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CHAPTER 11

Host specialization and dispersal in avian haemosporidians

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Abstract In order to be able to understand the ecological and evolutionary processes involved in the emergence of infectious diseases, one needs to comprehend how parasites arrive at new geographical ranges and how they manage to maintain viable populations and even expand their ranges. We discuss host specificity in avian haemosporidians and how encounter and compatibility filters affect the dispersal of avian haemosporidians, and how these filters affect avian haemosporidian assemblages at different spatial and evolutionary scales. There are at least three important barriers to the dispersal of avian haemosporidians: (i) geographic barriers, (ii) environmental barriers and, (iii) interspecies barriers. In this chapter, we discuss the factors involved in these barriers and their effects on the structure of avian haemosporidian assemblages. Host specificity plays an important role in parasite dispersal, and in the case of avian haemosporidians that are vector-borne parasites, it needs to be evaluated both at the vector and bird host level. Understanding the effects of these factors on host-vector-parasite dynamics is important to unravel the dispersal and diversification mechanisms of avian haemosporidians. We end this chapter reviewing host specialization in avian haemosporidians of tropical regions, discussing the mechanisms involved in the

dispersal and specialisation of these parasites and point out important research gaps that need attention.

Keywords: host specificity, compatibility filter, encounter filter, parasite community assembly, host shifting, phylogenetic barriers, environmental barriers

11.1 Introduction

How do parasites arrive and establish themselves in new geographic locations? This is a very important question to be answered because of the increase in the emergence of infectious diseases (Jones et al. 2008). In order to answer this question, one needs to identify the barriers involved in the dispersal and establishment of parasites, how these barriers affect parasite community assembly and how these barriers affect **host shifts** (Combes 1991; Clark et al. 2018). More importantly, one needs to understand how these barriers work at different scales. For example, how does **host specificity** affect the establishment of novel parasite populations in newly colonized areas? Or how do hosts' life history strategies affect the maintenance of a parasite population within a given area?

Clark et al. (2018) identified three important barriers for avian haemosporidian dispersal: (i) **geographic barriers** (e.g., distance between regions, presence of mountain ranges, presence of water barriers or even scarcity of water between regions); (ii) **environmental barriers** (e.g., temperature and precipitation gradients, habitat differences between regions) and; (iii) **interspecies barriers** (e.g., ecological similarity of hosts, immunological similarity of hosts, phylogenetic relatedness of hosts, specificity of vertebrate host-vector relationships). These barriers work at different scales, with geographic and environmental barriers working at larger scales, while interspecies barriers will act at both local and regional scales (Fig. 11.1). At the local scale, diverse ecological communities could

reduce the spread of avian haemosporidians due to a **dilution effect** (Civitello et al. 2015), a hypothesis that has yet to be formally tested for avian haemosporidian parasites. For example, if vectors are not host specific, then encounter rates with the bird host could be reduced because of the large presence of other bird species that are incompatible hosts (Fig. 11.1c), a circumstance that may be particularly promoted by competition in highly diverse avian communities, where the abundance of compatible bird hosts could be reduced leading to a reduction in parasite abundance (Keesing et al. 2006; Civitello et al. 2015). However, if avian haemosporidians are capable of infecting a broad range of bird species (i.e., host generalists), then the dilution effect will be reduced (Fig 11.1b), and depending on the avian assemblage abundance structure an **amplification effect** is possible. Therefore, a specialized parasite lineage dispersing to a new location with a diverse host community might be less likely to encounter its host and persist than a generalist parasite (e.g., metacommunity dynamics; Suzán et al. 2015).

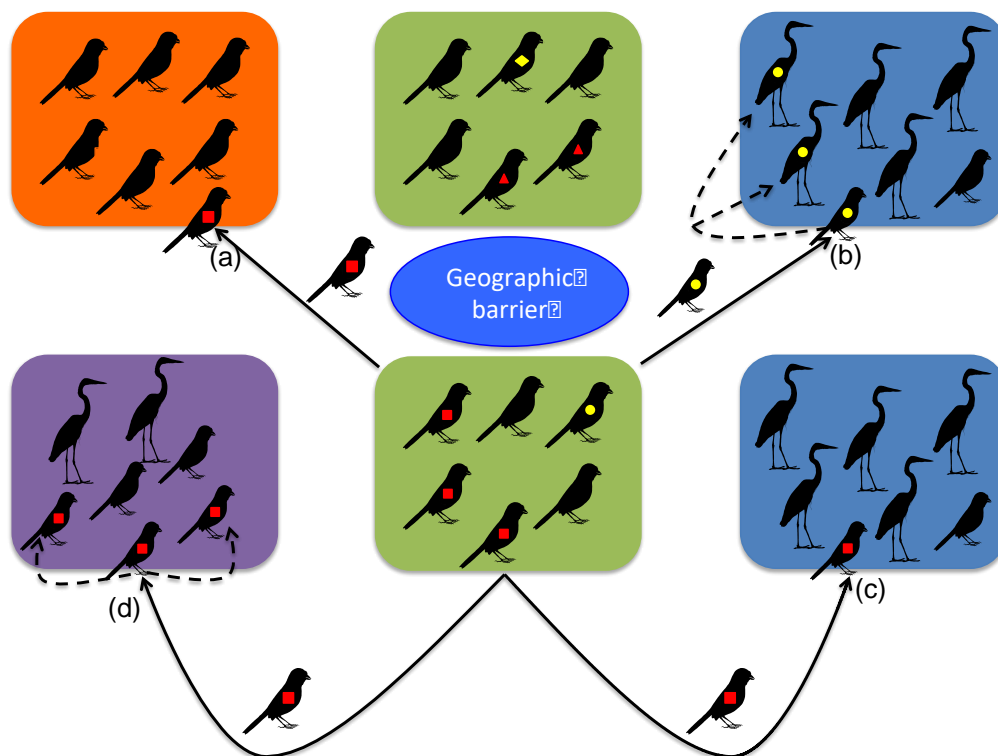


Fig. 11.1 The green communities are phylogenetically similar. However, because of a geographic barrier (e.g., water barrier), each community has its own avian haemosporidian lineages (represented by red squares, yellow circles, red triangles, and yellow diamond). The lines show dispersal of infected birds into novel communities and dashed lines when avian haemosporidians establish themselves in the novel community. Coloured rectangles represent communities that are environmentally similar. Avian haemosporidians can fail to colonize a novel community because of environmental barriers, such as lower precipitation in the novel community (a). Avian haemosporidians will also fail to colonize a novel community due to the interspecies barrier and a potential dilution effect because there will be a higher abundance of non-host species (c). However, avian haemosporidians are capable of shifting hosts when lineages are host generalist or re-encounter previously compatible host species (b). Colonization of novel communities by avian haemosporidians will be more likely to occur when the novel community presents phylogenetically similar hosts (i.e., ecological fitting) reducing the species barrier (d). Figure is adapted from Clark et al. (2018). Gabriel L. M. Rosa designed bird silhouettes.

Host specificity measures the degree of specialization of a parasite, and is inversely proportional to the number and diversity of host species it can infect (Poulin 2007). In the case of avian haemosporidians (i.e., vector-borne parasites), host specificity applies to both birds and dipteran vectors. According to Combes (1991), two filters should determine the distribution of parasites: (i) an **encounter filter** and (ii) a **compatibility filter**. Vectors will determine the bird hosts that avian haemosporidians will encounter among those available in the local parasite community (Fig. 11.2a). In general, there seems to be a vector-family specificity in avian haemosporidians (Valkiūnas 2005; Santiago-Alarcon et al. 2012a). However, blood-sucking dipterans can present plastic feeding behaviour that extends across

different vertebrate groups (Santiago-Alarcon et al. 2012a,b; Santiago-Alarcon et al. 2013; Pettersson et al. 2013; see Chaps. 5 and 6 for a thorough description of blood sucking dipteran vectors and a synthesis of research on vectors involved in the **transmission** of avian haemosporidians across tropical regions). This behaviour can lead to host shifts in birds when avian haemosporidians encounter other suitable hosts, influencing the distribution of parasites in a local community (Santiago-Alarcon et al. 2013). Conversely, vectors will influence the structure of parasite-host associations if they feed on a limited range of host species, which will restrict transmission of parasites to potentially suitable hosts (Hellgren et al. 2008; Malmqvist et al. 2004). Therefore, vectors may serve as ecological barriers to transmission because vectors will determine the routes of infection (i.e., network of hosts that vectors feed on).

The compatibility filter is influenced by both vector and bird hosts (Valkiūnas 2011; Medeiros et al. 2013; Gutiérrez-López et al. 2016; Clark et al. 2018). Dipterans can present resistance towards avian haemosporidians (Fig. 11.2b), which restricts the parasite lineages that are capable of completing their life cycle within a vector (Santiago-Alarcon et al. 2012a; Valkiūnas et al. 2013). Avian hosts can also show resistance towards avian haemosporidian lineages (Westerdahl et al. 2012, 2013, Sarquis-Adamson and MacDougall-Shackleton 2016), which can be qualitative (i.e., prevents parasite infection) or quantitative (i.e., reduces infection effects). This compatibility filter at the avian hosts will also structure parasite-host associations (Fig. 11.2b). For example, if a vector feeds on a resistant avian host, the parasite may not be able to be further transmitted, especially if the avian host is capable of clearing the infection (Westerdahl et al. 2012). The complex life cycle of avian haemosporidians suggests that these parasites should be host generalist (Noble et al. 1989; Poulin 2007) because high host and vector specificity could lead to local parasite extinction when parasites face low population sizes of their specific vector or avian host species (for evidence of the

evolutionary stability of host specific vs generalist parasite strategies, see Pérez-Rodríguez et al. 2015, Ellis and Bensch 2018). Understanding these compatibility filters is important because host shifting is common in avian haemosporidians with little evidence of co-speciation (Ricklefs et al. 2014; Ellis et al. 2015; Nylin et al. 2018).

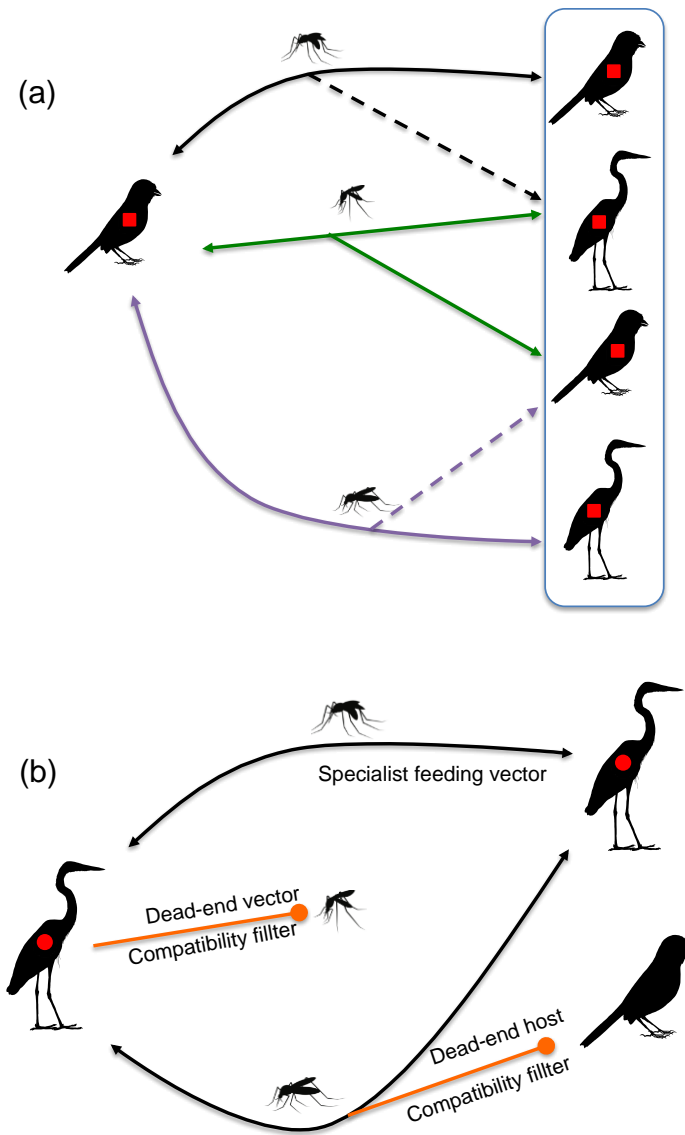


Fig. 11.2 Encounter (a) and compatibility (b) filters. In (a), each coloured line represents an infection pathway provided by a specific vector species. The blue rectangle represents the encounter filter, and dashed lines the avian hosts the vectors did not encounter. In (b), the compatibility filter (represented by the orange line), showing the possibility of a vector or

avian host acting as incompatible (dead-end) hosts (see **host compatibility** in the glossary) because of their resistance to the avian haemosporidian. Freepik designed Mosquito silhouettes, and Gabriel L. M. Rosa designed bird silhouettes.

11.2 Host specificity in avian haemosporidians

Highly specialized parasites are those that are restricted to a single host species, while generalist parasites are capable of infecting multiple taxa. However, categorizing a parasite as either specialist or generalist can be a difficult task. For example, if a parasite infects more than one host species within a genus, would it be considered a generalist? An alternative would be to quantify how phylogenetically distant hosts are (Poulin and Mouillot 2003; Hellgren et al. 2009; Clark and Clegg 2017), where generalist parasites would be those capable of infecting host species that are phylogenetically distant (e.g., infecting bird species from different orders). Also, it is important to consider how infection levels vary among the different host species being used. For example, parasites may have a main host species while infecting other host species at lower intensities or prevalence (Moens et al. 2016; Huang et al. 2018). Another important aspect to consider is the time scale of the processes involved in the host-parasite interaction. For example, recent adaptation to specific host attributes (such as its habitat niche) may be responsible for an increase in parasite compatibility (Clark and Clegg 2017; see Chap. 7 for an introduction to ecological niche modelling and its applications to host-parasite interactions). Conversely, ancient processes in the evolutionary history of a host-parasite interaction would cause ancestral habitat filtering. In the latter case, parasite success or failure in mechanisms such as adaptation to the host immune system and host dispersal could lead to the maintenance or loss of the parasite (Clark and Clegg 2017).

Therefore, host specificity is best seen on a gradient of host specialization that considers infection levels and prevalence (Moens et al. 2016; Huang et al. 2018).

The intensity of infection (or **parasitemia**) is difficult to measure (see below and Chap. 2 for a review of haemosporidian study methods), but an important attribute of the parasite that could lead to higher mosquito infection and an increase in parasite transmission (Cornet et al. 2014). It has been shown for *Plasmodium relictum* that mosquitos feeding during the acute phase of infection will have higher infection (Pigeault et al. 2015), which could lead to a higher transmission of this malaria parasite to other hosts. In accordance with this idea, it has also been shown that *Plasmodium relictum* will have higher within host parasitemia in the evening, which is when its vector *Culex pipiens* is most active (Pigeault et al. 2018). Moreover, *Plasmodium relictum* can react to the biting of uninfected vectors by increasing their replication within the host (i.e. higher parasitemia), which will lead to a better timing of replication with the presence of vectors, an important attribute in regions that have seasonal vector activity (Cornet et al. 2014; Pigeault et al. 2018). This is important because it shows that *Plasmodium relictum* during chronic infections can present flexibility regarding its replications that can lead to higher transmission of the parasite during chronic infections. Therefore, not only the prevalence of infections in a population will affect parasite dispersal, but also parasitemia within hosts can affect the dispersal of avian haemosporidians by the potential increase in the infection rate of vectors that could boost parasite transmission to other hosts.

Specialist parasites need to cope with fewer defence mechanisms (i.e., host species with different immune systems), which could make them more efficient at evading the hosts' immune system and allow them to efficiently replicate and transmit to other hosts (Poulin 1998). This more efficient performance should result in a greater infection rate (proportion of infected individuals – prevalence) and higher parasite intensity (number of parasites found in

an infected individual) within its host's population. Conversely, generalist parasites have to surpass different immune systems potentially reducing their replication and transmission rate (Hellgren et al. 2009). These ecological differences regarding host use can explain differences in parasite abundance and occupancy in local communities. According to the niche breadth hypothesis, generalist parasites will be more effective at colonizing different host communities allowing them to occupy larger distributional ranges when compared to specialist parasites (Drovetski et al. 2014). However, the trade-off hypothesis suggests that specialist parasites will trade **host range** for increased prevalence across the geographic range of their specific hosts. If these hosts have large distributional ranges, then specialist parasites will not only be locally abundant (i.e., highly prevalent), but will also be able to attain large distributional ranges themselves (Drovetski et al. 2014; Lima and Bensch 2014).

In vector-borne parasites, transmission to suboptimal or incompatible hosts may occur often, particularly in highly diverse bird communities such as in the Neotropical region (Civitello et al. 2015). In this case, generalist parasites might have a competitive edge because they will manage to increase their host encounter rate despite infecting suboptimal hosts (Keesing et al. 2006). For example, in a megadiverse forest in Ecuador, *Haemoproteus* lineages were considered to be more host generalist than *Haemoproteus* parasites of temperate forests (Moens and Pérez-Tris 2016). This is an interesting result because *Haemoproteus* lineages are usually considered host specific (Beadell et al. 2009; Hellgren et al. 2009; Olson-Pons et al. 2015; but see Ellis et al. 2015), but in the Neotropical region of South America, they show a more generalist pattern of host use (Belo et al. 2011; Svensson-Coelho et al. 2013; see Chap. 1 for a synthesis on avian haemosporidian research of the 20th century demonstrating that *Haemoproteus* are widespread and common across tropical avian assemblages). However, the Neotropical region is notorious for a large number of single lineage recoveries within communities (Lacorte et al. 2013, Fecchio et al. 2018a), which is

indicative of unsampled parasite diversity. Further research with increased sampling effort is needed to clarify whether these parasites are specific of single host species (which would somewhat contradict the expected low specialization of parasites in regions of high avian diversity), or whether they are rare but host generalist parasites.

At a local scale, the prevalence of avian haemosporidians can be associated with host abundance (at least at the parasite community level; Ellis et al. 2017), and both specialist and generalist avian haemosporidians can infect a similar number of individual hosts (Medeiros et al. 2014). Although a reduction in the number of compatible host species should reduce transmission and overall parasite prevalence - because the encounter of uninfected vectors with infected individuals will be reduced (Keesing et al. 2006) -, specialist avian haemosporidians could reach higher prevalence on their specific hosts when compared with generalist avian haemosporidians on those same hosts (Medeiros et al. 2014). Also, recent data suggests that even generalist parasites will fair better in a set of main host species (Huang et al. 2018), indicating that prevalence and infection intensity will vary on a host-by-host basis, further contributing to the continuous nature of parasite specificity. However, one of the difficulties in understanding these trade-offs is determining the intensity of infection (i.e., the number of individual parasites infecting a host), which is usually done using either microscopy or qPCR (Asghar et al. 2011, Ishtiaq et al. 2017, Huang et al. 2018). The use of microscopy is rather challenging because blood smears need to be of high quality and evaluated by experienced personnel (Valkiūnas et al. 2008; see Chap. 2 for a review of haemosporidian study methods). Also, wild birds will usually have low blood infection intensities lacking full-grown gametocytes, making it more difficult to detect and identify infections (Moens et al. 2016). Although qPCR methods can quantify infection intensity without the need to evaluate blood smears (Ciloglu et al. 2019), determining the standard curves using DNA samples of known infection intensity that is accessed by microscopic

analysis (e.g., Ishtiaq et al. 2017; Asghar et al. 2011; Moens et al. 2016) is required to generate comparable estimates of parasitemia. In addition, the direct observation of mature gametocytes in peripheral blood is the best standard for scoring a host species as a competent reservoir for the parasite (Moens et al. 2016). Therefore, the combination of microscopy and molecular techniques (for identification of lineages based on DNA sequence and quantification of parasite intensities) is vital to better understand the trade-offs of being a specialist or generalist parasite. For example, a parasite well adapted in exploiting its host should show a greater capacity of infection (i.e., have high prevalence) together with a greater capacity of reproduction (infection intensity) within its host (Huang et al. 2018). Moreover, adaptation to hosts can vary, and this variation should be reflected in the prevalence and intensity of infection. Therefore, in order to determine if an avian haemosporidian lineage is a generalist or specialist parasite, one needs to consider both the prevalence and infection intensities in each host species (Moens et al. 2016; Huang et al. 2018). With these data, one can answer questions such as 1) does the same avian haemosporidian lineage have similar prevalence and infection intensity in the same host species independent of locality? 2) Are there particular host species that are more susceptible to avian haemosporidians? And 3) how does infection intensity and prevalence vary when co-infections of avian haemosporidians occur? (e.g., Palinauskas et al. 2018). Answering these questions will greatly contribute to our understanding of parasite dispersal and host ranges.

Studies on the association between avian haemosporidian lineages and vectors are scarce (see Chap. 6 for a synthesis of the current knowledge on dipteran vectors of avian haemosporidian parasites). The difficulty resides in identifying the vector species (particularly in tropical regions; see Chap. 5 for a thorough introduction to blood sucking Diptera families across tropical regions), which lineages are capable of infecting vectors and also discovering the species that vectors prefer feeding on. The development of molecular

markers has allowed great advances in the study of avian malaria (Bensch et al. 2009; see Chap. 4 for a presentation and discussion of molecular methods used in avian haemosporidian research). However, the identification of avian haemosporidians lineages within insect vectors does not necessarily mean that they are capable of completing sporogony (see Chaps. 2 and 6; Njabo et al. 2011; Valkiūnas 2011). Current data on molecular markers suggests that most *Plasmodium* lineages are capable of infecting several vector species (Kimura et al. 2010; Martínez-de la Puente et al. 2011; Njabo et al. 2011; but see Gager et al. 2008). For example, *Plasmodium relictum*, can infect over 20 different mosquito species belonging to at least four different genera (Santiago-Alarcon et al. 2012a). Moreover, different vector species can share similar or identical *Plasmodium* lineages (Ferraguti et al. 2013). Data on vector competence of other avian haemosporidians also show several cases of large vector range for several *Haemoproteus* and *Leucocytozoon* lineages, as well as the same vector species being capable of harbouring several lineages (Santiago-Alarcon et al. 2012a). Data also suggest that the encounter filter might not be a strong driver in the structuring of *Plasmodium* assemblages (Medeiros et al. 2013). However, for *Leucocytozoon*, evidence suggests that vectors can work as encounter filters because blackflies feed on a subset of vertebrate hosts (Hellgren et al. 2008). Transmission success will depend on both the host and vector range of avian haemosporidians, wherein one extreme there will be lineages that are both vector and host generalist, and in the other extreme lineages that are both vector and host specialists. Understanding how transmission varies is important because it has direct consequences on the dispersal and transmission of diseases in the wild. For example, avian malaria parasites that are transmitted by a wide range of vectors and capable of infecting a wide range of birds should have high transmission and dispersal success (Martínez-de la Puente et al. 2011).

11.3 Dispersal and colonization of communities

Dispersal of avian haemosporidians relies mainly on the bird hosts because vector dispersal is usually limited (Ejiri et al. 2011; but see discussion in Ellis et al. 2019). Moreover, bird hosts are endotherms and have longer lifespans, which guarantees a more constant environment when compared to vectors that are ectotherm and have very short lifespans (Seghal et al. 2015; Fecchio et al. 2019; see Chap. 5). Vector specificity seems to play a minor role in the dispersal and structuring of avian haemosporidian communities (Gager et al. 2008; Njabo et al. 2011; Medeiros et al. 2013), probably because avian haemosporidian lineages are less selective regarding vector use (Kimura et al. 2010; Njabo et al. 2011) and vectors are less selective regarding which bird hosts they feed on (Santiago-Alarcon et al. 2012a,b; Santiago-Alarcon et al. 2013; Medeiros et al. 2013). However, some avian haemosporidian lineages can be vector specialists (Gager et al. 2008) and more studies are needed on vector use by avian haemosporidians, particularly experimental studies in order to determine vector specificity and other factors that can affect the transmission of these parasites (Valkiūnas et al. 2013; Palinauskas et al. 2015).

If the bird hosts indeed are the main drivers in avian haemosporidian distribution and dispersal, then one can expect lineage turnover to follow bird host turnover (with a role for vectors as parasite-vector and bird-vector relationships probably follow similar patterns). Indeed, bird community similarity can predict parasite similarity (Ellis et al. 2015; Clark et al. 2018; Fecchio et al. 2018a). Therefore, the overlap of host species across different communities will connect these communities and allow the dispersal of avian haemosporidians (Clark et al. 2018). For example, in the Amazonian region, areas of bird endemism also constrained the distribution of *Plasmodium* lineages despite them presenting low host specificity and lack of specific phylogenetic constraint (Fecchio et al. 2018a). Also, generalist avian haemosporidians should be able to disperse more easily because more than

one host species could provide a link between communities. However, dispersal will be limited if communities present interspecies barriers (Fig. 11.1). Indeed, phylogenetic host relatedness may to a variable extent determine avian haemosporidian turnover (Ellis et al. 2015; Clark and Clegg 2017; Clark et al. 2018), which suggests that dispersal will be more likely to occur between phylogenetically similar host communities (controlling for geographic distance, as phylogenetically similar host communities tend to be geographically close), a pattern that occurs for both generalist and specialist avian haemosporidians. Moreover, recalling what was discussed above, dispersal of avian haemosporidians between different populations of bird hosts from different bird communities is more likely to occur for avian haemosporidian lineages that have a large geographic range (Drovetski et al. 2014; Mata et al. 2015). For example, specialist avian haemosporidian lineages will only occur in more than one bird community or be able to cross biogeographic barriers if their specific bird host is abundant in both communities (Mata et al. 2015; Clark et al. 2018). Conversely, generalist lineages should be less limited geographically because of their capability of infecting several host species, which could increase their connectivity with different host communities (Ewen et al. 2012).

Environmental and ecological conditions can also affect the dispersal and distribution of avian haemosporidians (Fecchio et al. 2019; Clark et al. 2016, 2018). Climate will affect the distribution of host species and vectors (Fig. 11.3), but could also affect the development of avian haemosporidians directly when they are infecting their ectothermic vectors (Paijmans et al. 2010). For example, *Plasmodium relictum* requires a temperature of over 13°C to complete its development within the vector *Culex quinquefasciatus* (LaPointe et al. 2010). Moreover, evidence suggests that host specificity may be a labile trait that varies biogeographically, potentially as a response to climate variation (Fecchio et al. 2019). For example, regions that have marked rainfall seasonality or wetter dry seasons have more

specialized avian haemosporidian lineages (Fecchio et al. 2019). Interestingly, regions of high bird diversity such as the Amazonia and the Andes, which have high rainfall, tend to have less specialized lineages with host switching as the main diversification mechanism (Galen and Witt 2014; Moens and Pérez-Tris 2016; Fecchio et al. 2018b). However, water availability is an important environmental predictor of vector abundance (Smith et al. 2004; Okanga et al. 2013; Sehgal 2015; see Chaps. 5 and 6), which can lead to higher incidence of avian haemosporidians in wild birds (Wood et al. 2007; Krama et al. 2015; Ferraguti et al. 2018; Santiago-Alarcon et al. 2019). Landscape features and other environmental variables seem to be important in determining the distribution of avian haemosporidians lineages (Pérez-Rodríguez et al. 2013a; Sehgal et al. 2015; Ferraguti et al. 2018; see Chaps. 10 and 14). For example, temperature and distance to artificial water reservoirs can be important predictors of avian haemosporidian prevalence (Pérez-Rodríguez et al. 2013a; Sehgal et al. 2011; González-Quevedo et al. 2014). It is possible that at a more local scale, landscape features will have a stronger effect on vector distribution and abundance, which in turn will structure avian haemosporidian assemblages locally by increasing the incidence of infection and potential dispersal (i.e., spillover) to uninfected bird hosts (e.g., Renner et al. 2016; Santiago-Alarcon et al. 2019; Fig. 11.3).

Understanding host-parasite dynamics is crucial for understanding parasite dispersal and how different ecological factors will act on different scales. For example, increased vector abundance should lead to the increase of local parasite prevalence (Fig. 11.3). Even on a local scale, avian haemosporidian prevalence can vary substantially because of local environmental features such as distance to water, variation in vegetation cover and temperature (Wood et al. 2007; Seghal et al. 2011; González-Quevedo et al. 2014; Renner et al. 2016; Ferraguti et al. 2018). Also, prevalence can vary seasonally due to climatic differences and the entering of new recruits (after the breeding season) that are expected to be

immunologically naïve (Cosgrove et al. 2008), which in turn can increase the incidence of infection (Fig. 11.3). Therefore, dispersal of avian haemosporidians rely on several factors: (i) host and vector specificity; (ii) environmental factors that affect the distribution and abundance of vectors and bird hosts; (iii) breeding season of bird hosts (increase of immunologically naïve hosts); (iv) vector community composition (abundance, richness, phylogenetic diversity, phylogenetic similarities between different communities); and (v) bird community composition (abundance, richness, phylogenetic diversity, phylogenetic similarities between different communities). For example, bird communities that have high phylogenetic diversity and bird richness provide a more diverse array of available niches for parasites (Lacorte et al. 2013; Clark and Clegg 2017; Clark et al. 2018), which should lead to higher avian haemosporidian diversity (Fig. 11.3). Testing the effects of the factors presented in Figure 11.3 is important to determine how avian haemosporidians dispersal is affected and should help in the understanding of how avian haemosporidians communities are structured and connected locally and regionally.

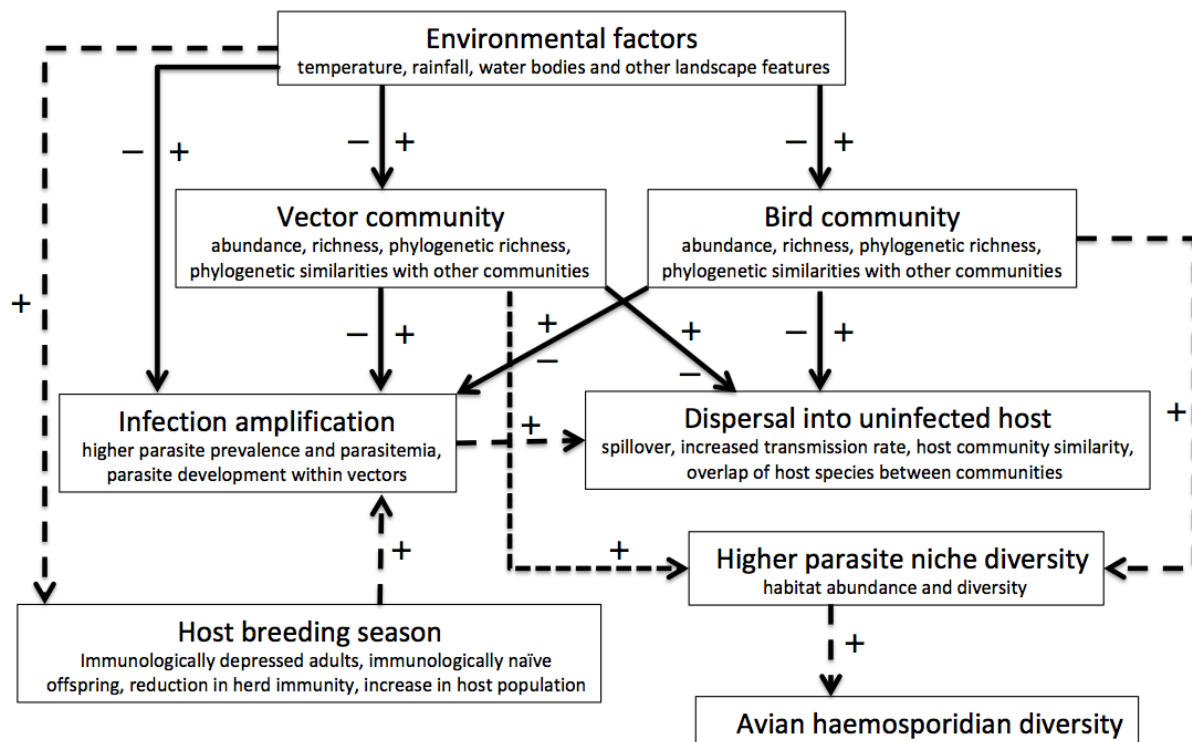


Fig. 11.3 Hypotheses on how environmental and biological factors can affect the incidence, transmission, and dispersal of avian haemosporidians. Understanding the effects of these factors on host-parasite dynamics should help unravel the dispersal and diversification mechanisms of avian haemosporidians, which in turn can help the understanding of the emergence of infectious diseases in wildlife and humans. Lines show positive and negative effects, while dashed lines show potential positive effects when there is an increase in one of the parameters inside the box. For example, vector communities that are richer in species and/or have higher abundance of vectors should have higher parasite niche diversity, which in turn should lead to an increase in avian haemosporidian diversity. The same idea applies for the bird community box. Conversely, host community similarity (i.e. high phylogenetic similarity between bird communities), should increase connectivity for many parasites species, which in turn could lead to more similar avian haemosporidian communities.

11.4 Dispersal of avian haemosporidians on islands

Colonization of islands by vector-borne parasites such as avian haemosporidians is a complex process. Avian haemosporidian must first manage to arrive at an island, which can occur via host migration or dispersal or even due to the arrival of vagrant hosts or windblown vectors (Clark and Clegg 2015; see Parker 2018 for a review of research on the Galápagos Islands). However, several factors are expected to affect the persistence of avian haemosporidians on islands (see Chap. 8 for a thorough review of research on avian haemosporidian island biogeography). For example, host specificity can play a significant role in determining the persistence of avian haemosporidians on islands, where generalist avian haemosporidian lineages are expected to have a higher probability of persistence (Ewen et al. 2012; Pérez-Rodríguez et al. 2013a; Clark et al. 2014) and also a higher probability of becoming invasive (Mack et al. 2000; see Chap. 15 for an in depth treatment of the role of parasites on invasion biology). Generalist parasites should be better colonizers because they could switch to other more abundant host species present on the invaded island, allowing them to persist despite having a low prevalence in the arriving host species (Ewen et al. 2012; Pérez-Rodríguez et al. 2013a). The presence of suitable vectors on islands is also important for the maintenance of arriving avian haemosporidians, which might have a greater difficulty of arrival (particularly for more isolated islands) and persistence. It is known that temperature and water availability are important elements for the development of vectors (Lapointe et al. 2010; Okanga et al. 2013; see Chaps. 5 and 6) and will also affect the prevalence of avian haemosporidians (Seghal et al. 2011; González-Quevedo et al. 2014; Ferraguti et al. 2018). Therefore, depending on the environmental conditions of the islands, vector abundance and diversity may be limited.

The diversity of haemosporidians on oceanic islands is lower than for continental areas (Clark et al. 2014), which is expected. Also, avian haemosporidian lineages that have large geographical range sizes or that are more common on the mainland will usually be more common on islands (Santiago-Alarcon et al. 2010; Ewen et al. 2012; Perez-Rodríguez et al. 2013a), and islands closer to the mainland tend to have higher avian haemosporidian diversity (Fallon et al. 2005; Ricklefs et al. 2011; Perez-Rodríguez et al. 2013a). Thus, dispersal of avian haemosporidians to islands is facilitated if islands are close to the continent or have been connected to mainland in the past (Fallon et al. 2005; Perez-Rodríguez et al. 2013a, Soares et al. 2017). Moreover, the prevalence on islands can be lower when compared to the mainland and can have lower temporal stability (Perez-Rodríguez et al. 2013a), which can lead to increase lineage turnover due to colonization and extinction events (Fallon et al. 2004).

Biogeographic patterns and dispersal can vary regarding *Plasmodium* and *Haemoproteus*. For example, *Haemoproteus* distribution in southern Melanesia was more associated with the presence and availability of bird hosts, while *Plasmodium* distribution was more associated with geography and local island conditions instead of host availability (Olsson-Pons et al. 2015). Moreover, generalist lineages are usually more common on islands (Ishtiaq et al. 2008; Clark and Clegg 2015). Evidence suggests that *Haemoproteus* lineages are less frequent on islands at the global scale (Clark et al. 2014), which could be explained by the fact that *Haemoproteus* parasites tend to be more specific regarding bird hosts (Beadell et al. 2004, 2009; but see Moens and Pérez-Tris 2016; Ellis et al. 2015) and vector species (Martínez-de la Puente et al. 2011). More research is needed, however, given the current island geographical sampling bias (i.e., Hawaii, Galápagos, Caribbean Antilles), where on some archipelagos *Haemoproteus* is the dominant avian haemosporidian genus (Parker 2018). It is also possible that there is a paucity of suitable vectors (Diptera:

Ceratopogonidae) for *Haemoproteus* parasites on islands or a lack of suitable vector habitat. Vector specificity would explain the lower colonization success of *Haemoproteus* compared to *Plasmodium*, a parasite genus that has been a protagonist of notorious cases of invasion of island bird communities (Beadell et al. 2006; Ewen et al. 2012).

11.5 Host specialization in tropical avian malaria

Understanding parasite diversity and specificity in tropical habitats is important for public health and the conservation of biodiversity. Tropical bird communities might be reservoirs of parasites that could cause tremendous problems if moved away from their native range, either by their impact on poultry or their effects on native wildlife (Vanstreels et al. 2014; Moens and Pérez-Tris 2016; see Chap. 15). Conversely, the valuable biodiversity of tropical habitats may be threatened by invasive parasites (Marzal et al. 2015). The degree of specificity of host-parasite interactions plays an undoubtedly prominent role in parasite exchange, both by determining the capability of tropical parasites to infect a wide range of host species (and therefore cause problems if moved outside their native range [Ewen et al. 2012; Moens and Pérez-Tris 2016]), or the compatibility of tropical bird species as hosts of generalist parasites that might be imported into the tropics, causing disease (Marzal et al. 2015, Ferreira-Junior et al. 2018, Ortiz-Catedral et al. 2019).

Most research on avian malaria parasites has traditionally been done in temperate regions of the world (Bensch et al. 2009; see Chap. 1 for a review of avian haemosporidian research in tropical regions of the world during the 20th century). Studies in tropical regions are scarce and are concentrated in a few areas (Clark et al. 2014). As a consequence, the current knowledge of the diversity and host specificity of avian malaria parasites in the tropics remains incomplete (Outlaw et al. 2017), making it difficult to establish general

patterns for tropical parasites. Various studies have tried to point out the singularity of tropical habitats from this perspective, aiming at identifying different factors that may affect diversity and specificity of parasites in the tropics (e.g., Svensson-Coelho et al. 2014). A general conclusion is that tropical and temperate communities are formed by different parasite species, with a minority of elements of parasite diversity being shared between regions (Svensson-Coelho et al. 2013; Moens and Pérez-Tris 2016). This is a remarkable observation, given the fact that migratory birds usually carry parasites acquired in temperate areas to the tropics and vice versa, yet the parasites typically fail to thrive in different regions (Hellgren et al. 2007, Pérez-Rodríguez et al. 2013b, Ricklefs et al. 2017; see Chap. 16 for a synthesis of current research on avian migration and its role on avian haemosporidian latitudinal dispersal). Knowing what keeps parasites confined to different transmission areas (from phylogenetic similarity of host communities to variable availability of competent vectors, see e.g. Ricklefs et al. 2017) is central to our understanding of the evolution of parasite specificity in the tropics.

The most immediate elements invoked to explain the structure of tropical parasite assemblages are climate and vector diversity. Environmental factors and most notably temperature may affect parasite life cycles, even blocking their development in vectors in climatically unsuitable habitat (LaPointe et al. 2010). This could explain why the transmission of avian haemosporidian lineages that are brought over by migratory birds in their peripheral blood is interrupted during the reproductive season (and reciprocally, temperate avian haemosporidian lineages fail to establish themselves in tropical nonbreeding habitats when birds return; Hellgren et al. 2007; Ricklefs et al. 2017). Parasites may be therefore constrained to exploit the subset of compatible host species that are encountered by their vectors during periods of favourable environmental conditions, increasing specificity as

a consequence. In fact, climate has recently been identified as a relevant factor explaining geographical variation in specificity of avian haemosporidian parasites (Fecchio et al. 2019).

However, climate is too variable in the tropics to make it possible to define a common scenario for the evolution of parasite specificity in the region, where sharp environmental gradients take place at small geographic scales compared with temperate regions (Malhi et al. 2010). For example, tropical mountain ranges such as the Andes create broad geographic areas characterised by sharp elevational gradients from the lowland rainforest at the sea level to the open Paramo ecosystem well above 3000 m asl. These gradients may contribute to the structuring of parasite assemblages among the bird species that occur at different elevations, increasing parasite diversity and specificity at the regional scale (Galen and Witt 2014). On the other hand, these gradients might favour environmentally generalist parasites that are capable of thriving across the broad range of environmental conditions that their hosts may encounter within short distances (i.e., from tens to couple hundred kilometres). Conversely, climate may constrain parasite geographic distributions if parasites are unable to thrive in unsuitable climatic regions (e.g., colder habitats at higher elevations, drier habitats such as tropical seasonally dry forests), although such climate constraints may attenuate due to global change, which is of major concern for tropical birds inhabiting high-elevation and geographically restricted habitats (Prieto-Torres et al. 2016; Liao et al. 2017). Whether regional climatic gradients promote or reduce parasite-host specificity remains an open question, on which research in tropical habitats may shed much light.

In combination with climatic effects, the specificity of parasite-vector associations may contribute to shaping the network of bird-parasite interactions, increasing or lowering the specificity of their relationship in different regions (Santiago-Alarcon et al. 2012a). As it was discussed above, the diversity of vectors changes across geographic regions, both qualitatively and quantitatively, and this may affect the patterns of parasite distribution

among bird hosts (see Chap. 6). Only a few studies have analysed the role of dipteran vectors in structuring bird-parasite relationships, showing that compatibility filter (Fig. 11.2) is more likely to be operating at the bird host level (Medeiros et al. 2013). However, we know too little on the diversity of vectors and the structure of parasite-vector interactions to confidently interpret the role of vectors in shaping bird-parasite relationships. This lack of knowledge is probably more limiting in the tropics (Santiago-Alarcon et al. 2012a; Chap. 6), where an increased diversity of dipteran species capable of transmitting parasites is probably increasing the complexity of bird-vector-parasite interactions, obscuring the role of vectors in the structuring of bird-parasite relationships (Svensson-Coelho et al. 2016).

If the diversity of vectors is an important factor explaining bird-parasite relationships in the tropics, the diversity of bird hosts may also be relevant in this regard. Tropical habitats are renowned by their great bird diversity, which may promote dilution effects and select for generalist strategies of host exploitation among avian malaria parasites (this may lead to amplification effects on other geographical areas with less host diversity, if such generalist parasites are able to reach them). Supporting this idea, the megadiverse rainforests of the Amazonian slopes of the Andes are home to the most generalist members of the genus *Haemoproteus* reported so far (Moens and Pérez-Tris 2016). However, this pattern is far from general: a comparison of two bird-parasite interaction networks (one in temperate and one in tropical habitat) failed to detect any difference in the degree of host specialization of both parasite communities. In fact, parasites showed high host specialization in both cases, meaning that a generalist strategy is not necessarily general among the parasites that occur in bird diverse regions (Svensson-Coelho et al. 2014). There is also evidence of environmental influences contributing to the variation in host specificity of avian malaria parasites. For example, in tropical Africa parasite diversity and specialization was found to be higher in lowland rainforests compared to the more climatically variable highland forests (Loiseau et

al. 2012). In addition, the diversity of host life histories may also contribute to increase the variation in parasite host ranges. For example, long-lived or abundant host species favour parasites that specialize in their exploitation (e.g., Santiago-Alarcon et al. 2016; Svensson-Coelho et al. 2016). These processes may increase modularity in the network of bird-parasite interactions, which in turn may increase variance in the success of specialists and generalist parasites among bird communities (Pinheiro et al. 2016). To sum up, we still know very little about the relative influence of habitat features and bird communities in shaping avian malaria relationships. This knowledge gap may be of conservation concern, because the above influences may prove critical for the understanding of human impacts on the ecology of wildlife diseases, such as those associated with habitat modification and hunting (Chasar et al. 2009; see Chap. 14).

To further complicate our understanding of bird-parasite relationships in the tropics, local variation in the intensity of infection among the many hosts infected by generalist parasites, indicates that even the most generalist parasites seem to be more specialized than they appear based solely on their list of infected species. For example, *Haemoproteus witti*, a parasite first discovered in hummingbirds, scores the greatest host range among parasites of its genus in various bird communities in the Neotropics, where it infects birds of several orders. However, this parasite is only found to produce gametocytes detectable in peripheral blood in hummingbirds, supporting the idea that *H. witti* is more specific than its reported list of infected hosts may suggest (Moens et al. 2016).

In summary, our knowledge of the patterns of host specialization and dispersal of avian malaria parasites is in its infancy. We are well aware of the importance of these attributes of parasites for understanding their patterns of global distribution, both in space and among host species, which ultimately determine (or are the result of) the capability of parasites to colonize new hosts or geographic regions (Ewen et al. 2012). In order to

anticipate future problems associated with disease emergence, we must disentangle the network of bird-vector-parasite interactions, and understand how its architecture promotes or constraints parasite transmission across species or geographic areas. Research in the tropics may prove influential in this field because of the existence of sharp environmental gradients associated with tropical mountains, which may facilitate the analysis of environmental influences on bird-parasite relationships at more local scales compared to other regions. From a conservation perspective, we also need to improve the current understanding of the impact of native and introduced parasites on tropical avifauna, in order to design management plans to avoid and/or contain parasite spread.

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References

- Asghar M, Hasselquist D, Bensch S (2011) Are chronic avian haemosporidian infections costly in wild birds? *J Avian Biol* 42:530–537
- Beadell JS, Gering E, Austin J et al (2004) Prevalence and differential host-specificity of two avian blood parasite genera in the Australo-Papuan region. *Mol Ecol* 13:3829–3844
- Beadell JS, Ishtiaq F, Covas R et al (2006) Global phylogeographic limits of Hawaii's avian malaria. *Proc R Soc B* 273:2935–2944
- Beadell JS, Covas R, Gebhard C (2009) Host associations and evolutionary relationship of avian blood parasites from West Africa. *Int J Parasitol* 39:257–266
- Belo NO, Pinheiro RT, Reis ES et al (2011) Prevalence and lineage diversity of avian haemosporidians from three distinct Cerrado habitats in Brazil. *PLoS ONE* 6:e17654
- Bensch S, Hellgren O, Pérez-Tris J (2009) MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome b lineages. *Mol Ecol Res* 9:1353–1358

Chasar A, Loiseau C, Valkiūnas G et al (2009) Prevalence and diversity patterns of avian blood parasites in degraded African rainforest habitats. *Mol Ecol* 18:4121–4133

Ciloglu A, Ellis VA, Bernotienė R et al (2019) A new one-step multiplex PCR assay for simultaneous detection and identification of avian haemosporidian parasites. *Parasit Res* 118:191–201

Civitello DJ, Cohen J, Fatima H et al (2015) Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proc Natl Acad Sci USA* 112:8667–8671

Clark NJ, Clegg SM, Lima MR (2014) A review of global diversity in avian haemosporidians (*Plasmodium* and *Haemoproteus*: Haemosporida): new insights from molecular data. *Int J Parasitol* 44:329–338

Clark NJ, Clegg SM (2015) The influence of vagrant hosts and weather patterns on the colonization and persistence of blood parasites in an island bird. *J Biogeogr* 42:641–651

Clark NJ, Wells K, Dimitrov D et al (2016) Co-infections and environmental conditions drive the distributions of blood parasites in wild birds. *J Anim Ecol* 85:1461–1470

Clark NJ, Clegg SM (2017) Integrating phylogenetic and ecological distances reveals new insights into parasite host specificity. *Mol Ecol* 26:3074–3086

Clark NJ, Clegg SM, Sam K et al (2018) Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Divers Distrib* 24:13–23

Combes C (1991) Evolution of parasite life cycles. In: Toft, CA, Aeschlimann A, Bolis L (eds) *Parasite-Host Associations: Coexistence or Conflict?* Oxford University Press, Oxford, p 62–82

Cornet S, Nicot A, Rivero A et al. (2014) Evolution of plastic transmission strategies in avian malaria. *PLoS Pathog* 10(9):e1004308

Cosgrove CL, Wood MJ, Day KP et al (2008) Seasonal variation in *Plasmodium* prevalence in a population of blue tits *Cyanistes caeruleus*. *J Anim Ecol* 77:540–548

Drovetski SV, Aghayan SA, Mata VA et al (2014) Does the niche breadth or trade-off hypothesis explain the abundance-occupancy relationship in avian haemosporidia? *Mol Ecol* 23:3322–3329

Ejiri H, Sato Y, Kim K-S et al (2011) Entomological study on transmission of avian malaria parasites in a zoological garden in Japan: bloodmeal identification and detection of avian malaria parasite DNA from blood-fed mosquitoes. *J Med Entomol* 48:600–607

Ellis VA, Collins MD, Medeiros MCI et al (2015) Local host specialization, host-switching, and dispersal shape the regional distributions of avian haemosporidian parasites. *Proc Natl Acad Sci USA* 112:11294–11299

Ellis VA, Medeiros MCI, Collins MD et al (2017) Prevalence of avian haemosporidian parasites is positively related to the abundance of host species at multiple sites within a region. *Parasit Res* 116:73–80

Ellis VA, Bensch S (2018) Host specificity of avian haemosporidian parasites is unrelated among sister lineages but shows phylogenetic signal across larger clades. *Int J Parasitol* 48:897–902

Ellis VA, Sari EHR, Rubenstein DR et al (2019) The global biogeography of avian haemosporidian parasites is characterized by local diversification and intercontinental dispersal. *Parasitology* 146:213–219

Ewen JG, Bensch S, Blackburn TM et al (2012) Establishment of exotic parasites: the origins and characteristics of an avian malaria community in an isolated island avifauna. *Ecol Lett* 15:1112–1119

Fallon SM, Ricklefs RE, Latta SC et al (2004) Temporal stability of insular avian malaria parasite communities. *Proc R Soc Lon B Biol Sci* 271:493–500

Fallon SM, Bermingham E, Ricklefs RE (2005) Host specialization and geographic localization of avian malaria parasites: a regional analysis in the Lesser Antilles. *Am Nat* 165:466–480

Fecchio A, Pinheiro R, Feli G et al (2018a). Host community similarity and geography shape the diversity and distribution of haemosporidian parasites in Amazonian birds. *Ecography* 41:505–515

Fecchio A, Bell JA, Collins MD et al (2018b) Diversification by host switching and dispersal shaped the diversity and distribution of avian malaria parasites in Amazonia. *Oikos* 127:1233–1242

Fecchio A, Wells K, Bell JA et al (2019) Climate variation influences host specificity in avian malaria parasites. *Ecol Lett* 22:547–557

Fecchio A, Bell JA, Pinheiro RBP et al (2019) Avian host composition, local speciation, and dispersal drive the regional assembly of avian malaria parasites in South American birds. *Mol Ecol*. doi:10.1111/mec.15094

Ferraguti M, Martínez-de la Puente J, Muñoz J et al (2013) Avian *Plasmodium* in *Culex* and *Ochlerotatus* mosquitoes from southern Spain: effects of season and host-feeding source on parasite dynamics. *PLoS ONE* 8(6):e66237

Ferraguti M, Martínez-de la Puente J, Bensch S et al (2018) Ecological determinants of avian malaria infection: an integrative analysis at landscape, mosquito and vertebrate community levels. *J Anim Ecol* 87:727–740

Ferreira-Junior FC, Dutra DA, Silveira P et al (2018) A new pathogen spillover from domestic to wild animals: *Plasmodium juxtannucleare* infects free-living passerines in Brazil. *Parasitology* 145:1949–1958

- Gager AB, Loaiza JDR, Dearborns DC (2008) Do mosquitoes filter the access of *Plasmodium* cytochrome b lineages to an avian host? *Mol Ecol* 17:2552–2561
- Galen SC, Witt CC (2014) Diverse avian malaria and other haemosporidian parasites in Andean house wrens: evidence for regional co-diversification by host-switching. *J Avian Biol* 45:374–386
- González-Quevedo C, Davies RG, Richardson DS (2014) Predictors of malaria infection in a wild bird population: landscape-level analyses reveal climatic and anthropogenic factors. *J Anim Ecol* 83:1091–1102
- Gutiérrez-López R, Martínez-de la Puente J, Gangoso L et al (2016) Do mosquitoes transmit the avian malaria-like parasite *Haemoproteus*? An experimental test of vector competence using mosquito saliva. *Parasit Vectors* 9:609
- Hellgren O, Waldenström J, Pérez-Tris J et al (2007) Detecting shifts of transmission areas in avian blood parasites - a phylogenetic approach. *Mol Ecol* 16:1281–1290
- Hellgren O, Bensch S, Malmqvist B (2008) Bird hosts, blood parasites and their vectors – associations uncovered by molecular analyses of blackfly blood meals. *Mol Ecol* 17:1605–1613
- Hellgren O, Pérez-Tris J, Bensch S (2009) A jack-of-all-trades and still a master of some: prevalence and host range in avian malaria and related blood parasites. *Ecology* 90:2840–2849
- Huang X, Ellis VA, Jönsson J et al (2018) Generalist haemosporidian parasites are better adapted to a subset of host species in a multiple host community. *Mol Ecol* 27:4336–4346
- Ishtiaq F, Guillaumot L, Clegg SM et al (2008) Avian haematozoan parasites and their associations with mosquitoes across southwest Pacific Islands. *Mol Ecol* 17:4545–4555
- Ishtiaq F, Rao M, Huang X et al (2017) Estimating prevalence of avian haemosporidians in natural populations: a comparative study on screening protocols. *Parasit Vectors* 10:127
- Jones KE, Patel NG, Levy MA et al (2008) Global trends in emerging infectious diseases. *Nature* 451:990–993.
- Keesing F, Holt RD, Osfeld RS (2006) Effects of species diversity on disease risk. *Ecol Lett* 9:485–498
- Kimura M, Darbro JM, Harrington LC (2010) Avian malaria parasites share congeneric mosquito vectors. *J Parasitol* 96:144–151
- Krama T, Krams R, Cīrulis D et al (2015) Intensity of haemosporidian infection of parids positively correlates with proximity to water bodies, but negatively with host survival. *J Ornithol* 156:1075–1084

- Lacorte GA, Félix GMF, Pinheiro RRB et al (2013) Exploring the diversity and distribution of Neotropical avian malaria parasites – a molecular survey from southeast Brazil. PLoS ONE 8(3): e57770
- LaPointe DA, Goff ML, Atkinson CT (2010) Thermal constraints to the sporogonic development and altitudinal distribution of avian malaria *Plasmodium relictum* in Hawai'i. J Parasitol 96:318–324
- Liao W, Atkinson CT, LaPointe DA et al (2017) Mitigating future avian malaria threats to Hawaiian forest birds from climate change. PLoS ONE 12:e0168880
- Lima MR, Bensch S (2014) Why some parasites are widespread and abundant while others are local and rare? Mol Ecol 23:3130–3132
- Loiseau C, Harrigan RJ, Robert A, et al (2012) Host and habitat specialization of avian malaria in Africa. Mol Ecol 21:431–441
- Mack RN, Simberloff D, Lonsdale WM et al. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710
- Malhi Y, Silman M, Salinas N, et al (2010) Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Glob Change Biol 16:3171–3175
- Malmqvist B, Strasevicius D, Hellgren O et al (2004) Vertebrate host specificity of wild-caught blackflies revealed by mitochondrial DNA in blood. Proc R Soc Lond B Biol Sci 271:S152–S155
- Martínez-de la Puente J, Martínez J, Rivero-de Aguilar J et al (2011) On the specificity of avian blood parasites: revealing specific and generalist relationships between haemosporidians and biting midges. Mol Ecol 20:3275–3287
- Marzal A, García-Longoria L, Cárdenas Callirgos JM et al (2015) Invasive avian malaria as an emerging parasitic disease in native birds of Peru. Biol Invasions 17:39–45
- Mata VA, da Silva LP, Lopes RJ et al (2015) The strait of Gibraltar poses an effective barrier to host-specialised but not to host-generalised lineages of avian Haemosporidia. Int J Parasitol 45:711–719
- Medeiros MCI, Hamer GL, Ricklefs RE (2013) Host compatibility rather than vector-host-encounter rate determines the host range of avian *Plasmodium* parasites. Proc R Soc Biol Sci Ser B 280(1760):20122947
- Medeiros MCI, Ellis VA, Ricklefs RE (2014) Specialized avian haemosporida trade reduced host breadth for increased prevalence. J Evol Biol 27:2520–2528
- Moens MAJ, Pérez-Tris J (2016) Discovering potential sources of emerging pathogens: South America is a reservoir of generalist avian blood parasites. Int J Parasitol 46:41–49
- Moens MAJ, Valkiūnas G, Paca A et al (2016) Parasite specialization in a unique habitat:

hummingbirds as reservoirs of generalist blood parasites of Andean birds. *J Anim Ecol* 85:1234–1245

Njabo KY, Cornel AJ, Bonneaud C et al (2011) Nospecific patterns of vector, host and avian malaria parasite associations in a central African rainforest. *Mol Ecol* 20:1049–1061

Noble ER, Noble GA, Schad GA et al (1989) *Parasitology: The Biology of Animals and Parasites*, 6th ed. Lea & Febiger, Philadelphia

Nylin S, Agosta S, Bensch S et al (2018) Embracing colonizations: a new paradigm for species association dynamics. *Trends Ecol Evol* 33:4–14

Okanga S, Cumming GS, Hockey PAR (2013) Avian malaria prevalence and mosquito abundance in the Western Cape, South Africa. *Malar J* 12:370

Olsson-Pons S, Clark NJ, Ishtiaq F et al (2015) Differences in host species relationships and biogeographic influences produce contrasting patterns of prevalence, community composition and genetic structure in two genera of avian malaria parasites in southern Melanesia. *J Anim Ecol* 84:985–998

Ortiz-Catedral L, Brunton D, Stidworthy MF et al (2019) *Haemoproteus minutus* is highly virulent for Australasian and South American parrots. *Parasit Vectors* 12:40

Outlaw DC, Harvey JA, Drovetski SV et al (2017) Diversity and distribution of avian haemosporidians in sub-Saharan Africa: an inter-regional biogeographic overview. *Parasitology* 144:394–402

Paaijmans KP, Blanford S, Bell AS et al (2010) Influence of climate on malaria transmission depends on daily temperature variation. *Proc Natl Acad Sci U S A* 107(34):15135–15139

Palinauskas V, Žiegtė R, Ilgūnas M et al (2015) Description of the first cryptic avian malaria parasite, *Plasmodium homocircumflexum* n. sp., with experimental data on its virulence and development in avian hosts and mosquitoes. *Int J Parasitol* 45:51–62

Palinauskas V, Žiegtė R, Šengau J et al. (2018) Different paths – the same virulence: experimental study on avian single and co-infections with *Plasmodium relictum* and *Plasmodium elongatum*. *Int J Parasitol* 48:1089–1096.

Parker PG (2018) *Disease ecology: Galapagos birds and their parasites*. Springer, Cham.

Pérez-Rodríguez A, Ramírez Á, Richardson DS et al (2013a) Evolution of parasite island syndromes without long-term host population isolation: parasite dynamics in Macaronesian blackcaps *Sylvia atricapilla*. *Glob Ecol Biogeogr* 22:1272–1281

Pérez-Rodríguez A, de la Puente J, Onrubia A et al (2013b) Molecular characterization of haemosporidian parasites from kites of the genus *Milvus* (Aves: Accipitridae). *Int J Parasitol* 43:381–387

Pérez-Rodríguez A, de la Hera I, Bensch S et al (2015) Evolution of seasonal transmission patterns in avian blood-borne parasites. *Int J Parasitol* 45:605–611

Petersson E, Bensch S, Ander M et al (2013) Molecular identification of bloodmeals and species composition in *Culicoides* biting midges. *Med Vet Entomol* 27:104–112

Pigeault R, Vézilier J, Cornet S et al (2015) Avian malaria: a new lease of life for an old experimental model to study the evolutionary ecology of *Plasmodium*. *Phil Trans R Soc B* 370:20140300

Pigeault R, Caudron Q, Nicot A et al (2018) Timing malaria transmission with mosquito fluctuations. *Evol Lett* 2-4:378–389

Pinheiro RBP, Félix GMF, Chaves AV et al (2016) Trade-offs and resource breadth processes as drivers of performance and specificity in a host–parasite system: a new integrative hypothesis. *Int J Parasitol* 46:115–121

Poulin R (1998) Large-scale patterns of host use by parasites of freshwater fishes. *Ecol Lett* 1:118–128

Poulin R (2007) *Evolutionary Ecology of Parasites*, 2nd edn. Princeton University Press, New Jersey

Poulin R and Mouillot D (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. *Parasitology* 126:473–480

Prieto-Torres DA, Navarro-Singüenza AG, Santiago-Alarcón D et al. (2016) Response of the endangered tropical dry forests to climate change and the role of Mexican protected areas for their conservation. *Glob Chang Biol* 22:364–379

Renner SC, Lüdke B, Kaiser S et al. (2016) Forests of opportunities and mischief: disentangling the interactions between forests, parasites and immune response. *Int J Parasitol* 46:571–579.

Ricklefs RE, Gray JD, Latta SC et al (2011) Distribution anomalies in avian haemosporidian parasites in the southern Lesser Antilles. *J Avian Biol* 42:570–584

Ricklefs RE, Outlaw DC, Svensson-Coelho M et al (2014) Species formation by host shifting in avian malaria parasites. *Proc Natl Acad Sci U S A* 111(41):14816–14821

Ricklefs RE, Medeiros M, Ellis VA et al (2017) Avian migration and the distribution of malaria parasites in New World passerine birds. *J Biogeogr* 44:1113–1123

Santiago-Alarcón D, Outlaw DC, Ricklefs RE et al (2010) Phylogenetic relationships of haemosporidian parasites in New World Columbiformes, with emphasis on the endemic Galapagos dove. *Int J Parasitol* 40:463–470

Santiago-Alarcón D, Palinauskas V, Schaefer HM (2012a) Diptera vectors of avian haemosporidian parasites: untangling parasite life cycles and their taxonomy. *Biol Rev* 87:928–964

Santiago-Alarcón D, Havelka P, Schaefer HM et al (2012b) Bloodmeal analysis reveals avian *Plasmodium* infections and broad host preferences of *Culicoides* (Diptera: Ceratopogonidae) vectors. PLoS ONE 7(2):e31098

Santiago-Alarcón D, Havelka P, Pineda E et al (2013) Urban forests as hubs for novel zoonosis: blood meal analysis, seasonal variation in *Culicoides* (Diptera: Ceratopogonidae) vectors, and avian haemosporidians. Parasitology 140:1799–1810

Santiago-Alarcón D, MacGregor-Fors I, Kücknert K et al. (2016) Avian haemosporidian parasites in an urban forest and their relationship to bird size and abundance. Urban Ecosyst 19:331–346

Santiago-Alarcón D, MacGregor-Fors I, Falfán I et al. (2019) Parasites in space and time: a case study of haemosporidian spatiotemporal prevalence in urban birds. Int J Parasitol 49:235–246.

Sarquis-Adamson Y, MacDougall-Shackleton EA (2016) Song sparrows *Melospiza melodia* have a home-field advantage in defending against sympatric malarial parasites. R Soc open sci 3:160216.

Sehgal RNM, Buermann W, Harrigan RJ et al (2011) Spatially explicit predictions of blood parasites in a widely distributed African rainforest. Proc R Soc Biol Sci Ser B 278:1025–1033

Sehgal RNM (2015) Manifold habitat effects on the prevalence and diversity of avian blood parasites. Int J Parasitol Parasites Wildl 4:421–430

Smith DL, Dushoff J, McKenzie FE (2004) The risk of a mosquito-borne infection in a heterogeneous environment. PLoS Biology, 2(11):e368

Soares L, Latta SC, Ricklefs RE (2017) Dynamics of avian haemosporidian assemblages through millennial time scales inferred from insular biotas of the West Indies. Proc Natl Acad Sci USA 114:6635–6640

Svensson-Coelho M, Blake JG, Loiselle BA et al (2013) Diversity, prevalence and host specificity of avian *Plasmodium* and *Haemoproteus* in a Western Amazon assemblage. Ornithol Monogr 76:1–47

Svensson-Coelho M, Ellis VA, Loiselle BA et al (2014) Reciprocal specialization in multihost malaria parasite communities of birds: A temperate-tropical comparison. Am Nat 184:624–635

Svensson-Coelho M, Loiselle BA, Blake JG et al (2016) Resource predictability and specialization in avian malaria parasites. Mol Ecol 25:4377–4391

Suzán, G, García-Peña GE, Castro-Arellano I et al. (2015) Metacommunity and phylogenetic structure determine wildlife and zoonotic infectious disease patterns in time and space. Ecol Evol 5:865–873

Valkiūnas G (2005) Avian Malaria Parasites and Other Haemosporidia. CRC Press, Boca Raton

Valkiūnas G, Iezhova TA, Križanauskienė A et al (2008) A comparative analysis of microscopy and PCR-based detection methods for blood parasites. J Parasitol 94:1395–1401

Valkiūnas G (2011) Haemosporidian vector research: marriage of molecular and microscopical approaches is essential. Mol Ecol 20:3084–3086

Valkiūnas G, Kazlauskienė R, Bernotienė R et al (2013) Abortive long-lasting sporogony of two *Haemoproteus* species (Haemosporida, Haemoproteidae) in the mosquito *Ochlerotatus cantans*, with perspectives on haemosporidian vector research. Parasitol Res 112: 2159–2169

Vanstreels RET, Kolesnikovas CKM, Sandri S et al (2014) Outbreak of avian malaria associated to multiple species of *Plasmodium* in Magellanic penguins undergoing rehabilitation in southern Brazil. PLoS ONE 9:e94994

Westerdahl H, Asghar M, Hasslquist D et al (2012) Quantitative disease resistance: to better understand parasite-mediated selection on major histocompatibility complex. Proc R Soc Lond B Biol Sci 279(1728):577–584

Westerdahl H, Stjernman M, Råberg L et al (2013) MHC-I affects infection intensity but not infection status with a frequent avian malaria parasite in blue tits. PLoS ONE 8(8):e72647

Wood MJ, Cosgrove CL, Wilkin TA et al (2007) Within-population variation in prevalence and lineage distribution of avian malaria in blue tits, *Cyanistes caeruleus*. Mol Ecol 16: 3263–3273

Glossary of technical terms

Amplification effect. A positive correlation between host diversity and parasite transmission success. In avian haemosporidians an amplification effect may be expected when the parasite increases host range (i.e., becomes more generalist) in diverse ecological communities.

Compatibility filters. The different biological barriers that prevent certain elements in the network of host-vector-parasite relationships from establishing an interaction.

Dilution effect. A negative correlation between host diversity and parasite transmission success. In avian haemosporidians a dilution effect may be expected when the proportion of incompatible or suboptimal hosts increases in diverse ecological communities.

Encounter filter. The ecological barriers that prevent the parasite to encounter a potential compatible host.

Environmental barrier. Environmental features that potentially affect the distribution of species (parasite, host and vector). For example regions may have different habitats,

macroclimates, topography and landscape (i.e., variation in the land surface regarding the distribution of habitats)

Geographic barrier. Natural geographic features that act as physical barriers to the dispersal of avian haemosporidians between different regions. These physical barriers are present in the land surface, such as the presence of a mountain range or a water body.

Host compatibility. The capacity of a bird species to act as a suitable host for a parasite. Incompatible hosts, also known as dead-end hosts, cannot be successfully exploited by the parasite, either because the host clears the infection before the parasite can be transmitted by vectors (i.e., the host is resistant to the infection) or because the parasite fails to develop transmissible blood stages. Host compatibility can also be applied to vector species

Host range. Also known as host breadth. It represents the diversity of host species that a parasite can exploit, which can be measured by the richness or phylogenetic diversity of compatible host species.

Host shift. The event that leads to the colonization of a new host species in the evolutionary history of interactions of a parasite.

Host specificity. The degree to which a parasite is specialized in a subset of the vertebrate host or vector species.

Host susceptibility. The degree to which a host may be exploited by a parasite. When hosts are not susceptible at all they are termed incompatible or non-competent hosts.

Interspecies barrier. The variation in the attributes of host and vector species that prevent the transmission/spread of parasites into different host and vector species. These attributes can include ecological traits, such as nesting and foraging behaviour of hosts, vector feeding behaviour and microhabitat use of both hosts and vectors. Immunological similarities of hosts and vectors (i.e., phylogenetic relatedness) should also have an important role.

Parasitemia. An index of infection level. When applied to avian haemosporidian parasites, it is measured as the proportion of circulating red blood cells that are occupied by parasites.

Transmission. The passage of a parasite from one vertebrate host to the next assisted by an insect vector.