# **Chapter 5 Avian Disease Ecology in the Neotropics**



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# **5.1 Introduction**

Globally, birds are the best studied taxonomic group of vertebrates. Over 10,000 bird species have radiated and spread across the Earth's biomes (Avibase; [avibase.](http://avibase.bsc-eoc.org) [bsc-eoc.org](http://avibase.bsc-eoc.org)), and ornithologists have mapped and dated the diversifcation of all extant bird species worldwide (Jetz et al. [2012\)](#page-30-0). Through ecological studies, ornithologists have uncovered the high taxonomic and functional diversity of birds, their biogeographical patterns and the drivers of these patterns across different regions and scales (Rahbek and Graves [2001](#page-32-0); Herzog et al. [2005;](#page-30-1) Moura et al. [2016;](#page-32-1) Matuoka et al. [2020;](#page-31-0) Sol et al. [2020](#page-33-0)). However, parasite species affecting bird populations and communities have received fewer research efforts, hindering our capacity to manage and conserve bird species. Bird species play a critical role as hosts of a large array of parasite species that affect animal and human health (Dobson et al.

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[2008;](#page-29-0) Nabi et al. [2021\)](#page-32-2). Birds have been reported to harbor as many zoonoses as those found in fying mammals, such as in bats (Order Chiroptera; Mollentze and Streicker [2020](#page-32-3)). Moreover, birds latitudinal and altitudinal migration movements between wintering and breeding areas are implicated in the geographical spread of major parasitic species (e.g., infuenza viruses, West Nile virus; Feare [2010](#page-29-1); Winker and Gibson [2010](#page-34-0); Lee et al. [2015;](#page-31-1) Morin et al. [2018;](#page-32-4) Mine et al. [2019\)](#page-32-5). For example, Avian Infuenza viruses (AIVs) are known to successfully complete reassortment processes (i.e., the processes in which gene segments are exchanged between different infuenza viruses) in geographical hotspots for viral transport and mixing, where breeding areas are shared between North American and Asian migrant bird species (Morin et al. [2018\)](#page-32-4). In the Beringia region, phylogeographic analyses have shown that viral reassortment has likely occurred between highly pathogenic infuenza strains originating in China (e.g., Asian H5N8) and North American infuenza lineages that have ultimately spread across the continental United States (Saito et al. [2015\)](#page-33-1).

Avian parasites can have negative effects on their host populations and ecosystems (Møller [2005](#page-32-6)). Parasites can signifcantly affect host ftness by changing their behavior and sexual selection and can regulate avian populations by negatively impacting host reproduction (i.e., affecting the fecundity or survival of individuals) (May and Anderson [1978;](#page-31-2) Møller [2005](#page-32-6)). Parasites can also mediate intraspecifc competition, predator–prey interactions, and food web stability and determine host community structure (Møller and Erritzøe [2000](#page-32-7); Navarro [2004;](#page-32-8) Lafferty et al. [2006;](#page-31-3) Wood et al. [2007\)](#page-34-1). Moreover, they can exert evolutionary pressures on their hosts' immune systems, promoting greater investment in immune function that produces ftter and more viable host populations (Møller and Erritzøe [2002\)](#page-32-9). For example, avian malaria (genus *Plasmodium*) has produced epizootic die-offs in immunologically naive Hawaiian insular avifauna (LaPointe et al. [2012](#page-31-4)), causing population declines and signifcant altitudinal shifts in the distribution of susceptible forest birds (e.g., Hawaii amakihi; *Hemignathus virens*) (Samuel et al. [2011](#page-33-2)). While such population declines are commonly associated with acute malaria infections that result in increased predation or starvation of avian hosts, chronic infections in continental avifauna produce long-term subclinical effects that can indirectly impair reproductive success (e.g., *Plasmodium*-infected male songbirds have been observed to reduce song frequency, potentially impacting sexual selection) (Gilman et al. [2007;](#page-30-2) Meza-Montes et al. [2023](#page-31-5)).

Although parasitic species such as avian malaria and related haemosporidians are constrained to affect avian populations, others have had critical effects on both avian and human populations. Such is the case for the neurotropic and zoonotic West Nile virus (WNV), which has produced massive bird die-offs in highly susceptible hosts (e.g., American crows; *Corvus brachyrhynchos*), and neurological outbreaks of disease in humans across Europe and the United States (LaDeau et al. [2011;](#page-31-6) George et al. [2015](#page-30-3); Hadfeld et al. [2019](#page-30-4)). WNV is capable of infecting over 608 species of birds (Tolsá et al. [2018\)](#page-34-2); however, not all bird species are amplifying hosts for maintaining and transmitting the infection (Komar et al. [2003](#page-31-7)). Similarly, not all infected avian species are affected by neurologic illness and death (Steele

et al. [2000\)](#page-33-3). The effects of WNV on birds have affected only a few susceptible host species (Kilpatrick and Wheeler [2019](#page-31-8)), but WNV-associated declines of avian populations have had indirect ecological and health effects on other species. For instance, abundance variation in susceptible WNV species such as American robins promoted shifts in mosquito feeding preferences to humans and other avian species, increasing the prevalence of human disease (Kilpatrick et al. [2006\)](#page-31-9).

Avian hosts can also produce important effects on parasite populations and communities. For example, when infected by vector-borne viruses, bird species can exert selection pressures over parasite genetic populations, removing variants of lower fitness and affecting intrahost viral diversity (Jerzak et al. [2005](#page-30-5)). This regulation has been observed for WNV, where strong processes of purifying selection can evolutionarily constrain its genetic diversity in bird hosts (Jerzak et al. [2008\)](#page-30-6). On a much broader scale, avian host ecological traits (e.g., body mass, geographic range size, and relative abundance) can infuence a parasite's colonization success, reproduction, and contact with susceptible hosts, affecting parasite diversity and community composition (Poulin and Valtonen [2001](#page-32-10); Dáttilo et al. [2020](#page-29-2)). Moreover, the phylogenetic relatedness of hosts can drive the phylogenetic diversity of parasites across spatial scales (Clark and Clegg [2017\)](#page-29-3).

Few study systems are well understood in relation to the effects of the ecology of avian parasites on the ecology of avian host populations (and vice versa). Additionally, the potential for bird parasites to produce spillover events and emerge as novel zoonoses remains unclear. This stems from the fact that, in general, very little is known about the global parasitic faunas of birds. Most studies on the ecology of birds and their parasites have been performed in temperate regions (i.e., Nearctic and Palearctic) (Titley et al. [2017](#page-34-3)). Accordingly, a gap in knowledge on avian disease ecology remains for other biogeographical regions, such as the Neotropics. This scenario is worrying, as the Neotropical region is home to approximately 30% of the global avifauna and a high number of endemic species (Reboreda et al. [2019\)](#page-32-11). The high diversity of Neotropical bird species provides a diverse set of ecological niches for parasites (Hudson et al. [2006](#page-30-7); Poulin [2014](#page-32-12)). Furthermore, host species diversity has been shown to be a positive driver of parasite species diversity (Dobson et al. [2008;](#page-29-0) Poulin [2014;](#page-32-12) Kamiya et al. [2014\)](#page-31-10). Consequently, the Neotropical region is predicted to harbor not only a great proportion of the world's avifauna but also an extraordinary amount of parasite species (Dobson et al. [2008;](#page-29-0) Santiago-Alarcon and Rojas Soto [2021\)](#page-33-4).

In the context of global change, parasites are most likely to jump across species and disproportionately affect endangered and naïve native avian populations (e.g., Ortega-Guzmán et al. [2022\)](#page-32-13). Yet, some parasite species are also predicted to decline in abundance and geographical range size due to climate change and habitat destruction (Dobson et al. [2008](#page-29-0)). This will be contingent on the complexity of a parasites' life cycle, their dependence on host population density, their type of transmission, their host specifcity, and the geographical range size of their hosts, among other factors (Dobson et al. [2008\)](#page-29-0). Unfortunately, Neotropical species tend to have smaller range sizes than those inhabiting temperate or polar regions (Jetz and Rahbek [2002](#page-30-8)); hence, it is likely that their population declines will lead to the decline of their parasitic faunas (Dobson et al. [2008\)](#page-29-0). This is predicted to impact several ecosystem services that parasite species provide, including regulation of host abundance, increase in food web connectance, concentration and removal of pollutants from their hosts, among others (Sures [2004;](#page-34-4) Møller [2005;](#page-32-6) Lafferty et al. [2006\)](#page-31-3). Because parasites represent fundamental components of biodiversity, understanding their ecological and evolutionary interactions with their host species will aid to maintain animal, human, and ecosystem health.

In this chapter, we conducted an extensive search in the Web of Science Core Collection for current information regarding parasite ecology in birds across the Neotropical region from 2000 to 2021. The Web of Science Core Collection is a selective and balanced database that uses relevant information from multiple sources (Birkle et al. [2020\)](#page-29-4). Our frst search aimed to retrieve studies focused on parasite groups (i.e., virus, bacteria, protozoa, fungi, and disease), birds (i.e., birds, avian, aves, and avifauna), and the Neotropical region (i.e., Neotropic, South America, and Latin America). We excluded all scientifc papers that reported avian parasites in captive bird species, review papers, laboratory/experimental studies, and museum collection studies.

Our second search aimed to retrieve studies that show how anthropogenic (i.e., fragmentation, land use, landscape, urban, and habitat perturbation) and ecological (i.e., temperature, latitude, altitude, precipitation, humidity, and climate change) factors can be associated with the prevalence and diversity of each parasite group. According to prior knowledge, anthropogenic and ecological keywords were chosen regarding fundamental factors that infuence the prevalence and diversity of parasite species in their hosts, environment, and space. Last, we conducted a third search seeking to retrieve studies that explicitly assessed the relation between anthropogenic/ecological factors and the prevalence, diversity and/or richness of specifc parasite genera or species within each parasite group. We selected one parasite species (or genus) per parasite group (i.e., the parasite species or genus that had the highest number of observations in our frst search). An avian parasite record was considered to be an independent observation of a parasite genus or species in a particular Neotropical country, locality, and year. Boolean codes for all three searches can be found in Appendix Table [5.4](#page-26-0).

#### **5.2 Results**

In our frst search, we retrieved and assessed 3064 studies. Only papers that contained parasite group and/or species, avian order and/or species and country were selected, leaving a total of 1338 studies. Only 11 of 26 were conducted in Neotropical countries (i.e., Brazil, Peru, Argentina, Colombia, Chile, Ecuador, Mexico, Venezuela, Costa Rica, Dominican Republic, French Guiana, Panama, Guatemala, Bolivia, and Uruguay), and 15 Neotropical countries were not represented (i.e., Belize, El Salvador, Honduras, Nicaragua, Paraguay, Guyana, Suriname, Cuba, Jamaica, Haiti, and Puerto Rico). We found that Brazil is the Neotropical country

that contains the highest number of avian parasite records (553 observations), followed by Colombia (268 observations), Peru (252 observations), Argentina (86 observations), Chile (53 observations), Mexico (28 observations), and Ecuador (27 observations) (Fig. [5.1](#page-5-0)). In terms of groups of parasites, Brazil and Mexico were the only countries that had parasite records of all fve groups considered in this chapter: Virus, Bacteria, Fungi, Protista, and Animalia (i.e., parasitic insects, worms, cestodes, and rotifers) (Fig. [5.1](#page-5-0)). Brazil mainly had records of parasitic insects (i.e., Arthropoda, Fig. [5.2\)](#page-5-1), but it also had a signifcant number of protozoa of the phylum Mizozoa (subphylum Apicomplexa) (e.g., avian haemosporidian parasites) (Fig. [5.3](#page-6-0)) and of viral families such as Orthomyxoviridae, Coronaviridae, and Bornaviridae (e.g., avian coronaviruses, avian infuenza, and avian bornaviruses) (Fig. [5.4\)](#page-6-1). Mexico mainly contained records of viral families such as Flaviviridae (e.g., West Nile virus) (Fig. [5.4\)](#page-6-1), platyhelminthes and rotifers (Fig. [5.2](#page-5-1)), and Apicomplexa protozoa (i.e., avian haemosporidians) (Fig. [5.3\)](#page-6-0).

Chile followed Brazil and Mexico in number of groups of parasites, showing records of parasitic arthropods, nematodes, and platyhelminthes (Fig. [5.2](#page-5-1)) but also containing records of Apicomplexa protozoa (Fig. [5.3](#page-6-0)), and of Orthomyxoviridae and Poxviridae viral families (e.g., Avian Pox and Infuenza viruses) (Fig. [5.4\)](#page-6-1). Argentina mainly contained records of parasitic platyhelminthes (Fig. [5.2](#page-5-1)) and of the Orthomyxoviridae, Adenoviridae, Coronaviridae, Paramyxoviridae, and Bunyaviridae families (e.g., avian infuenza virus, avian adenovirus, avian infectious bronchitis virus, and avian paramyxovirus) (Fig. [5.4\)](#page-6-1). After Brazil, Colombia contained the most records of parasitic arthropods (Fig. [5.2](#page-5-1)) and an important number of records of parasitic protozoa (i.e., both Mizozoa and Euglenozoa phyla) (Fig. [5.3](#page-6-0)). Following Colombia, Peru also contained an important number of records of parasitic arthropods (Fig. [5.2\)](#page-5-1) and showed records of viral families such as Orthomyxoviridae and Adenoviridae (e.g., avian infuenza, Siadenoviruses, and Mastadenoviruses) (Fig. [5.4](#page-6-1)). Brazil and Argentina contained most studies focusing on avian bacteria (Fig. [5.1](#page-5-0)), mainly the phyla Proteobacteria (e.g., *Escherichia coli*, *Vibrio cholerae*, *Salmonella* spp), Firmicutes (e.g., *Bacillus* spp., *Clostridium* spp.), and Chlamydiota (e.g., *Chlamydia psittaci*) (Fig. [5.5\)](#page-7-0).

Brazil also represented the country with the highest parasite species richness (*S* = 243), followed by Argentina (*S* = 58), Colombia (*S* = 48), Peru (*S* = 43), and Chile  $(S = 44)$  (Fig. [5.6\)](#page-7-1). These five countries contained most of the studies that we were able to retrieve (Fig. [5.6\)](#page-7-1). Additionally, our frst search revealed that almost all avian parasites included in our study (over 800 observations out of 1338 total parasite observations) are being recorded and studied in bird species of the order Passeriformes  $(n = 72$  studies), followed by birds of the order Columbiformes  $(n = 27$  studies), Charadriiformes ( $n = 18$  studies), and Psittaciformes ( $n = 17$  studies) (Fig. [5.7\)](#page-8-0). Most records observed in the order Passeriformes belong to parasitic insects of the phylum Arthropoda (Fig. [5.8](#page-8-1)), followed by Apicomplexa protozoa (Fig. [5.9\)](#page-9-0), and by viral species of the Poxviridae, Flaviviridae, and Bunyaviridae families (Fig. [5.10](#page-9-1)). Studies that focused on avian bacteria were mostly observed in the orders Psittaciformes, Charadriiformes, and Cathartiformes (Fig. [5.11](#page-10-0)).

<span id="page-5-0"></span>

**Fig. 5.1** Number of parasite records belonging to the kingdoms Virus, Animalia (i.e., Arthropoda, Nematoda, Platyhelminthes, Rotifera), Protista, Bacteria, and Fungi per studied country in the Neotropical region

<span id="page-5-1"></span>

**Fig. 5.2** Number of records of avian parasitic arthropods, nematodes, platyhelminthes and rotifers per studied country in the Neotropical region

<span id="page-6-0"></span>

**Fig. 5.3** Number of records of avian protozoa per studied country in the Neotropical region

<span id="page-6-1"></span>

**Fig. 5.4** Number of records of viral families per studied country in the Neotropical region

<span id="page-7-0"></span>

**Fig. 5.5** Number of records of bacterial phyla per studied country in the Neotropical region

<span id="page-7-1"></span>

**Fig. 5.6** Parasite species richness as a function of avian species richness as analyzed in the Neotropical region. *N* represents the number of studies retrieved from each country. The Y axis was transformed to Sqrt (square root)

In our second search, we retrieved 1100 and 268 studies where anthropogenic and ecological factors, respectively, were studied concerning the prevalence and diversity of each parasite group. However, only in eight studies, parasite prevalence and/or diversity were explicitly assessed (i.e., using mathematical modeling) in relation to anthropogenic (e.g., land use type, distance to urban sites, forest fragment size, etc.) and ecological (i.e., temperature, precipitation, latitude, etc.) factors (Table [5.1](#page-11-0)). The parasite groups assessed in these eight studies included Apicomplexa protozoa (i.e., avian haemosporidians), avian viruses (i.e., West Nile virus, St Louis

<span id="page-8-0"></span>

**Fig. 5.7** Number of parasite records belonging to the kingdoms Virus, Animalia (i.e., Arthropoda, Nematoda, Platyhelminthes, Rotifera), Protista, Bacteria, and Fungi, per taxonomic bird order. Numbers next to bars represent the number of studies found per bird order

<span id="page-8-1"></span>

**Fig. 5.8** Number of records of avian parasitic arthropods, platyhelminthes, nematodes, and rotifers per taxonomic bird order

<span id="page-9-0"></span>

**Fig. 5.9** Number of records of avian protozoa per taxonomic bird order

<span id="page-9-1"></span>

**Fig. 5.10** Number of records of viral families per taxonomic bird order

<span id="page-10-0"></span>

**Fig. 5.11** Number of records of bacterial phyla per taxonomic bird order

Encephalitis virus, Avian pox virus), parasitic arthropods (i.e., *Amblyomma* spp.), and helminth communities (Table [5.1](#page-11-0)).

Finally, our third search retrieved 287 and 62 studies for anthropogenic and ecological factors, respectively. Of these, 12 (Table [5.2\)](#page-13-0) and 17 (Table [5.3\)](#page-17-0) were studies where the prevalence and/or diversity of each parasite genus/species was explicitly assessed for anthropogenic and ecological factors. All studies analyzed avian haemosporidian parasites.

## **5.3 Discussion**

Parasite ecology in birds has gained greater attention in the last two decades. Animal and public health concerns linked to avian disease outbreaks (e.g., highly pathogenic avian fu and West Nile fever) underscore the importance of investigating the ecological and evolutionary relationships between avian parasites, their host communities, and their environments (e.g., Robles-Fernández et al. [2022](#page-33-5)). Despite this, our research suggests that avian parasite diversity surveys remain rudimentary in most countries of the Neotropical region, and therefore, we have a poor understanding of disease dynamics as a function of ecological and anthropogenic factors.

Our extensive search revealed that within the Neotropics, most avian parasites are being detected in Brazil, Colombia, and Peru. This is not surprising, as these countries represent the three most bird-rich countries in the world ([birdlife.org\)](http://birdlife.org). Several studies have shown that parasite species richness follows host species



<span id="page-11-0"></span>**Table 5.1** Summary of the selected (second search) studies that explore the association between anthropogenic/ecological factors and parasite prevalence/



Country	Avian order	Explanatory variables	Response variables	Effect type	References
Ecuador	<b>NA</b>	Forest fragment size	Prevalence (Plasmodium)	Nonpredictive	Sebaio et al. (2010)
		Forest fragment size	Prevalence (Haemoproteus)	Nonpredictive	
		Forest dependence	Prevalence (Plasmodium)	Predictive	
		Forest dependence	Prevalence (Haemoproteus)	Nonpredictive	
Ecuador	Passeriformes	Fragment area	Infection status (Haemosporidian)	Nonpredictive	Rivero de Aguilar
		Forest quality	Infection status (Haemosporidian)	Nonpredictive	et al. (2018)
		Tree cover around fragments	Infection status (Haemosporidian)	Nonpredictive	
		Mist-net location (edge or interior)	Infection status (Haemosporidian)	Nonpredictive	
		Date	Infection status (Plasmodium)	Predictive	
		Cover	Infection status (Haemoproteus)	Predictive	
<b>Brazil</b>	Passeriformes	Proportion of native vegetation	Probability of infection (Haemosporidian)	Predictive	Fecchio et al. (2021)
		Distance to urban regions	Probability of infection (Haemosporidian)	Nonpredictive	
<b>Brazil</b>	<b>NA</b>	Habitat type (disturbed and undisturbed)	prevalence (Haemosporidian)	Predictive	Fecchio et al. (2021)
		Habitat type (disturbed and undisturbed)	prevalence (Haemoproteus)	Predictive	
		Habitat type (disturbed and undisturbed)	Prevalence (Plasmodium)	Predictive	
		Habitat type (disturbed and undisturbed)	Diversity (Plasmodium)	Predictive	
		Habitat type (disturbed and undisturbed)	Diversity (Haemosporidian)	Predictive	

<span id="page-13-0"></span>**Table 5.2** Summary of the selected (third search) studies that explore the association between anthropogenic factors and parasite prevalence/diversity in Neotropical avifauna

Country	Avian order	Explanatory variables	Response variables	Effect type	References
México	Passeriformes	Land use types	Lineage richness (Haemosporidian)	Predictive	Hernandez- Lara et al. (2020)
		Land use types	Prevalence (Haemosporidian)	Predictive	
		Land use types	Parasitemia (Haemosporidian)	Nonpredictive	
		Land use types	Aggregation (Plasmodium)	Nonpredictive	
<b>Brazil</b>	Passeriformes	Habitat type qué tipos?	Prevalence (Haemosporidian)	Predictive	Belo et al. (2011)
			Diversity (Haemosporidian)	Predictive	
Argentina, Uruguay, Bolivia. Mexico, Brazil, Peru, and Guatemala	Passeriformes	Host species diversity	Prevalence (Haemoproteus)	Predictive	Doussang et al. (2021)
Argentina, Uruguay, Bolivia. Mexico, Brazil, Peru, and Guatemala	Passeriformes	Host species diversity	Prevalence (Plasmodium)	Predictive	
Guadeloupe and	Passeriformes	Habitat loss	Prevalence (Haemosporidian)	Predictive	Perez- Rodriguez et al. (2018)
Martinique		Habitat fragmentation	Prevalence (Haemosporidian)	Predictive	

**Table 5.2** (continued)

Country	Avian order	Explanatory variables	Response variables	Effect type	References
<b>Brazil</b>	<b>NA</b>	Proportion native forest	Prevalence (Haemoproteus)	Nonpredictive	Fecchio et al. (2021)
			Taxonomic diversity (Haemoproteus)	Nonpredictive	
			Phylogenetic diversity (Haemoproteus)	Nonpredictive	
		Host functional	Prevalence (Haemoproteus)	Nonpredictive	
	Host Host	diversity	Taxonomic diversity (Haemoproteus)	Nonpredictive	
			Phylogenetic diversity (Haemoproteus)	Nonpredictive	
		phylogenetic diversity	Prevalence (Haemoproteus)	Nonpredictive	
			Taxonomic diversity (Haemoproteus)	Nonpredictive	
			Phylogenetic diversity (Haemoproteus)	Nonpredictive	
		taxonomic	Prevalence (Haemoproteus)	Nonpredictive	
		diversity	Taxonomic diversity (Haemoproteus)	Predictive	
			Phylogenetic diversity (Haemoproteus)	Nonpredictive	
		Proportion native forest	Prevalence (Plasmodium)	Predictive	
			Taxonomic diversity (Plasmodium)	Nonpredictive	
			Phylogenetic diversity (Plasmodium)	Nonpredictive	

**Table 5.2** (continued)





Country	Avian order	Explanatory variables	Response variables	Effect type	References
Chile,	Passeriformes	Altitude	Prevalence	Predictive	Doussang.
Costa			(Haemoproteus)		et al. (2021)
Rica. Bolivia,			Prevalence (Plasmodium)	Predictive	
Peru, and Argentina			Genetic diversity (Haemoproteus)	Nonpredictive	
			Genetic diversity (Plasmodium)	Nonpredictive	
		Latitude	Prevalence (Haemoproteus)	Predictive	
			Prevalence (Plasmodium)	Predictive	
			Genetic diversity (Haemoproteus)	Nonpredictive	
			Genetic diversity (Plasmodium)	Nonpredictive	
<b>Brazil</b>	Apodiformes, Passeriformes, Columbiformes. Accipitriformes, Galbuliformes, Psittaciformes	Humidity	Infection (Haemosporidian)	Predictive	Ferreira de Souza et al. (2020)
Peru	Passeriformes	Altitude	Prevalence (Plasmodium)	Predictive	Jones et al. (2013)
Chile	Passeriformes	Latitude	Prevalence (Plasmodium)	Predictive	Cuevas et al.
			Diversity (Plasmodium)	Predictive	(2020)
			Prevalence (Leucocytozoon)	Predictive	
			Diversity (Leucocytozoon)	Predictive	
			Prevalence (Haemoproteus)	Predictive	
			Diversity (Haemoproteus)	Nonpredictive	

<span id="page-17-0"></span>**Table 5.3** Summary of the selected (third search) studies that explore the association between ecological factors and parasite prevalence/diversity in Neotropical avifauna

Country	Avian order	Explanatory variables	Response variables	Effect type	References
Chile	<b>NA</b>	Latitude	Prevalence (Leucocytozoon)	Predictive	Merino et al. (2008)
			Prevalence (Plasmodium)	Predictive	
			Prevalence (Haemoproteus)	Predictive	
			Prevalence (Haemosporidian)	Predictive	
			Parasite richness (Leucocytozoon)	Nonpredictive	
			Parasite richness (Plasmodium)	Nonpredictive	
			Parasite richness (Haemoproteus)	Nonpredictive	
			Parasite richness (Haemosporidian)	Nonpredictive	
Ecuador	Passeriformes	Precipitation	Prevalence (Haemosporidian)	Predictive	Cadena- Ortiz et al. (2019)
		Site	Parasitemia (Haemosporidian)	Predictive	
Colombia	Passeriformes	Precipitation	Prevalence (Haemosporidian) Eucometis penicillata	Predictive	Pulgarin-R et al. (2018)
			Prevalence (Haemosporidian) Manacus manacus	Predictive	
			Diversity (Haemosporidian)	Nonpredictive	
<b>Brazil</b>	Passeriformes and Columbiformes	Temperature	Prevalence (Plasmodium)	Predictive	Rodriguez et al. (2021)
			Prevalence (Haemoproteus)	Nonpredictive	
		Rainfall	Prevalence (Plasmodium)	Nonpredictive	
			Prevalence (Haemoproteus)	Nonpredictive	

**Table 5.3** (continued)

Country	Avian order	Explanatory variables	Response variables	Effect type	References
Peru	Passeriformes, Caprimulgiformes,	Precipitation	Parasite turnover (Haemosporidian)	Predictive	McNew et al.
	Apodiformes, Strigiformes,	Temperature	Parasite turnover (Haemosporidian)	Nonpredictive	(2021)
	Cuculiformes, Galbuliformes,	Elevation	Parasite turnover (Haemosporidian)	Predictive	
	Piciformes, Tinamiformes, Trogoniformes, and	Net primary production	Parasite turnover (Haemosporidian)	Predictive	
	Columbiformes	Host turnover	Parasite turnover (Haemosporidian)	Predictive	
		Precipitation	Taxonomic diversity	Nonpredictive	
		Temperature	Taxonomic diversity	Nonpredictive	
		Elevation	Taxonomic diversity	Predictive	
		Net primary production	Taxonomic diversity	Predictive	
		Host turnover	Taxonomic diversity	Predictive	
Mexico	Columbiformes, Cuculiformes, Apodiformes, Strigiformes, Coraciiformes, Piciformes. Passeriformes	Elevation	Prevalence (Plasmodium)	Predictive	Rodríguez- Hernandez et al. (2021)
			Prevalence (Haemoproteus)	Predictive	
			Prevalence (Leucocytozoon)	Predictive	
			Parasitemia (Plasmodium)	Predictive	
			Parasitemia (Haemoproteus)	Predictive	
			Parasitemia (Leucocytozoon)	Predictive	
			Aggregation (Plasmodium)	Predictive	
			Aggregation (Haemoproteus)	Predictive	
			Aggregation (Plasmodium)	Predictive	
			Prevalence (Haemosporidia)	Predictive	
			Parasitemia (Haemosporidia)	Predictive	
			Aggregation (Haemosporidia)	Predictive	

**Table 5.3** (continued)

Country	Avian order	Explanatory variables	Response variables	Effect type	References
Mexico	Columbiformes, Cuculiformes, Apodiformes,	Temperature	Lineage community composition	Predictive	Alvarez- Medizabal et al. (2021)
	Strigiformes, Coraciiformes, Piciformes. Passeriformes	Precipitation	Lineage community composition	Predictive	
<b>Brazil</b>	Passeriformes	Number of water bodies	Probability of infection (Haemosporidian)	Nonpredictive	Fecchio et al. (2021)
		Precipitation	Probability of infection (Haemosporidian)	Predictive	
		Temperature	Probability of infection (Haemosporidian)	Predictive	
Mexico	Passeriformes	Seasonality	Prevalence (Haemosporidia)	Predictive	Hernandez- Lara et al. (2020)
			Prevalence (Haemoproteus)	Predictive	
			Prevalence (Plasmodium)	Predictive	
			Parasitemia (Haemosporidia)	Predictive	
			Aggregation (Haemosporidia)	Predictive	
<b>Brazil</b>	NA	Temperature	Prevalence (Plasmodium)	Nonpredictive	Fecchio et al. (2021)
			Taxonomic diversity (Plasmodium)	Nonpredictive	
			Phylogenetic diversity (Plasmodium)	Nonpredictive	
			Prevalence (Haemoproteus)	Nonpredictive	
			Taxonomic diversity (Haemoproteus)	Nonpredictive	
			Phylogenetic diversity (Haemoproteus)	Nonpredictive	
Mexico	Passeriformes	Seasonality	Prevalence	Predictive	Hernandez-
			Parasitaemia	Predictive	Lara et al. (2017)
			Aggregation	Nonpredictive	

**Table 5.3** (continued)

Country	Avian order	Explanatory variables	Response variables	Effect type	References
<b>Brazil</b>	Passeriformes and Columbiformes	Seasonality	Prevalence	Nonpredictive	Ferrerira et al. (2017)
Ecuador	Passeriformes	Seasonality	Infection status (Plasmodium)	Nonpredictive	Rivero de Aguilar et al. (2018)

**Table 5.3** (continued)

richness (Dobson et al. [2008](#page-29-0); Poulin [2014](#page-32-12); Kamiya et al. [2014\)](#page-31-10). Consequently, these three bird-rich countries offer a high diversity of hosts for parasites to occupy, increasing the likelihood of parasite detection. Most observations for Brazil, Colombia, and Peru are of parasitic Arthropoda, which are mainly represented by chewing lice of the genus *Myrsidea* sp. Avian chewing lice are ubiquitous and highly diverse ectoparasites of birds in Neotropical regions (Soto-Madrid et al. [2020\)](#page-33-9). Apart from being studied for their relevance as members of Neotropical communities, arthropods such as chewing lice are methodologically more straightforward to detect than other groups of parasites (e.g., viruses). We suggest that their vast diversity, direct detection, and usefulness as parasite models to understand ecological interactions explains the high number of arthropod records observed in Brazil, Colombia, and Peru.

Following arthropod insects, avian protozoa comprised the next best-studied parasite group in the Neotropics. Brazil, Peru, Colombia, Mexico, and Chile contained most avian protozoa records. Phylum Mizozoa (subphylum Apicomplexa) represented most of the observations, mainly including avian haemosporidian parasites (*Plasmodium* sp., *Haemoproteus* sp., and *Leucocytozoon* sp.). Apicomplexan parasites such as avian haemosporidians have become a model system for ecological and evolutionary studies of bird–parasite interactions (e.g., see chapters in Santiago-Alarcon and Marzal [2020b](#page-33-10)). Their importance for avian conservation, worldwide distribution, and high probability of detection in blood smears and PCR molecular samples has contributed to more scientists dedicating their research to this highly diverse parasite system (Valkiūnas and Atkinson [2020;](#page-34-6) Bensch and Hellgren [2020](#page-28-2)). Although much effort to detect and understand avian haemosporidian diversity in tropical settings has taken place in the last decade, most of their studies have been performed in temperate regions (Santiago-Alarcon and Marzal [2020a](#page-33-11); Chapa-Vargas et al. [2020](#page-29-12)). Moreover, haemosporidian haplotype sequence divergence has suggested that haemosporidian genetic richness could match worldwide avian species richness (i.e., 10,000 bird species) (Bensch et al. [2004;](#page-28-3) Bensch and Hellgren [2020\)](#page-28-2). Consequently, detection of avian haemosporidian diversity will help to understand complex antagonistic interactions – particularly of vector-borne parasites – and should be prioritized within Neotropical settings considered hotspots for host and parasite biodiversity (Santiago-Alarcon and Rojas Soto [2021](#page-33-4)).

After avian protozoa, avian viruses were the next best-studied group. In particular, we found that the Poxviridae, Orthomyxoviridae, Flaviviridae, and Coronaviridae families have been the most studied avian viruses in Neotropical countries. Ecuador, French Guiana, Guatemala, Chile, and Venezuela contained all studies focusing on avian pox virus. Avian pox viruses have been observed in over 350 species of birds (Williams et al. [2021\)](#page-34-7). Because their incidence has increased over the last 10 years, avian pox has been considered an emerging viral disease (Alehegn et al. [2014\)](#page-28-4), mainly affecting songbirds, birds of prey, marine birds, and poultry within tropical regions. A high prevalence of the disease has been observed in remote populations (e.g., Galapagos Islands), suggesting a threat to naive endemic insular avifauna in the Neotropical region (Williams et al. [2021\)](#page-34-7). In wild continental birds, pox prevalence has been highly variable, and information regarding host specifcity, strain virulence, and strain diversity remains elusive (Williams et al. [2021](#page-34-7)). In addition to fnding many observations on avian pox viruses, our results showed avian infuenza viruses (AIV) as the second most studied avian viruses in Neotropical countries. Brazil, Argentina, Peru, Ecuador, Chile, and Guatemala contained most AIV observations. Research efforts have been conducted worldwide to better understand the ecology of AIVs in wild birds (Wille and Barr [2022](#page-34-8)). Today, we know that highly pathogenic AIVs (HPAIVs) circulate on all continents except Australia and Antarctica (Willie and Barr [2022\)](#page-34-8). Moreover, HPAIVs have caused recent outbreaks in South America, killing over 22,000 wild birds, mainly Peruvian pelicans (*Pelecanus thagusI*) and boobies (*Sula variegata*) (Gamarra-Toledo et al. [2023\)](#page-30-15). Apart from these species, HPAIV has affected the near-threatened Guanay cormorant (*Leucocarbo bougainvillii*) across the coastline of Peru and has been suggested to be a potential threat to scavenger species such as the Andean condor (*Vultur gryphus*) (Gamarra-Toledo et al. [2023\)](#page-30-15). Researchers are calling for epidemiological surveillance to better understand the extent to which such outbreaks could progress.

Following avian infuenza, West Nile virus was the third most studied avian virus in the Neotropical region. Mexico and the Dominican Republic contained all of the records. WNV belongs to the Flavivirus genus, and its transmission cycle involves mosquitoes as vectors and wild birds as their vertebrate hosts. For more than 20 years, this virus has represented a threat to bird populations with persistent impacts on some wild bird species in North America (Passeriformes comprises the order with more susceptible avian species for this virus) and on human populations producing outbreaks of neurological disease (LaDeau et al. [2007;](#page-31-15) George et al. [2015\)](#page-30-3). However, despite its importance for bird conservation, human health, and evidence suggesting migratory birds are important carriers of this virus, WNV is poorly known in the Neotropical region. A worldwide study showed that Mexico, Guatemala, and Argentina are countries with serological and molecular evidence in wild birds (Tolsá et al. [2018\)](#page-34-2). However, WNV has already been classified as a neglected tropical disease because funding and research efforts have declined over time (Ronca et al. [2021](#page-33-12)).

Regarding bacteria, we found few records, even though birds are recognized as hosts of many bacterial species relevant to avian and human health (Reed [2002;](#page-33-13) Benskin et al. [2009\)](#page-29-13). *Escherichia coli* was the best-represented bacterial species in our search and was studied in Brazil, Chile, Costa Rica, and Argentina mainly in Charadriiformes, Psittaciformes, and Sphenisciformes hosts. In the Neotropics, the study of *E*. *coli* should be a priority because it has been associated with mass dieoffs of various wild bird species, which are suggested to act as carriers of multidrugresistant *E*. *coli* (Reed [2002](#page-33-13); Smith et al. [2020](#page-33-14)). The genus *Salmonella* was the second most studied bacteria in the Neotropics, mainly in Peru and Argentina in the Charadriiformes and Passeriformes. Various studies have shown that this genus, specifcally *Salmonella typhimurium,* is commonly isolated in intestinal samples of wild birds and has been associated with mass mortality events (Smith et al. [2020\)](#page-33-14).

Fungi was the least studied parasite group in the Neotropics  $(n = 19)$ . The bestrepresented species were *Cryptococcus neoformans* and *Aspergillus* spp. *Cryptococcus neoformans* was identifed infecting the order Columbiformes (pigeons and doves) in Brazil, Venezuela, and Colombia. *Cryptococcus* spp. have been found in avian orders such as Passeriformes, Anseriformes, Accipitriformes, Apterygiformes, Psittaciformes, and Columbiformes, with wide variability in susceptibility between bird species (Johnston et al. [2016](#page-31-16)). Additionally, *Aspergillus* spp. were identifed in samples of Sphenisciformes, Suliformes, and Charadriiformes in Brazil, Argentina, and Mexico, respectively. At the parasite species level, we also recorded *Aspergillus fumigatus*, a common parasite among wild and domestic birds, with a prevalence of approximately 95% (Arné et al. [2021](#page-28-5)).

# *5.3.1 Parasite Dynamics as a Function of Anthropogenic and Ecological Factors*

Understanding parasite infection patterns, their diversity and distribution in relation to environmental, spatial, and anthropogenic factors remains a challenge for infectious disease ecology. Our synthesis found that the main anthropogenic variables associated to prevalence and diversity of avian parasites are land-use or habitat type, habitat fragmentation or loss, the proportion of native vegetation, and habitatassociated host diversity in its taxonomic, phylogenetic, and functional forms. These variables often relate differently to each parasite system, sometimes producing opposing trends even within the same parasite taxa. For example, the prevalence of avian pox viruses has increased with agricultural intensifcation (Zylberberg et al. [2013\)](#page-34-5). In contrast, the probability of haemosporidian parasite infection has increased with higher proportion of native vegetation cover (Fecchio et al. [2020](#page-30-9)) or decrease with advanced stages of forest succession (Ferreira Junior et al. [2017\)](#page-30-13). In the case of avian haemosporidians, parasite genera can produce these contrasting results because each Haemosporidian genus is transmitted by different Diptera families and species whose reproduction and development depend on different microclimatic conditions (Rodríguez-Hernández et al. [2021](#page-33-8)). For instance, the *Plasmodium* genus might be favored by anthropogenic transformation, while the *Haemoproteus* genus might be more prevalent in preserved forests (Hernández-Lara et al. [2020\)](#page-30-11).

This shows how the response of parasites to anthropogenic drivers of prevalence varies spatially and may be contingent on the host–parasite system.

Habitat-associated host diversity has also been related to contrasting infection patterns and parasite diversity in systems such as avian haemosporidians. Increased host functional diversity in preserved remnants of the Brazilian Atlantic Forest decreased *Plasmodium* lineage diversity (Fecchio et al. [2021\)](#page-30-10). However, high host taxonomic diversity within the same locations increased *Plasmodium* taxonomic lineage diversity but decreased *Plasmodium* phylogenetic lineage diversity (i.e., more diverse avian communities in preserved remnants harbored more taxonomically diverse but phylogenetically clustered parasite assemblages). Apparently, different facets of avian host diversity (e.g., functional, taxonomic, and phylogenetic) can produce differential effects over the taxonomic and phylogenetic components of haemosporidian parasite diversity, underscoring the complexity and relevance of assessing the spatial patterns of host diversity in all of its facets as drivers of parasite diversity and distribution.

Beyond the diverse effects of anthropogenic factors, the prevalence and diversity of avian parasites can be driven by ecological factors (i.e., environmental and spatial factors). We found that latitude, altitude, temperature, precipitation, humidity, and seasonality are the most studied ecological drivers of parasite prevalence and diversity in the Neotropics. For instance, the inverse relationship between altitude and temperature has been associated with the differential distribution of avian haemosporidian genera across elevational gradients in different settings (Zamora-Vilchis et al. [2012](#page-34-9); van Rooyen et al. [2013](#page-34-10); Álvarez-Mendizábal et al. [2021\)](#page-28-1). Similarly, an inverse latitudinal diversity gradient has explained the infection probability and phylogenetic diversity of *Leucocytozoon* parasites in New World birds (Fecchio et al. [2019](#page-29-14)). Moreover, within Neotropical countries such as Mexico and Brazil, haemosporidian parasite prevalence, diversity, and community composition have been explained by temperature, precipitation, humidity, and seasonality (Hernández-Lara et al. [2017](#page-30-12); Hernández-Lara et al. [2020;](#page-30-11) Ferreira de Souza et al. [2020\)](#page-29-9). In the Caatinga of Brazil, there was a high frequency of hemoparasites in birds due to high levels of humidity and rainfall (Ferreira de Souza et al. [2020\)](#page-29-9). Similarly, contrasting patterns in prevalence among bird species were reported in Colombia (e.g., grayheaded tanagers, *Eucometis penicillata*, exhibited higher prevalence rates in locations with less precipitation, while white-bearded manakins, *Manacus manacus,* showed higher prevalence in locations with high precipitation) (Pulgarín-R et al. [2018\)](#page-32-16). In Mexico, increased infection rates have been associated with wet seasons, where there is an increase in the abundance of mosquito vectors, and coincide with avian host breeding seasons, where reproduction generates a trade-off between immune function and reproductive output (Hernández-Lara et al. [2020](#page-30-11)).

Environmental and spatial heterogeneity can structure the distribution and diversity of avian parasites and their hosts and vectors. However, a wide variation in responses to the heterogeneity in ecological factors can be observed for most host– parasite systems. The relative importance of environmental versus spatial drivers of parasite infection and diversity can also depend on the scale of the study (e.g.,

microclimatic variables can explain parasite distribution patterns at local-landscape scales, while geographic barriers or latitude could be more important drivers at regional and global scales). Consequently, it is fundamental to continue studying avian host–parasite systems in regions that provide this type of environmental heterogeneity (i.e., tropical and subtropical) at different spatiotemporal scales to better understand the relative importance of such drivers for specifc parasite systems.

#### **5.4 Conclusions and Synthesis**

Our study showed that arthropod insects, protozoa, and viruses are the main parasite groups being studied in birds across the Neotropical region. Although bacteria and fungi have been less studied, the potential for these parasites to produce diseases in avian populations should not be overlooked. Most of the published information regarding parasite ecology in Neotropical birds has been directed to the order Passeriformes, mainly because of its high number of species and because there is a sampling bias for passerine birds when using understory mist nets. This has allowed in-depth knowledge of parasite dynamics within some passerine populations (e.g., West Nile virus infecting American robins); however, the diversity and distribution of avian parasites among nonpasserine birds remains scarce, and it is an area of opportunity to advance the feld. Our data showed that parasite species richness was higher in Brazil, Argentina, Colombia, Peru, and Chile than in the other analyzed Neotropical countries. This was certainly associated with the high bird species richness that these countries harbor, and it should also be associated with the high number of studies that we retrieved for those countries. The low parasite and bird species richness that was observed for countries, such as the Dominican Republic, Guatemala, Bolivia, and Uruguay, is likely explained by the few studies that we found, suggesting that parasite surveillance and scientifc publication in these countries is insuffcient. The lack of studies focusing on avian disease ecology in Neotropical islands (e.g., Cuba, Jamaica, Haiti, Puerto Rico; but see (Parker [2018](#page-32-17)) for synthesis of disease ecology research in the Galápagos Islands) underscores the need to focus our scientifc research on parasite dynamics of endemic insular avifauna.

We identifed several anthropogenic and ecological factors affecting parasite prevalence and diversity across space. However, our synthesis did not include all relevant factors that could potentially drive parasite diversity and distribution (e.g., host-associated factors such as life-history traits). Although we showed that the diversity and distribution of some Neotropical avian parasites have been thoroughly assessed concerning anthropogenic and ecological drivers (e.g., avian haemosporidians), most parasite systems remain understudied in the Neotropical region (i.e., their presence in avian hosts is not assessed as a function of relevant drivers of disease), and their diversity is yet to be uncovered (Fernandez Correa et al. [2019](#page-30-16)). We underscore the large knowledge gap when considering the temporal aspect of

disease ecology (e.g., Rubio et al. [2017](#page-33-15)). Future research efforts should focus on determining how the temporal component (e.g., variation across the day and across seasons or months) (Castro-Arellano et al. [2010](#page-29-15)) affects the ecological dynamics of host-parasite systems.

## **Appendix A: Supplementary Data**

First search	
General overview of parasite groups	((virus* OR bacteria* OR protozoa* OR *parasite* OR fungi* OR disease*) AND (birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry))
Second search	
Anthropogenic factors/ parasite groups	(birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) AND (fragmentation OR land use OR landscape OR urban*OR habitat perturbation) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry) AND (virus*)
	(birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) AND (fragmentation OR land use OR landscape OR urban*OR habitat perturbation) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry) AND (bacteria*)
	(birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) AND (fragmentation OR land use OR landscape OR urban*OR habitat perturbation) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry) AND (fungi* OR fungus)
	(birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) AND (fragmentation OR land use OR landscape OR urban*OR habitat perturbation) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry) AND (protista OR protozoa*)
	(birds OR avian OR aves OR avifauna) AND (neotropic* OR South America OR Latin America) AND (fragmentation OR land use OR landscape OR urban*OR habitat perturbation) NOT (review* OR laboratory OR experiment*) NOT (zoos OR captivity OR domestic OR poultry) AND (Arthropoda OR Platyhelminthes OR Nematoda OR Rotifera)

<span id="page-26-0"></span>Table 5.4 Boolean codes used for our first, second, and third searches



**Table 5.4** (continued)





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