Chapter 10

Effects of ecological gradients on tropical avian haemoparasites

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Abstract This chapter provides a brief overview of how natural gradients (e.g., latitude, altitude, landscape gradients) affect host-parasite interactions involving blood parasites in wildlife, and how biotic and abiotic factors act as disruptors. These gradients have a direct impact on prevalence, parasitemia, and the observed relationships between parasites and hosts. In the tropical zone, altitudinal gradients imitate the behavior of the latitudinal gradient, since low temperatures are common both at higher altitudes and higher latitudes. Temperature is one of the determining factors of the diversity of vectors, hosts, and vegetation that affect parasite transmission cycles. Furthermore, within landscapes there may be many types of elements producing gradients. For instance, increasing distance from water sources, anthropogenic degradation, and even sequential stages of succession and interspersed vegetation communities would affect host-parasite-vector interactions. However, such effects do not always operate in the same direction because responses are context-sensitive. We also discuss the

importance of an integrative diagnosis, using microscopic and molecular approaches, which allow better approximations and analyses at the parasite species level, thus producing stronger conclusions. The same detail is recommended for studies on the hematophagous fauna of potential vectors. The life cycle of different parasite species has its own set of characteristics and it corresponds to the researchers to unravel the puzzle and to avoid unwarranted generalizations.

Keywords Blood parasites, Vector-borne diseases, Latitudinal and Altitudinal effects, Landscape heterogeneity, Haemosporida, avian malaria, *Haemoproteus*, *Leucocytozoon*

10.1 Introduction

Gradients in ecological systems may be defined as gradual changes in some characteristic of interest that may influence some ecological process (Stevens 1992; Rohde 1992). There are many types of gradients in nature and they may operate at different spatial scales. In addition, the effects of different types of gradients on ecological processes may interact, thus either enhancing or disrupting the response of the process involved. Some examples of gradients are those originating from latitude (i.e., position within continents in relation to the Equator), elevation, temperature, distance from water sources, and distance from different types of anthropogenic degradation or natural disturbances to name a few (Fig. 10.1).

Latitude is perhaps the type of gradient generating the largest variation in biological diversity. Species richness for most taxonomical groups increases from the poles towards the equator (Turner et al. 2001). Although haemosporidians have been recorded throughout most of the planet and are only absent from polar regions (Merino et al. 1997a; Valkiūnas 2005; Martínez et al. 2018), they also follow the latitudinal gradient (Durrant et al. 2006; Merino et al. 2008; Szöllösi et al. 2011; Oakgrove et al.

2014). Indeed, diversity of haemosporidian morphospecies and lineages is highest near the equator (see Chap. 9 for a thorough introduction to macroecology and ecological networks). Patterns of prevalence may also change throughout latitudinal gradients (Dousang et al. 2019) and in many cases the variable analyzed in parasites studies of gradients is prevalence and not species richness, probably due to difficulties to assign species to blood parasites (see for example Nilsson et al. 2016). The gradient in species richness imposed by latitude is further modified by distance from coastal lines. In general, within continents, species richness is usually highest near the coastline and decreases towards inland areas due to the change in humidity (Turner et al. 2011). Because Diptera vectors have higher reproductive rates associated to high humidity, haemosporidian transmission and diversity are likely higher in moist environments in comparison to dry lands (Lacorte et al. 2013). However, dry environments such as desserts also provide opportunities for vector reproduction such as the presence of water sources (e.g., springs, rivers and tributaries, and cacti which hold water; see Chaps. 5 and 6 for an in depth introduction to Diptera families involved in avian haemosporidian transmission, as well as on an ecological synthesis of vector research in avian haemosporidians).

Altitude is an important driver of variation in climate and in vegetation; in general, higher altitudes have cooler conditions, and mountains tend to receive more precipitation in comparison to valleys. However, due to water runoff, foothills receive some of the highest amount of humidity, and are crossed by rivers and tributaries in areas that are complex in topography, usually carrying running water with high oxygen contents (Butler and Hogsette 1998; Turner et al 2001). Within some climatic regions such as those in which slopes face coastlines, where humidity tends to be high, vegetation varies partially as a response to the temperature gradient associated to

altitude, but also as a response to other factors such as slope and aspect (Swanson et al. 1988). At finer scales, vegetation is further influenced by soil types and by the large variety of microclimates that originate by the complex patterns that topography produces (Swanson et al. 1988). Haemosporidians, their hosts, and vectors respond to these sources of environmental variation. Consequently, fine-scale patterns in haemoparasite diversity and in prevalence are likely associated to these complex patterns (e.g., Renner et al. 2016). In general, diversity of haemoparasites and their vectors, as well as prevalence decreases with decreasing temperature; however, each haemosporidian genus may respond differently to the same environmental features (e.g., Santiago-Alarcon et al. 2019a). A recent meta-analysis revealed that haemosporidian diversity is closely related to patterns of host endemism in the Andes ecosystems, peaking at mid-elevations (i.e., 2000-2500 m asl); furthermore, the spatial distribution of avian haemosporidians was closely associated with areas of avian endemism across large geographical scales in the tropical Andes (Gil-Vargas and Sedano-Cruz 2019).

Natural and anthropogenic disturbances and habitat degradation dramatically modify structure and composition of natural vegetation communities, thus creating additional environmental gradients (e.g., Hernández-Lara et al. 2017). Trends in parasite-vector-host interactions frequently respond to these disturbances and to habitat degradation. Responses to degradation depend on the type of impact; whereas some types of degradation may influence haemosporidian positively, other sources may have negative effects (e.g., Sehgal et al. 2011; Renner et al. 2016; see Chap. 13 for an introduction to urban and landscape ecology, and Chap. 14 for a synthesis of anthropic impacts on avian haemosporidian ecology). In the following sections, we provide a more detailed review of current knowledge regarding some of the above-mentioned

types of gradients, and how these gradients may influence haemosporidian parasite-vector-host interactions within the Neotropics (Fig. 10.1).

10.2 Latitudinal gradients in bird blood parasite richness

The existence of latitudinal gradients in species richness of free-living organisms has been reported in many studies (Pianka 1966; Rohde 1992; Stevens 1992; Huston 1999; Chown and Gaston 2000; see Chap. 9). However, there are very few cases reported for pathogenic organisms (see Hillebrand et al. 2001; Curtis et al. 2002; Nee 2003; Guernier et al. 2004; Guégan et al. 2005) and even less if we look at avian blood parasites (Durrant et al. 2006; Merino et al. 2008; Szöllősi et al. 2011; Oakgrove et al. 2014). Based on these data the initial hypothesis is that there will exist a maximum of diversity or richness of parasites in tropical areas (i.e., low latitude) and that these values will decrease as we move towards the poles where climatic conditions will limit the growth of vector populations and transmission of blood parasites. For example, several studies report low incidence of blood parasites in birds from polar areas as compared with prevalence at other latitudes (Greiner et al. 1975; Merino et al. 1997a; Loiseau et al. 2012; Martínez et al. 2018; but see Meixell et al. 2016).

Probably the first insight on the prevalence of blood parasites of birds and latitude was the report by White et al. (1978) indicating that the Neotropics showed much lower parasite prevalence and a near absence of *Leucocytozoon* infections (this is partly explained by lack of research in tropical areas; see Lutz et al. 2015; Outlaw et al. 2017 for reviews) in comparison with a similar review of Nearctic avian haematozoan distribution reported by Greiner et al. (1975) (see Chap. 1 for a thorough review of avian haemosporidian research conducted during the 20th. century). Among the papers reporting blood parasite differences between latitudes we can also cite the work by

Durrant et al. (2006), who found a higher prevalence of *Haemoproteus* and *Plasmodium* in birds from Guyana as compared to prevalence in bird species from Uruguay. They also observed higher prevalence of infection by *Plasmodium* than by *Haemoproteus*. These results are in contrast with those from Chile (found at similar latitudes of Uruguay) where Merino et al. (2008) found higher prevalence of *Haemoproteus* and lower prevalence by *Plasmodium*. These facts were attributed to different vector abundance or activity in Chile compared to Uruguay. Differences could also be related to dissimilarities in habitat and climate conditions between the Atlantic and the Pacific sides of the continent, even at the same latitude (Merino et al. 2008). Studying the distribution of several genera of blood parasites infecting birds along a latitudinal gradient that includes the world's southernmost forest ecosystems, Merino et al. (2008) found a positive significant relationship between prevalence and latitude for *Leucocytozoon* lineages and a negative relationship for *Haemoproteus*, *Plasmodium* and mixed infections. However, they did not find a significant relationship between parasite diversity and latitude, suggesting that some parasite lineages may evolve locally in isolation within some host species (see also Clark 2018). By using a global database of lineage distributions of *Plasmodium* and *Haemoproteus*, Clark et al. (2014) tested the relationship between diversity among those parasites and their avian hosts across 13 geographic regions. They found that geographic distributions of parasite genera differed, with *Haemoproteus* spp. being absent from the majority of oceanic regions while *Plasmodium* spp. being cosmopolitan and especially diverse in the Neotropics. Overall these authors found a biogeographic pattern of higher diversity of blood parasites in low latitude tropical areas. They suggested that there are differences in the way avian haemosporidian diverge and colonize new communities, but also that better estimates of avian haemosporidian diversity patterns are needed. Clark (2018) failed to

find a latitudinal gradient in global variation in avian haemosporidian phylogenetic diversity, pointing toward an effect of differences in hosts-switching tendencies or the timing of avian evolutionary radiations to explain biogeography of these blood parasite infections. However, his results could be affected by biases in sampling effort that concentrates in higher latitudes in North America and Europe (Clark et al. 2014).

Szöllősi et al. (2011) found that prevalence of *Plasmodium* and *Haemoproteus* differed consistently between parasite lineages and host populations of Blue tits (*Cyanistes caeruleus*) across Europe, indicating that the transmission success of parasites is lineage specific but also dependent on locality. They also found that parasites with high prevalence were widely distributed among Blue tit populations and were found to infect more host species. Thus, they suggested that parasites with high local prevalence can have a wide distribution at a global scale and that neighboring host populations shared more parasite lineages compared to geographically more distant locations.

In another work, Oakgrove et al. (2014) studied resident and migratory bird species across a latitudinal gradient in Alaska and looked for associations between bioclimatic conditions and the distribution of parasite prevalence. They found an effect of latitude on *Haemoproteus*, *Plasmodium* and *Leucocytozoon* prevalence, which decreases towards the north, but they detect other factors affecting these parasites. For example, *Leucocytozoon* was the genus with the highest diversity, prevalence, and co-infection prevalence; temperature seasonality, precipitation, and tree cover were the environmental factors affecting the prevalence of co-infection probably, which indicates the need for a minimum of temperature, water, and tree cover for development and successful transmission of these parasites.

It is difficult to conclude and generalize what specific factors affect parasite latitudinal gradients. Hence, we next discuss some of the factors that we consider most relevant that could affect the existence of latitudinal gradients in diversity and prevalence of avian blood parasites. We group them by their origin in two sets, biotic and abiotic disruptors of ecological gradients, but in some cases one disruptor could be included in both categories.

10.2.1 Disruptors of biotic origin

There exist a large taxonomic diversity of blood parasites infecting birds (see Chaps. 1 and 2). These taxa have different life cycles and require different conditions to complete their cycles (Valkiūnas 2005). Therefore, ideal conditions for one parasite may not be optimal for another and vice versa. For example, *Leucocytozoon* appears to be better adapted to complete their cycle in cold and mountainous climates that may not be suitable for other parasite genera (Merino et al. 1997b; Merino et al. 2008; Oakgrove et al. 2014). This could be, at least partially, by the fact that black flies, the main vectors of *Leucocytozoon*, need running water for their development and reproduction (see Chaps. 5 and 6). Such water conditions are common in mountainous areas after the melt of snow. Thus, a potential disrupting factor when looking for latitudinal gradients of blood parasites infecting birds is the inclusion of different study areas, which will be more or less suitable for different vector taxa, as well as the parasites they transmit. For example, Merino et al. (2008) found a positive significant relationship between prevalence and latitude for *Leucocytozoon* lineages, but a negative relationship for *Haemoproteus*, *Plasmodium*, and mixed infections. The different pattern for *Leucocytozoon* could be attributable to more suitable habitats for simuliid vectors at

high latitudes in Chile. This relationship between Leucocytozoids and high latitudes has been reported previously in other regions (see Greiner et al. 1975).

There are some host species and families that appear to be less susceptible to infections by blood parasites, and their inclusion in studies of latitudinal gradients of blood parasites may yield results that complicate the identification of the gradient. For example, Psittaciformes and many sea birds are not frequently infected with blood parasites (Quillfeldt et al. 2011). The explanation for this fact is not clear and many hypotheses have been suggested; among them, the lack of favorable habitat for at least some vectors, the resistance of the taxa involved, or even eating habits (see Martínez–Abrain et al. 2004; Mendes et al. 2005; Quillfeldt et al. 2014; Masello et al. 2018). In this respect, Quillfeldt et al. (2010) showed that latitude appears to have an effect on the prevalence of infection on seabirds, with polar species showing lower prevalence than those from milder climates. Although the lack of suitable vectors could be part of the explanation in this case, the presence of vectors that may adapt to cold conditions could change this conclusion, but this most likely differs among bird and parasite taxa. For example, birds in polar and marine environments where (liquid) fresh water is scarce could be infected by parasites transmitted by mites and ticks instead of mosquitoes and other dipterans. This is the case of *Babesia* in gulls and penguins (Merino 1998; Montero et al. 2016), *Hepatozoon* in boobies (Merino et al. 2014), or *Lankesterella* in snow buntings (Martínez et al. 2018). Conversely, other groups of birds tend to be infected frequently by various genera of blood parasites and, therefore, seem very susceptible to infections, as is the case of thrushes and finches (e.g., Greiner et al. 1975; White et al. 1978; see also Chap. 1). Reasons for this are also unclear, but habitat, body mass, abundance, nest type and plumage brightness, and foraging and social behavior among other factors could be part of the explanation (e.g., Scheuerlein and Ricklefs

2004; Fecchio et al. 2011; González et al. 2014; Lutz et al. 2015; Santiago-Alarcon et al. 2016). In order to avoid bird taxonomic and phylogenetic noise in susceptibility to infection, it would be ideal to look for latitudinal gradients using the same bird species or a well-defined set of bird species, and using a homogeneous sampling design (i.e., same or similar number of samples of each species at each location). Age and sex of the sampled birds could also affect the results because the incidence of infection is frequently related to these factors (Valkiūnas 2005). The season of sampling can also affect parasite detection and therefore the results of the analysis on the presence of latitudinal gradients. It is known that in general many blood parasite infections are chronic and suffer relapses during the bird-breeding season, probably triggered by hormonal changes during breeding season or other type of stressors (Valkiūnas 2005; Santiago-Alarcon et al. 2019b; but see Pérez-Rodríguez et al. 2015). The reproductive season of birds also coincides with mild climate that also favors the development of vectors and allows for successful parasite transmission. In particular, latitudinal migratory birds are subjected to parasite transmission both during their summer and winter quarters, and must therefore increase their defenses to cope with a larger array of parasites year round in two completely different areas (Møller and Erritzøe 1998; Møller and Szép 2011; see Chap. 16 for a review of avian haemosporidian research in relation to migratory behavior). Migratory birds can act as vectors spreading diseases by carrying more or less generalist parasites through their migration routes and exposing them to the populations of sedentary birds along these routes. For example, Merino et al. (2008) reported that specificity at the host-family level was only found for *Haemoproteus* lineages infecting birds in the family Emberizidae and that individuals of a long distance migrant, the white-crested elaenia (*Elaenia albiceps*), were found infected by the same parasite lineages in localities separated by 20° of latitude.

Infections by these lineages were detected in other sedentary birds, especially in juveniles and nestlings of different bird species. They concluded that long distance migrants are able to distort the presence of latitudinal gradients of diseases due to their potential role in spreading infections (see Chap. 16).

Another potential barrier to the spread of parasites is the requirement of competent hosts and vectors. In this sense, generalist parasites capable of developing in different hosts are more likely to spread than those with more specific requirements. Generalist species of parasites are also more likely to remain in places where the density of each host species is low, because they can complete their transmission among different host species. This is an expected situation in the tropics where we find a great diversity of potential host species, but with low population density (see Moens and Pérez-Tris 2016; Fecchio et al. 2018a,b). The same also applies to the invertebrate hosts that act as vectors of blood parasites. Those blood parasites that are able to infect vectors successfully, i.e., able to complete their cycle in different vectors and produce infective stages, will have more chances of reaching their vertebrate host than those with more specific vector needs (see Chap. 6). Moreover, parasites with highly specific host requirements could have higher risk of extinction if their hosts also go extinct (Windsor 1995).

The current scenario of climate change can also potentially act as a disruptor of latitudinal gradients (Garamszegi 2011). Climate change may cause the movement of species including their expansion with the arrival of more benign weather conditions (Merino 2019). Parasites and pathogens typically follow hosts in their expansion, although there is usually a lag in timing. Low density in host invasion fronts could produce serial founder events leading to local extinctions and absence of parasites from frontal host populations (e.g., Coon and Martin 2014). However, the parasites

eventually catch up with their hosts in the recently colonized areas (Phillips et al. 2010). Invasive species may also play an interesting role in this kind of studies. For example, it is known that House sparrows (*Passer domesticus*) have aided the geographical expansion of a detrimental lineage of *Plasmodium* across their new range (Marzal et al. 2011), and the introduction of blood parasites and their vectors in some areas have produced important impacts on the native avifauna (van Riper et al. 1986; Tompkins and Gleason 2006; see Chap. 15 for a review of invasion biology in relation to parasites).

Finally, we can mention different types of disruptors associated with human activity that can affect latitudinal gradients in birds' blood parasites. Humans can create or eliminate reproductive areas for disease vectors, as it occurs when drying up wetlands to eliminate the incidence of malaria in humans (Naranjo-Ramirez et al. 2016), or the creation of swamps and water reserves that can be used by vectors for reproduction (Martínez and Merino 2011; Sehgal 2015). Several studies also focus on the effect of forest fragmentation on both birds and their parasites. Although deforestation could negatively affect the relationship between vectors, hosts and parasites, the effect between prevalence and deforestations is not always straightforward (Sehgal 2015). Urbanization in relation to latitudinal gradients can also affect the results obtained in terms of the incidence, lineage richness, and assemblage abundance structure of blood parasites (e.g., Carbó-Ramírez et al. 2017). Infections can be reduced in cities by effects of pollution, urbanization, or augmented by the presence of locations with water (e.g., ponds, stagnant water), which are appropriate for vector reproduction (Sehgal 2015; Martínez de la Puente et al. 2016; Abella-Medrano et al. 2018; see Chaps. 13 and 14 for an introduction and synthesis of urban ecology and its relationship with avian parasites).

10.2.2. Disruptors of abiotic origin

Apart from the biological characteristics of the involved organisms, other factors exist that may affect the existence of latitudinal patterns in the distribution and incidence of blood parasites. The existence of certain geographical barriers can isolate populations of vectors, birds, or parasites making it harder to spread diseases (e.g., Prieto-Torres et al. 2019 for birds isolated in neotropical seasonally dry forests). For example, the existence of deserts around tropical areas can operate as barriers to the extension of vectors and parasites since, in many cases, conditions for disease transmission are confined to the few oases and streams present in desert areas (e.g., Ayadi et al. 2017). It is common to find low prevalence of blood parasites in birds living in desert or semi-desert environments (Barrientos et al. 2014; Martínez et al. 2016).

Great mountain barriers (e.g., the Andes) can also serve as impediment for several diseases due to the difficulty for some vectors to reproduce and spread successfully at high altitudes (see section of altitudinal gradients). In this case the effect of the altitude is the same as that of the latitude where high altitudes correspond with high latitudes. Another factor that can influence the existence or act as a disruptor of latitudinal gradients is the different conformation of continents in both hemispheres. This can cause differences in biodiversity distribution as pointed by Chown et al. (2004). The proportion of oceanic to land surface in the Northern hemisphere is approximately 1:1 whereas in the Southern hemisphere is about 16:1 for latitudes between 30 and 60°. This implies a marked influence of oceans in landmasses of the Southern hemisphere generating mild climates as compared to the northern landmasses across the same latitude. Obviously, this affects the distribution and diversity of species at all ecological levels including microorganisms (Merino and Potti 1996; Bonan 2002;

Harvell et al. 2002). The higher extension of landmasses in the East-West direction in Eurasia compared with other continents with a predominant landmass distribution in North-South direction has been also suggested as a potential factor facilitating expansion of diseases across Eurasia, given that conditions did not vary considerably for landmasses across the same latitude (i.e., Eurasia) than in continents where the latitude effect is more marked (Diamond 1997). For example, in the case of southern South America the height and extension of landmass is reduced as we move towards the south. This implies an oceanic influence on the south of the continent that tends to ameliorate the climate favoring the existence and development of vectors and the possibility of diseases transmission, even at high latitudes (Merino et al. 2008). Finally, islands also have a clear effect of oceans on their climate, but usually infections are less frequent due to the lack of appropriate vectors (Scheuerlein and Ricklefs 2004; Barrientos et al. 2014; Gangoso et al. 2019). However, the naïve native avifauna on islands could be severely affected when a new parasite is introduced (van Riper 1991; Parker 2018; see Chap. 8 for a synthesis on island biogeography of avian haemosporidians in the Neotropics).

2.2.3. Recommendations

There are many factors that can influence the finding of latitudinal gradients of bird blood parasites. We should keep these factors in mind when determining if a gradient exist or does not. In this sense, it is necessary to try to homogenize the samples; for example, by habitats and species composition, or preferably by comparing common species. It is also necessary to try to prevent or at least control for the effect of factors such as urbanization, deforestation, the presence of dammed areas, host phylogeny, and the proportion of sampling from different host sexes and ages. Geographical gradients

in prevalence of avian haematozoa may differ between parasite genera and hemispheres, probably in relation to the existence of appropriate vector–parasite–host interactions. In this respect there is much work to be done especially in terms of the distribution of vectors (biting midges, blackflies, ticks, mosquitoes, mites, etc.) and the diseases they spread. In addition, the majority of studies have focused on Europe and North America and it would be of interest to include other geographical areas, particularly tropical ones. It is also recommendable to always include both microscopic and molecular techniques for detection of parasites (Valkiūnas et al. 2006; see Chap. 2 for an introduction to avian haemosporidian life cycles and study methods).

10.3. Altitudinal gradients

Several authors propose that the richness of mammals, reptiles, amphibians, birds, and insects decreases with altitude (Stevens 1992; Ya’Cob et al. 2016). Nevertheless, there is evidence that this rule is only valid for specific taxonomic groups (Rohde 1996). Mountains can be considered as continental Islands due to their isolation from surrounding vegetation, and given their distinctive climatic characteristics some species have evolved *in situ* (i.e., endemics) and species living there need particular adaptations (e.g., hematological changes for high altitudes; Ishtiaq and Barve 2018). In this context, it is generally accepted that the prevalence of parasites decreases with increasing elevation (van Rooyen et al. 2013). However, there are few well-documented reports on haemosporasite population parameters and diversity in tropical areas in relation to highlands and altitudinal effects. Elevational gradients provide an excellent means of understanding the distribution, prevalence, and richness of species and to test what climatic factors influence them the most. Temperature is closely related to elevation, and in only short geographic ranges significant differences in temperature can be

observed. Temperature is a critical environmental factor determining vector presence, host distribution and abundance, and consequently the prevalence of parasites (Jones et al. 2013; Harrigan et al. 2014).

The richness of hosts and the potential vectors that are present in an area are responsible for the prevalence of parasites detected there (Pulgarín-R et al. 2018; Gil-Vargas and Sedano-Cruz 2019). In fact, Poulin (2014) stated that there exists a strong covariance between host and parasite species richness. The primary drivers of the current geographic distribution of parasites are the result of an interaction among ecological and environmental characteristics, physiological features, evolutionary processes, and anthropogenic changes that affect hosts and vectors (Ricklefs 1987, 2004; Jones et al. 2018). To explore this in more detail, we discuss some studies analyzing two of the most important biotic and abiotic factors (i.e., vectors, temperature) that influence parasite prevalence along elevational gradients in the tropics, as well as some study cases.

10.3.1 Vectors

The natural distributional patterns of arthropods, some of them vectors, are largely determined by altitude, temperature, rainfall, and relative humidity (Tanga et al. 2010). The prevalence of haemoparasites also is influenced by arthropod vector abundance, host species, and susceptibility of the host to infection (Atkinson et al. 2001; see Chaps. 5 and 6 for a in depth review of Diptera vectors and their role as vectors of avian haemosporidians and other diseases; see Chap. 11 for a synthesis on avian haemosporidian host specificity; see Chap. 17 for a in depth analysis of experimental parasitology).

Recently, in the Andean Mountains of Colombia, Mantilla et al. (2018)

conducted a study analyzing how the ENSO (El Niño-Southern Oscillation) period affects the prevalence of *Leucocytozoon* and their possible vectors along an elevational gradient from 1800 to 4750 m asl in three different ecoregions: Andean and sub-Andean forest and Paramo. There was a negative association between Simuliidae species richness and elevation, which agrees with findings by Ya’Cob et al. (2016). Moreover, Simuliidae species composition change across ecoregions, and during the ENSO periods there were marked changes in the altitudinal distribution and occurrence of some Simuliid species. The most dramatical changes in simuliid population were observed in the Paramo ecosystem, during el Niño. In this period, warm water is pushed towards the eastern Pacific coast of South America, causing atypical climate changes, and affecting the abundance and distribution of organisms at large scales (Larkin and Harrison 2005). During El Niño, it was not possible to find some *Gigantodax* species, previously detected during la Niña phase (la Niña refers to periods in which surface temperatures at the eastern Pacific coast of South America are lower than average). Besides, the prevalence of *Leucocytozoon* also was different between two ENSO periods, being higher during la Niña. It means that changes in the prevalence of *Leucocytozoon* were directly associated with the dynamic of the observed simuliid communities (Mantilla et al. 2018; Illera et al. 2017).

It is worth noting that in South America the Andean mountains are the only known Neotropical ecosystem where *Leucocytozoon* transmission has been confirmed by both microscopic and molecular tools. This narrowly confined transmission of *Leucocytozoon* contrasts with that observed in the Old World, where transmission occurs both in the lowlands and highlands (Illera et al. 2017; Valkiūnas 2005; Sehgal et al. 2006). Even though in the South American lowlands *Leucocytozoon* is found in migratory birds and the family of their main vector, blackflies (Simuliidae), is also

present and highly diverse (Adler 2019), transmission is not completely demonstrated and only a single report of *Leucocytozoon* detected by molecular tools was recently published (Fecchio et al. 2018c). Lotta et al. (2016) hypothesized that a specific genus of Simuliidae such as *Gigantodax* spp. that is distributed only in the Andean ecosystems might be the vector of *Leucocytozoon* spp. which might explain such restricted distribution. Further investigations are needed throughout lowland areas in the Neotropics in order to rule out the local transmission of parasites of the genus *Leucocytozoon*.

Other important variables, which affect the dynamic of transmission was studied by Atkinson et al. (2014), which compared changes in avian malaria prevalence through a period of 20 years, and the occurrence of mosquito larvae of *Culex quinquefasciatus* along an elevational gradient in the Hawaiian Islands. During that period, the prevalence of infection increased significantly at the three sampled sites across the altitudinal range and was more marked at 1100 m asl. At the same time the detection of *Culex* larvae and the mean air temperature also increased, and those changes were accompanied with declining precipitation and changes in streams flow across the area. Overall, it is important to mention that each vector species can be affected in different ways by the same environmental conditions.

10.3.2. Temperature

Temperature is one of the primary abiotic variables driving elevational distribution of species in different taxa. In this case, it is a very important variable that regulates the development of parasites (Santiago-Alarcon et al. 2012; see Chap. 2). Haemoparasites undergo several developmental stages in vertebrate hosts, which represent a shelter for the parasites from external abiotic conditions. However, haemosporidians need

ectothermic hosts (haematophagous invertebrates) where with few exceptions the sexual cycle occurs and produces the infective parasite stage (sporozoites; see Chaps. 5 and 6). These vectors are affected by climatic conditions (Morand 2015) that positively or negatively impact the life cycle of the parasites they transmit (Lapointe et al. 2010). In this way, it is logical to conclude that variations on parasites' geographic distribution are highly dependent on vectors life history traits and adaptations to abiotic environments such as temperature and humidity, which also affect the parasites speed of development inside the vector.

One of the most dramatic avian haemoparasite impacts is the case of avian malaria in Hawaii caused by *Plasmodium relictum* and transmitted by *Culex quinquefasciatus*; as a result of this exotic pathogen, in addition to habitat loss, fragmentation and destruction, and introduced predators, half of the Hawaiian honeycreepers (Drepanidinae) became extinct (van Riper et al. 1986). Some bird species are altitudinal migrants on the islands, which helped them escape avian malaria transmission. Researchers hypothesized that those birds escaped infection because the mosquito vector was not able to reproduce at those altitudes. However, an elegant study by Lapointe et al. (2010) demonstrated that low temperatures and not the distribution of the vector *Cx. quinquefasciatus* was responsible for preventing the development of sporozoites and consequently *Plasmodium* transmission did not occur in highlands.

Under warmer temperatures the time for the completion of the parasite's cycle in the vectors is shorter (Santiago-Alarcon et al. 2012). The opposite is expected in the highlands where low temperatures predominate. This is one of the explanations that Zamora-Vilchis et al. (2012) provided for the finding of low prevalence of haemoparasites in highlands of Queensland, Australia. However, in the Neotropical region parasites of the genus *Leucocytozoon* are distributed only in the highlands at

altitudes above 2100 m asl, and the peak of prevalence occurs in the Paramo ecosystem (> 3100 m asl). Furthermore, *Leucocytozoon* is the only genus found at 4000 m asl in the Colombian Andes where on average the temperature is low (-4°C with a maximum at 6°C), indicating that *Leucocytozoon* parasites and their vectors are well adapted to these environmental conditions (Lotta et al. 2016).

There is growing concern about the behavior of vector-borne diseases under the scenario of climate change. Given the previously reported effects of ENSO, it is possible that under a scenario of global warming, we could also face the extinction of specialists and the expansion of generalist parasites (Carlson et al. 2017). Along with the expansion of generalist parasites, there would be a gradual change in vegetation composition and structure, and new adaptations of vectors to be able to overcome these novel environmental conditions (Mantilla 2016). Overall, the research findings indicate that host populations at high altitudes in a scenario of climate warming will face population declines and extinctions because of a possible distribution of new vectors and host species migrating from lower elevations, which would represent potential competitors, pathogens, or predators for naïve locally adapted species.

Despite the lack of marked seasons in the tropics (implying favorable conditions occurring year-round for parasite transmission), there are dry and wet seasons, which are also marked variables governing the presence and distribution of avian haemoparasites. For instance, Zamora-Vilchis et al. (2012) reported in birds from the Australian wet tropics that parasite prevalence was positively associated with annual temperature, and it was higher than expected during the dry season independently of elevation. The seasonality of rainfall can also directly impact haemosporidian host specificity in the tropics (Fecchio et al. 2019).

10.3.2. Study cases

Illera et al. (2017) evaluated the prevalence and richness of avian haemosporidians in both Mediterranean and Atlantic temperate mountain ranges, and the main conclusion was that each genus of *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* (Table 10.1) parasites shows different biotic and abiotic preferences, and one of the most critical factors affecting prevalence was host richness. In this study, in agreement with other studies in the old World, parasites of the genus *Leucocytozoon* were found both in lowlands and highlands, in contrast to the current situation observed in the New World.

In South America, the Andes ecosystem is an interesting natural system for the evaluation of the importance of latitudinal and altitudinal gradients in the transmission of avian haemoparasites. In this ecosystem researchers have investigated *Zonotrichia capensis* (Rufous Collared Sparrow), which has a broad geographic distribution from southern Mexico to Patagonia in Argentina, and which occupies open spaces, from sea level to 4600 m asl (Cheveiron et al. 2008; Doussang et al. 2019; Cadena-Ortiz et al. 2018; Mantilla et al. 2016; Escallón et al. 2016). Doussang et al. (2019) evaluated the distribution of avian haemoparasite prevalence in both latitudinal and altitudinal gradients from Central and South America, and they found that in this bird species the most frequent infections are caused by parasites of the genus *Haemoproteus*. However, *Plasmodium* spp. lineage diversity is higher in comparison to *Haemoproteus*. Several studies compared the prevalence of infection in the Rufous Collared Sparrow across elevational gradients in South America, which concluded that despite the fact that at high elevations the overall prevalence of haemoparasites is lower, the elevation at which these phenomena occurs is variable, depending mainly on the landscape features and the ecosystem type (Table 10.1; see section 10.4 and Chap. 14 for anthropic impacts on hosts and parasites).

González et al. (2014) found that in Colombia the prevalence of the genus *Leucocytozoon* increased with elevation in agreement with results from other studies in Switzerland (van Rooyen et al. 2013) and Peru (Galen and Witt 2014); whereas the prevalence of *Trypanosoma* and microfilariae decreased with elevation (Fig. 10.2). The overall prevalence of the genera of *Plasmodium* and *Haemoproteus* did not vary significantly with elevation; however, elevational changes in prevalence were evident when the analyses were conducted at the species or lineage level (Mantilla 2016).

González et al. (2015) and Mantilla (2016) demonstrated that there is a change in the parasite species distribution and their lineages along elevational gradients in the Andean Mountains in Colombia. This is also related to changes in the vegetation, running water, and temperature that changed avian and vector composition. This pattern agrees with the study of Galen and Witt (2014) in the Peruvian Andes, where the elevational distribution of avian haemosporida lineages of the same genus did not overlap, implying a high parasite lineage turnover as altitude changes, which might actually be related to the change of ecosystem types at different altitudes. Zamora-Vilchis et al. (2012) found that avian haemoparasite species richness declined with elevation. Bearing in mind the evidence, it is critical not to make generalizations, since parasite species distributed at high elevations usually are not shared with those found in lowland areas, even *Haemoproteus* or *Plasmodium* lineages, which are widespread along different altitudes (see also Table 10.1).

10.3.3. Recommendations

Avian haemoparasite species and lineages vary along altitudinal gradients depending on the hosts, landscape, and environmental conditions. Future research must consider the species or lineages of the parasite, rather than only considering genera and infection

status. Likewise, we emphasize the importance of examining vector communities at the species level, in order to detect subtle changes in their distribution and occurrence as a function of environmental changes.

Under the current climate change, vector-borne diseases can reach higher elevations and infect naïve hosts. Management plans should be carefully designed to anticipate and to avoid biodiversity losses, and even avoid extinctions of threatened and endemic bird species, particularly in highlands. Understanding how different sources of heterogeneity at the landscape level may influence parasite-vector-host interactions could help with the design of strategies aimed at compensating for the effects of climate change at larger latitudinal and altitudinal scales.

More surveys in tropical regions are needed to be able to make accurate conclusions about avian haematozoa biodiversity, richness, and distribution because current knowledge in the tropics and particularly the Neotropics is still fragmentary and restricted mainly to a few countries (e.g., Colombia, Brazil, Mexico; see also Chap. 1 for a synthesis of the research conducted in tropical areas during the last century, and Chap. 6 for current knowledge on avian haemosporidian vectors of tropical areas).

10.4 Within-landscape gradients

Ecological landscapes are geographical areas that are spatially heterogeneous in some features of interest (e.g., anthropogenic impacts) (Turner et al. 2001). This heterogeneity creates environmental gradients that may influence ecological processes such as parasite-vector-host interactions. There are many different types of within-landscape gradients and they may function as disruptors of other gradients, such as the ones that have been discussed in the previous sections. Some examples of within-

landscape gradients that may influence interspecific interactions involving haemoparasites include distance from water sources, levels of habitat degradation due to human activities, urbanization intensity, vegetation successional stages, interspersed vegetation types such as those existing in altitudinal gradients and on relatively large geographical areas, and incremental levels of exposure to pollutants (Wood et al. 2007; Knowles et al. 2014; Lachish et al. 2011, 2013; Renner et al. 2016; Hernández-Lara et al. 2017). Thus, the focus of this section is at finer scales.

10.4.1. Effect of water

Water sources within landscapes may include lakes, lagoons, natural, and artificial ponds, rivers and tributaries, and finer-scale elements that hold small volumes of water or humidity such as rocks, soil, and live or dead vegetation. Because dipteran vectors require water or at least some moisture for the viability of some stages of their life cycles (Borkent 2004; see Chaps. 5 and 6), these landscape elements facilitate haemosporidian dispersal (Lapointe et al. 2012), and it is likely that some of the most diverse and abundant vector populations for either haemosporidia or other types of haemoparasites are often those inhabiting humid ecosystems (Lachish et al. 2013). Indeed, reported infection rates and richness of haemosporidian assemblages tend to be higher in tropical moist ecosystems in comparison with dry environments (Lacorte et al. 2013). Due to the high humidity in these environments, vector community attributes and prevalence may be high and constant within entire landscapes. It has been reported that mosquito communities in humid landscapes of Central Veracruz, Mexico are very similar in species richness and composition regardless of land use type, changing only in abundance structure (Abella-Medrano et al. 2015). Similarly, temperature was a significantly better predictor of *Plasmodium* spp. prevalence in comparison to moisture

in central Africa (Sehgal et al. 2011). However, in the same study areas, prevalence of *Trypanosoma* spp. was better predicted by moisture and secondarily by temperature and elevation. Therefore, an alternative is that even in these moist landscapes there may be some variations in both vector abundances and haemoparasite prevalence resulting from varying distances to water sources, degree of habitat degradation, within-landscape connectivity or other landscape features that may act as disruptors (e.g., Hernández-Lara et al. 2017; Abella-Medrano et al. 2018).

In environments where moisture varies as a function of vegetation types (e.g., altitudinal gradients), topography determines availability and spatial distribution of water sources such as lakes ponds, rivers, and tributaries (e.g., Swanson et al. 1988). Rivers and tributaries in these landscapes provide well-oxygenated running water, which is necessary for the successful development of the larval phase of dipterans from the Simuliidae family, also known as black flies, the main vectors of Leucocytozoids (Butler et al. 1998). *Leucocytozoon* spp. infections are usually recorded at high altitudes (González et al. 2014; Harrigan et al. 2014), and in these mountainous landscapes prevalence by this genus is often high (e.g. Rodríguez et al. 2009; Gonzalez-Quevedo et al. 2016). Distance to rivers and tributaries in these conditions may influence black fly abundance, causing *Leucocytozoon* spp. prevalence vary according to topographic features in environments having high and intermediate humidity values. However, to our knowledge, the effect of distance from such rivers and tributaries on black fly diversity and abundance and on *Leucocytozoon* infection is currently understudied in tropical regions. One recent study from northern South America, reported that diversity and prevalence of *Plasmodium* and *Haemoproteus* responded to host species and to host by climate interactions, but not to water availability (Pulgarín-R et al. 2018). In contrast, in drier environments that are topographically less complex, recorded prevalence of

Leucocytozoon is usually extremely low (e.g., Belo et al. 2012; Reinoso-Pérez et al. 2016; Ham-Dueñas et al. 2017).

Finally, in dry lands, infection may respond to water availability and seasonal rainfall patterns, but the responses may vary among avian and haemoparasite species. In the UK, for instance, transmission rates of *Plasmodium circumflexum* in Blue tits and in Great tits (*Parus major*) strongly varied among years, and decreased with distance from the Thames river. The effect of the river, however, was not recorded for *P. relictum*, and differences among years in transmission rates were strong (Lasch et al. 2011, 2011). Similarly, it has been suggested that temperature and humidity in arid ecosystems may influence vector distribution and abundance (Belo et al. 2012). Therefore, whenever there is water available, as in proximity to ponds, springs, or other water reservoirs, or during periods of intense rain, prevalence may be high, and infection rates could decrease with distance from these landscape elements (Belo et al. 2012). Therefore, in some dry landscapes such as in Arizona, absence of haemosporidians may result from very limited water availability (Deviche et al. 2005). In other cases, such as in dry scrublands of central Mexico, where local inhabitants build water ponds for livestock management and where the density of these ponds is high, haemosporidian assemblages are species rich and both prevalence and parasitaemia decrease with increasing distance from such water sources, but again, the magnitude of response varies among bird and parasite species (Reinoso-Pérez et al. 2016; Ham-Dueñas et al. 2017). Moreover, in this region, the effect of distance from water ponds may be confounded with habitat degradation (see section 10.4.2 below). Therefore, studies in dry lands where the density of water sources is low and some water sources are away from human settlements, may help to disentangle the effect of water sources from that of other fine scale factors such as small human settlements (e.g., Tinajero et al. 2019).

10.4.2. Human activities

Human activities have dramatically altered the structure and composition of natural landscapes at a massive scale (Primack 1993). These changes may have strong influences on parasite-host-vector interactions (see Chap. 14 for an in depth synthesis of Anthropropic effects on host-parasite interactions). Some examples of human degradation which may alter such relations include land use changes that convert areas covered by natural vegetation to agricultural fields, where avian, vector, and parasite communities may be different from the original ones (e.g., Patz et al. 2000; Abella-Medrano et al. 2015; Hernández-Lara et al. 2017; MacGregor-Fors et al. 2018). Introduction of livestock may promote increased abundance of vector populations (Patz et al. 2000). Establishment of urban areas where vector and parasite incidence may be higher or lower, and their communities may contain novel species and lineages (Patz et al. 2000; Carbó-Ramírez et al. 2017; Abella-Medrano et al. 2018), and introduction of toxic substances such as agrochemicals, metals, and metalloids dumped into the environment by mining activities which may affect hosts and/or vectors (Valkiūnas 2005; Ruiz-García 2017; Santiago-Alarcon and Delgado-V 2017; Monzalvo-Santos 2018). All these types of degradation may create local environmental gradients and alter parasite-vector-host interactions.

Although haemoparasite prevalence seems to be low in urban in comparison to rural areas (Geue and Partecke 2008; Santiago-Alarcon et al. 2019a; see Chap. 14), small human settlements, by modifying the surrounding landscape, may have a different type of effect on interspecific relationships involving haemoparasites (e.g., Tinajero et al. 2019). In semiarid scrublands of central Mexico, for instance, numerous small villages (< 500 inhabitants) were established during the late XIXth. and early XXth.

centuries, and for nearly 100 years, tree extraction and overgrazing by goats have been the most common land uses surrounding these villages. In these areas, the tree layer has been almost eliminated, and due to the browsing by goats, shrubs occur in low densities and are short in height, creating a particularly open habitat. Contrastingly, at relatively large distances from the villages (>10km), scrublands have been subject only to moderate disturbance. In these habitats trees and shrubs occur at higher densities, and shrubs have higher heights. Within this gradient, the highest and lowest haemosporidian parasitaemia values in two bird species, the House finch (*Haemorrous mexicanus*) and the Canyon towhee (*Melozone fusca*), were found in villages and in relatively undisturbed scrublands, respectively (Reinoso-Pérez et al. 2016). It is possible that ecological stress for the House finch and the Canyon towhee is high at the sub-optimal habitat (i.e., villages and surrounding degraded scrublands) and thus, birds' immunological capacity to fight off infections may be impaired. Most water ponds present in these landscapes have been built by humans and are located at or close to the villages. Hence, habitat degradation may be correlated with the presence of water ponds, which provides suitable breeding habitat for vectors. Therefore, additional research is needed to disentangle the potential simultaneous effects of water sources and habitat degradation (e.g., Santiago-Alarcon et al. 2019b). Some additional information supporting the potential effect of habitat degradation pertains to the Black-throated Sparrow (*Amphispiza bilineata*) and the American Kestrel (*Falco sparverius*). These species are well adapted to open habitats (Pidgeon et al. 2003 2006; Smallwood and Bird 2002). A recent study reported significant lower prevalence in Black-throated Sparrows at degraded scrublands adjacent to the villages in comparison to the relatively undisturbed scrublands (Ham-Dueñas et al. 2017). Moreover, ecological stress, measured through the heterophyl/lymphocyte ratio (Ellis et al. 2012), was lower in the

open preferred habitat. The degraded scrublands resemble the preferred, open habitat, for the Black-throated Sparrow; therefore, in spite of being a degraded habitat, this is an almost optimal habitat for the sparrow, where feeding resources are abundant, and competitors as well as predators may occur in low numbers. Regarding the American Kestrel, lower prevalence and parasitaemia values have been recorded in agricultural fields and undisturbed scrublands in comparison to villages (Tinajero et al. 2019). Agricultural fields are open habitats in which some power poles and isolated trees are present; this type of habitat facilitates visibility and provides perches that kestrels use while foraging for mice and small arthropods (Smallwood and Bird 2002). These conditions consisting of abundant feeding resources and presence of habitat elements which facilitate prey acquisition may guarantee an environment where stress is moderate, and thus kestrels may allocate a considerable amount of energy to cope with infection. Moreover, the potential presence of agrochemicals in these agricultural fields may negatively affect vectors and decrease infection rates, thus indirectly providing a benefit to Kestrels.

A study in Venezuela did not detect differences in haemosporidian prevalence and lineage richness between distant sites (>500 km) (Belo et al. 2012) possibly because habitat disturbance in this landscape occurs at a very local scale. There are many other examples of effects of habitat degradation on parasite prevalence in different habitat types, these effects sometimes increase infection rate in some African rainforest birds (Chasar et al. 2009), but they may also decrease prevalence such as in tundra habitats of North America (e.g. Bennett et al. 1992) and in Neotropical montane forests of Veracruz, Mexico (Hernández-Lara et al. 2017), or be neutral (Fokidis et al. 2008; see Chap. 14). The presence and direction of effects of these types of gradients may thus be context sensitive.

10.4.3. Toxic substances

Human-generated substances that may be toxic to organisms, also known as novel entities (*sensu* Steffen et al. 2015), may strongly influence parasite-vector-host interactions (Santiago-Alarcon and Delgado-V 2017). Through anthropogenic activities ecosystems have been exposed to thousands of these pollutants; some of the most common types of toxic substances include agrochemicals, metals that are dumped in the environment by the mining industry, hydrocarbons, and colorants. The purpose of some of these pollutants, such as organochlorine agrochemicals is to control populations of arthropods that attack crops (Landis et al. 2011). Other pollutants, such as metals, hydrocarbons, and colorants are not intended to control arthropod pests. However, many of these novel entities have negative effects not only on arthropods, but also on other organisms, including vertebrates (Santiago-Alarcon and Delgado-V 2017). Because novel entities have the capacity to kill arthropods (Landis et al. 2011), abundance of vector populations is likely to be low in exposed areas, but increase with distance from polluted sites. Consequently, haemoparasite prevalence in hosts may increase with distance from such polluted areas, or may at least be significantly higher in unexposed than in exposed sites (reviewed in Valkiūnas 2005). On the other hand, pollutants may also negatively affect vertebrate hosts through various mechanisms including damage to the DNA, the endocrine and the immunological system, to physiological pathways, morphological changes, and by inducing changes in reproduction and survival rates (Landis et al. 2011). When vertebrates are exposed to such negative effects, their ability to cope with infections may be impaired. Consequently, the probability of acquiring an infection and the intensity of the infection may be higher. Due to the simultaneous

effects of pollutants on both vectors and hosts, the resulting effect is difficult to predict and may vary among bird and vector species depending on the physiological ability to fight infection and to resist exposure to a specific substance. An additional factor to be considered is the combination of different types of pollutants in the environment, and the interacting effects that they may have (Chapa-Vargas et al. 2010; Monzalvo-Santos et al. 2016). The number of studies investigating effects of pollutants on prevalence and infection intensity is very low (reviewed in Valkiūnas 2005), particularly in tropical areas (see Santiago-Alarcon and Delgado-V 2017). However, results of ongoing research suggest that prevalence decrease with increasing amounts of heavy metals (antimony, arsenic, and lead) in feathers of birds from central Mexico, possibly due to the negative effect of these metals on vectors (e.g., Raymis- Keller et al. 1998; Migliorini et al. 2004). In addition, it was estimated that bird physiological stress (estimated through the heterophyl/lymphocyte ratio) was greater in sites exposed to metals than in unexposed sites (Monzalvo-Santos 2018). Similarly, it was found that haemosporidian prevalence and parasitaemia decreased with increasing amounts of organochlorines (endosulfide) in bird feathers (Ruiz-García 2017). In order to better understand the effects of different types of pollutants on parasite-vector-host interactions, investigations involving many different host species in different types of environments, and exposed to different types of pollutants should be implemented. In addition, studies should evaluate how exposure to pollutants influences vector abundances, and prevalence of haemosporidians in birds and vectors, and the concentration of pollutants in vectors themselves should be evaluated.

10.4.4 Recommendations

Field studies should be designed in such a way that within landscape local heterogeneity (i.e., local environmental gradients such as distance to water sources, pollutants, and vegetation structure) can be evaluated in such a way that individual factor effects on host-vector-parasite dynamics can be separated and determined. Within landscapes, there are many other potential factors that may generate environmental gradients; some examples include natural disturbances (e.g., fire, tree fall gaps, floods) and vegetation succession. The effects of these local scale gradients on parasite-vector-host relationships have not been studied, but these effects may be relevant because they can disrupt or act in synergy with the effects of other gradients at both local and regional scales (e.g., van Hoesel et al. 2019).

10.5 Conclusions

There is a vast body of evidence favoring the existence of effects of different types of environmental gradients on parasite-vector-host interactions involving haemoparasites in wild vertebrates. Understanding the fine details related to these gradients is a very complex issue. Often times, the effects are highly dependent on context, and some gradients may interact with the effects of others. Latitudinal gradients, for instance may not be evident if a disruptor such as an altitudinal gradient is present. Moreover, some environmental gradients, such as those imposed by pollution sources may act simultaneously on more than one organism involved in the parasite-vector-host interaction, and the type and direction of response may be difficult to predict. In spite of this complexity, current knowledge indicates that some general trends include higher prevalence, parasitaemia, and parasite lineage richness towards the equator, at lower and intermediate altitudes, at shorter distances from water sources, in degraded habitats, and in areas that are not exposed to pollutants. However, these patterns may not always

hold; therefore, context as well as idiosyncratic responses of individual bird, vector, and parasite species are very important (e.g., Schmitz 2010).

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Figure Legends

Fig. 10.1. Summary of factors influencing host-vector-parasite relationships involving haemoparasites.

Fig. 10.2. Distribution of the prevalence of six parasite taxa by elevation (m asl). PLoS ONE 9: doi: 10.1371/journal.pone.0100695

Table 10.1. Studies investigating avian Haemosporidian prevalence across different elevational gradients. Numbers in parenthesis represent sample sizes.

Species or order (n)	Elevation masl	Prevalence	Sampling sites	Additional information	Author
<i>Zonotrichia capensis</i> (184)	4105 3700 435 80	18% 42% 15% 0%	Peruvian Andes		Jones et al. 2013
<i>Zonotrichia capensis</i> * (13) (26) (15) (20)	3300 2100 1500 600	8% 35% 73% 31%	Ecuadorian Andes	There is no relationship between levels of testosterone (an immunosuppressor) and elevation	Escallon et al. 2016
<i>Zonotrichia capensis</i> * (28)/(125) (60)/ (244) (76)/(427)	1850 2400 2560	3.6%/10.5* 3.3%/26.63 25/10.5	Colombian Andes	Prevalence of haemoparasites vary depending on host species	Mantilla et al.2016.
<i>Zonotrichia capensis</i> (23) (6) (12) (35) (68) (16)	3077 3849 1666 1643 588 104	60.9% 100% 58.3% 35% 89.7% 6.3%	Perú Argentina Chile Chile Chile Uruguay	Prevalence differed markedly between genera. <i>Haemoproteus</i> was most prevalent at higher altitudes up to approximately 2200 m asl, and <i>Plasmodium</i> was most prevalent at lower altitudes.	Dousang et al.2019
<i>Troglodytes aedon</i> (140)	129– 4454	30%	Peruvian Andes	<i>Leucocytozoon</i> parasites strongly associated with montane habitats.	Gallen and Witt 2014
Passeriformes (1445)	28- 2090		Iberian mountains	<i>Plasmodium</i> prevalence and richness was inversely associated to altitude, while <i>Leucocytozoon</i> and <i>Haemoproteus</i> were	Illera et al. 2017

				positively related to altitude.	
Passeriformes and Apodiformes (428)	3227 2182 1235 119	50% 60% 12% 8%	Ecuadorian Andes	Higher prevalence was found at highlands (with lower mean annual temperatures)	Harrigan et al. 2014
Passeriformes and Falconiformes (415)	1650	15%	Chichibu mountains, Japan	The most prevalent parasite was <i>Leucocytozoon</i>	Imura et al. 2013
<i>Parus major</i> (55)			Western Switzerland	Altitude did not affect overall prevalence. However, it influences the genera prevalence: <i>Leucocytozoon</i> parasites are more prevalent at high altitudes, <i>Plasmodium</i> spp. re more prevalent at lower altitudes, and the prevalence of <i>Haemoproteus</i> spp. increases with altitude.	Van Rooyen et al. 2013

* It shows the comparison between avian haemoparasite prevalence obtained only in *Zonotrichia capensis* compared to that of all Passeriformes sampled.