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REVIEW ARTICLE

Ecology and Evolution of Avian Malaria: Implications of Land Use Changes and Climate Change on Disease Dynamics

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Abstract | Malaria is the deadliest of all mosquito-borne diseases. Thousands of malaria parasite species exploit squamate reptiles, birds, and mammals as vertebrate hosts as well as dipteran vectors. Among these, avian malaria and related parasites have revealed an extensive genetic diversity as well as phenotypic diversity with varying virulence, host range, distribution—offering an amenable experimental system which has played a key role in understanding the ecology and evolution of human malaria parasites. Since its discovery in 1885, avian malaria contributed a great deal to the success of the U.S. antimalarial program during World War II. From modelling the links between climate change and health from a conservation and public health perspectives, avian malaria offered new opportunities and a relatively tractable system which were otherwise diluted by socio-economic, vector control and infra-structural changes in the human malaria context. In this review, I highlight the importance of avian malaria research in understanding the influence of climate change, land use and deforestation on disease dynamics, and how this helps to understand the ecology and evolution of the disease both from human and wildlife perspectives.

Keywords: *Climate change, Habitat loss, Malaria, Mosquito, Plasmodium*

1 Introduction

One hundred and thirty-six years have elapsed since the discovery of malaria parasites in birds and even today avian malaria has remained a popular model system for exploring the selection pressures shaping the ecology and evolution of both the host and parasite—advancing the research on human malaria.

In 1880, Charles Louis Alphonse Laveran discovered gametocytes (the infective stage) circulating in the peripheral blood of human patients. Subsequently, Danilewsky in 1884 in Ukraine discovered the presence of intracellular malaria-like parasites in infected birds. Most importantly, this was the first investigation which showed a pathological effect of these parasites on their avian hosts in a similar fashion to the pathological effects caused by malaria parasites in humans[1]. In 1898, Ronald Ross demonstrated for the first time in India that mosquitoes could serve as an intermediate host for bird malaria. He carried out controlled experiments in *Plasmodium relictum*-infected *Culex* mosquitoes to demonstrate the complete life cycle ending as sporozoites in the salivary glands of the mosquitoes and succeeded in transmitting this infection via mosquito-bites to healthy birds[2]. Since then, avian malaria has been the oldest experimental system for investigating the biology and transmission mechanism of *Plasmodium* parasites.

By 1940, avian malaria and related hematozoa were classified into three genera of haemosporidians parasites—*Plasmodium, Haemoproteus* and *Leucocytozoon*. These parasites are transmitted by dipteran insects, e.g., mosquitoes (*Plasmodium*), biting midges or hippoboscid flies

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(*Haemoproteus*), and black flies (*Leucocytozoon*)[3]. With a combination of microscopy and molecular techniques, a huge amount of genetic diversity, which corresponds with phenotypic diversity, revealed that these parasites are more ubiquitous and cosmopolitan (except Antarctica)[4] than the other vertebrate malarias. To date, over 3600 unique parasite lineages have been identified based on variation in cytochrome *b* (*cytb*) gene [see MalAvi database,[5]]. The extensive diversity and distribution of avian blood parasites provided vast opportunities for exploring evolutionary and ecological questions related to speciation[6], co-evolution[7, 8], life-history trade-offs[9, 10], the evolution of virulence[11, 12], sexual selection[13], competition and community structure[14–16], enemy release hypothesis[17, 18], biogeographical patterns[19], and climate change[20, 21].

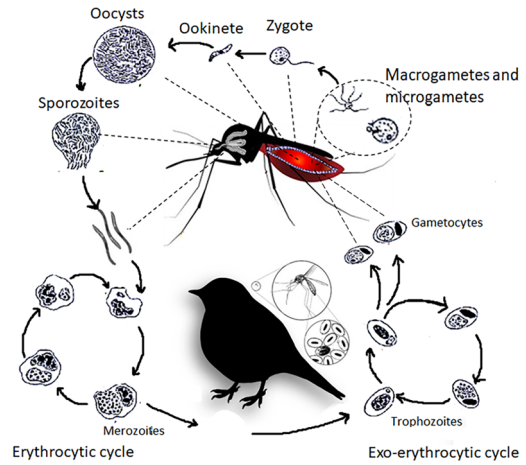

Figure 1: Life cycle of Avian *Plasmodium* in vertebrate and invertebrate hosts.

1.1 Parasite Biology and Transmission Dynamics

In general, the biology of haemosporidians is driven by many ecological (season, habitat, vector dynamic, host diversity), life-history traits (host migration strategy), physiology (hypoxia) and abiotic factors (temperature, humidity, rainfall). The transmission dynamics of malaria parasites hinges upon three main factors: (i) presence of competent arthropod vector, (ii) mature parasite stages in their host, (iii) conducive environmental conditions to transmit the parasite to a susceptible host in a limited time period. For example, the extrinsic incubation period (EIP) of *Plasmodium* is dependent on temperature and generally takes 8–14 days to develop, so most adult mosquitoes are likely to die before the age at which they could potentially transmit the parasites[22–24].

In general, the life cycle of avian malaria (*Plasmodium*) parasites has two main phases—the sexual phase inside the arthropod vector and the asexual phase inside the vertebrate host. The life cycle in the avian host for all genera can be divided into erythrocytic and exoerythrocytic stages[4]. The presence of gametocytes is the key parameter to ascertain the host competency and infective stage of the parasite in bird, whereas the presence of sporozoites in salivary glands of arthropod vectors defines them as competent vectors (Fig. 1). Therefore, to determine the true species composition of the haemosporidians in each naturally infected individual host, a combination of both microscopy and molecular methods is important[4]. Furthermore, molecular methods combined with microscopy revealed that malaria parasites are virulent in birds due to the exo-erythrocytic development in various organs which can cause extensive damage and abortive development in non-adapted avian hosts (e.g., penguins)[25].

The dynamics of parasitemia of malaria parasites in bird goes through an acute (high parasitemia) phase of infection followed by a later chronic phase (low parasitemia). In the acute phase of infection, parasitemia increases steadily to a peak, approximately 6–12 days after parasites first appear in the blood. After this acute phase, intensity appears to be influenced by the complex interplay of host immunity, seasonal photoperiod, and hormones associated with reproduction (Fig. 2). During the acute phase of infection, anemic birds are more vulnerable to indirect mortality due to environmental stressors such as predation, starvation, or inclement weather[26]. In birds that survive the infection, the acute phase is followed by a decline in the intensity of parasitemia to chronic levels—chronic infections can persist for the lifetime of infected birds at low intensities and serve as a source for recrudescing infections[27, 28].

In temperate regions, birds with latent (chronic) infections experience a spring relapse (recrudescence) with an increase in parasite numbers visible in the blood stages[29]. Breeding is the most physiologically stressful period of the annual cycle when increased corticosterone levels suppress the immune system, thereby increasing the chances of a new infection or causing a relapse of a pre-existing infection[30, 31]. Recrudescence (from exo-erythrocytic latent parasite stages) of chronic infections is believed to facilitate seasonal transmission in temperate climates

Parasitemia: The ratio between infected and non-infected red blood cells, is a measure for the quantity of parasites in a host's peripheral blood and thus, of the severity of infection.

Extrinsic Incubation Period (EIP): The parasite development period inside the mosquito before the parasite is transmissible.

Recrudescence: Increase in parasitemia from the multiplication of persistent circulating blood stages.

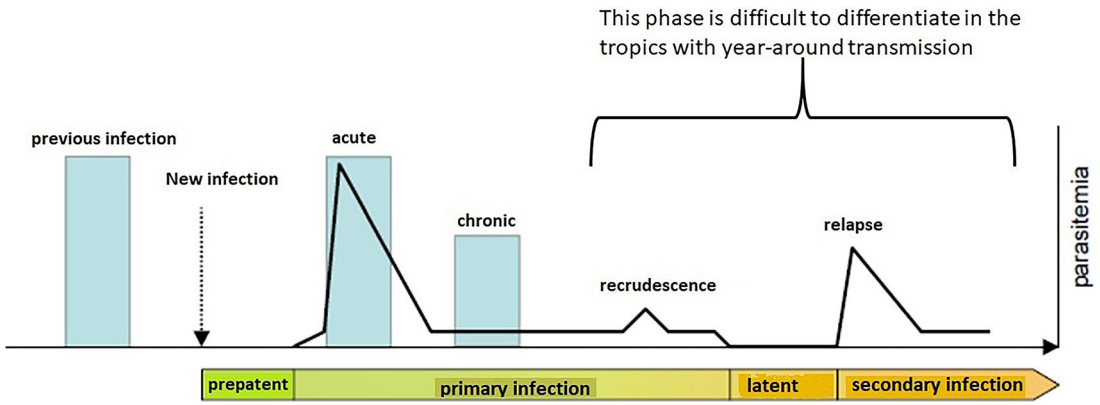

Figure 2: Dynamics of parasitemia in bird blood.

where the time of vector emergence coincides with breeding birds. However, vector competence and vector-parasite specificity do not allow all parasite lineages to be easily transmitted across regions. For example, in Europe, the absence of some lineages of *P. relictum* in hatch-year birds indicates that transmission occurs on the wintering rather than the breeding grounds[32]. This further implies that haemosporidian prevalence and the diversity of parasites vary significantly across the annual cycle—with bimodal patterns of spring and autumn infection peaks followed by marked decreases in prevalence during winters[33, 34]. In contrast, tropical climates facilitate the transmission of parasites throughout the year[35] and it is difficult to distinguish between relapse and recrudescence.

1.2 Ecology and Conservation Biology of Avian Malaria

Avian malaria and related parasites can have significant negative effects on host survival and longevity[36], reproductive success and body condition[37, 38]. Avian haemosporidians have been endemic to the tropics for millions of years, and birds and parasites have co-evolved and engaged in arms races in most parts of the world. These associations have led to close correlations between virulence traits of pathogen strains (or species) and the host's resistance genes, finally leading to diversification and balancing selection on both virulence and resistance genes i.e., Major Histocompatibility Complex (MHC;[39]). O'Connor et al.[40] showed how pathogens drive the evolution of migration strategies – the selection on immune genes in species varies between high pathogen areas (wintering grounds) to low pathogen areas (pathogen escape/release) and thereby response to novel virulent parasites (pathogen exposure) influencing selection regimes on diverse immune genes[41].

Whilst an emerging disease only occurs when the hosts are highly susceptible, there are two main scenarios in which a parasite is likely to have such an impact that a disease reaches epidemic proportions. First, the introduction of a parasite to a new geographic area upon host introduction and host colonization, when such co-evolved parasites subsequently invade a naive individual, they can be extremely virulent due to the lack of an evolved immune response of the new host to this parasite[42]. For example, the introduction of *Plasmodium relictum* to the Hawaiian Islands resulted in a catastrophic decline in the endemic avifauna[43, 44]. Avian malaria became a serious threat for Hawaiian honeycreepers when the mosquito vector *Culex quinquefasciatus* was introduced in the early twentieth century[43, 45]. Prevalence of infection and of parasitemia were high in honeycreepers, and the infection induced a substantial drop in body mass and hematocrit and finally a high mortality[44, 46], which almost resulted in the extinction of honeycreeper populations in lowland areas. Nowadays, populations of one of the honeycreepers, the amakihi (*Hemignathus virens*), have recovered in number but still suffer from high malaria prevalence (24–40% if estimated by microscopy, 55–83% if estimated by serology)[47].

Second, due to adaptation or mutation, a parasite can gain increased virulence. In addition, a change in abiotic factors can affect the equilibrium of the host and parasite. A change in climate may result in a longer transmission season to which birds might not be able to adapt quickly enough. In addition, new climatic conditions might result in the spread of the parasites,

Hematocrit: The proportion of red blood cells in blood.

where they encounter new and possibly susceptible naive hosts. It is difficult to predict whether avian malaria should be considered as a threat of an emerging infectious disease for many populations, however, isolated populations that have evolved without these parasites (e.g., endemic Hawaiian birds or avifauna in malaria-free zones) can be particularly vulnerable to climate change. Nonetheless, avian malaria model is an excellent model system to understand to evaluate the effect of climate, habitat and host diversity on the range expansion of the disease.

1.3 Climate Change

The impact of climate on disease epidemiology, vector range expansion and host diversity patterns has been explored primarily in three main ways: (a) latitudinal gradients, (b) ecological gradients, (c) bird, vector and parasite phenologies.

(a) Latitudinal gradient

The latitudinal gradient is central in ecology in defining species diversity and distribution over a large spatial scale with variable climatic factors explaining biotic interactions. As a generality of the pattern, the number of plant and animal species declines as one moves away from the equator[48–50]. This pattern holds for parasite and infectious diseases suggesting that similar mechanism and ecological factors drive pathogen distributions[51]. In this context, the maximum range of precipitation is the best predictor of pathogen and disease distribution – the pathogen species, their vectors or hosts tend to be adapted to tropical regions with a range of contrasting wet and dry conditions throughout the year. Several studies showed this pattern with a low prevalence of blood parasites in birds from polar areas as compared with prevalence at other latitudes[52–54]. Based on the empirical data, Loiseau et al.[53] predicted habitat suitability for *Plasmodium* under a global-warming scenario in Alaska. A similar pattern has been explored at a local scale, Loiseau et al.[55] investigated whether variation in environmental variables account for spatial variation in malaria (*Plasmodium relictum*) in House sparrows (*Passer domesticus*) in France. Based on the empirical data it was suggested that the mean diurnal and temperature seasonality range will increase in the future and lead to a higher prevalence of avian malaria in this region. In contrast, based on a global dataset, Clark et al.[56] showed no evidence of latitudinal gradient in avian haemosporidians. Fecchio et al.[57] found an inverse latitudinal gradient in New World birds by showing that the probability of decrease in diversity and prevalence of *Leucocytozoon* parasites with an increase in temperature. A similar pattern was shown in Western Palaearctic birds with *Leucocytozoon* diversity increasing towards the poles whereas *Haemoproteus* diversity increasing towards the equator in regions with higher vegetation density [58].

(b) Ecological gradient

Analogous to the latitudinal gradient in species richness, species richness declines with an increase in elevation due to decreases in temperature and a consequent decrease in productivity[59, 60]. Temperature is the key driver of mosquito population dynamics and parasite transmission intensity[23]. Simulations based on surveillance studies in human malaria suggest that human-induced climate change may alter both the geographic range and local abundance of malaria pathogens. Most importantly, the parasites depend on the abundance and distribution of arthropod vectors, which seem to respond sensitively to global warming[23, 61]. In Africa, where average temperatures are expected to increase between 3 °C and 4 °C by 2100 (roughly 1.5 times the global mean response[61], hotspots for human malaria risk are predicted to shift toward higher elevations and to increase the relative burdens of dengue fever over malaria across the Sub-Saharan region[62]. As the environment changes, some habitats that are currently too cool to sustain vector populations may become more favourable, whereas others that are drying may become less conducive to vector reproduction. Therefore, the geographic ranges of mosquitoes may expand or be reduced, which may cause parallel changes in the population of malaria pathogens they transmit. Additionally, a slim rise in ambient temperature and rainfall can also extend locally the breeding season of mosquitoes[63, 64]. Such expansion also increases the time window of malaria transmission resulting in a larger number of generations of parasites per year that can positively affect parasite abundance[34]. Finally, the dynamics and distribution of malaria are strongly determined by climatic factors[65]. There is substantial evidence from studies of human, as well as avian malaria that the development of *Plasmodium* parasites within mosquitoes is exquisitely temperature-sensitive[66]. Malaria pathogens may themselves benefit from increased temperatures,

as the incubation period of human *Plasmodium* within the mosquito is highly sensitive to temperature and below 15 °C, their development is completely blocked[23, 67]. Similarly, in Hawaii, the threshold temperature for transmission of avian *Plasmodium relictum* has been estimated to be 13 °C, whereas peak *Plasmodium* prevalence in *Culex quinquefasciatus* occurs in mid-elevation forests where the mean ambient summer temperature is 17 °C[20]. Therefore, there is no malaria transmission in high-elevation forests due to low mosquito abundance, and temperatures not conducive to parasite development. To understand the ecology and transmission risk of malaria, there is a need for higher resolution studies of environmental and biological data. Contemporary surveillance studies in Hawaii have revealed that malaria patterns in native island birds are influenced by global warming[68–70]. Warming climate is expanding the optimal habitat range for malaria-transmitting mosquitoes, thereby increasing the threat posed by avian malaria (*Plasmodium* spp.) to endemic hosts that have evolved without adaptive immunity [e.g., Hawaii;[68]. Nearly 7% of globally threatened bird species have declined due to avian malaria[71]. However, except for this limited endemic case, the consequences of environmental changes for the prevalence and distribution of avian malaria at the global level remain obscure. There is a lack of quantitative studies which has limited our capacity to understand and predict these changes in other threatened ecosystems.

Montane species have evolved physiological strategies to cope with changing seasonal demands (e.g., haematological adaptations with change in oxygen pressure with high altitude)[72], to exploit food resources and to escape parasites[73]. Mountain ecosystems are especially vulnerable to climate change and provide an excellent model system to understand the prevalence, distribution, and species turnover in parasite diversity as a function of temperature. In this context, many studies have shown that the prevalence of *Plasmodium* and *Haemoproteus* parasites decreases with increasing elevation[74–76] but see[77]. However, *Leucocytozoon* prevalence and diversity increases with elevation. *Leucocytozoon* is the only genus recorded above 2100 m in Neotropical region and Western Himalayas[76, 78]. These results corroborate finding from other studies in Switzerland[75] and Peru[79]. Furthermore, there was a high turnover in *Leucocytozoon* lineages with altitude[79]. Temperature and presence of competent vector species are key drivers that determine parasite transmission intensity. *Leucocytozoon* spp. are transmitted by blackflies (simuliids) which breed in clear stream waters and can thus increase in parasite prevalence within a cool environment.

Using Briere parametrization of the EIP and Bayesian parameter inference, Mozzaffer et al.[80] described how year-round parasite transmission is influenced by temperature variations in the western Himalaya by showing that high elevation sites (2600–3200 m) do not support human *Plasmodium* development throughout the year. Temperature conditions are not conducive to avian *Plasmodium* transmission from September to April at 2600 m and throughout the year at 3200 m. Using climate models, we predicted that by 2050, high elevation sites (above 2600 m) will have a temperature range conducive for malaria transmission[80].

These studies on the effects of climate change on the avian blood parasite have significantly contributed to our understanding of the impacts of changing environmental conditions on disease ecology[67]. With human malaria, vector control and human movements can mask climate effects, making it difficult to tease apart which are the variables that determine and constrain the distribution of arthropod vectors.

Bird migration phenology, vector emergence and parasite biology

Annual migration is common across animal taxa. Migration phenology shapes the patterns in disease transmission in many ways—(i) migration facilitates the geographical spread of pathogens, ii) migration exposes a host to multiple habitats, thereby enabling interactions between a diverse set of host species and pathogens [e.g.,[32]], (ii) long-distance movement is energetically demanding and migration can have a culling effect by removing infected individuals (migratory culling)[81], thus reducing the infection risk or by interrupting pathogen transmission for part of the year (migratory escape). Accelerating changes in climate, reflected in temporal changes of temperature, precipitation, and seasons, are shifting the migration phenology, vector population dynamics and disease transmission in new regions, either by disrupting or bridging novel host-parasite interactions[67].

In general, haemosporidian prevalence and diversity of parasites vary significantly across the annual cycle[82, 83]. Given the diversity of parasite lineages identified in birds, the specific temporal patterns vary across parasite lineages[82], host

Migration: Regular, seasonal movement of an animal population to and from a given area.

Phenology: Study of the timing of life cycle events at the population level, most often focusing on responses to climate change. It often makes use of long-term records and includes events such as flowering, leaf fall, hatching and annual migration.

Vector: an organism that spreads infection by transmitting pathogens from one host to another.

populations,[84] and migration strategies[42]. These findings highlight that different parasite lineages have evolved different transmission strategies, which, in turn, are influenced by the presence of compatible vector species. Thus, mismatches in vector emergence and timing at stopover points could also lead to an absence of shared parasite lineages between migrant and resident birds[82–84].

The empirical research considers breeding success as a parameter to evaluate the impact of pathogens at the population level [e.g., [85, 86]] but does not evaluate how parasitism negatively influences bird migration [but see[87]]. Depending on the parasite biology, infection with certain parasite genera can be detrimental to a host species. Most studies do not quantify the parasitemia and degree of anemia in migrants during migration routes. In addition, poor diet and habitat quality influences body condition and thereby increases susceptibility to disease, so individuals with better body conditions can develop effective immune responses[88, 89]. Large fat reserves and good body condition are key parameters for migratory behaviour and are often compromised in immune-challenged birds leading to delayed migration, reduced migration speed and higher mortality[90–93]. Møller et al.[94] showed the spring arrival date to the breeding grounds in barn swallows (*Hirundo rustica*) is predicted by parasite intensity. Early arriving males usually gain access to superior habitat, mates thereby having much higher reproductive success than average individuals[91].

Temperature is considered as the main driver for vector emergence and spring phenology. The overlap in the phenology of parasites and vectors produces spring relapses and new infections in breeding host populations[92]. Generally, mosquito-borne pathogens rely on frequency-dependent transmission where abundance, community composition and their contact rates govern the parasite transmission[95]. Vector phenology and abundance are mainly driven by ambient temperatures that trigger larval development[96] and precipitation that provides egg-laying opportunities. However, vector populations respond non-linearly to both temperature and precipitation, e.g., increasing temperatures and precipitation favour reproduction and may result in higher abundances, but this will be reversed when exceeding the thermal optimum or a precipitation threshold[97].

Understanding how environmental variables influence the abundance and distribution of mosquitoes is a key issue in disease ecology, as these are crucial for determining distribution, incidence and dynamics of vector-borne diseases. Insects are among the groups of organisms most likely to be affected by climate change because the climate has a particularly strong direct influence on their development, reproduction, and survival[98–100]. There are currently no studies undertaken to understand the influence of environmental factors on vector phenology and abundance and what changes in the vectors' distribution ranges are expected with climate change.

1.4 Land Use Changes and Deforestation

Anthropogenic modification (e.g., fragmentation, tree cover loss, edge effects) of the ecosystem has greatly influenced the spatial distribution of hosts and vectors, likely impacting disease transmission dynamics[101]. Land use change for agriculture is the largest driver of land cover change across the globe[102].

The prevalence and diversity of avian blood parasites in free-living host species in the tropics has shown contrasting patterns in altered landscapes. Whilst the effect of habitat fragmentation on the prevalence of avian haemosporidians has remained inconclusive across regions and is largely context-dependent and difficult to generalize, it is evident that these patterns are driven by deforestation, change in temperature and community structure of arthropod vectors[103]. For example, mosquitoes are the most sensitive insects to habitat degradation, change in land-cover factors are known to influence the spatial distribution of mosquito and alter the intensity, seasonality, incidence and geographic range of malaria transmission[103].

Empirical studies show a variable pattern in parasite prevalence with forest disturbance – Bonneaud et al.[104] found an increase in *Plasmodium* prevalence in intact forested areas compared to deforested areas in Cameroon. Loiseau et al.[105] reported a decrease in parasite prevalence with increased forest fragmentation in Ghana. Tchoumbou et al.[106] recently found that selective logging favoured an increase in the prevalence of *Plasmodium* in insectivores. Similarly, several studies have shown no effect of habitat degradation on haemosporidian prevalence [e.g., [107, 108]]. Gonzalez-Quevedo et al.[109] found that temperature and the distance to artificial water bodies were related both positively and negatively to avian malaria. Ferraguti et al.[110] reported a positive relationship between the distance to man-made water reservoirs with the prevalence and diversity of *Plasmodium* parasites in the house

sparrow. Sehgal et al.[111] found across different habitat types (i.e., primary forest, secondary forest, ecotone), that temperature was the most important abiotic factor related to an increase in avian malaria prevalence.

Spatial heterogeneity in infection probability *may* change in response not only to environmental filters but also to changing host species distributions that provide new ecological opportunities for a parasite to expand its host range and increase its local prevalence[112]. Land use change and seasonality can have a strong influence on vector composition and abundance, enabling the spread of vector species into previously uninhabitable areas—tropical deforested habitats are more open and warmer than primary forests[113], which may increase the survival and growth rates of mosquito larvae[114, 115]. In general, disturbed habitats harbour generalist parasite lineages and are associated with a high spillover risk of zoonotic disease transmission in regions experiencing land-use changes[116, 117]. For avian haemosporidians, the parasite community composition is driven by host species assemblages in disturbed habitats which facilitates the phylogenetic host specificity by infecting closely related species. Menzies et al.[108] found parasite diversity showed a positive association with host abundance in logged habitat suggesting that altered habitats are supporting higher local densities of several insectivorous bird species as well as high parasite diversity. Furthermore, disturbed habitats support host-specific lineages and probably opportunities for parasites to shift to distantly related hosts are low and constrained by the limited niche. In contrast, undisturbed habitats support a broad community of host species which allows for parasite switching—the high avian diversity in undisturbed habitats could contribute to a dilution effect[112].

Similarly, urbanisation has severely altered host-parasite interactions by introducing new predators, competition, and pollution [e.g., [118]]. Urban greenspaces harbour higher parasite richness than their nonurban counterparts[119] a combination of increased temperature and water availability at the micro-habitat level supports vectors which facilitates year-round transmission of parasites[120]. Increases in parasite prevalence have also been shown to have a negative effect on the body condition of urban birds[121].

1.5 Future Perspectives

There is a long history of research on avian haemosporidians in the tropical regions which primarily focused on the prevalence and diversity of parasite genera with taxonomic descriptions[122, 123]. McClure et al.[124] conducted the largest survey of avian haemosporidians on the Indian sub-continent. Since then, using traditional microscopy and molecular methods, many studies provide snapshots of the prevalence and diversity of avian haemosporidians in the Indian sub-continent[125–128]. Despite common and abundant avian hosts and geographical variation, a major knowledge gap drives the need for longitudinal studies to understand the spatio-temporal patterns in epidemiology of avian haematozoa. Our understanding of within-host processes and epidemiological dynamics in natural populations is currently hampered by a lack of longitudinal studies. Most studies on avian malaria parasites only provide snapshots of prevalence. Long-term datasets for host–pathogen systems are a rare and valuable resource for understanding the infectious disease dynamics in wildlife. In the Indian context, we had a handful of studies exploring how the parasite diversity is shaped by geography and host species resulting in generalist and specialist parasite community in a tropical sky-island[127]. Menzies et al.[108] explored similar patterns in relation to habitat quality by showing that primary forest plots accumulate generalist parasite lineages. We need fine-scale studies to understand the relationship between avian malaria and habitat degradation in shaping parasite and vector communities on bird populations. Insects are among the groups of organisms most likely to be affected by climate change because the climate has a particularly strong direct influence on their development, reproduction, and survival[98]. There are currently no studies undertaken to understand the influence of environmental factors on vector phenology and abundance and what changes in the vectors' distribution ranges are expected with climate change.

Most ecological studies are biased towards single pathogens specialising on a single host species[129]. To advance our predictive power in disease modelling and to understand the complexities of infection dynamics, we need longitudinal studies and data on multi-host and multi-pathogen systems[130]. Many modelling studies have explored mechanisms of directly transmitted disease in migrants[131], and the effects of climate change on host migration[132]. Until now, models have not been developed that utilise empirical data to explore climate-driven effects on the host and vector distributions and

phenology. Understanding how environmental variables influence the abundance and distribution of mosquitoes is a key issue in disease ecology, as these are crucial for determining distribution, incidence and dynamics of vector-borne diseases.

Using longitudinal studies and mathematical modelling as a tool, on multiple birds, vectors and parasites, will generate essential data needed to understand the mechanism of malaria dynamics which will enable predictions of the future spread of disease that is of relevance from both a conservation and public health perspective.

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Code Availability

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Conflict of Interest

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Consent to Participate.

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