16 Host-parasite interactions and climate change

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16.1 Introduction

Several models predict that climate change will modify the distribution of several diseases. However, although an increasing number of examples of host-parasite interactions modified by climate change exist in the literature, empirical data on this issue are still lacking. Here, I review published findings from the last ten years since the previous edition of this book was published (Merino and Møller, 2010).

We not only incorporate data from papers published since 2010, but also data from several papers published prior to 2010 that were not included in the previous edition. In addition, we include studies on parasites that do not directly affect birds but have similar life cycles to those that do. Although we attempted a comprehensive literature search, some papers may have been overlooked. However, we are confident that the most relevant studies related to this topic have been included.

The differences between the current scenario of climate change and the one presented in 2010 are not considerable, and although some models have been refined and modified, the predictions have not changed substantially (see Rohr et al., 2011). Thus, researchers studying the effect of climate change on bird-parasite interactions still expect an expansion of the geographical range of several diseases and a potential decrease in others, depending on a variety of factors and the idiosyncrasies of each disease (Lafferty, 2009). Furthermore, if the global climate becomes warmer and wetter, parasites in general are still expected to achieve

greater transmission over longer periods, with changes in virulence as a likely consequence (Harvell et al., 2002; Kutz et al., 2005; Polley and Thompson, 2009). However, we must again stress that both parasites and hosts are living beings with the capacity to evolve and adapt, thus making it difficult to predict their exact response to environmental changes (Martínez and Merino, 2011). For instance, many parasites spend a part of their life cycle independent of their vertebrate hosts and, therefore, are highly affected by environmental conditions during that period. In these cases, climate change may severely affect the development and survival of a parasite and thus its transmission to a vertebrate host. In other cases, climate can affect the bird hosts, resulting in changes in population size, behaviour and physiology that make it easier or more difficult for parasites to complete their life cycles (Morley and Lewis, 2014). Parasites can also be brought to new areas by their hosts or switch hosts in response to a reduction in original host abundance and an increase in the abundance of other hosts (Phillips et al., 2010). Introduced host species present a special case. Since they are often free of parasites or resistant to endemic parasites, they can generally outcompete endemic host species. Introduced species can also introduce their own parasites, which may greatly impact endemic host species (Marzal et al., 2011; Lymbery et al., 2014). In any event, we cannot expect to observe a linear relationship between environmental change and parasite populations due to the varying influence of different factors such as environmental thresholds, host resistance, interactions between parasites and between parasites and their predators, or interactions between several of these variables (Sutherst, 2001; Lafferty, 2009).

16.2 Climate change and changes in phenology of parasites and their hosts

Climate and climate change can potentially affect many events in the lives of both hosts and parasites, including their interactions with each other. For example, the breeding season can be adjusted by temperature and rainfall directly or indirectly by their effect on food availability. Changes in the synchrony between breeding season and food availability may have important consequences for host or parasite fitness. Warmer winters or earlier springs due to climate change may alter the magnitude and timing of peak parasite transmission, thus affecting host health (Polley and Thompson, 2009). As a result, climate change is expected to affect the phenology of parasites and hosts, ultimately altering their interactions.

One of the best examples of how phenological changes in response to climate change can influence bird-parasite interactions is the study of cuckoos *Cuculus canorus* and their hosts by Saino et al. (2009). Cuckoos that migrated to Europe for the breeding season arrived late relative to their hosts that were short-distance migrants. There was less of a mismatch between the arrival times of cuckoos and their hosts that were long-distance migrants. Saino et al. (2009) predicted that cuckoo races that specialize on short-distance migrants will disappear, as they will have fewer opportunities for successful parasitism. To further support their hypothesis, they compared areas across Europe that have different degrees of increase in spring temperature, expecting to find less parasitism of residents or short-distance migrants in areas that experience greater increases in temperature. Specifically, they compared the relative frequency of parasitism of two host categories in 23 European countries before and after 1990 and found that parasitism of residents and short-distance migrants decreased, and it was positively related to increases in spring temperature. In conclusion, their data

support the hypothesis that the change in host use by the common cuckoo is at least partially driven by climate change (Møller et al., 2011).

We should interpret these types of results with caution because a study examining the effects of changes in breeding phenology of the great spotted cuckoo *Clamator glandarius* and its magpie host *Pica pica* in Europe found different results in cross-sectional versus longitudinal analyses (Avilés et al., 2014). Cross-sectional analyses, which assess correlations between climate conditions and phenological mismatch between host and parasite at the population level, revealed that climate affects laydate and cuckoos were able to adjust their breeding phenology to that of their magpie hosts. In contrast, longitudinal analyses, which examined within-individual variation in breeding phenology, revealed high individual consistency in magpie host phenology and a low influence of climate. These findings suggest that the phenological mismatch between cuckoos and magpies at the population level is not explained by the host's response to climatic conditions (Avilés et al., 2014).

Other examples that demonstrate changes in phenology of bird parasites linked to climate change are scarce. However, several studies of different tick species that can use birds as hosts have shown or predicted changes in phenology associated with environmental conditions. For example, *Ixodes scapularis* is the principal tick vector of the Lyme borreliosis agent *Borrelia burgdorferi* and other tick-borne zoonoses in northeastern North America. Although the life cycle of this parasite is linked primarily to small mammals and humans, recent research has shown that birds also act as reservoirs, thus contributing to the propagation of these tick-borne diseases (Newman et al., 2015). The seasonal phenology of these ectoparasites is partly controlled by ambient temperature. Therefore, climatic changes may affect the degree of seasonal synchrony of the different tick stages.

Furthermore, seasonal synchrony among tick nymphs and larvae may affect the type of diseases they transmit. Asynchrony between nymphs and larvae will favour the transmission of persistent pathogens by allowing infected nymphs to inoculate a population of naive hosts that can subsequently transmit the pathogen to larvae and complete the transmission cycle. However, synchrony between nymphs and larvae favours transmission of pathogens that produce short-lived infections in hosts (Levi et al., 2015).

In another study, Ogden and collaborators (2008) mathematically simulated the phenology of *I. scapularis* for a site in southern Ontario, Canada under monthly temperatures projected under emissions scenario A2 of the Intergovernmental Panel on Climate Change. Following this, they simulated pathogen transmission in a population of white-footed mice (*Peromyscus leucopus*) using a susceptible–infected–recovered (SIR) model. Their results showed that the fitness of pathogens transmitted by ticks differed according to the seasonal pattern of immature tick activity, which was different for each predicted temperature scenario. Although, in general, long-lived, highly transmissible and low virulent pathogens were the fittest, under some scenarios of seasonal tick activity, the fitness of shorter-lived, less efficiently transmissible and more virulent pathogens increased. Thus, Ogden and co-authors concluded that climate change may affect the evolutionary processes of pathogens transmitted by the tick *I. scapularis* via effects of temperature on tick seasonality.

Using data gathered over 19 years, Levi et al. (2015) analysed the seasonal synchrony of nymph and larval stages of *I. scapularis*. These authors showed that the phenology of nymphal and larval ticks advanced almost three weeks during years in which May and August were warmer compared with years in which these

months were colder. However, increased synchrony was not observed. Warmer weather in October was associated with fewer larvae feeding concurrently with nymphs during the following spring. Based on these data and projected warming by 2050, Levi et al. (2015) hypothesized that the timing of nymphal and larval activity will advance on average by 8–11 and 10–14 days, respectively. Thus, climate warming should maintain or increase transmission of persistent pathogens, but may inhibit pathogens that do not produce long-lasting infections (Levi et al., 2015).

16.3 Climate change and changes in prevalence and intensity of parasitism

Increases in temperatures can accelerate the emergence of some parasitic stages, thus increasing their prevalence and intensity in hosts. For instance, both cercarial production within snails, the first intermediate host of trematodes, and their emergence from these hosts is accelerated in response to temperature increases (Poulin, 2006). Thus, global warming may increase the cercarial output of trematodes, potentially impacting hosts, including bird hosts. However, this impact may be mitigated, to some extent, as higher temperatures also decrease the lifespan of cercariae (Poulin, 2006). These parasites can indirectly affect birds by reducing the amphipod populations on which they prey, as well as directly affect birds through schistosomatid infections, which are associated with changes in climatic conditions (Mas-Coma et al., 2009). These particular trematode parasites have been studied primarily for the cercarial dermatitis ("swimmers itch") they cause in humans swimming in lakes. This disease causes an itchy skin rash but is

not contagious (Horak et al., 2000). The increasing incidence of this disease is associated with climate warming as bird host populations are spending more time in lakes, thus changing their migratory behaviour (Guillemain et al., 2013). The increased presence of birds, along with the accelerated production of cercariae with milder temperatures, has increased the prevalence and intensity of these parasites in lakes that previously never or rarely produced the disease. In Europe, cercarial dermatitis is caused by cercariae of the genera *Trichobilharzia*, *Bilharziella* and *Gigantobilharzia*, all of which are known to parasitize birds (Mas-Coma et al., 2009). These parasites also cause severe diseases in their bird hosts (Levine et al., 1956; Horak et al., 2000).

The nematode *Heterakis gallinarum* presents another potential example that may provide insight into the rise of incidence of parasite infection associated with increases in temperature. This parasite of chickens and related bird species is transmitted after larval development has occurred within eggs previously deposited in the environment. Increases in temperature cause accelerated development of larvae (Más-Coma et al., 2008), and thus, a potential increase in the prevalence of infection by this parasite. As the climate changes, *Heterakis* should be closely monitored as it may have commercial implications for the poultry industry.

Several studies have linked environmental conditions and infections by avian blood parasites (for a summary, see Sehgal, 2015). For example, Sehgal et al. (2011) collected blood samples from olive sunbirds (*Cyanomitra olivacea*) from 28 different localities in central and western Africa and found that temperature was the most important predictor of *Plasmodium* prevalence whereas humidity appeared to be more important for trypanosomes. In another study, Berthelot's

pipits (*Anthus berthelotii*) that inhabited locations with higher minimum temperatures on Tenerife (Canary Islands) were more likely to be infected by malaria (Gonzalez-Quevedo et al., 2014). Some mathematical models have indicated that the prevalence of *Leucocytozoon*, a malaria-like blood parasite of birds, is influenced by seasonal changes in temperature by affecting the emergence of the insect vector, black flies, in the Colorado Rocky Mountains (Murdock et al., 2013). Climate warming is expected to affect the distribution and the incidence of insect vectors, increasing their altitudinal and latitudinal ranges and, as a consequence, affecting the prevalence of the blood parasites transmitted by them. For example, *Plasmodium* prevalence has increased with increasing global temperatures, especially during the last two decades, as shown by Garamszegi (2011; see Figure 1). In this study, the author compiled publications on avian malaria infections over the last seven decades and analysed variation in parasite prevalence in more than 3,000 bird species. The prevalence of other blood parasites has also been positively linked to temperature in a bird community of the Australian Wet Tropics along an elevation gradient (Zamora-Vilchis et al., 2012). This effect has been explained by both the increase in vector abundance with temperature and the accelerated development of blood parasites within vectors at elevated temperatures. Based on the regression of parasite prevalence on temperature found in this study, the authors predicted a 10% increase in prevalence of parasites for each 1°C increment in temperature (Zamora-Vilchis et al., 2012). A similar relationship between blood parasites and altitudinal gradient has also been reported in New Zealand (Niebuhr et al., 2016).

Insert Fig 1. here

In the case of ectoparasites things could be different because they depend more on ambient temperatures for development and completion of their life cycles. Consequently they may be more directly affected by climate change than endoparasites, which once in their bird host are less affected by environmental climatic conditions. However, some ectoparasites live in tight contact with their hosts and it could be expected that direct effects of climate barely affect that parasites. Nonetheless, some studies show how, even in those cases, climate affects ectoparasites. For example, the intensity of feather mites was positively related to temperature across an elevation gradient in five of six species of passerines in Spain (Meléndez et al., 2014). Thus, the effect of climate change along this altitudinal gradient may be affecting mite intensities on their hosts.

Several studies have linked the incidence and the prevalence of the parasitic diptera *Philornis downsi* with climatic events. Although the adult flies feed on fruit, they deposit their eggs in bird nests, and the resulting larvae feed on the blood and tissues of nestlings (O'Connor et al., 2010a), which causes high mortality in some bird species (O'Connor et al., 2010b). Dudaniec et al. (2007) found higher intensities of infection by this parasite in nests of Darwin's finches in a high rainfall year yet lower numbers of parasites in a dry year. However, the authors concluded that this effect is more likely due to an increase in clutch size during years with higher rainfall and not a direct effect of climate on the parasite. This conclusion is in agreement with the results by Koop et al. (2013), who reported that neither the prevalence nor the abundance of *P. downsi* decreased significantly in a dry year compared with an earlier wet year thus concluding that this species is capable of withstanding the extreme climatic fluctuations characteristic of the Galápagos Islands. However, Antoniazzi et al. (2011) reported that high average maximum

temperature and increased rainfall were significantly and positively correlated with mean *Philornis torquans* intensity in Argentinian birds.

In another study, Møller and collaborators (2013) analysed paired information on 89 parasite populations of 24 bird host species using data collected some years ago and again in 2010 with an average interval of 10 years between collection dates. The parasite taxa studied included protozoa, feather parasites, diptera, ticks, mites and fleas. The study finds that non-dipteran parasites (blood-sucking fleas, ticks and mites) were the only group that tended to decrease in prevalence between sampling years although differences with other groups were not statistically significant. However, a significant increase in temperature over time was detected, as was an increase in parasite prevalence and abundance. Nevertheless, these variables were not directly related to each other. This finding, and the fact that temperature can significantly affect host variables such as clutch size and body condition, which are also related to parasite infection, led the authors to conclude that the apparent effect of temperature on parasites was mediated through an effect on hosts.

In a recent study, Castaño et al. (2018) experimentally increased the temperature inside nestboxes of a small passerine, the blue tit *Cyanistes caeruleus*, and assessed the effects on both nest-dwelling ectoparasites and flying insect vectors. An average increase of 3°C produced an average reduction of 5.2% in relative humidity within nestboxes. Although populations of the blow fly *Protocalliphora azurea* (based on pupae) and the mite *Dermanyssus gallinoides* were significantly reduced, other parasite populations were unaffected. The effect of temperature on humidity might have mediated these effects given that several arthropods are highly sensitive to water loss (Figure 2; Castaño et al., 2018).

Insert Fig 2 here

In general, an increase in temperature does not necessarily increase the prevalence and the abundance of parasites. Rather, this is dependent on the association between temperature and other climatic characteristic such as rainfall and the type of parasite and its particular life cycle requirements. In addition, the effects of increased temperatures on hosts may prove to be more important for parasites than any direct effects of climate.

16.4 Range expansion and host-parasite interactions

One of the main predictions of models linking host-parasite interactions with climate change relates to range expansion. Based on a meta-analysis, Chen et al. (2011) estimated that terrestrial vertebrates are expanding their ranges between two and three times faster than previously reported. This study also estimated a distributional change to higher elevations at a median rate of 11.0 metres per decade and to higher latitudes at a median rate of 16.9 kilometres per decade following changes in climate. However, these changes varied considerably among species (Chen et al., 2011). Although parasites and pathogens typically follow hosts in their expansions, there is usually a lag in timing given their absence from host invasion fronts prior to expansion. This absence is likely due to serial founder events in low-density frontal host populations that produce local extinctions and hamper pathogen transmission. Thus, hosts at invasion fronts may temporarily reduce their investment in immune responses, which may facilitate their expansion into new territories. However, the parasites eventually catch up with

their hosts in the recently colonized areas (Phillips et al., 2010). The case of birds is especially relevant for range expansions because birds are highly mobile and thus able to expand their range more easily compared to other vertebrates. Moreover, species with migratory behaviour and those introduced by humans are more likely to expand at a fast rate following climate change.

Some studies have directly or indirectly studied range expansions of bird hosts and their association with climate change. For example, in general, latitudinal and altitudinal changes in the range of avian malaria are expected. Avian malaria is already effectively transmitted in Alaska, and it is expected that the expansion of warmer temperatures due to climate change to more northern regions will extend the northern limit of its transmission, which will also allow the development of other vectors and parasites in those areas (Loiseau et al., 2012). Similar results were found for malaria transmission in France (Loiseau et al., 2013). Increases in temperature and rainfall are also expected to increase transmission of avian malaria at higher elevations as has been predicted for Australia and Hawaii (Zamora-Vilchis et al., 2012; Liao et al., 2015).

A good example of birds potentially expanding the range of disease is the case of *Ixodes scapularis* ticks, the primary tick vector of the Lyme disease pathogen *Borrelia burgdorferi* in North America. The range expansion of *I. scapularis* in Canada has led to the emergence of Lyme disease in that country. Although temperature appears to be the most important determinant for tick population establishment, long-distance dispersal of ticks by migratory birds and local dispersal by resident hosts appear to be the main factors determining tick range expansion (Leighton et al., 2012). By analysing stable hydrogen isotopes of rectrices from birds carrying ticks, Ogden and collaborators (2015) were able to

determine where birds breed and how far north they could migrate. Based on these findings, they concluded that migratory birds have the ability to extend the range of the ticks they carry farther north, even to regions that are presently climatically unsuitable for the establishment of ticks. Thus, under current climate change scenarios, it is expected that ticks will be able to extend their range to more northern regions in the future. In Europe, migrant passerines are known to transport *Ixodes ricinus* ticks infected by a variety of *Borrelia* species to more northern localities (Hasle et al., 2011). Moreover, a range expansion of this tick in some areas of Europe has been predicted on the basis of an ecological niche model under a climate change scenario. However, contractions in other areas have also been predicted (Boeckmann and Joyner, 2014).

Birds are also considered the primary hosts and reservoirs responsible for spreading West Nile virus (WNV). High summer temperatures and heavy rainfall are also associated with WNV transmission. Since the introduction of this virus in the United States in 1999, WNV has been expanding rapidly throughout the country, and new associations with native vectors and birds have been developing (Darsie and Ward, 2005; Tabachnick, 2010). Furthermore, the summer droughts facilitate contact between birds and mosquitoes around the few remaining sources of water, with later rainfalls facilitating the spread of infected birds and mosquitoes. A subsequent period of drought again forces contact between hosts and vectors, thus amplifying the virus. Later rainfalls then allow transmission from infected vectors to humans and other host animals. Although the entry and establishment of WNV in the United States does not appear to be related to climate change, it could have a potential effect on the transmission of WNV (Tabachnick, 2010). Other pathogens affecting migratory birds are expected to increase their

geographic ranges as a consequence of climate change, although the mechanisms linking these effects are still far from clear, and more ecological studies are clearly needed (Fuller et al., 2012). Multiple factors can affect host-switching during range expansion and they merit further research. Distributional ecology (Estrada-Peña et al., 2014), ecological fitting (Agosta et al., 2010) and the biodiversity-buffers-disease paradigm (Civitello et al., 2015) are among those that still need to be explored in depth.

16.5 Climate change and changes in virulence

Virulence is considered the net effect of parasites on their hosts and, therefore, is a factor in host-parasite interactions (Toft and Karter, 1990; Poulin and Combes, 1999). In fact, a parasite can show different levels of virulence in different hosts. Thus, climate change may affect virulence when new host-parasite interactions emerge during range expansions. Climate warming may increase the virulence of parasites infecting newly arrived hosts in the expanded areas, or new parasites may be introduced to native hosts of these areas. In both cases, an increase in virulence is expected if warmer temperatures allow parasites to complete their life cycles more rapidly, thus increasing parasite density (Marcogliese, 2001; see also section 16.3). Similar processes may also affect introduced species and their parasites (Rahel and Olden, 2008). However, there are very few examples of increased virulence mediated by climate change in birds. As noted above, Møller et al. (2013) compared different populations of birds and their parasites across Europe at two different times and found that clutch and brood sizes and body condition were associated with changes in both temperature and parasitism. These

authors suggest that these parasites, perhaps mediated through the indirect effects of temperature, are affecting the fecundity and body condition of their hosts.

Increased virulence can also be observed for West Nile virus (WNV) in migratory bird hosts (and mammals) in which new highly virulent strains have evolved following range expansion (Kilpatrick, 2011). The virulence of these strains may be related to climate, as in the case of the WN02 strain, which evolved in North America and is more efficiently transmitted by mosquitoes. The difference in transmission of this strain increases with temperature under laboratory conditions, as expected if this strain replicates at a higher rate compared with other strains (Kilpatrick, 2011; see 16.4 above).

However, in some cases, lower virulence is observed as increases in temperature reduce parasite populations or their activity. For example, ticks use to find its hosts by climbing vegetation and adopting a sit-and-wait tactic, and this questing activity is reduced at elevated temperatures (Randolph, 2009; Dantas-Torres and Otranto, 2013).

16.6 Climate change and changes in anti-parasite defences of hosts

Adaptations by birds may emerge following changes in bird-parasite interactions due to the effects of climate change. Both increases and decreases in body temperature are known to affect immune responses against pathogens. However, prior acclimation of individuals to thermal conditions removes the immunosuppressive effect of stress (Martínez and Merino, 2011). In any case, the association between thermal stress and immunosuppression leading to a disease episode or an increase in susceptibility has rarely been reported, although several

studies have linked the onset of epidemic outbreaks to extreme fluctuations of heat or cold (Travers et al., 2008; Wegner et al., 2008; McClanahan et al., 2009).

One example in birds is a study of the effect of temperature along an altitudinal gradient on both blood parasite infections and major histocompatibility complex (MHC) variation (Zamora-Vilchis et al., 2013). Although parasite intensity was related to both temperature and MHC variability, the authors did not find a relationship between these two factors, concluding that the relationship between immunity and temperature is indirect and mediated by parasite abundance. Birds have defensive behaviours against parasites that may increase or decrease in function, depending on the level of parasite pressure, a factor that can be affected by climate change. For example, female grooming and nest sanitation activities decrease when ectoparasite infestation was experimentally reduced in nests of pied flycatchers (*Ficedula hypoleuca*) (Cantarero et al., 2013). Thus, increases in the abundance of parasites due to climate change will likely affect the amount of time birds devote to hygienic activities.

16.7 Climate change and changes in coevolutionary interactions

Changes in host-parasite interactions may result from processes in which parasites “missing the boat” offer some advantages to hosts that expand into new areas (MacLeod et al., 2010). However, some diseases adapt easily to new conditions, thus establishing new host-parasite interactions that allow propagation of diseases. An example of this is the aforementioned case of West Nile virus, which has infected new mosquito species in North America and adapted to bird species in that continent (Tabachnick, 2010). Other potential examples of parasites adapting

to new conditions are migratory cuckoos in Europe that adapt to species available for nest parasitism (Møller et al., 2011) or the effect of *Philornis* parasitism on birds in the Galapagos Islands (Dudaniec et al., 2007). In this respect, generalist parasites introduced into new areas/hosts favoured by climate change may have an advantage, although ecological-fitting, the process whereby organisms (in this case parasites) form novel associations with other species (in this case hosts) as a result of the suites of traits that they carry at the time they encounter the novel condition, should also be taken into account (Agosta et al., 2010). Furthermore, the capacity of parasites to adapt to different temperatures may also be the difference between failure and success in establishing a new host (see also Carlson et al., 2017).

16.8 Effects of climate change on bird-parasite interactions: future directions

Birds attract our attention due to their colourful plumages and songs and the ease by which they can be observed. Some of these reasons also contribute to why they are objects of intense research. The contrary can be said of most parasitic species; however, diseases that affect beautiful birds would also be expected to attract great scientific attention. In this chapter, I offer a summary of research advances on bird–parasites interactions related to climate change since the publication by Merino and Møller in 2010. Much of the research attempting to understand how climate change will affect birds and their parasites has centred on certain groups of pathogens, especially zoonotic species that can affect humans. Thus, the majority of the studies that I found link or potentially link climate change with migratory birds are the tick vectors of Lyme disease or the spread of the West Nile

virus. Another disease attracting great attention is avian malaria, probably for its parallels with human malaria. Even for lesser studied parasites, their potential direct effects on humans are the main cause for their study as, for example, in the case of cercarial infections in waterbirds.

It is logical that all of these studies attract our attention. However, more studies on the effect of climate change on the expansion, prevalence, intensity, virulence and coevolutionary relationships of bird parasites are required. Such studies will also be important for humans because birds and parasites are major components of ecosystems (Kuris et al., 2008).

Most studies use data collected in the field to help generate models, including those that make predictions of how changes in temperature may alter future bird-parasite interactions. However, there is still a lack of experimental approaches that produce empirical data to improve these models. The possibility to study bird-parasite interactions under different climatic scenarios also exists, which may provide a better understanding of how these interactions vary with climate effects. The introduction of other variables along with climatic ones in models of bird-parasite relationships have clearly improved our understanding and have shown that even closely related parasites can respond in different ways to the same environmental factors. For example, Pérez-Rodríguez et al. (2013) studied avian blood parasites of different genera in several Iberian populations of blackcap *Sylvia atricapilla* and assess the relative importance of several potential determinants of variation in the diversity of these parasites, including climate, landscape features and host population migration. They found that prevalence and richness of parasites were predominantly related to climate but also to landscape features and host migration. In addition, they found that each parasite genus was

affected in different ways by different variables even when infecting the same host species.

Another promising field of study for bird-parasite-climate research in coming years will revolve around invasive species, including not only those introduced by humans but also those that have extended their ranges. There are very few studies of the potential effect of climate and parasitism on the success of invasive species. However, there is little knowledge about how the expansion of non-native species under a climate change scenario may be affected if these species were freed from their common parasites, or if the potential introduction of pathogens of invasive species may be favoured by climate change. The potential response of bird hosts to new infections is also difficult to predict. Therefore, future research should also focus on whether birds can adapt to new challenges produced by the arrival and the adaptation of new pathogens due to climate change. To date, very few studies have investigated the development of resistance in birds challenged by new diseases (e.g. Atkinson et al., 2013). However, the survival of several bird species will likely depend on their capacity to adapt to the presence of novel pathogens.

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Figure legends:

Figure 1. The relationship between climate change and the prevalence of avian malaria due to *Plasmodium*. The regression line was fitted to the appropriately transformed data (for a transparent illustration, the Y-axis is left transformed). The data points are species observations from different studies and are colored based on the geographic origin (red, Africa; green, Europe; yellow, Asia; blue, North America; orange, South America). Taken from Garamszegi (2011) with permission (©John Wiley and Sons).

Figure 2. Mite numbers were related to temperature ($r_s = -0.564$, $n = 28$, $P = 0.001$) and relative humidity ($r_s = 0.372$, $n = 28$, $P = 0.050$) in blue tit (*Cyanistes caeruleus*) nests following a treatment that increased the temperature inside nests. Data from control (squares) and treated nests (crosses) are shown together. Data from Castaño et al. (2018).