OCUs (1 to 5), temperate climate OCUs (6 and 7), and Tropical OCUs (8 to 10) (Table 6). The general predicted trend for all models shows that between 60% and 100% of the area of suitable climate conditions for haemosporidian for the recorded prevalence would be lost by 2070, in both RCP 4.5 and RCP 8.5 scenarios (Table 7). Potential permanence or continuity of suitable haemosporidian climate varies between OCUs. In the “optimistic” scenario (RCP 4.5), current climate conditions are expected to be less affected at higher elevations, as seen in the projections for OCUs 4, 6, and 7, but less so under RCP 8.5, and it improves for some of the same OCUs, such as 4 and 6 (Table 7, Fig. 6).

Table 7. Climate projections for all Operational Climate Units (OCU) under Representative Concentration Pathway scenarios 4.5 and 8.5. Each percentage represents the estimated area reduction (deficit), expansion (gain) and continuity of the distributions of suitable climate associated with haemosporidian prevalence.

	RCP 4.5			**RCP 8.5**		
	Suitable climate niche deficit (%)	Suitable climate niche gain (%)	Suitable climate niche continuity (%)	Suitable climate niche deficit (%)	Suitable climate niche gain (%)	Suitable climate niche continuity (%)
OCU01	95.9	0	4.1	99.8	0	0.2
OCU02	100	0	0	100	0	0
OCU03	100	0	0	100	0	0
OCU04	71.5	2.4	26.1	50.8	7	42.2
OCU05	71.3	12.9	15.8	96.6	3.4	0
OCU06	72	0.1	27.8	42.8	25.5	31.7
OCU07	0	0	100	97.3	0	2.7
OCU08	60.7	19.6	19.7	72.9	20.6	6.5
OCU09	96.3	3.7	0	99.7	0.3	0
OCU10	69	23.8	7.2	73.7	25.3	0.9

For the semi-arid OCUs (1 to 5), climate projections predict the loss of suitable climate distribution in both scenarios, ranging from 71% to 100% in the RCP 4.5 scenario and 50.8% to 100% in the RCP 8.5 scenario. OCUs 2 and 3 show a 100% complete change of suitable climate distribution projection in both scenarios. Both climatic units are in the physiographic region of the Mexican Plateau in San Luis Potosí, and OCU2 contains the driest survey sites (Charcas), with some of the lowest haemosporidian prevalence recorded in the study for that region. The complete change of haemosporidians' suitable climate is in line with the expected increases in temperature and decreases in precipitation, affecting arid climates under both RCP scenarios (Table 7).

In temperate climatic units, the OCU6 (Tamasopo) presented a higher decrease of suitable climate for the observed haemosporidian prevalence under the

RCP 4.5 scenario (-72%) and less change (42.8%) under the RCP 8.5 scenario. Interestingly, projections for the OCU7 (Mirador-Cinco Palos) showed that under the RCP 4.5 scenario, the entirety of haemosporidian prevalence suitable climate could potentially continue to exist in 50 years. Conversely, under the projections for the RCP 8.5 scenario, 97.3% of this suitable climate could be lost. The study sites contained in the OCU7 correspond to the physiographic region of Sierra Madre Oriental and include the most humid sites of the study, with the highest combined haemosporidian prevalence for the state of Veracruz (Table 3, Fig. 5). The OCUs also showed the highest percentage of climate continuity for 2070: 27.8% to 100% under the RCP 4.5 scenario and 2.7% to 31.7% under the RCP 8.5 scenario, as well as a small geographic expansion (gain: 0.1% to 25.5%) of suitable climate areas for haemosporidian presence on the western slopes of the Sierra Madre Oriental under RCP 8.5 scenario (Table 7, Fig. 6).

The last climate category corresponds to the tropical OCUs 8-10, located in the Gulf of Mexico Coastal Plain. Climate projections for OCU8 (Rinconada-Amelco) under the RCP 4.5 scenario showed a decreased suitable habitat that could reach 60.7% and 72.9% under RCP 8.5. For OCU9 (Paso de Ovejas), the loss of suitable habitat reaches close to 100% for both scenarios and a minor gain under RCP 4.5 scenario of 3.7% (Table 7). OCU10 (La Mancha) is predicted to lose between 69% and 73.7% of haemosporidian prevalence suitable habitat in scenarios RCP 4.5 and RCP 8.5, respectively. However, it could have a suitable climate gain of over 20% under both climate change scenarios. These potential increases of suitable climate represent only a small percentage; however, it becomes important when compared to the areas of predicted suitable habitat loss.

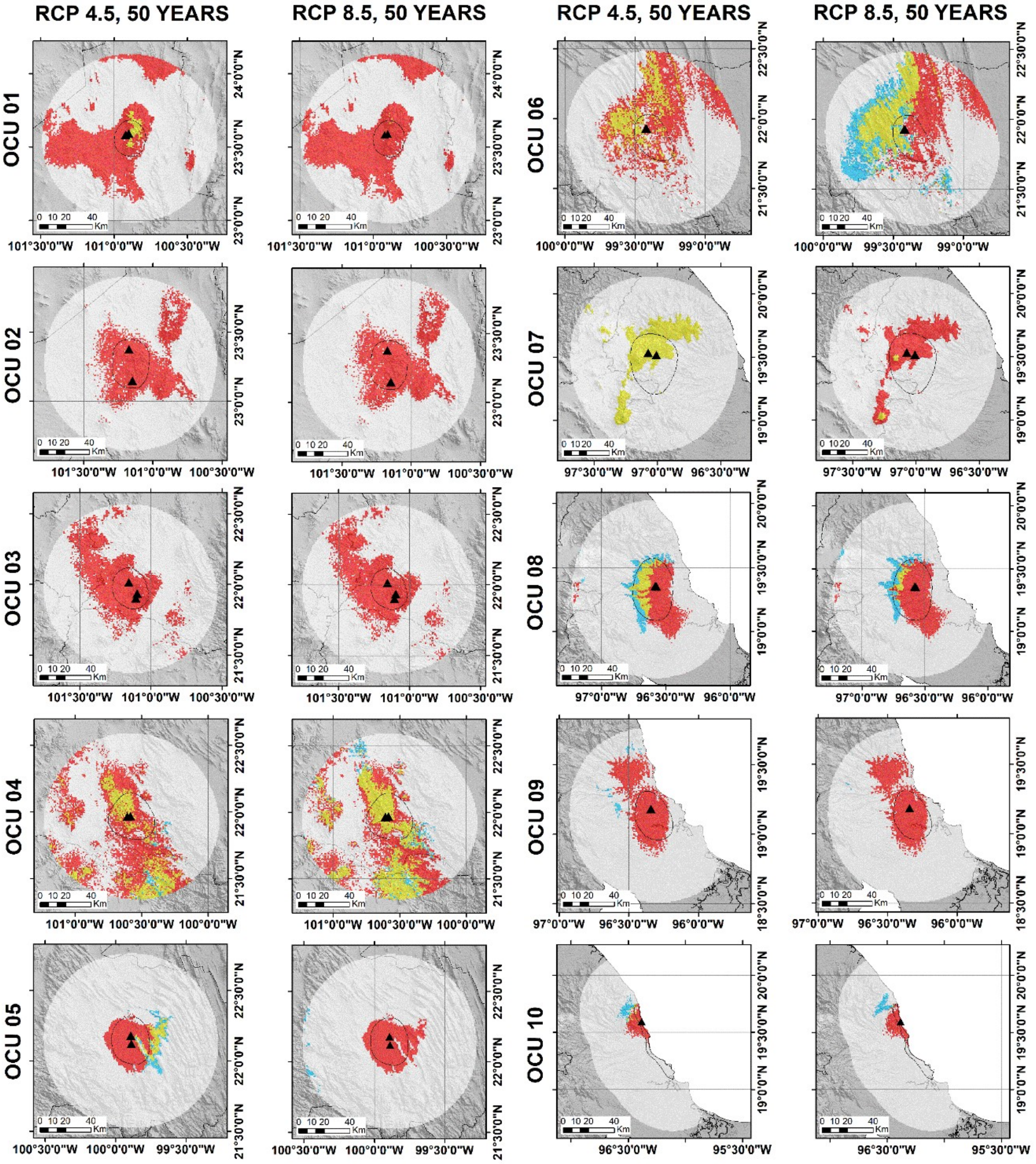

Figure 6. Mapped projection of suitable climatic conditions associated with haemosporidian prevalence for the 2070 decade under climate change scenarios RCP 4.5 & 8.5. The white contour corresponds to the 50km buffer applied for the models and the colored areas represents the different projections regarding suitable climatic habitat for the observed haemosporidian prevalences under current climate trends: Red grid cells represent a potential deficit of suitable climatic habitat under climate change scenarios RCP 4.5 and 8.5, yellow grid cells represent the area of climatic habitat that will potentially continue despite the effects of climate change, and the blue grid cells represent the area of climatic habitat added. The black

contours within the buffer from which the colored areas stem from represent the polygons of each OCU.

DISCUSSION

Despite it was expected that climate possess an effect on the distribution of haemosporidian communities, it is important to highlight that temperature was the main driving bioclimatic factor for these parasite-vector-host associations, at least for the region and the scale of the study. Although, in some cases, those variables related to precipitation were the most important (Table 2), particularly in relation to the potential geographic expansion of suitable climate areas for haemosporidian presence on the western slopes of the Sierra Madre Oriental. In general, it became evident that under both climate change scenarios – RCP 4.5 and RCP 8.5 – the range of 50% to 100% of the current climate distribution that favors haemosporidian prevalence could be lost by 2070. The projected distribution of remaining suitable haemosporidian climate and potential newly suitable areas converge around higher elevation habitats located in five of our climatic units (OCUs 4-8) (Fig. 6). Rather than modelling around individual sites, we clustered our survey sites into OCUs based on shared climate characteristics due to proximity, to better visualize the distribution trends obtained from our climate projections.

The results indicate that haemosporidian prevalence could change significantly in the study region. However, these results do not necessarily mean that birds and their parasites communities would be deeply modified; what we can suggest is that climate change could potentially change the dynamic of infections and the community compositions. Although we do not know the degree of the modifications, if they were to be profound, the haemosporidians, their vectors, and the birds could be affected to the same degree.

As previously mentioned, the arid and semi-arid ecosystems of central-northwestern Mexico occupy more than 50% of the national territory and are home to diverse communities of flora and fauna (Cavazos*, et al.* 2013; SEMARNAT 2016). Climate change will accelerate the desertification process in this region, and the local biodiversity will face resource limitation problems (mainly water), changes in ecological functionality and population decreases (Liverman & O'Brien 1991; Whitford & Duval 2020). For temperate and tropical ecosystems like those found in Veracruz, climate change scenarios show potential trends of haemosporidian suitable climate deficit that could be related to the temperature increases and shifts on the local precipitation regimes. However, there is also the possibility that some of this suitable haemosporidian climate could remain in some areas at higher elevations. Also, in some areas, the climate could become suitable for haemosporidian prevalence at the same levels that we found nowadays in our surveys. These findings are consistent with other studies focusing on haemosporidian prevalence in avian communities of Hawaii, Australia, Europe, and Africa (Benning*, et al.* 2002; Garamszegi 2011; Zamora-Vilchis*, et al.* 2012; Paaijmans & Thomas 2013; Atkinson*, et al.* 2014), where the temperature was the main driving factor behind the dispersion and transmission of haemosporidian infections in birds. The main difference between those studies and what we found here is that temperature increases in Hawaii, Australia, Europe, and Africa associate positively with haemosporidian prevalence of infection; while in central-eastern Mexico, our climate change projections seem to suggest that haemosporidian prevalence could decline as the temperature increases because local temperatures would surpass the optimal haemosporidian developmental and transmission threshold, as well as the Diptera vector tolerance for breeding and development (Loiseau*, et al.* 2013; Rooyen*, et al.* 2013; Atkinson*, et al.* 2014; Liao*, et al.* 2017; Ferraguti*, et al.* 2018). The climate change projections show that a global temperature increase of 2 to 3° C (as projected by scenario RCP 4.5), could potentially manifest in an important reduction of suitable climate areas for haemosporidian parasites in the study region. The projection under scenario RCP 8.5 is even more dramatic, showing a potential deficit of around 73.7% or higher of the suitable climate distribution area for haemosporidian parasites in San Luis Potosí and Veracruz. These results were somewhat unexpected, as the projected trends in other regions show that a suitable climate for haemosporidian prevalence moves the altitudinal gradient upward while remaining in its original distribution (Benning *et al.,* 2002). However, the projected temperature increases of both the "optimistic" and "pessimistic" climate change scenarios would most likely affect avian communities too by other means, i.e., such as the limitation of resources due to the desertification associated with temperature increases, as well as unforeseen changes in the population-regulation function provided by haemosporidian infections (Fuller*, et al.* 2012; Ilgūnas*, et al.* 2016).

Though the potential climate distribution for haemosporidians is likely to decrease its range, the prevalence of *Plasmodium* or *Leucocytozoon* species could potentially increase in some areas of the study region. Particularly in those regions where vectors could find the necessary conditions for their development, such as in portions of the higher altitude areas where topography favors water retention, water runoff, and humidity levels necessary for the development of simulid and culicid larvae for the transmission of *Leucocytozoon* and *Plasmodium*. In steep topography, however, water retention could become scarce, diminishing suitable conditions for the reproduction of vectors for *Haemoproteus* and *Plasmodium*, but potentially maintaining favorable conditions for *Leucocytozoon* prevalence at high elevations, at hillsides and slopes in the form of running waters where simulid vectors could reproduce (Ferreira*, et al.* 2020). Other studies support that landscape features such as mountain ranges are especially favorable for the prevalence of *Leucocytozoon* infections in birds (Galen & Witt 2014; Harrigan*, et al.* 2014; Illera*, et al.* 2017) due to water availability and lower temperatures found at higher elevations. Alternatively, *Leucocytozoon* spp. might suffer severely due to the loss of mountain habitats and the desertification process entailed by climate change, particularly in the drier environments of the Mexican Plateau.

Haemoproteus dominated infection prevalence in San Luis Potosí, while *Plasmodium* prevalence was higher in Veracruz in lowland tropical areas. These results suggest that local climate variation among regions may influence the presence of different types of dipteran vectors. For San Luis Potosí, these prevalence trends coincide with the findings of previous studies, reporting *Haemoproteus* species as the most frequent in 31 bird species from the neighboring states of Tamaulipas and Nuevo Leon (Bennett*, et al.* 1991) and from San Luis Potosí (Reinoso-Pérez*, et al.* 2016; Ham-Dueñas*, et al.* 2017). Although *Haemoproteus* and *Plasmodium* infections share some climatic similarities, there are also some differences in their preferences, and they do not have similar prevalence rates across the study region. These differences are intimately linked to the reproductive requirements of their transmitting vectors. *Haemoproteus* parasites are transmitted by ceratopogonid and hippoboscid flies (Friend & Franson 1999; Ferreira*, et al.* 2020). Ceratopogonid insects show high ecological flexibility and tolerate temperature ranges from 4° C to 30° C (Sprygin*, et al.* 2014). Several species acting as haemosporidian vectors can breed in animal excrements, the rotting fruit of cacti and other vegetation detritus (Wanji*, et al.* 2019). All these conditions are available in our study sites from San Luis Potosí covering the physiographic region of the Mexican Plateau. In addition, residents of the Mexican Plateau region build artificial water bodies to maintain cattle and crops. These structures are common and scattered across the landscape, making it easier for *Haemoproteus* ceratopogonid vectors to find suitable reproductive habitats. These artificial water bodies could also provide the aquatic habitat that *Plasmodium* culicid vectors require for reproduction and larval development (Grech*, et al.* 2019) in the Mexican Plateau. Nevertheless, since these insects have an optimal development range located around the 16° C isotherm, the high temperature variability in the region could be limiting their abundances, hence the lower *Plasmodium* prevalence for San Luis Potosí. With current and projected temperature increases and rainfall reduction caused by climate change, the availability of moist soils and organic detritus, as well as the smaller artificial water bodies that could be helping sustain ceratopogonid vectors of *Haemoproteus* and culicid vectors of *Plasmodium*, could disappear or become scarce across the landscape, changing haemosporidian prevalence in this region of San Luis Potosí, and probably in the large Mexican Plateau.

The arid and semi-arid ecosystems in Mexico are already threatened by desertification due to unsustainable agriculture and urban development (SEMARNAT 2016). However, it is estimated that, with climate change, the annual precipitation regime for central and northeastern Mexico could experience a 40% to 50% reduction that will negatively affect the productivity, biodiversity, and functionality of these landscapes (Cavazos*, et al.* 2013). In contrast, tropical climates with higher precipitation regimes are more suitable for the culicid vectors responsible for *Plasmodium* transmission. Our reported prevalence for the state of Veracruz coincided with those reported in another study comparing haemosporidian infection rates between bioclimatic regions, where the neotropical site was located in Veracruz and had a significatively higher local prevalence of *Plasmodium* compared to the *Haemoproteus* and *Leucocytozoon* genera (Carbó-Ramírez*, et al.* 2017). The streams or rivers easily found in the Sierra Madre Oriental of Veracruz likewise explain the more limited distribution and prevalence of *Leucocytozoon* infections, as black flies (Simuliidae) occur only in habitats with fast flowing waters (Crosskey 1993). The combination of running water and low temperatures necessary for *Leucocytozoon* transmission is rare in the Mexican Plateau. It can only be found in the Sierra Madre Oriental in the southeastern portion of the state, near the border with the state of Veracruz. The projected effects of climate change in temperate and tropical climates such as those found in Veracruz do not appear to be as severe as those predicted for the arid regions. However, models still estimate a rainfall reduction of 20% for the Gulf of Mexico Coastal Plain. Mountain habitats have already shifted more than 500m upwards during the last three decades across the Trans-Mexican Volcanic Belt (Jiménez-García*, et al.* 2021).

Half of the surveys made for this study focused on estimating haemosporidian prevalence from drylands. These ecosystems are often less studied than tropical and temperate ecosystems, where the highest bird endemism and avian richness levels are located. This lack of knowledge has resulted in an information gap regarding avian haemosporidian ecology for arid and semi-arid ecosystems, despite them containing around 30% of the global biodiversity and constituting one of the most extensive yet vulnerable systems worldwide. For regions with a high rate of environmental degradation like the ecosystems in central-eastern Mexico, further studies into the ecology of avian haemosporidian infections and bird hosts should be considered. Besides, other important variables include habitat loss, urbanization, and desertification, especially when setting conservation strategies to curb the effects of climate change over host-parasite dynamics.

CONCLUSION

Our findings support the hypothesis that the prevalence trends can be explained and predicted by bioclimatic variables at the local and landscape level. Distributions and prevalence of haemosporidians are driven by temperature and humidity conditions that are directly related to their specific vectors' the reproductive ecology. The Operational Climate Units showed a clear altitudinal migration trend of haemosporidian parasites in response to climate change projections under two contrasting scenarios (RCP 4.5 and RCP 8.5), particularly those located in temperate climates. For the arid and semi-arid ecosystems, a suitable climate for haemosporidians is predicted to decrease drastically, except in smaller areas concentrated at higher elevations of the mountainous habitats of the Mexican Plateau.

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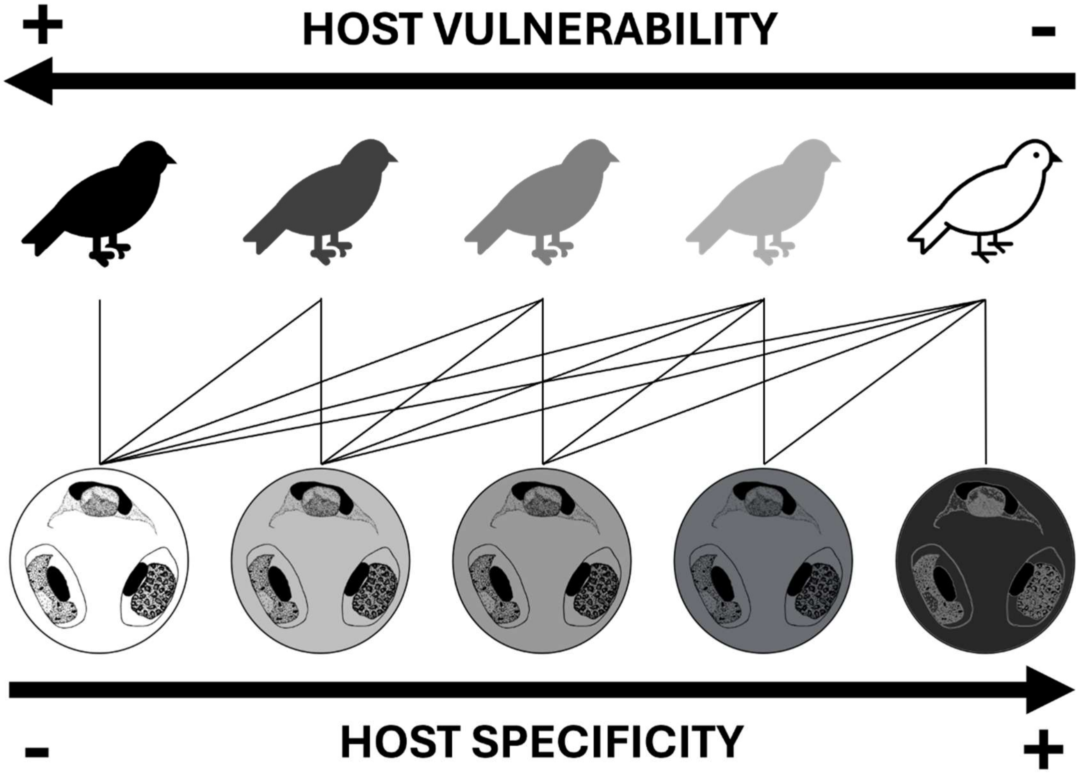
CHAPTER II

SPECIALIST VS GENERALIST: PREDICTING ENVIRONMENTAL SUITABILITY TRENDS IN HAEMOSPORIDIAN LINEAGES WITH OPPOSITE INFECTION STRATEGIES



ABSTRACT

We assessed the environmental tolerance of generalist vs specialist haemosporidians recorded in continental North America. We identified the most influential bioclimatic predictor variables associated with the potential distribution of these two types of parasites and projected them into 20 years between 2061 and 2080 under two contrasting climate change scenarios (SSP2-4.5 and SSP5-8.5) from the newly implemented CMIP6. We assessed the host specificity of a 19 haemosporidian lineage sample at a continental scale (*γ* dimension) and a regional scale (*α* dimension). Nine lineages fit the criteria to be classified as specialists for the α dimension. However, at a larger scale (γ dimension), the proportion of specialist vs generalist lineages changes significantly, with only five lineages fitting in the specialist category. We also found two different trends for generalist lineages: (1) Those that interacted with avian hosts randomly distributed in the phylogeny (classified as random), and (2) lineages with MPD values above the average. Once we identified host specificity trends, we chose the generalist (pSEIAUR01) and specialist (lCNEORN01) lineages with the highest number of georeferenced occurrence records to create a spatial projection of the optimal climate conditions in which each haemosporidian type could be inferred. Under both scenarios, climate suitability models predicted a northward migration of the climatic niche and a potential reduction of the optimal climate that haemosporidian parasites can use. Specialist lineages have a potentially higher risk of losing most of their spatial distribution of suitable climates by 2061.

Keywords: avian haemosporidians, specificity index, environmental tolerance, climate change

INTRODUCTION

Avian haemosporidian parasites, which include genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*, exhibit a wide range of host specificity (i.e., their capability to infect different host species within a geographical range, as well as the phylogenetic distance between hosts and propensity for host shifting) (Poulin*, et al.* 2011; Wells & Clark 2019). Specificity varies even among parasites within the same genus, from extreme generalism to extreme specificity (Okanga*, et al.* 2014), and these relationships serve as an indicator of how a parasite and its hosts have been associated over much of their evolutionary history (Hoberg*, et al.* 1997). The extent of host specificity and host shifts among a group of parasites can be directly tested by comparing the match between the phylogenetic trees of the parasites and their hosts (Brooks 1988). A strong match suggests strong host specialization and co-speciation. A poor match would imply that host shifts have happened repeatedly over evolutionary time and that potential host species are at substantial risk of being invaded by novel parasites (Toft & Karter 1990; Newton 1998).

For vector transmitted parasites such as avian haemosporidians, host specificity could offer fitness advantages in host-rich communities (Ventim et al. 2012). Higher prevalence rates are often associated with host-generalist lineages because being able to infect a wide array of potential hosts increases the possibility of encountering suitable hosts to infect (Ventim 2012). In the other side of the spectrum, host-specialist lineages can optimize their infection rates by controlling the abundance of their suitable hosts and being more effective than generalists in infecting them (Keesing et al. 2006; Moens & Perez-Tris 2015). However, host specificity is not a fixed attribute (Fecchio*, et al.* 2019a). The degree of host specificity exhibited by avian haemosporidian parasites is also influenced by a variety of other factors, including the ecological conditions in which the parasite and host interact (Brooks & Hoberg 2007; Samuel*, et al.* 2011; Atkinson*, et al.* 2014; Ferraguti*, et al.* 2018; Rodríguez-Hernández*, et al.* 2021), the evolutive history between the interacting organisms (Hoberg*, et al.* 1997), and their ecological fitting, that is, the required physiological and behavioral overlap needed for infection to happen (Wells & Clark 2019). Therefore, environmental variables play an important role in the transmission, dispersion, and distribution of generalist and specialist haemosporidian lineages (Fallon*, et al.* 2005; Loiseau*, et al.* 2012).

The environmental space occupied by haemosporidian parasites consists of two ecological dimensions: the host complex (vectors and final hosts) (Hoberg*, et al.* 1997; Brooks & Hoberg 2007; Morand & Krasnov 2010; Loiseau*, et al.* 2012; Santiago-Alarcon*, et al.* 2012; Lotta*, et al.* 2016) and the vector-parasite-host's environment (Benning*, et al.* 2002; Fallon*, et al.* 2005; Santiago-Alarcon*, et al.* 2012; Ferraguti*, et al.* 2018; Fecchio*, et al.* 2019a; Chapa-Vargas*, et al.* 2020; Martina Ferraguti*, et al.* 2020). Both ecological dimensions influence the spatial expression of parasitism within the geography. Highly specific parasites may be restricted to certain geographic regions or habitats because the hosts they infect are geographically and environmentally restricted in the same way (Fallon*, et al.* 2005; Rodríguez-Hernández*, et al.* 2021), while more generalist parasites may have a wider distribution because of the extensive variety of hosts they can infect (Beadell*, et al.* 2004). Environmental factors such as seasonality, temperature, humidity, habitat modification, vegetation cover, food availability for avian hosts, proximity to human settlements, and vector availability can also impact parasite survival and transmission processes (Valkiūnas 2005; Schröder & Schmidt 2008; Møller 2010; Garamszegi 2011; Clark*, et al.* 2016; Fecchio*, et al.* 2019a; Chapa-Vargas*, et al.* 2020; Rodríguez-Hernández*, et al.* 2021). Many studies have focused on the environmental changes that occur at the host level to predict modifications to the transmission rates and distribution ranges of these parasites (Ricklefs & Fallon 2002; Fallon*, et al.* 2005; Ellis*, et al.* 2020), but the transmission process has rarely been studied from the perspective of haemosporidian presence as an indicator of environmental suitability for the parasite-host complex.

Since haemosporidian infections are common in wild bird communities, they represent a potential conservation issue due to the unpredictable effects of climate change over parasite-host interactions (Khasnis & Nettleman 2005; Stresman 2010). Host specificity could play a role in how haemosporidian parasites adapt to climate change, and this phenomenon could express through the following situations: 1) shifts in prevalence and coinfection rates (Zamora-Vilchis*, et al.* 2012; Clark*, et al.* 2016), 2) potential changes on transmission risk (Huijben*, et al.* 2007; Garamszegi 2011), 3) species turnover (Clark 2018; Álvarez-Mendizábal*, et al.* 2021), and 4) changes in distribution and development thresholds (Marcogliese 2008; Paaijmans & Thomas 2013). Spatial modelling could provide information to predict, describe, and assess these potential responses to climate change at different resolution levels, as has been done for the study of vector-borne human diseases (Martens*, et al.* 1999; Patz & Reisen 2001)

Regarding the distribution of avian haemosporidians, Greiner et al. (1975) analyzed these parasites in North America, examining their regional distribution, distribution by host families, and by vertical stratification of the hosts nesting sites and feeding behavior of their known vectors. They found that haemosporidian prevalence is strongly associated with the vertical stratification of host nesting sites within a delimited region, but prevalence distribution varied from region to region and showed no correlation when pooled across the continent (Greiner*, et al.* 1975). Other studies demonstrate a direct correlation between temperature increases and increased reproduction rates of parasites and vectors (Garamszegi 2011). Likewise, proximity to freshwater reserves fosters the reproduction of the Dipteran vectors responsible for haemosporidian transmission (Krama et al., 2015; Ferraguti et al., 2018). With temperature and humidity being the primary environmental variables that influence haemosporidian prevalence, projection models might provide information on the potential shifts in distributional trends of haemosporidian infections in response to climate change (particularly across altitudinal and latitudinal gradients), comparable to what has been reported in Hawaii, Europe, and Africa (Benning*, et al.* 2002; Garamszegi 2011; Atkinson*, et al.* 2014).

The climate change projections made by the IPCC for the near term of 2021-2040 estimate an increase of 1.5° C in the global temperature according to their most recent scenario-based projections from the Coupled Model Intercomparison Project Phase 6 (O'Neill*, et al.* 2016; Lee*, et al.* 2021; Stockhause*, et al.* 2021). The updated climate change scenarios proposed for the CMIP6 replace the RCP scenarios with five narratives grounded on different socioeconomic development pathways called the SSP scenarios (Shared Socioeconomic Pathways) (Riahi*, et al.* 2016; Stockhause*, et al.* 2021). These scenarios are summarized in Table 1:

Table 1. The five CMIP6 Shared Socioeconomic Pathway scenarios. Each SSP is associated with one of the previously used Random Concentration Pathway scenarios and includes a socioeconomic prediction based on global economic trends, technological progress, and geopolitical developments coupled with its expected mitigation strategies by the end of the century.

Scenario	Pathway name	Associated RCP scenario	Temperature increases by 2100	End of the century CO2 ppm	Socioeconomic growth predictions	Mitigation strategies
SSP1	Green and sustainable	RCP1.9	≤1.5° C	~390	Strong economic growth	Societies are actively involved in environmental policies
					Emphasis on human well-being	Development respects environmental boundaries
					Inequality is reduced globally	Lower material growth
		RCP2.6	≤1.8° C	~450	Policies focus on education and healthcare	Lower energy demands
					Socioeconomic inequality decreases globally	Strong reduction of fossil fuel use Net-zero global C02 emissions by 2050 Nations develop carbon capture technologies
SSP2	Medium	RCP4.5	≤2.7° C	~600	Historical trends define socioeconomic development	Slow progress in achieving sustainable development
					Uneven economic growth between countries	Environmental systems face degradation
					Moderate global population growth	Use of resources and energy decline
					Socioeconomic inequality persists	Challenges for conservation remain
					Gradual progress toward sustainability strategies	Societies struggle to implement emissions mitigation policies
SSP3	Regional rivalry	RCP7.0	≤3.6° C	~880	Increase in regional conflicts and issues	Inconsistent legislation on energy and resources exploitation

					Decline in education investment and technological development Slow socioeconomic development High population growth in developing countries Low population growth in industrialized countries Global cooperation collapses	Environmental concerns hold low priority Strong environmental degradation Carbon emissions rise steadily Drastic climatic changes
SSP4	Inequality	RCP3.4	≤2.4° C	~480	Increasing socioeconomic disparities Development is greatly uneven between countries Social cohesion and cooperation degrade Local and regional conflict increases	Environmental policies focus on local issues Conservation occurs in middle- and high-income areas Lower income regions face higher environmental degradation
SSP5	Fossil-fueled development	RCP8.5	4.4° C	~1130	Heavy reliance on fossil fuel resources Societies become more participative Technological development is favored Global markets are increasingly integrated and competitive Strong investments in health,	Local environmental problems are managed successfully Social trust in ability to effectively manage social and ecological issues Human capital development favors sustainable development Stronger mitigation strategies for greenhouse gas emissions are needed Heavy exploitation of fossil fuel resources

	education, and institutions Global population peaks and declines by the end of the century	Adoption of alternative energy resources

These newly revised climate narratives have a more nuanced output than the previous RCP scenarios since they consider the ability of society to adapt to a changing environment. These new models offer to be far more accurate in predicting the potential impacts of climate change on the Earth’s environment and its biological systems.

In a healthy environment, parasitism is merely another category of ecological regulation interactions that help maintain the structure of the ecosystem. Parasites regulate host populations by either influencing host behavior, modifying their hosts’ phenotype or altering their hosts’ fitness (competition, reproduction, survival, etc.) (Poulin 1999). However, the impact of climate change on parasitic interactions such as avian haemosporidian parasites is a topic of concern because these parasites can cause significant health problems in wild birds, including chronic anemia, reduced reproductive success, and increased mortality rates in vulnerable populations (Benning*, et al.* 2002; Huijben*, et al.* 2007; Carlson*, et al.* 2011). The potential for host switching by some haemosporidian lineages also poses a risk of introducing new parasites to bird populations that may be more vulnerable to infection, especially in populations where haemosporidian infections are rare or virtually non-existent (i.e., like boreal regions) (Ricklefs & Fallon 2002).

The main objective of this study was to assess the environmental tolerance of generalist and specialist haemosporidians present in continental North America. By identifying the most influential bioclimatic predictor variables associated with haemosporidian presence in the continent, we can model their potential present distribution and evaluate whether there is a correlation between environmental conditions and the distributional variations of these two types of parasites. Also, by identifying these likely environmental trends, we associated the recorded haemosporidian prevalence in our study sites to their temperature and humidity conditions and projected them into a 20-year period between 2061 and 2080 under the two contrasting climate change scenarios (SSP2-4.5 and SSP5-8.5) to assess the potential effects of climate change over the geographic distribution of generalist and specialist haemosporidian lineages. For both types of parasites, we predicted a potential prevalence increase at higher latitudes (represented by a northward migration of the parasites' distribution models for each climate change scenario), and a decreasing prevalence at lower latitudes (with a reduction of the distribution area in lower latitudes) as a direct result of climate change, where increases in temperature of already hot environments along with lower humidity are likely to interrupt the life cycle of both Diptera vectors and haemosporidians. As highly specific parasites may be geographically restricted in relation to the distribution of their hosts, we predicted the northward migration and potential reduction of the optimal environmental niche to be more noticeable for specialist haemosporidian lineages in contrast to what is expected for generalist haemosporidians.

METHODS

Data collection and haemosporidian specificity analysis. We had data from a previous study conducted in Mexico, where we evaluated climate suitability for haemosporidian infections in bird communities found in Central to Eastern Mexico (Ortega-Guzmán*, et al.* 2022). To obtain appropriate sample sizes for environmental modelling at a continental scale, we used the lineage list from that study as a template list and then compiled and filtered georeferenced presence data for lineages from that list reported across continental North America (Canada, United States and Mexico) from the MalAvi database (Bensch*, et al.* 2009). Lineages associated with taxonomically related avian hosts were also included to test for specialization. We selected a total of 19 lineages, of which 12 fit the appropriate criteria for having over 15 georeferenced locations of presence data distributed across continental North America, making them viable for the climate characterization models. The remaining seven lineages were chosen for their association with closely related avian taxa, were registered in less than 10 georeferenced locations, and thus were used solely for testing the specificity index.

Next, we calculated the extent of host specificity (referred as specialization index or SI) of our 19 haemosporidian lineages to compare potential environmental trends between haemosporidian lineages with opposing infection strategies (generalists vs specialists). Using the birdtree.org phylogenetic database to build a maximum credibility clade tree created from a random sample of 1000 Hackett phylogenetic trees (Hackett*, et al.* 2008; Jetz*, et al.* 2012), we created a phylogenetic distance matrix for the avian host species of each lineage at two geographic scales: 1) Mexico (representing the "local" haemosporidian diversity, *α* dimension), used to characterize the phylogenetic SI of the 19 haemosporidian lineages and associated hosts (47 avian host species) limited to georeferenced locations in Mexico; and 2) Continental North America (representing the global haemosporidian diversity, *γ* dimension), which assessed the phylogenetic SI of our 19 haemosporidian lineages using the total associated hosts (156 avian host species) registered in Canada, the United States, Mexico, and Central America. Both scales include information from our previous study plus records obtained from the MalAvi Database.

To classify the SI into our two main categories (specialist and generalist), we then calculated the Mean Pairwise Distance (MPD) between the 19 lineages and their avian hosts with the Picante package (Kembel*, et al.* 2010) in R. MPD is an effective summary statistic used to compare different biological communities and determine if the species of a given group are closely related, and has been used frequently as a reliable measurement of the phylogenetic diversity of the hosts with which a parasite interacts (Tsirogiannis & Sandel 2014). In the Picante package, this is done by estimating the MPD for randomly generated communities (made by shuffling the tips of the branches of the phylogenetic and functional trees used to calculate distance matrices for the entire community with the function ses.mpd) and reporting Standardized Effect Sizes (SES) that are equivalent to -1 times the net-relatedness index (NRI) and nearest taxon index (NTI). Negative values of the observed MPD value for the community (mpd.obs.z or mntd.obs.z), combined with low p values ($mpd.obs.p < 0.05$), indicate phylogenetic clustering, meaning the species within the community are more closely related than what is expected by randomness and thus exhibit a tendency for specificity to the associated avian taxons. Higher MPD values ($mpd.obs.p > 0.05$) for avian haemosporidians represent parasites with generalistic tendencies (Svensson-Coelho & Ricklefs 2011; Barrow*,* *et al.* 2021). We categorized all 19 lineages into one of the two SI categories and compared the results for both the *α* and *γ* dimensions to contrast the differences between both scales.

Climate data. We used the newly implemented Coupled Model Intercomparison Project Phase 6 (CMIP6) models (Stockhause*, et al.* 2021) from WorldClim to characterize the climatic niche associated with presence data for the selected lineages. The CMIP6 models incorporate new emission scenarios derived by different socio-economic assumptions known as Shared Socio-economic Pathways (SSPs), which allow for higher climate sensitivity (Riahi*, et al.* 2016; Hausfather 2018; Stockhause*, et al.* 2021), and chose two contrasting emission scenarios (SSP2-4.5, and SSP5-8.5) at a spatial resolution of 2.5 minutes for our climate change projection modelling. Since haemosporidian infections peak during the warmest and most humid months of the year (May to September in the Northern Hemisphere), we chose to run the environmental tolerance models using eight WorldClim bioclimatic variables associated with temperature and precipitation fluctuations for that period of the year, where temperature anomalies and water availability may have a direct effect over the seasonal distributions of our haemosporidian lineages (Table 2).

Table 2. List of Worldclim's bioclimatic variables used to run the final models

Code	Bioclimatic variable
BIO01	Annual Mean Temperature
BIO05	Max Temperature of Warmest Month
BIO07	Temperature Annual Range (BIO5-BIO6)
BIO10	Mean Temperature of Warmest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter

Environmental tolerance models. To characterize and compare the environmental tolerance between generalist and specialist lineages, we modeled the eleven lineages with more than fifteen georeferenced occurrence records to obtain reliable model accuracy. For the sake of brevity for this chapter, we display the results of the two best represented lineages from each category, but the models for the rest of the lineages will be available once we publish the paper. Representing the specialist haemosporidians, lCNEORN01 is a well sampled lineage in North America, particularly across the Canadian Nearctic region. From the generalist category, pSEIAUR01 is one of the more evenly sampled lineages in our sample, found across the United States and south to Mexico.

The environmental tolerance models were generated with the help of the presence-only distribution-modelling algorithm Maxent (Phillips*, et al.* 2006) included in the NicheToolBox (NTBox) R package (Osorio-Olvera*, et al.* 2020). The Maxent algorithm (Phillips*, et al.* 2006) uses the information from the known occurrence points and the data from the bioclimatic variable layers to provide an estimate of presence across a study area. Other methods require true absence data or either assume the existence of such information, so Maxent is a powerful tool for evaluating and interpreting environmental niche models where only the presence of the species is known (Phillips & Dudík 2008). A binary map of presence/absence of the bioclimatic conditions for haemosporidian prevalence was obtained by applying a binary threshold (10 percentile training presence) to the projection of probability distribution for the current climate and the climate change scenarios. Climate change projection models for the potential distribution of haemosporidian lineages lCNEORN01 and pSEIAUR01 based on SSP scenarios 2-4.5 and 5-8.5, were projected to a 20-year period between 2061 and 2080.

As these parasites are present in a diverse array of avian hosts, of which a considerable number of species have migratory and/or resident populations (Supplementary material, Table A), we modelled the potential distributions of each lineage in relation to the status of the avian hosts during the season of peak haemosporidian infections. We created a total of eighteen environmental projections for our two representative lineages, lCNEORN01 and pSEIAUR01, for the following combinations: Three models (Current climate and climate change scenarios SSP2-4.5 and SSP5-8.5) for the lineage documented in migratory avian hosts, three models for the lineage documented in resident avian hosts, and three models combining the registers for migratory and resident hosts.

Niche suitability ellipsoid models. NicheToolBox (NTBox) is an R package allowing users to create ecological niche models based on n-dimensional Minimum Volume Ellipsoids (MVE). These models use Mahalanobis distances to measure the distance of the sample populations toward the ellipsoid centroid and visually represent the structure of the environmental space occupied by a given species (Osorio-Olvera*, et* *al.* 2020). According to the abundant niche-center hypothesis, the *n*-dimensional niche space has an approximately ellipsoidal structure, and the centroid represents the virtual area where a species' maximum abundance and fitness (environmental suitability) occurs (Brown 1984; Sagarin & Gaines 2002). Other algorithms frequently used for generating correlative niche models —such as GARP, MaxENT, or BIOCLIM— are not as effective for assessing species fitness, as they do not provide direct means to measure niche structure (Osorio-Olvera*, et al.* 2020).

RESULTS

Haemosporidian host specificity index (SI). Our sample included six *Plasmodium* lineages, five *Haemoproteus* lineages, and eight *Leucocytozoon* lineages, and each group has at least one representative specialist or generalist lineage. From our 19 haemosporidian lineage list in the *α* dimension, nine lineages have not been recorded in Mexico, and therefore we could not obtain their specificity index. Similarly, the SI analysis could not sort two lineages (hAMPBIL02 and hBNOW03) into either the generalist or specialist label due to each being reported in a single avian host species. Since the basis for the SI is calculating the phylogenetic distances between hosts of a given lineage, the analysis cannot calculate an MPD value for a single branch of a phylogenetic tree. The remaining eight lineages were evenly split into four specialists (mpd.obs.p < 0.05; lCB1, lCNEORN01, pBAEBIC02, and pBAEBIC04) and four generalists (mpd.obs.p > 0.95; pBT7, pLAIRI01, pPADOM09, and pSEIAUR01) (Table 3).

In comparison, the SI analysis for the *γ* dimension (continental North America) showed that ten lineages (hAMPBIL02, hDENPEN02, lCATGUT02, lCATMIN01, lCATUST11, lCB1, lCNEORN01, lCOBRA13, pBAEBIC02, and pBAEBIC04) have MPD values significantly different to those expected by randomness (mpd.obs.p < 0.05), suggesting that their avian hosts are clustered and not randomly distributed within the phylogenetic tree, thus allowing us to classify them as specialist parasites. Six lineages (hBNOW03, lCOBRA02, pBT7, pLAIRI01, pPADOM09, and pSEIAUR01) in the γ dimension are associated to avian hosts arbitrarily distributed (mpd.obs.p > 0.95) within the phylogenetic tree, indicating the hosts are not closely related, thus providing the basis to classify these lineages as generalists. Only three lineages (hCAMRUB03, hCOBRA01, and lCOBRA05) could not be sorted into either category since they were reported for a single avian host species, respectively (Table 3).

Table 3. Specificity index (SI) classification for the 19 haemosporidian lineages in Mexico (α dimension) and for continental North America (γ dimension). The letter before the name of each lineage represents the haemosporidian genus they belong to (h = *Haemoproteus*, p = *Plasmodium* or l = *Leucocytozoon*). Columns Host spp., Orders, Families, and Genera represent the taxonomic breakdown of the avian hosts infected by each lineage. Lineages marked 'Yes' in ENM were chosen for environmental niche modelling.

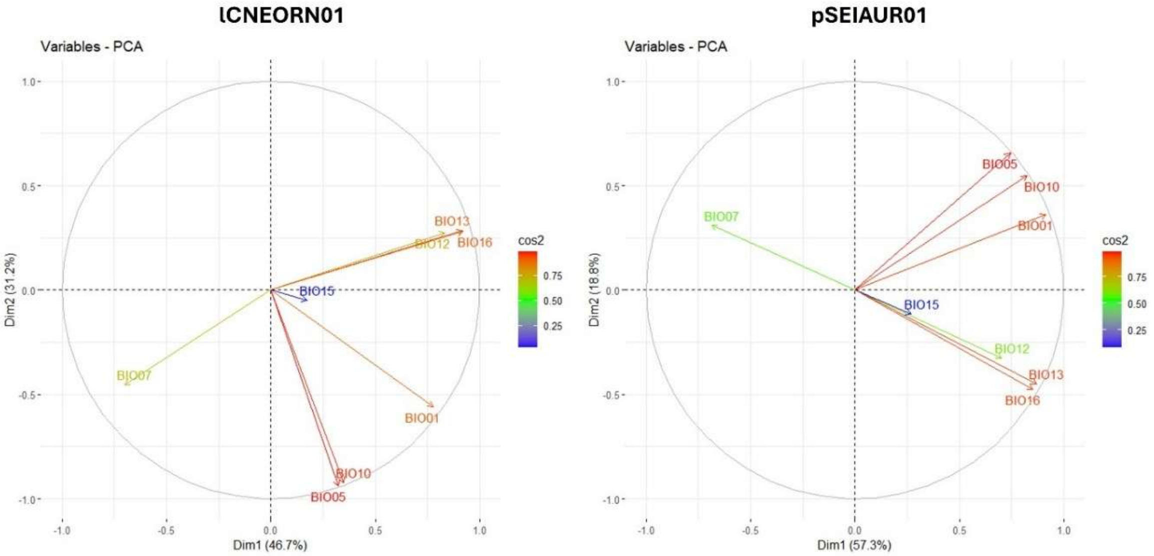
Lineage	α dimension						γ dimension						ENM
	Host spp	Orders	Families	Genera	mpd.obs.p	SI	Host spp	Orders	Families	Genera	mpd.obs.p	SI	
hAMPBIL02	1	1	1	1	NA	NA	2	1	1	2	0.001	**Specialist***	No
hBNOW03	1	1	1	1	NA	NA	2	2	2	2	0.199	Generalist	No
hCAMRUB03	0	0	0	0	NA	NA	1	1	1	1	NA	NA	No
hCOBRA01	0	0	0	0	NA	NA	1	1	1	1	NA	NA	No
hDENPEN02	0	0	0	0	NA	NA	7	1	4	5	0.007	**Specialist***	**Yes**
lCATGUT02	0	0	0	0	NA	NA	3	1	2	1	0.005	**Specialist***	**Yes**
lCATMIN01	0	0	0	0	NA	NA	4	1	1	2	0.003	**Specialist***	**Yes**
lCATUST11	0	0	0	0	NA	NA	2	1	1	1	0.001	**Specialist***	No
lCB1	2	1	1	2	0.004	**Specialist***	42	1	9	27	0.001	**Specialist***	**Yes**
lCNEORN01	8	1	4	7	0.001	**Specialist***	37	1	9	24	0.001	**Specialist***	**Yes**
lCOBRA02	0	0	0	0	NA	NA	3	2	2	3	0.856	Generalist	No
lCOBRA05	0	0	0	0	NA	NA	1	1	1	1	NA	NA	No
lCOBRA13	0	0	0	0	NA	NA	3	1	1	3	0.001	**Specialist***	No
pBAEBIC02	18	2	8	14	0.05	**Specialist***	31	2	11	24	0.007	**Specialist***	**Yes**
pBAEBIC04	1	1	1	1	0.0395	**Specialist***	5	1	3	4	0.001	**Specialist***	**Yes**
pBT7	3	1	3	3	0.804	Generalist	46	5	16	38	0.996	Generalist	**Yes**
pLAIRI01	10	1	8	10	0.782	Generalist	32	4	16	28	0.704	Generalist	**Yes**
pPADOM09	19	1	8	18	0.999	Generalist	33	4	14	31	0.994	Generalist	**Yes**
pSEIAUR01	10	2	7	10	0.476	Generalist	55	5	17	43	0.996	Generalist	**Yes**

NA = Not available.

Generalist lineages are so because they have the capability to infect avian hosts in different taxonomic orders, which indirectly demonstrates a broad environmental tolerance of these parasites. We also found that four of the six *Plasmodium* lineages behave as generalists, as we originally expected. *Leucocytozoon* also appears to have a predisposition to specialism, as six of the eight lineages in our sample were classified as such by the SI analysis. The infection trends for *Haemoproteus* were not as clearly defined since we could not calculate the SI for two of its lineages. In regard of the lineages that could not be categorized by the SI analysis due to lack of host diversity, this result can either be interpreted as 1) these lineages are strongly specialized in the avian species where they have been found, or 2) the lineage is not particularly abundant and has not been sampled in other species as a result. With the available information it is difficult to ascertain whether these lineages are too specific to their reported avian hosts or if they are being underrepresented in our host samples. There is a possibility that the former scenario might be the case for the hCOBRA01 and lCOBRA05 lineages, as they have been consistently reported in the single species from which the lineage derives their name (*Corvus brachyrhynchos*).

Haemosporidian environmental tolerance models. The models created a geographical projection for the climate conditions in which each haemosporidian lineage could be inferred using the three different climatic scenarios: current climate, and scenarios SSP2-4.5 and SSP5-8.5. Since we chose the bioclimatic variables associated with the season of peak haemosporidian infection, we ran a Principal

Component Analysis (PCA) to evaluate how the variables are influencing the models. We observed strong positive correlations between the temperature variables BIO05, BIO10, and BIO01 and negative correlations with the precipitation variables BIO12, BIO13, and BIO16 for the generalist lineage pSEIAUR01. In contrast, for the specialist lineage lCNEORN01, the projections respond positively with the precipitation variables BIO12, BIO13, BIO16. The temperature variables BIO05 and BIO10 are strongly correlated but correlate negatively with the precipitation variables in the projections for the genus (Fig. 1).



lCNEORN01

pSEIAUR01

Figure 1. PCA loading plot showing the correlation between the bioclimatic variables used in the models for the specialist lineage lCNEORN01 and the generalist lineage pSEIAUR01.

lCNEORN01 has been reported in a total of 37 avian species, of which 23 have migratory populations and 14 have resident populations. pSEIAUR01 has been reported in 55 avian species, 27 of which have migratory populations and 28 with resident populations. We divided the projections of each lineage in relation to the behavioral status of the avian hosts. For lCNEORN01 found in migratory hosts, the current climate environmental projection shows a fragmented distribution following the limit with the subarctic line of the continent. Interestingly, under the conditions estimated under climate change scenario SSP2-4.5, the probability distribution of suitable bioclimatic space for ICNEORN01 shows a trend of northward climate migration, with patches of suitable bioclimatic space appearing toward the Alaskan Arctic and the northeastern Canadian Nearctic region in the Labrador Peninsula (Fig. 2). Under scenario SSP5-8.5, the northward migration of suitable bioclimatic space is minor but still represents a potential expansion compared to the projected distribution for the contemporary climatic conditions.

For lineage pSEIAUR01 reported in migratory hosts, the current climate projections show that the bioclimatic space of this lineage is fragmentary but reaches the arctic region of the continent. However, under scenarios SSP2-4.5 and SSP5-8.5, the lineage could potentially lose its northern bioclimatic space in the Canadian tundra located west from the Labrador Peninsula but affect the general potential bioclimatic distribution for the lineage differently. The projection for the moderate climate change scenario SSP2-4.5 shows a potential increase of suitable bioclimatic space along the Rocky Mountains, the Interior Plains region, and the Great Lakes. In contrast, under pessimistic scenario SSP5-8.5, the projection predicts a reduction of suitable bioclimatic space similar to the projection for ICNEORN01 (Fig. 2).

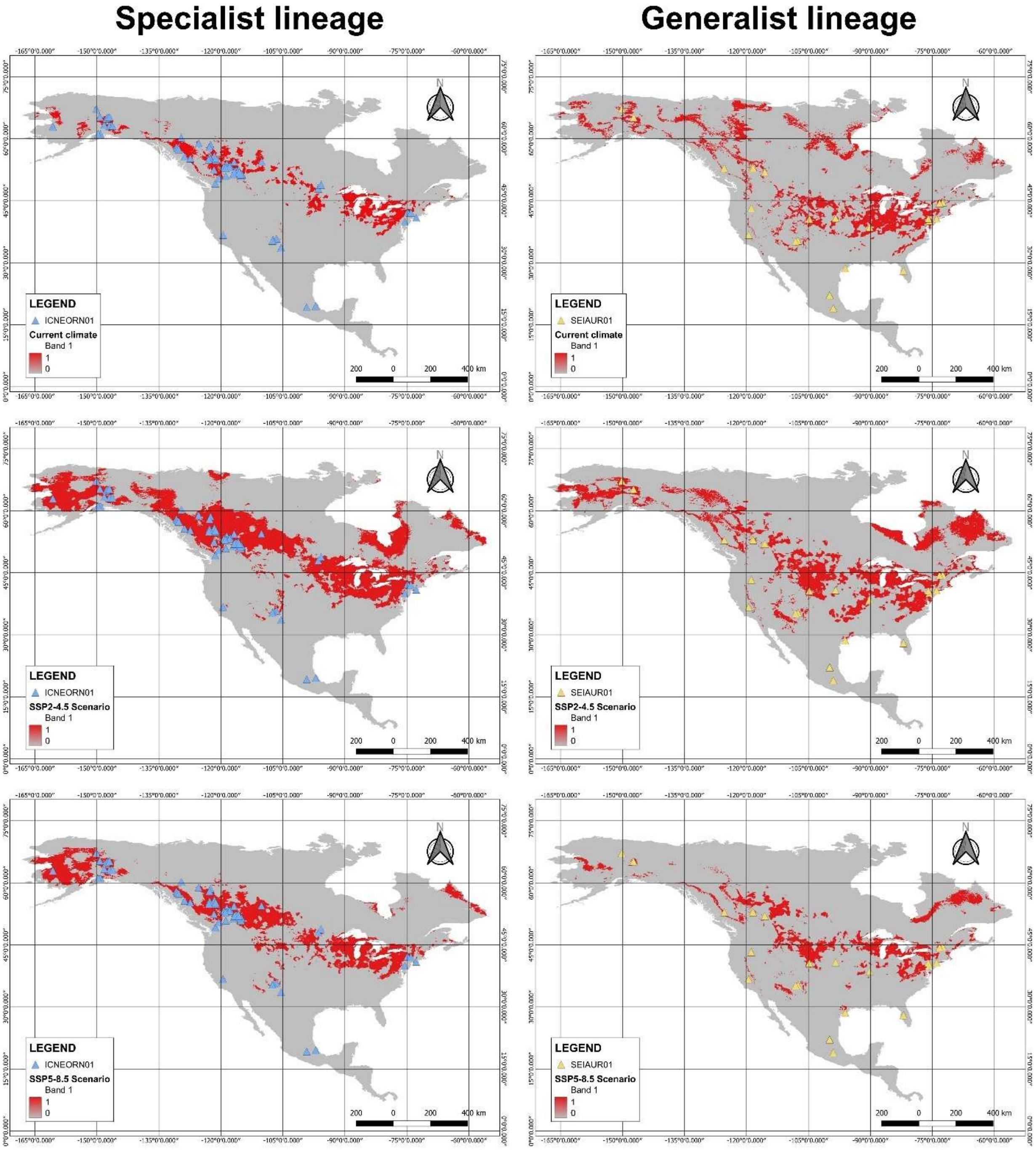


Figure 2. Environmental tolerance projections for the lineages ICNEORN01 (left) and pSEIAUR01 (right) using the records of their known migratory avian hosts.

The projections for ICNEORN01 found in avian hosts with resident populations, the projections a limited distribution of suitable bioclimatic space. For the current climate conditions, the distribution follows the mountainous ranges of the Rocky Mountains in the north, south toward the Sierra Madre Occidental, the Mexican Trans-Mexican Volcanic Belt, and fragmentary bioclimatic space in the Sierra Madre of Chiapas toward Central America. However, this fragmentary distribution could virtually disappear under climate change scenarios SSP2-4.5 and SSP5-8.5 (Fig. 3).

The bioclimatic space projections for pSEIAUR01 reported in resident avian hosts appear more stable, concentrating along the Appalachian region, the Central Plains, the Florida Peninsula, and Gulf of Mexico, with minor differences between the projections for the current climate and SSP2-4.5 scenarios. Under scenario SSP5-8.5, the lineage could face a reduction of suitable, particularly in the Central Plains region, the Florida Peninsula, and the Gulf of Mexico (Fig. 3).

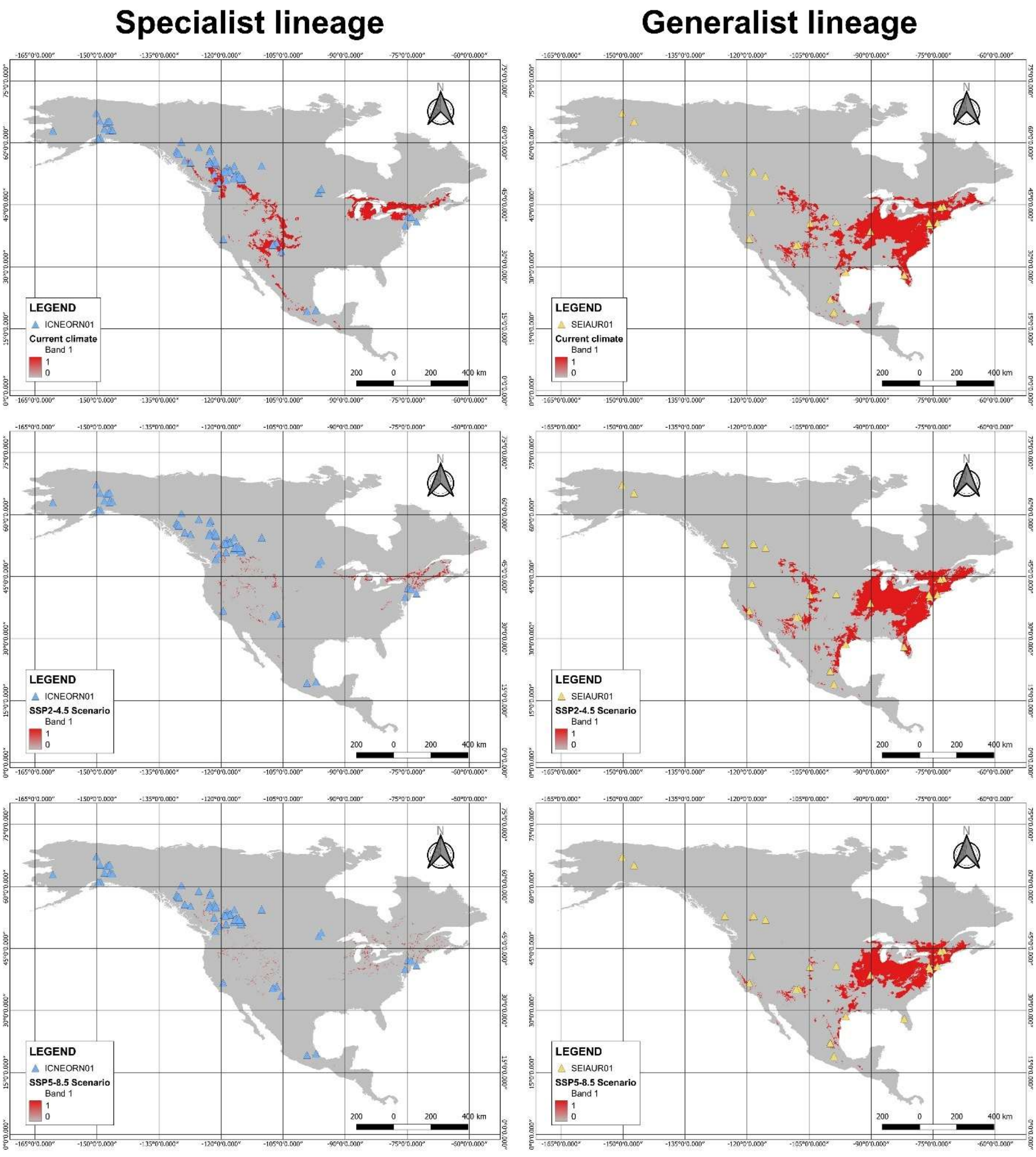


Figure 3. Environmental tolerance projections for the lineages ICNEORN01 (left) and pSEIAUR01 (right) using the records of their known resident avian hosts.

The projections combining the total avian hosts depict less discernible bioclimatic trends due to the conflation of both types of avian hosts (Fig 4). Since the migratory hosts of both lineages tend to reach higher latitudes during reproductive season (which coincides with peak haemosporidian infection season) while the resident hosts remain in their respective distribution areas, the models calculate an overfitted distribution in both cases. For lineage ICNEORN01, these projections display a rather homogeneous distribution of bioclimatic space along the Canadian Nearctic region. Under these conditions, the projections for climate change scenarios SSP2-4.5 and SPP5-8.5 display an expansion of the bioclimatic space, with a northward latitudinal migration. For lineage pSEIAUR01, the projection for scenario SSP2-4.5 shows a reduction of bioclimatic space along its westernmost distribution. In contrast, the projection for climate change scenario SPP5-8.5 shows that most of its original distribution remains and adds a potential northward latitudinal migration of the suitable bioclimatic space along the coast of the Hudson Bay, between the Labrador Peninsula and the Northwest Territories (Fig 4).

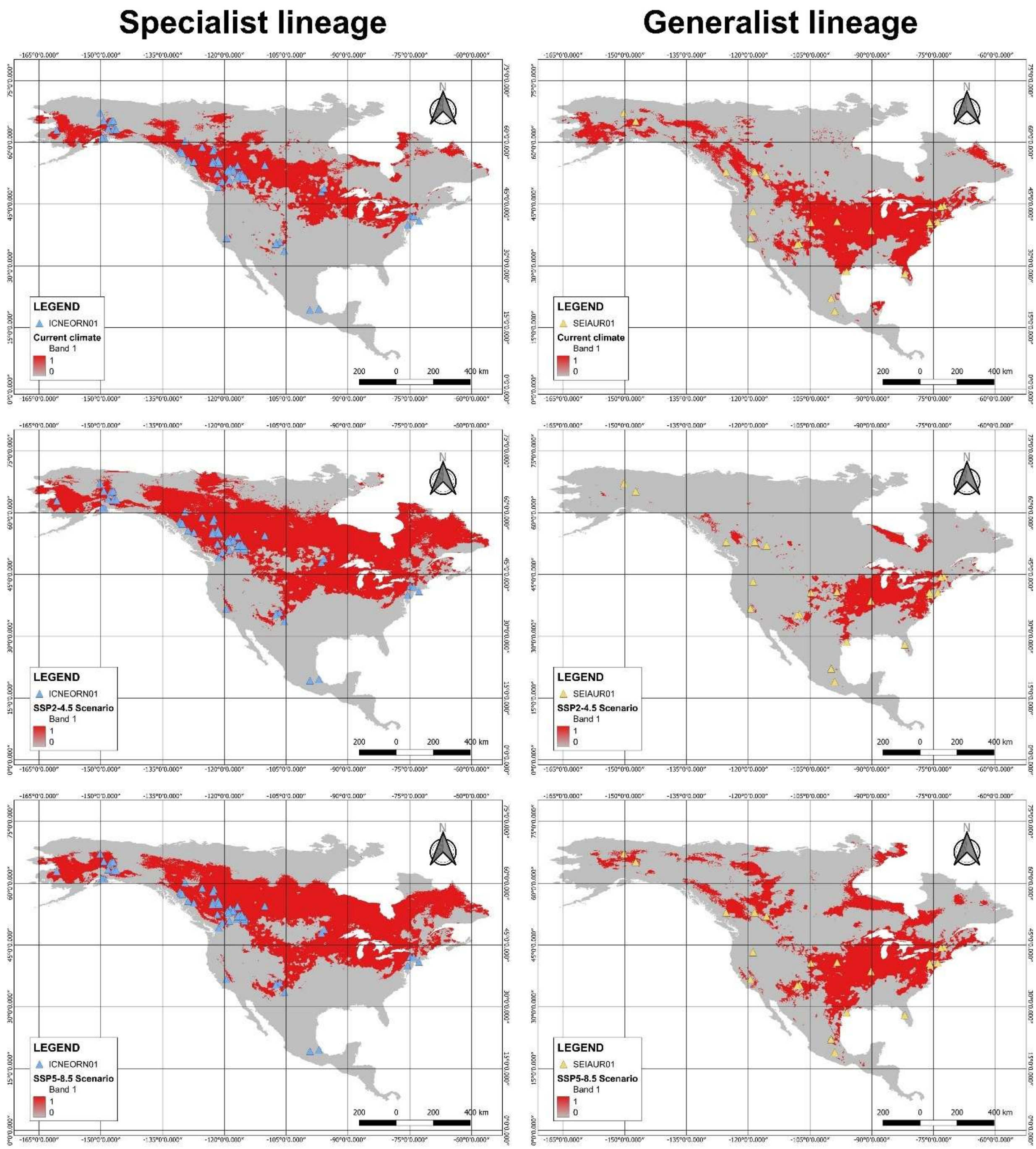


Figure 4. Environmental tolerance projections for the lineages ICNEORN01 (left) and pSEIAUR01 (right) using the total records of their known avian hosts.

Niche suitability models. The geographic projections of the haemosporidian environmental tolerance show the potential changes of the bioclimatic space distribution of ICNEORN01 and pSEIAUR01 across continental North America.

However, these changes do not represent climate suitability. With the NTBox package, we calculated the ellipsoid structure of the niche space for both lineages. Since the PCA showed that the precipitation variables had a positive correlation over the bioclimatic space distribution models of lCNEORN01, we chose variables BIO13 and BIO16, and temperature variable BIO05, to build the MVE model of the lineage. We found that lCNEORN01 occupies bioclimatic niche heavily constituted of less than optimal bioclimatic space in all climate scenarios. In contrast, we built the the niche suitability models for generalist lineage pSEIAUR01 using the temperature variables with higher loadings in the PCA (BIO05 and BIO10), as well as the precipitation variable BIO16. The niche structure for pSEIAUR01 includes a significant portion of suboptimal bioclimatic space but the centroid of the lineage is wider, indicating its higher environmental tolerance. Yet, the effects of climate change over the structure of the niche space for lCNEORN01 and pSEIAUR01 is clear: as the bioclimatic conditions get affected by the changing regimes of temperature and precipitation under scenario SSP2-4.5 and SSP5-8.5, haemosporidian parasites could potentially be facing the loss of suitable climate space in the near future (Fig. 5).

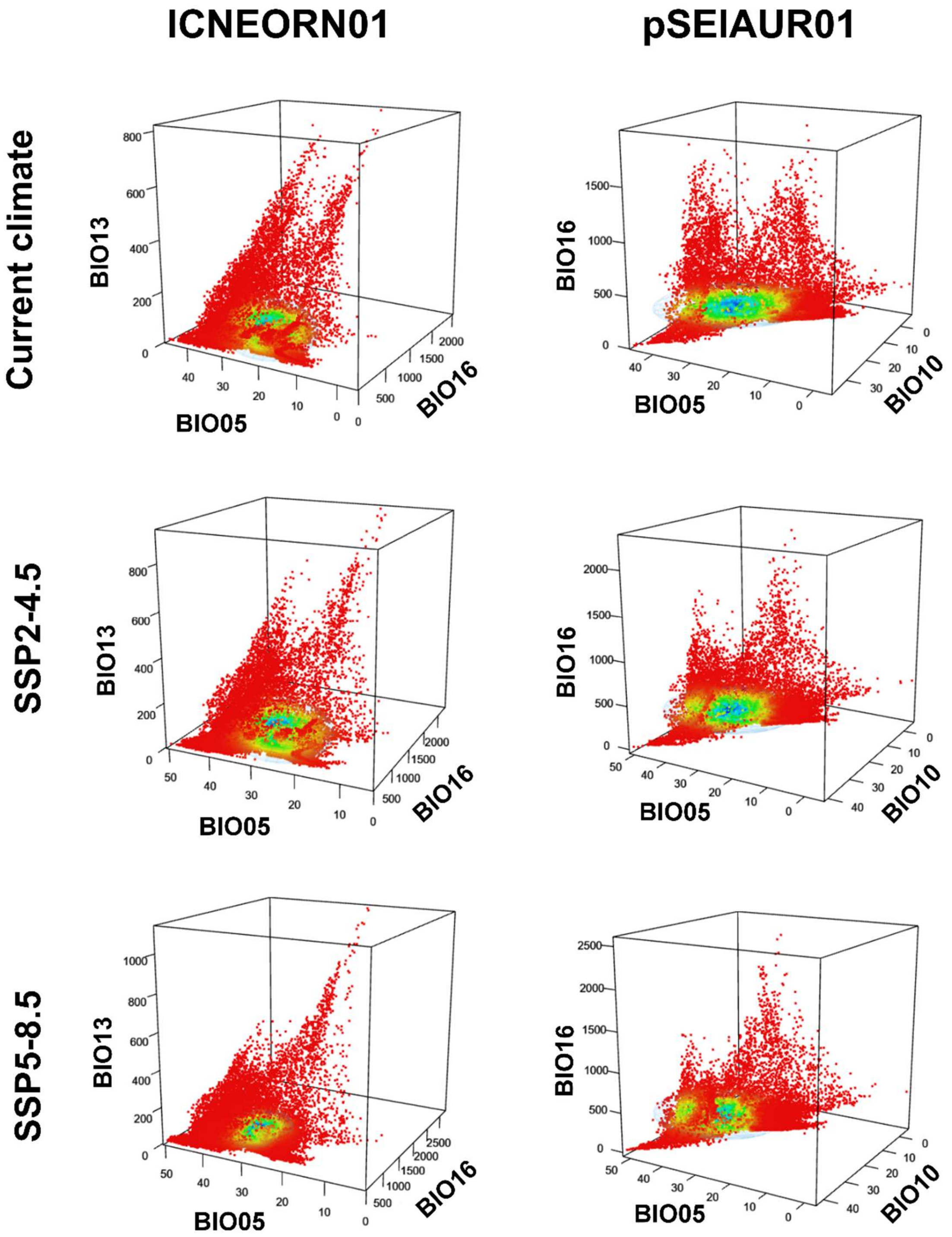


Figure 5. Graphical representation of the niche space for ICNEORN01 and pSEIAUR01. Niche ellipsoid models show changes in climate suitability under each climate change scenario. Each color represents the distance to niche centroid (DNC). Green = populations nearer to the niche centroid, Yellow = populations inside the niche but not belong to the centroid, Red = populations outside the suitable niche range. Axes represent the temperature ranges (° C) from the bioclimatic variables BIO01 (Annual mean temperature), BIO06 (Minimum temperature of the coldest

month), and BIO11 (Mean temperature of the coldest quarter), the three variables that had the highest (positive) gain for predicting the distribution of haemosporidian occurrence data on the environmental tolerance models.

DISCUSSION

As the effects of climate change worsen over time, host specificity could play a more significant role in how haemosporidian parasites adapt to it. Each haemosporidian genus is associated with different bioclimatic thresholds: *Plasmodium* and *Haemoproteus* prevalences are positively correlated with temperature and humidity (Lindsay & Martens 1998; Benning*, et al.* 2002; Stresman 2010; Garamszegi 2011), while the temperature thresholds for the prevalence of *Leucocytozoon* parasites are lower, as the genus is better adapted to colder climates (Valkiūnas 2005) associated with altitudes over 2200 masl (Galen & Witt 2014; Lotta*, et al.* 2016), and higher latitudes (Ramey*, et al.* 2014; Smith*, et al.* 2016; Fecchio*, et al.* 2019b). For this reason, we originally assumed that the *Plasmodium* and *Haemoproteus* lineages would show a tendency toward generalism, since their environmental requirements are not as restrictive as those observed for Leucozoonoid parasites and, in turn, expected *Leucocytozoon* lineages to behave mostly as specialists due to their most distinctive environmental requirements. However, by calculating the Specificity Index, we confirmed that the infection strategies of the lineages are a consequence of the coevolutive history of the parasites and their hosts, while the environment shapes how these relationships occur in relation to the environmental thresholds of the haemosporidian parasites, their hosts, and vectors.

Our specialist lineage lCNEORN01 does appear to have a lower environmental tolerance than the generalist lineage pSEIAUR01. This environmental tolerance is related to the environmental tolerance of the associated avian hosts of the lineage. The ICNEORN01 lineage belongs to the genus *Leucocytozoon*, and Leucozoonoid parasites are well adapted to colder climates (as observed in de bioclimatic projections), where the conditions usually have higher precipitation and overall humidity that limit *Haemoproteus* and *Plasmodium* infections but are suitable for the Simulidae vectors of Leucozoonoid infections in birds (Forrester & Greiner 2008; Harrigan*, et al.* 2014; Illera*, et al.* 2017; Ferreira*, et al.* 2020) and favor the the asexual reproduction or sporogony —the phase of the life cycle where the bird-infective stages are formed— of the parasites in the genus develop (temperatures ranges between 15 and 20° C) (Valkiūnas 2005). Our niche suitability results situate the temperature thresholds (between -10° C to 15° C) for ICNEORN01 well within the temperature thresholds reported in the literature. As this represent the lowest temperature threshold (Valkiūnas 2005; Ramey*, et al.* 2014; Smith*, et al.* 2016) of the three main haemosporidian genera (*Haemoproteus*, *Plasmodium* and *Leucocytozoon*) included in our samples, it's coherent that the environmental and geographical spaces of a parasite with such a limited environmental tolerance get affected negatively under contrasting climate change scenarios. Also, *Leucocytozoon* infection rates and lineage diversity have been reported to decrease at higher latitudes (Fecchio*, et al.* 2019b), so it makes sense that the spatial turnover and lower environmental tolerance could directly affect their distribution patterns and even potentially produce local extinctions for *Leucocytozoon* lineages. If the birds (and vectors) lose suitable bioclimatic space, ICNEORN01 could be facing a potentially important loss of suitable climate due to climate change unless the environmental pressure promotes a switch of the infection strategy of the lineage.

In contrast, the generalist lineage pSEIAUR01 belongs in the genus *Plasmodium*, and its prevalence has been positively correlated with temperature and humidity increases (Lindsay & Martens 1998; Benning*, et al.* 2002; Valkiūnas 2005; Stresman 2010; Garamszegi 2011; Atkinson*, et al.* 2014). For generalist lineages, their environmental tolerance seems to be directly associated with the wide variety of avian hosts they can infect. For *Plasmodium* infections like pSEIAUR01, their prevalence and the distribution and abundance of its vectors is positively correlated with temperature (Lindsay & Martens 1998; Atkinson 1999; Benning*, et al.* 2002; Garamszegi 2011), which explains why the climate change scenarios appear to affect generalist infections less negatively and even expand their distribution range under scenario SSP2-4.5. Also, it is worth noting that the northward range shift has been observed on other groups (Niven & Butcher 2014; Pélissié*, et al.* 2022), but with parasitic organisms like haemosporidians, these latitudinal distribution shifts continue to be hard to assess, mainly because different parasite groups present different distribution patterns in response to latitude and local climate trends (Kamiya*, et al.* 2014). However, this northward spatial turnover appears to be a response to the observed widening of the tropical width (Staten*, et al.* 2018), were the limits of the arid and semi-arid regions in the subtropics are shifting toward the poles as a result of anthropogenic climate change.

By comparing haemosporidian lineages that exhibit different ranges of host specificity we expected to offer a new approach to assess the effects of climate change over avian haemosporidian infections. The evolutive history of host-parasite relationships explains the appearance of opposing infection strategies such as specificity, where the lineages have adapted to infect certain avian hosts taxa, or generalism, where the parasites have adapted to infect the widest range of hosts possible. However, host specificity of avian haemosporidian parasites remains an underused attribute for niche modelling projections (Wells & Clark 2019).

Since host specificity is not a fixed attribute, the observed distribution changes under the chosen climate change scenarios (SSP2-4.5 and SSP5-8.5) open the possibility that haemosporidian lineages could adopt different infection strategies than what they have under the current climate. This means that lineages that in the present are behaving as specialist parasites and infecting avian hosts with non-random Specificity Indexes ($p < 0.05$) could either 1) potentially adapt to generalist infection strategies or 2) potentially disappear after the distribution of their suitable climate gets reduced because of the effects of climate change. Either outcome would also relate to how climate change is going to affect the distribution and abundance of their avian hosts and dipteran vectors. On the other hand, current generalist lineages could potentially increase their range in certain regions and replace specialist lineages, leading to the turnover of haemosporidian lineages. For this reason, we consider that host specificity provides a promising attribute that can help make better predictions in relation to the potential dispersion trends and infection risks posed by avian haemosporidians in wild bird populations across the globe. By including host specificity, the behavioral status of the avian hosts (migratory vs. resident species) or by modelling each haemosporidian lineage, we consider that environmental projections can provide a more nuanced analysis of the effects of climate change over haemosporidian infections, as well as providing a new approach to assessing which avian hosts could be at a potentially higher risk of infection, species turnover rates and changes of distribution of haemosporidians.

The impact of climate change on the transmission and dispersion of avian haemosporidians is becoming a prominent issue of concern for bird conservation around the world. Since the haemosporidian host-parasite complex is highly dependent on temperature and humidity conditions, predictive models provide useful information on potential shifts on the geographical expression of haemosporidian infections in response to climate change (particularly across altitudinal and latitudinal gradients) (Benning*, et al.* 2002; Garamszegi 2011; Atkinson*, et al.* 2014). When modelling environmental tolerance for generalist and specialist haemosporidian lineages at a continental scale, we found that the bioclimatic variables with higher statistical impact over the models are temperature-related (BIO01 annual temperature, BIO06 minimum temperature of the coldest month, and BIO11 mean temperature of the coldest quarter). For our lineages, BIO11 was the environmental variable that proved more statistically effective for positively predicting the distribution of haemosporidian occurrence data (AUC 0.7958). This is similar to the findings in studies done at smaller scales (Schröder & Schmidt 2008; Zamora-Vilchis*, et al.* 2012; Álvarez-Mendizábal*, et al.* 2021). We also inferred that the presence of each haemosporidian lineage is indirectly linked to the presence of their dipteran vectors. As such, models like the ones presented here can be used to indirectly measure the potential distribution shifts of the climate behind vector presence and identify areas where vector research is needed.

It is also worth noting that specialized and well curated online databases like MalAvi (Bensch*, et al.* 2009) are proving to be very useful tools for investigating issues such as the emerging diseases of wildlife, as they provide a means to compile and distribute data from researchers around the world. These tools not only provide access to the state of the art on the guild, but they also allow researchers to supplement their data for more sophisticated analyses. Also, the taxonomy used to build the birdtree.org phylogenetic trees used to calculate the Specificity Index for our sample lineages is, to date, the only available and reliable phylogenetic resource containing over 9000 avian species (Rubolini*, et al.* 2015; Li*, et al.* 2019). The metrics that measure phylogenetic distances seem constant and are useful for community measurements, which is the approach we used here, and thus why we consider the analysis to be quite solid in relation to the calculation of the specificity index of our haemosporidian lineages.

CONCLUSION

The contrasting environmental tolerances between specialist and generalist lineages highlight the vulnerability of host-specific haemosporidians, which may face local extinctions as their suitable bioclimatic space diminishes as a direct result of climate change, especially under the most severe scenarios. Meanwhile, generalist lineages, benefiting from having broader environmental tolerances and a wider availability of potential hosts to infect, may expand or maintain their distribution ranges under moderate climate change scenarios (i.e. SSP2-4.5), illustrating a potential shift in the dynamics of avian haemosporidian infections in a period of 20 years between 2061 and 2080. Since the environmental variables most strongly associated with haemosporidian prevalence in our models correspond with temperature values (mean annual temperature, minimum temperature of the coldest month, and mean temperature of the coldest quarter), severe climate change scenarios (SSP5-8.5) not only could affect the distribution ranges for both types of parasites but also significantly reduce the suitability of niche space for haemosporidians in general. In this regard, our original predictions were partially met. We had predicted a clear northward migration of the environmental range for both types of haemosporidian lineages; however, by projecting the bioclimatic space of our lineages without considering which behavioral pattern was being followed by their hosts we obtained distribution projections that were far too homogeneous, so the spatial turnover is very subtle to notice. Nevertheless, the environmental range of the specialist lineage showed a noticeable trend of migrating toward higher latitudes under both climate change scenarios when taking into consideration its migratory avian hosts. We also had predicted that the potential reduction of suitable environmental niche would be more significative for specialist haemosporidian lineages rather than for generalist haemosporidians and found a clear trend to the reduction of bioclimatic space for the resident avian hosts under both climate change scenarios and a deterioration of the niche structure for both lineages under climate change scenarios SSP2-4.5 and SSP5-8.5. in contrast to the more stable niche space of the generalist lineage pSEIAUR01, supporting our hypothesis that generalist lineages have a higher degree of tolerance to climate change.

By integrating host specificity into predictive models, researchers can gain valuable insights into the potential changes in infection patterns and risks faced by avian populations as climate conditions evolve. Furthermore, the role of well-curated databases and updated phylogenetic resources will enhance the accuracy of these models, fostering a more comprehensive understanding of the ecological and evolutionary implications of climate change on haemosporidian parasites. Ultimately, acknowledging the complex interplay between host specificity, climate change, and avian health is crucial for developing effective conservation strategies to mitigate the risks posed by emerging infectious diseases in wildlife.

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FINAL CONCLUSIONS

Climate plays an important role in shaping the distribution and dynamics of avian haemosporidian infections. While precipitation-related variables have some influence, temperature remains the dominant bioclimatic driver of these vector-parasite-host associations, both at finer geographical scale (central-eastern Mexico) and at coarser scale (continental North America). In central to eastern Mexico, our projections under both climate change scenarios (RCP 4.5 and RCP 8.5) suggest a dramatic loss of suitable climate areas for haemosporidians by 2070, with the potential to impact parasite prevalence and community composition. As climate change exacerbates the desertification of arid regions and modifies precipitation regimes in tropical areas, these changes could affect the broader ecological dynamics. The impact of climate change on avian haemosporidian communities is particularly concerning in regions with high biodiversity and vulnerable ecosystems. Our study highlights the need for further research into the ecological dynamics of these infections in arid and semi-arid habitats, which have been underrepresented in previous studies.

Furthermore, another factor that could be playing a significant role in shaping how avian haemosporidian parasites react to the ongoing challenges posed by climate change is host specificity. The contrasting environmental tolerances between specialist lineages (i.e. ICNEORN01), and generalist lineages, (i.e. pSEIAUR01), reveal that host specificity may be a necessary factor to take into consideration for understanding how parasites might adapt to shifting climate conditions. Specialist parasites, with their narrow ecological requirements, are more vulnerable to the loss of suitable climate zones, especially in high-altitude and temperate regions. In contrast, generalist parasites, which can infect a wide range of avian hosts and have a wider environmental tolerance, appear to be more resilient to climate change, and their range may even expand as temperatures rise and humidity levels increase.

This study aims to contribute to the ever-growing body of evidence that demonstrates how climate change can significantly alter the ecological balance of infectious disease transmission. Predictive models that incorporate bioclimatic factors, host specificity, and the unique dynamics of avian haemosporidian systems offer valuable tools for understanding and anticipating future risks, improving our ability to protect vulnerable bird species and their ecosystems from the ever-evolving threat of climate-induced changes in disease patterns.

SUPPLEMENTARY MATERIAL

Table A. List of the registered avian host species for each of the nineteen lineages, their taxonomic classification and behavioral status.

Lineage	Host species	Family	Order	Host status
hAMPBIL02	*Spizella pallida*	Passerellidae	Passeriformes	Migratory
	Amphispiza bilineata	Passerellidae		Resident
pBAEBIC02	*Basilinna leucotis*	Trochilidae	Apodiformes	Resident
	Xiphorhynchus flavigaster	Furnariidae	Passeriformes	Resident
	Mionectes oleaginosus	Tyrannidae		Resident
	Baeolophus bicolor	Paridae		Resident
	Sitta carolinensis	Sittidae		Resident
	Troglodytes aedon	Troglodytidae		Resident
	Catharus frantzii	Turdidae		Resident
	Arremonops rufivirgatus	Passerellidae		Resident
	Arremon aurantiirostris			Resident
	Arremon brunneinucha			Resident
	Passerella iliaca			Resident
	Melospiza melodia			Resident
	Melospiza lincolnii			Resident
	Aimophila rufescens			Resident
	Pipilo maculatus			Resident
	Atlapetes albinucha			Resident
	Dolichonyx oryzivorus	Icteridae		Migratory
	Icterus chrysater			Resident
	Icterus graduacauda			Resident
	Molothrus ater			Resident
	Dives dives			Resident
	Parkesia noveboracensis	Parulidae		Migratory
	Geothlypis poliocephala			Resident
	Geothlypis trichas			Migratory
	Setophaga pensylvanica			Migratory
	Setophaga coronata	Parulidae		Migratory
	Basileuterus lachrymosus			Resident
	Basileuterus rufifrons			Resident
	Basileuterus culicivorus			Resident
	Cardellina pusilla			Migratory
	Habia rubica	Cardinalidae		Migratory
pBAEBIC04	*Poecile carolinensis*	Paridae	Passeriformes	Resident
	Poecile atricapillus			Resident
	Baeolophus bicolor			Resident
	Dumetella carolinensis	Mimidae		Migratory
	Arremonops rufivirgatus	Passerellidae		Resident

Lineage	Host species	Family	Order	Host status
hBNOW03	*Tyto alba*	Tytonidae	Strigiformes	Resident
	Falco sparverius	Falconidae	Falconiformes	Resident
pBT7	*Anser canagicus*	Anatidae	Anseriformes	Migratory
	Cygnus columbianus			Migratory
	Spatula discors			Migratory
	Anas acuta			Migratory
	Bonasa umbellus	Phasianidae	Galliformes	Resident
	Tympanuchus phasianellus			Resident
	Canachites canadensis			Resident
	Pluvialis fulva	Charadriidae	Charadriiformes	Migratory
	Calidris melanotos	Scolopacidae		Migratory
	Accipiter striatus	Accipitridae	Accipitriformes	Migratory
	Corvus brachyrhynchos	Corvidae	Passeriformes	Resident
	Poecile atricapillus	Paridae		Resident
	Poecile hudsonicus			Resident
	Tachycineta bicolor	Hirundinidae		Migratory
	Petrochelidon pyrrhonota			Migratory
	Troglodytes aedon	Troglodytidae		Resident
	Troglodytes troglodytes	Troglodytidae		Introduced
	Cistothorus platensis			Migratory
	Dumetella carolinensis	Mimidae		Migratory
	Ixoreus naevius	Turdidae		Migratory
	Catharus fuscescens			Migratory
	Catharus minimus			Migratory
	Catharus ustulatus			Migratory
	Catharus guttatus			Migratory
	Turdus migratorius			Migratory
	Passer domesticus	Passeridae		Introduced
	Pinicola enucleator	Fringilidae		Migratory
	Spinus pinus			Resident
	Spizella pallida	Passerellidae		Migratory
	Passerella iliaca			Resident
	Junco hyemalis			Resident
	Zonotrichia leucophrys			Resident
	Zonotrichia albicollis			Resident
	Ammospiza leconteii			Migratory
	Passerculus sandwichensis			Migratory
	Melospiza melodia			Resident
	Melospiza lincolnii			Resident
	Melospiza georgiana			Resident
	Pipilo erythrophthalmus			Migratory

Lineage	Host species	Family	Order	Host status
	Seiurus aurocapilla	Parulidae		Migratory
	Parkesia noveboracensis			Migratory
	Mniotilta varia			Migratory
	Leiothlypis celata			Migratory
	Geothlypis trichas			Migratory
	Setophaga coronata			Migratory
	Cardinalis cardinalis	Cardinalidae		Resident
hCAMRUB03	*Setophaga coronata*	Parulidae	Passeriformes	Migratory
ICATGUT02	*Perisoreus canadensis*	Corvidae	Passeriformes	Resident
	Catharus minimus	Turdidae		Migratory
	Catharus ustulatus			Migratory
	Catharus guttatus			Migratory
ICATMIN01	*Catharus minimus*	Turdidae	Passeriformes	Migratory
	Catharus ustulatus			Migratory
	Catharus guttatus			Migratory
	Hylocichla mustelina			Migratory
ICATUST11	*Catharus minimus*	Turdidae	Passeriformes	Migratory
	Catharus ustulatus			Migratory
ICB1	*Perisoreus canadensis*	Corvidae	Passeriformes	Resident
	Cyanocitta cristata			Resident
	Corvus corax			Resident
	Poecile carolinensis	Paridae		Resident
	Poecile atricapillus			Resident
	Poecile gambeli			Resident
	Poecile hudsonicus			Resident
	Baeolophus bicolor			Resident
	Tachycineta bicolor	Hirundinidae		Migratory
	Tachycineta thalassina			Migratory
	Corthylio calendula	Regulidae		Migratory
	Troglodytes aedon	Troglodytidae		Resident
	Anthus rubescens	Motacillidae		Migratory
	Leucosticte australis	Fringilidae		Resident
	Haemorhous mexicanus	Fringilidae		Resident
	Acanthis flammea			Resident
	Loxia curvirostra			Resident
	Loxia leucoptera			Resident
	Spinus pinus			Resident
	Spizelloides arborea	Passerellidae		Migratory
	Passerella iliaca			Resident
	Junco hyemalis			Resident
	Zonotrichia leucophrys			Resident

Lineage	Host species	Family	Order	Host status
ICNEORN01	*Zonotrichia albicollis*		Passeriformes	Resident
	Passerculus sandwichensis			Migratory
	Melospiza melodia			Resident
	Melospiza lincolnii			Resident
	Melospiza georgiana			Resident
	Pipilo chlorurus			Migratory
	Pipilo maculatus			Resident
	Parkesia noveboracensis	Parulidae		Migratory
	Mniotilta varia			Migratory
	Leiothlypis peregrina			Migratory
	Leiothlypis celata			Migratory
	Geothlypis trichas			Migratory
	Setophaga petechia			Migratory
	Setophaga striata			Migratory
	Setophaga caerulescens			Migratory
	Setophaga palmarum			Migratory
	Setophaga coronata			Migratory
	Setophaga townsendi			Migratory
	Cardellina pusilla			Migratory
	Poecile gambeli	Paridae		Resident
	Phylloscopus borealis	Phylloscopidae		Migratory
	Psaltriparus minimus	Aegithalidae		Resident
	Cistothorus palustris	Troglodytidae		Migratory
	Dumetella carolinensis	Mimidae		Migratory
	Spizella passerina	Passerellidae		Migratory
	Spizella pallida			Migratory
	Spizelloides arborea			Migratory
	Junco hyemalis			Resident
	Junco phaeonotus			Resident
	Zonotrichia capensis			Resident
	Zonotrichia leucophrys			Resident
	Zonotrichia albicollis			Resident
	Passerculus sandwichensis			Migratory
	Melospiza melodia			Resident
	Melospiza lincolnii			Resident
	Pipilo maculatus			Resident
	Pipilo erythrophthalmus			Migratory
	Atlapetes pileatus			Resident
	Dolichonyx oryzivorus	Icteridae		Migratory
	Icterus galbula			Migratory
	Agelaius phoeniceus			Resident

Lineage	Host species	Family	Order	Host status
	Quiscalus quiscula			Migratory
	Parkesia noveboracensis	Parulidae		Migratory
	Leiothlypis peregrina			Migratory
	Leiothlypis celata			Migratory
	Leiothlypis ruficapilla			Migratory
	Geothlypis trichas			Migratory
	Setophaga ruticilla			Migratory
	Setophaga petechia			Migratory
	Setophaga striata			Migratory
	Setophaga coronata			Migratory
	Setophaga townsendi			Migratory
	Basileuterus belli	Parulidae		Resident
	Cardellina canadensis			Migratory
	Cardellina pusilla			Migratory
	Cardinalis cardinalis	Cardinalidae		Resident
hCOBRA01	*Corvus brachyrhynchos*	Corvidae	Passeriformes	Resident
lCOBRA02	*Anser canagicus*	Anatidae	Anseriformes	Migratory
	Spatula discors			Migratory
	Corvus brachyrhynchos	Corvidae	Passeriformes	Resident
lCOBRA05	*Corvus brachyrhynchos*	Corvidae	Passeriformes	Resident
lCOBRA13	*Cyanocitta cristata*	Corvidae	Passeriformes	Resident
	Aphelocoma woodhouseii			Resident
	Corvus brachyrhynchos			Resident
hDENPEN02	*Poecile atricapillus*	Paridae	Passeriformes	Resident
	Acanthis flammea	Fringilidae		Resident
	Zonotrichia leucophrys	Passerellidae		Resident
	Setophaga petechia	Parulidae		Migratory
	Setophaga pensylvanica			Migratory
	Setophaga coronata			Migratory
	Cardellina pusilla			Migratory
pLAIRI01	*Anas acuta*	Anatidae	Anseriformes	Migratory
	Colinus virginianus	Odontophoridae	Galliformes	Resident
	Strix varia	Strigidae	Strigiformes	Resident
	Tyrannus vociferans	Tyrannidae	Passeriformes	Migratory
	Gymnorhinus cyanocephalus	Corvidae		Resident
	Aphelocoma californica			Resident
	Aphelocoma woodhouseii			Resident
	Corvus corax			Resident
	Poecile gambeli	Paridae		Resident
	Baeolophus ridgwayi			Resident
	Baeolophus atricristatus	Paridae		Resident

Lineage	Host species	Family	Order	Host status
	Tachycineta thalassina	Hirundinidae		Migratory
	Troglodytes aedon	Troglodytidae		Resident
	Thryomanes bewickii			Resident
	Henicorhina leucophrys			Resident
	Lamprotornis iris	Sturnidae		Introduced
	Toxostoma curvirostre	Mimidae		Resident
	Sialia mexicana	Turdidae		Migratory
	Sialia currucoides			Migratory
	Catharus ustulatus			Migratory
	Turdus grayi			Resident
	Turdus migratorius			Migratory
	Loxia curvirostra	Fringilidae		Resident
	Spinus psaltria			Migratory
	Arremonops rufivirgatus	Passerellidae		Resident
	Amphispiza bilineata			Resident
	Zonotrichia albicollis			Resident
	Passerculus sandwichensis			Migratory
	Dolichonyx oryzivorus	Icteridae		Migratory
	Quiscalus mexicanus			Resident
	Setophaga coronata	Parulidae		Migratory
	Cardinalis cardinalis	Cardinalidae		Resident
pPADOM09	*Anser cygnoides*	Anatidae	Anseriformes	Introduced
	Larosterna inca	Laridae	Charadriiformes	Vagrant
	Puffinus puffinus	Procellariidae	Procellariiformes	Migratory
	Myiopagis viridicata	Tyrannidae	Passeriformes	Resident
	Elaenia martinica			Resident
	Myiarchus tyrannulus			Resident
	Pitangus sulphuratus			Resident
	Megarynchus pitangua	Tyrannidae		Resident
	Tyrannus melancholicus			Resident
	Poecile carolinensis	Paridae		Resident
	Tachycineta thalassina	Hirundinidae		Migratory
	Troglodytes aedon	Troglodytidae		Resident
	Pheugopedius maculipectus			Resident
	Henicorhina leucophrys			Resident
	Dumetella carolinensis	Mimidae		Migratory
	Hylocichla mustelina	Turdidae		Migratory
	Turdus grayi			Resident
	Passer domesticus	Passeridae		Introduced
	Arremonops rufivirgatus	Passerellidae		Resident

Lineage	Host species	Family	Order	Host status
pSEIAUR01	*Zonotrichia capensis*			Resident
	Dolichonyx oryzivorus	Icteridae		Migratory
	Dives dives			Resident
	Mniotilta varia	Parulidae		Migratory
	Geothlypis trichas			Migratory
	Setophaga striata			Migratory
	Setophaga coronata			Migratory
	Basileuterus lachrymosus			Resident
	Basileuterus culicivorus			Resident
	Loriotus luctuosus	Thraupidae		Migratory
	Chlorophanes spiza			Resident
	Volatinia jacarina			Resident
	Coereba flaveola			Resident
	Saltator coerulescens			Resident
	Somateria mollissima	Anatidae	Anseriformes	Migratory
	Larosterna inca	Laridae	Charadriiformes	Vagrant
	Tyto alba	Tytonidae	Strigiformes	Resident
	Megascops kennicottii	Strigidae	Strigiformes	Resident
	Strix varia			Resident
	Melanerpes aurifrons	Picidae	Piciformes	Resident
	Colaptes auratus			Migratory
	Perisoreus canadensis	Corvidae	Passeriformes	Resident
	Cyanocorax yncas			Resident
	Aphelocoma californica			Resident
	Poecile carolinensis	Paridae		Resident
	Poecile atricapillus			Resident
	Baeolophus bicolor			Resident
	Tachycineta bicolor	Hirundinidae		Migratory
	Salpinctes obsoletus	Troglodytidae		Resident
	Thryomanes bewickii			Resident
	Dumetella carolinensis	Mimidae		Migratory
	Catharus minimus	Turdidae		Migratory
	Catharus ustulatus			Migratory
	Hylocichla mustelina			Migratory
	Turdus migratorius			Migratory
	Passer domesticus	Passeridae		Introduced
	Passer montanus			Introduced
	Euphonia hirundinacea	Fringilidae		Resident
	Haemorhous mexicanus			Resident
	Arremonops rufivirgatus	Passerellidae		Resident
	Spizella passerina			Migratory

Lineage	Host species	Family	Order	Host status
	Spizella pallida	Passerellidae		Migratory
	Spizella pusilla			Migratory
	Junco hyemalis			Resident
	Zonotrichia leucophrys			Resident
	Zonotrichia albicollis			Resident
	Passerculus sandwichensis			Migratory
	Centronyx henslowii			Migratory
	Melospiza melodia			Resident
	Melospiza georgiana			Resident
	Pipilo maculatus			Resident
	Pipilo erythrophthalmus			Migratory
	Dolichonyx oryzivorus	Icteridae		Migratory
	Agelaius phoeniceus			Resident
	Molothrus ater			Resident
	Dives dives			Resident
	Quiscalus mexicanus			Resident
	Seiurus aurocapilla	Parulidae		Migratory
	Mniotilta varia			Migratory
	Geothlypis trichas			Migratory
	Setophaga citrina			Migratory
	Setophaga pensylvanica			Migratory
	Setophaga striata			Migratory
	Setophaga coronata			Migratory
	Cardinalis cardinalis	Cardinalidae		Resident
	Pheucticus ludovicianus			Migratory
	Pheucticus melanocephalus			Migratory
	Passerina cyanea			Migratory
	Spiza americana			Migratory