

# Chapter 14

## Anthropogenic Effects on Avian Haemosporidians and Their Vectors



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**Abstract** With a population of nearly 8 billion humans, the planet is going through rapid unprecedented change. Human activities cause deforestation, desertification, urbanization, and climate change, all of which are affecting the tropical regions of the world. For example, it is clear that anthropogenic disturbance in tropical forests can rapidly increase biodiversity loss, and global environmental change may severely further degrade forests in the future. With regard to avian haemosporidians, it is not entirely clear how these changes will affect the prevalence, diversity, and pathogenicity of the parasites, but several studies have provided insights into how human impacts in the tropics will affect birds, vectors, and blood parasites. This chapter summarizes recent work that investigates the human effects on haemosporidian disease ecology.

**Keywords** Anthropocene · Diptera · Haemosporida · Land use change · Landscape epizootiology and epidemiology · Parasite ecology · Urban parasitology

### 14.1 Multiple Threats to Tropical Biodiversity

Human activities have impacted natural environments for at least 10,000 years, mostly through changing landscapes in the form of agriculture, forest management, building of canals and terraces, and more recently through the construction of cities (Piperno 2007; DeClerck et al. 2010; Forman 2014; MacGregor-Fors and

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Escobar-Ibáñez 2017). The main threats to tropical biodiversity are deforestation and habitat fragmentation (Pfeifer et al. 2017), followed by other factors such as land use changes (e.g., agriculture, urbanization) (Aratrakorn et al. 2006; Shochat et al. 2010), species introductions (Marzal et al. 2015), and climate change (Ramírez-Villegas et al. 2014).

### ***14.1.1 Deforestation and Habitat Fragmentation***

Rainforest fragmentation is rapidly affecting all tropical areas of the world, and the number of forest fragments will increase substantially over the next decades (Taubert et al. 2018). The increased numbers of forest edges will impact the overall biodiversity and restructure ecological communities on a global scale (Pfeifer et al. 2017). In general, it is thought that deforestation has contributed significantly to the emergence of diseases, both in humans and in wildlife (Patz et al. 2000; Stephens et al. 2016). For example, we now know that HIV-AIDS originated in chimpanzees (Gao et al. 1999) and that human contact with wildlife in the tropics may lead to further outbreaks of unknown diseases.

Birds are affected by many of the same types of pathogens as humans (viruses, bacteria, and parasites), and thus they can serve as sentinels for the study of emerging diseases. Avian communities are significantly affected by tropical rainforest fragmentation (Ferraz et al. 2007); therefore, we expect that their parasite communities will be similarly impacted. The avian haemosporidian blood parasites have complex life cycles that include two hosts: an insect and a bird (see Chap. 2 for an introduction on avian haemosporidian life cycles and study methods). Based on their ecology, insects and birds will be affected by changing environments differently. Insects will be more sensitive to changes in temperature and microclimates (see Chap. 6 for a synthesis on vectors of avian haemosporidians in the tropics), whereas birds will be affected by changes in forest patch size, shape, isolation, and other landscape features (Carrara et al. 2015). To date, it has been difficult to model exactly how changes in habitat, and in particular deforestation and forest fragmentation, will affect parasite communities.

The major questions that researchers are studying regarding avian haemosporidians can be distributed into three broad areas:

1. How do forest fragmentation and habitat destruction affect the prevalence and diversity of parasite communities?
2. What will be the impact on the distribution of parasite species and will certain generalist species dominate?
3. How will changes in haemosporidian communities affect overall avian health?

Several research studies addressing these questions have been published, but although there are trends in the data, it is clear that more investigations are needed.

Previous research has been done in several tropical areas of the world to answer these questions (Sehgal 2015). In Sub-Saharan Africa, studies have shown that

overall, the prevalence and diversity of avian haemosporidians is quite variable, but deforestation appears to affect parasite communities. For example, in Ghana, in one bird species (*Cyanomitra olivacea*), a decrease in the prevalence and parasitemia of avian malaria was associated with increased forest disturbance (Loiseau et al. 2010). When comparing pristine forests to deforested areas in Cameroon, results showed that the prevalence of the genus *Plasmodium* in the community of birds was higher in the intact forested areas (Bonneaud et al. 2009). Another study in Cameroon analyzed the diversity and prevalence of *Plasmodium* and *Haemoproteus* in two widespread species of African rainforest birds from paired disturbed and undisturbed habitats. Results revealed that in deforested areas, the prevalence of some parasite species increased, while the prevalence of others decreased, highlighting the importance to treat each parasite species/lineage separately (Chasar et al. 2009). More recently, in the Caribbean islands of Guadeloupe and Martinique, areas of high habitat fragmentation were associated with a higher prevalence of *Plasmodium* and *Haemoproteus*. Interestingly, habitat fragmentation was more important than habitat loss in predicting increased parasite prevalence (Pérez-Rodríguez et al. 2018). Thus, the loss of forests and the increase in forest edges with fragmentation will have a profound impact on the overall composition of haemosporidian communities. With these changes in prevalence and parasite diversity, it is becoming evident that wild birds will be affected. The ramifications of these global changes for overall avian health will be an important area of future studies.

### 14.1.2 Agriculture

Archeological evidence (e.g., Mesoamerica) demonstrates that humans have altered tropical habitats in a way that landscapes are dominated by a few tree species favored by humans (DeClerck et al. 2010). Hence, much of the original vegetation in tropical areas has been lost, and most of the human uses include vast extensions of monocultures (e.g., pineapple, banana, oil palm, and cattle ranches creating severe habitat loss and fragmentation; Harvey et al. 2005a). In the future, tropical forests of South America and Africa will be threatened by oil palm development: both regions are characterized as harboring high species biodiversity (Vijay et al. 2016). In Thailand, the conversion of forests to oil palm and rubber plantations reduced bird species richness by 60%. Species of insectivores and frugivores appear to be most affected (Aratrakorn et al. 2006). The same pattern has also been reported for other vertebrate (Danielsen and Heegaard 1995), as well as invertebrate taxa (i.e., beetles) (Chung et al. 2000). However, there are crops that are more biodiversity friendly, such as shade coffee and shade cacao plantations, that when dominating the landscape matrix provide refuge to wildlife unable to thrive in habitats that differ from the original ones (e.g., sun coffee; Rice and Greenberg 2000; Harvey et al. 2005a; Bisseleua et al. 2008; DeClerck et al. 2010; Clough et al. 2011; MacGregor-Fors et al. 2018). At smaller regional and local scales (range between <10 m and 200 km), it is important to consider heterogeneity in land uses. At such

scales, landowners do not equally manage bio-friendly plantations where land use change, soil type, and biotic interactions become more relevant, and their influence will have different impacts depending on the taxonomic group or interaction under study (Greenberg et al. 1997a; Cruz-Angón and Greenberg 2005; Harvey and González Villalobos 2007; Philpott et al. 2008; also see Peterson et al. 2011 for a review). For instance, at a local scale, birds were more abundant in forests, bats in riparian forests, and beetles in secondary forests (Harvey et al. 2006). Moreover, without a tree stratum in the matrix, biodiversity will decline, and ecosystem services will be lost (DeClerck et al. 2010), which is particularly relevant for avian species, such as frugivorous birds, that are sensitive toward deforestation (e.g., Luck and Daily 2003). Landscape features, such as forest patches and living fences (i.e., fences delimiting private properties constructed using live trees) connecting such patches, are relevant for biodiversity conservation (Harvey et al. 2005b). In open habitat types (e.g., cattle ranches), the presence of living fences or some isolated trees are required for maintaining higher species richness and connecting local forest patches (Greenberg et al. 1997b; Lang et al. 2003; Harvey et al. 2005b). Therefore, it is a priority to understand how the different land use types change the landscape matrix and affect biodiversity (see Chap. 13).

Focusing on birds, it is known that responses to landscape matrix composition will depend on local conditions and functional groups (e.g., Deconchat et al. 2009). For instance, in the Atlantic forest of Brazil, small isolated native vegetation patches surrounded by a low permeability matrix (e.g., sugar cane) were particularly detrimental for understory insectivores due to their low dispersal capacity, making apparent the need to create a connected landscape (Uezu and Metzger 2011). In some regions, it is more beneficial for birds to have a large connected landscape of small native vegetation patches compared to a single large patch, in particular when species assemblages are not deterministically structured and nested (i.e., species found in several small patches are not a subset of species found in a large forest patch; several small patches can contain more species than a single large one, e.g., Mohd-Azlan and Lawes 2011). Generalization of biodiversity patterns at large geographical scales can be misleading; therefore, for effective biodiversity conservation, the study and understanding of the local landscape context is necessary.

### **14.1.3 Urbanization**

The urbanization process has rapidly increased during the last decades, and cities around the world are becoming a common feature of landscapes (Alberti 2008; Forman 2014). More than half of the human population will be living in cities by the year 2050, imposing environmental demands at different spatial and temporal scales (McDonnell and Pickett 1990; Grimm et al. 2008; Montgomery 2008). Due to major landscape modifications related to the settlement of novel urban structures and to cover human basic needs (e.g., food, energy, water; McDonnell and Pickett 1990), urbanization has been identified as a major threat to biodiversity (Czech et al.

2000; McKinney 2002; Berkowitz et al. 2003; Alberti 2008; Shochat et al. 2010), directly affecting >3000 species listed as threatened or near-threatened according to the IUCN Red List (Maxwell et al. 2016). The most important threats to birds arising from the urbanization process are predation by cats, collisions with windows and with vehicles; together these factors amount to billions of death birds in the USA and Canada (Loss et al. 2015). Although less well documented, the same pattern arises in Latin American cities (Santiago-Alarcon and Delgado-V 2017).

At large spatial scales, there are high similarities in bird species richness between urbanized and semi-natural systems (Pautasso et al. 2011). When zooming into the urban landscape, complex patterns can be identified. For example, in the southwestern part of Mexico City, bird communities are dominated by a few generalist species in areas with commercial components, whereas there is higher evenness in green areas, suggesting that species richness and abundance are sensitive to site-specific characteristics (Ortega-Álvarez and MacGregor-Fors 2009). Within the urban landscape, granivores and insectivores dominate the avian community in the green areas, whereas omnivores are the dominant guild in the residential and commercial areas (Ortega-Álvarez and MacGregor-Fors 2009). In India, urban bird communities are dominated by granivores and omnivores with clear absences of insectivores, which are present in forested rural areas (Sengupta et al. 2014), suggesting that urbanization tends to homogenize avian communities. Hence, urban features of the landscape must be considered in biodiversity studies, as some characteristics of the urban matrix, such as urban forests and greenspaces, are highly valuable for bird conservation (Croci et al. 2008; Aronson et al. 2014; MacGregor-Fors et al. 2018).

#### 14.1.4 Introduction of Species

Another factor relevant for the conservation of native birds is the introduction of exotic species or biological invasions due to human activities (Mack et al. 2000). When organisms reach new areas they have to face novel environments and challenges, and the few that become naturalized may turn into a latent threat to native species (e.g., *Passer domesticus*, MacGregor-Fors et al. 2010) because they have escaped from their natural enemies (e.g., Turchin et al. 2003; Marzal et al. 2011) and found areas where they can thrive and displace native birds (MacGregor-Fors et al. 2010; Jiménez-Peñuela et al. 2019; Santiago-Alarcon et al. 2019). In general, invasive organisms can cause extinctions of native species via predation, competition for food, habitat modification, alteration of species interactions, and introduction of novel pathogens (Mack et al. 2000; Roemer et al. 2002; Perkins et al. 2008; Marzal et al. 2015). In the case of birds, the successful establishment of introduced species hinges on their population of origin in terms of growth rate, dispersal capacity, and life history (e.g., minimum population size to avoid Allee effects, geographical range size), characteristics of the place of introduction (e.g., climate), and specific features of the introduction event, such as the number of birds introduced to the new location (Duncan et al. 2003). Because most bird introductions begin with

small numbers, they usually fail to establish (Pimm 1991). The success of an introduction also decreases when there are large differences in terms of physical conditions between the original and introduced environments (Duncan et al. 2003). Given that human activities homogenize the environment (Aronson et al. 2014), bird species able to adapt to such conditions (Fischer et al. 2015) will be more likely to become invasive outside their native ranges. The invasive birds could potentially be more resistant to both native and exotic pathogens as compared to native birds (e.g., avian malaria; van Riper et al. 1986; see Chap. 15 for a review of invasion biology and parasites).

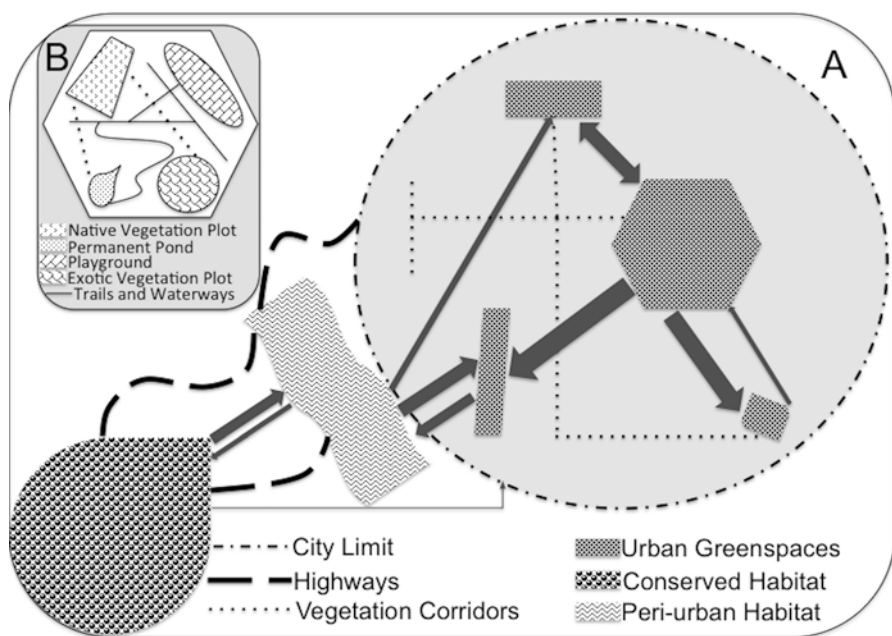
### **14.1.5 Climate Change**

Climate change in the last century caused by anthropogenic activities has generated shifts in the range, abundance, survival, phenology, disease emergence, reproductive success, and extinctions of many species (Condit et al. 1996; Pounds 2001; Hickling et al. 2006; Lavergne et al. 2006; Menéndez et al. 2006; Parmesan 2006; Wilson et al. 2007; Lurgi et al. 2012). Though climate change is generally not considered to be the primary threat to biodiversity at present, it will become the main conservation concern in future decades (Jetz et al. 2007). In general, species will move to higher latitudes and higher elevations in order to find “similar” climatic conditions (Wilson et al. 2007; Chen et al. 2011; Ramírez-Villegas et al. 2014). Studies in the tropics indicate that species from lowlands would have to travel longer distances in order to find suitable climatic conditions, which would increase their vulnerability to climate change depending on their dispersal capacity (Bertrand et al. 2011). Perhaps the most endangered habitats are the alpine forests, grasslands, and shrublands because of the drastic and accelerated reduction of suitable climatic conditions: it is likely that high altitude species will face higher extinction risks (Pounds 2001; Williams et al. 2007).

### **14.1.6 Conclusion**

Summarizing, all of the above-discussed human factors that impact biodiversity via global environmental changes have led to the new geological epoch known as the Anthropocene, mainly due to increases in global temperature, climate anomalies, pollution, and species declines (Waters et al. 2016). For example, historical museum bird collections (spanning 100–150 years) have demonstrated increases of toxic chemicals that bioaccumulate (e.g., mercury), increases in prevalence of infectious diseases, as well as changes in diet and migratory routes (Schmitt et al. 2018). One of the most threatened avifauna is the endemic Hawaiian honeycreepers that currently face habitat loss, invasive species including predators and pathogens, and their precarious situation will be exacerbated by climate change (Paxton et al. 2018).

Conservation management suggestions include mosquito control, protection of key habitats for forest birds, disentangling the genetic underpinnings of disease immunity, predator control, reintroductions and translocations, and increasing captive breeding efforts among others (Paxton et al. 2018). A prime example of conservation success is the avifauna of the Galapagos Islands, where no recorded extinctions exist and successful eradication programs of non-native species (e.g., goats, pigs, pigeons) have been successfully completed (Parker 2018). However, more severe El Niño events due to climate change could endanger endemic birds that have small population sizes such as the Galapagos penguin (*Spheniscus mendiculus*) and the Galapagos cormorant (*Phalacrocorax harrisi*), an effect that can act in synergy with native and non-native parasites (Santiago-Alarcon and Merkel 2018). Moreover, a host generalist ectoparasitic fly found in nests, *Philornis downsi*, causes high mortality in chicks of various bird species and is currently the ectoparasite which poses the most serious conservation challenges for native birds in the Galapagos archipelago (Fessler et al.



**Fig. 14.1** (a) Regional landscape showing native pristine and modified habitats (e.g., conserved forests, peri-urban forests, city), connected by animal dispersion (arrows; the thickness of arrows indicates influx rate among habitats). (b) Detail of an urban greenspace, where a large degree of heterogeneity is observed in habitat structure at this local scale. This scheme conveys a visualization of available regional species pools and potential ecological interactions at different spatial scales, where metapopulation and metacommunity dynamics can easily develop, even within cities (see b for the heterogeneity of an urban greenspace; e.g., Carbó-Ramírez et al. 2017), for both free-living organisms and their symbionts

2018). Hence, a current major research focus in bird conservation is the ecology of pathogens, particularly in relation to anthropogenic impacts (Fig. 14.1).

## 14.2 Consequences of Human Activities on Host–Parasite Dynamics

Environmental changes and biodiversity loss favor generalist vectors and parasites, increasing the risk of host-switches and emerging diseases in wildlife (Hernández-Lara et al. 2017; Abella-Medrano et al. 2018). Homogenization of host communities could lead to an amplification effect, meaning there would be more competent hosts (or vectors). The increase in the abundance of competent hosts means that the chance of a vector feeding on an infected individual and passing the parasite to another susceptible host is higher, having as a result an increase in infection rate (see Ostfeld et al. 2008). Genetic diversity is also affected by alteration and destruction of natural habitats; a decrease in hosts' genetic diversity could have a negative effect on their ability to respond to infections (Vourc'h et al. 2012). Particularly, endemic species and isolated populations could be at risk of extinction and should become a conservation priority. Transformation of natural habitats into agricultural lands, cattle ranches, and cities can pose a threat to less adaptable species in terms of behavior, for example, by increasing competition for resources (e.g., food, water, breeding sites). This competition and resource scarcity may generate significant stress on birds, causing potential negative effects on immune responses and host health.

### 14.2.1 Abiotic Factors Are Determinant for Parasite Distribution

Some of the factors explaining the prevalence of avian Haemosporida through disturbance gradients are temperature (Sehgal et al. 2011; Gonzalez-Quevedo et al. 2014), precipitation (Jones et al. 2013), proximity to water bodies (Mendenhall et al. 2013), and pollution (Bichet et al. 2013) (Table 14.1). Temperature, precipitation and water bodies are mainly related to the parasite's development within the vector. Temperature limits the completion of sexual life stages of haemosporidians within the vector (Paaijmans et al. 2013). Particularly, *Plasmodium* spp. require warmer temperatures (LaPointe et al. 2010), while species of *Leucocytozoon* are favored by lower temperatures (Carlson et al. 2018). But even species from *Leucocytozoon* and *Haemoproteus* have a temperature threshold under which they cannot complete their life cycle within the vector. Precipitation is another abiotic factor closely related to the transmission of avian



**Table 14.1** Studies of avian Haemosporida focusing on the effects of habitat anthropogenic changes to host-parasite interactions in tropical regions

Site	Vegetation type/land use	Host species	Parasitological parameter	Response direction	Explaining variables	Reference
Cameroon	Mature rainforests and agroforests	Tufted olive sunbird (Nectariniidae), yellow-whiskered Greenbul, and little Greenbul (Pycnonotidae)	Pr (P)	+	Undisturbed sites	Bonneaud et al. (2009)
			Pr (H, L)	+	Undisturbed sites	Chasar et al. (2009)
Cameroon	Undisturbed rainforests and agricultural sites	Olive sunbird (Nectariniidae)	Pr (P)	=	Disturbed vs. undisturbed	
			Pr (L)	+	Undisturbed sites	
			Pr (P)	+	Disturbed sites	
			Pr (P)	-	Fragmented forest and young oil palm plantation	
Cameroon	Undisturbed forests, fragmented forests, and young palm oil plantations	85 species (27 families)	Pr (H)	=	Disturbance	Tchoumou et al. (2020)
			Pr (P)	+	Tree cover and precipitation	
Ghana	High deforestation and drier, low deforestation, intermediate	Olive sunbird (Nectariniidae)	Pa	+	Least disturbed site	Loiseau et al. (2010)
			Pr	=	Disturbance	
Brazil	Intact and disturbed Cerrado, transition area Amazonian rainforest-Cerrado	122 species (29 families)	Pr	+	Most disturbed site	Belo et al. (2011)
			Pr	+	Disturbed (urban) vs. intact Cerrado	
			Pr	=	Transition area and intact Cerrado	
			Pr	=	Transition area and disturbed (urban) Cerrado	

(continued)

Table 14.1 (continued)

Site	Vegetation type/land use	Host species	Parasitological parameter	Response direction	Explaining variables	Reference
Costa Rica	Vegetation type/land use Landscape features, spatial scales, and landscape habitat configurations	Orange-billed nightingale-thrush (Turdidae)	Pr (P)	+	Proximity to the nearest river	Mendenhall et al. (2013)
				+	Increased forest element edge and decreased forest element area	
				+	Smallest forest elements and most deforested agricultural plots	
Tenerife	Anthropogenic, natural, biotic, and abiotic environmental factors	Berthelot's pipit (Motacillidae)	Pr (P)	+	Minimum temperature of the coldest month	González-Quevedo et al. (2014)
				+	Interaction distance to artificial bodies of water and minimum temperature of the coldest month	
				=	Host density	
				=	Vegetation type	
				-	Distance to artificial bodies of water	
				-	Distance from the nearest poultry farm	

Mexico (contrasted with Germany)	Urban greenspaces from three biogeographical regions	27 species (17 families)	Pr	=	Nearctic and Neotropical sites	Carbó-Ramírez et al. (2017)			
							Pr	-	Paleartic vs. Neotropical
							Pr (P)	+	Neotropical vs. Nearctic
							Pr (P)	+	Neotropical vs. Palearctic
							Pr (P)	=	Nearctic vs. Palearctic
									Host community composition higher at Neotropical site
Mexico	Cloud forest, shade coffee plantation, periurban forest, urban greenspace, and cattle ranch	Chestnut-capped Brushfinch (Emberizidae)	Pr	+	Urbanization	Hernández- Lara et al. (2017)			
			Pr (P)	-	Bush cover <sup>a</sup>				
			Pr (P)	-	Canopy cover <sup>b</sup>				
			Pa	+	Urban forest				
			Pa	-	Shade coffee plantation				
			Pa	-	Bush cover				
			Pa	+	Leaf litter ground cover				
			Ag	-	Cattle field <sup>b</sup>				
			Ag	+	Preserved forest <sup>a</sup>				

(continued)

Table 14.1 (continued)

Site	Vegetation type/land use	Host species	Parasitological parameter	Response direction	Explaining variables	Reference
Ecuador	Preserved rainforest and forest fragments	18 species (8 families)	Pr (P, H)	=	Disturbance gradient	Rivero de Aguilar et al. (2018)
Mexico	Non-urban (agricultural) and urban	House sparrow (Passeridae)	Pr	-	Urban vs. non-urban	Santiago-Alarcon et al. (2018)
Mexico	Cloud forest, shade coffee plantation, periurban forest, urban greenspace, and cattle ranch	Common chlorospingus (Passerellidae)	Pr (H) Pr (P) Parasite richness	- + -	Urbanization Urbanization Urbanization	Hernández-Lara et al. (2020)
Islands of Guadeloupe and Martinique	Habitat loss, habitat fragmentation, and landscape heterogeneity	Antillean bullfinch (Thraupidae)	Pr (P, H)	+	Forest fragmentation	Pérez-Rodríguez et al. (2018)

(Pr) prevalence, (Pt) parasitemia, (Ag) aggregation, (P) *Plasmodium*, (H) *Haemoproteus*, and (L) *Leucocytozoon*

<sup>a</sup>Dry season

<sup>b</sup>Rainy season

Haemosporida, as well as the presence of permanent water bodies. During the rainy season, precipitation creates temporal ponds and small water reservoirs in plants (i.e., phytothelmata) that are necessary for the development of the larval stages of dipteran vectors. This, in turn, allows an increase in blood-sucking dipteran populations and subsequently the transmission of blood parasites. Therefore, at sites with marked seasonal precipitation, there is generally a peak of infection during the rainy season (Cosgrove et al. 2008). Another factor is environmental pollution, which can reduce the ability of a host to fight off infections, exposing birds to pollutants that make them prone to acquiring infections (Bichet et al. 2013), and dying due to high parasitemia.

### ***14.2.2 Alteration of Forest Structure Modifies the Host–Parasite Interaction***

Vegetation structure is related both to the life history of insect vectors and vertebrate hosts and is therefore a complex variable to study. For example, a forest with dense tree cover would produce a thick layer of leaf litter, favoring the development of food resources (e.g., arthropods) for some bird species. In addition, a forest with dense tree cover would have more breeding and perching sites for birds and, in theory, would yield flowers, nectar, and fruits (important food sources for birds). Thus, we could expect that birds living in a habitat with plenty of resources would be in better condition and immunologically better prepared to fight off infections. On the other hand, a dense tree cover would create favorable microclimatic conditions for the development of dipterans, which could increase the risk of infection if abundant species are competent vectors. Proximity to the edge of the forest has been identified as another important variable explaining the parasitemia of avian Haemosporida, where parasitemia increases as birds are closer to the edge (Knowles et al. 2010). Near the edge of the forest, food resources become scarce and predation increases, both considered to be stressing factors for birds (Knowles et al. 2010). As stress negatively impacts the host immune response (Sapolsky 1992; Loiseau et al. 2008), it leads to a higher probability of a bird acquiring an infection, presenting high parasitemia, and even dying from the infection. Pollutants have been related to a suppressed immune response, reducing host fitness, and increasing host mortality (Sehgal 2015).

There are only a few studies in tropical areas focusing on the effects of land use change (Hernández-Lara et al. 2017) and urbanization (Carbó-Ramírez et al. 2017; Santiago-Alarcon et al. 2018) on host–parasite dynamics of avian haemosporidians (Table 14.1). In some cases, prevalence increases with habitat disturbance (Belo et al. 2011), but in others, the result is the opposite (Bonneaud et al. 2009), or even prevalence may remain similar across disturbance levels (Chasar et al. 2009). So, it seems that responses to habitat disturbance are dependent on the specific host–parasite system and location under study. The ability of a host to control an

infection is related to its ability to cope with habitat disturbance in terms of its stress response, adaptability, tolerance to infection, as well as its competence to host generalist parasites (as they become dominant in disturbed habitats; Hernández-Lara et al. 2020).

### ***14.2.3 Urbanization, an Extreme Habitat for Parasites***

Cities represent the most drastic habitat alteration because all the environmental factors (temperature, water availability, vegetation structure) and host and vector diversity are considerably altered when compared to their undisturbed counterparts. The effects of urbanization on the dynamics of bird-Haemosporida systems have mainly been studied in temperate regions, where the diversity of hosts, parasites, and vectors is much lower than in tropical areas (e.g., Fokidis et al. 2008; Evans et al. 2009). Another important difference is that urbanization develops differently across countries. In some places, it develops in an organized manner, but in others the development is erratic without much urban planning (MacGregor-Fors and Escobar-Ibáñez 2017). Therefore, results from different countries, in particular between temperate and tropical regions, should not be generalized.

Within cities, only a handful of native species remain and are subject to new threats and stressing factors (Santiago-Alarcon and Delgado-V 2017), having to compete for resources with non-native species that are well adapted to cities (e.g., pigeons). They have to face new predators (domestic cats and dogs), pollution (e.g., chemicals, noise, light), and other urban elements such as buildings and cars (Seress and Liker 2015). One would think that this is not a problem for birds because they can fly long distances, but in fact, some forest birds may not be able to move from one patch to the other (e.g., chestnut-capped brush finch). Hence, isolation of small populations could potentially lead to local extinctions. However, in some cases, birds are confined to parks and greenspaces, which can serve as refuge for birds not adapted to highly built areas (e.g., urban avoiders, urban utilizers). Actually, urban greenspaces have been shown to harbor high richness of avian haemosporidian lineages across different biogeographical regions, suggesting that urban greenspaces are important reservoirs for biodiversity and are able to keep similar ecological dynamics to nonurban counterparts (Carbó-Ramírez et al. 2017; Fig. 14.1). Furthermore, environmental conditions within urban areas differ from those in the surrounding environments, which can generate urban heat islands (i.e., increased temperature at local and micro spatial scales within cities), improving conditions for parasite year-round transmission (e.g., Buczek et al. 2014). For example, higher temperatures within cities and stable water sources can allow the permanent presence of insect vectors throughout the year in temperate areas, opening opportunities for continued parasite transmission, which might negatively affect hosts during winter months when resources are scarce, damaging their immune response as a result of lower body condition compared to conspecifics inhabiting more suitable nonurban habitats (e.g., Jiménez-Peñuela et al. 2019; Fig. 14.1). At the individual level,

there are immunological responses to habitat alteration, in particular to factors (e.g., chemicals, pollution) that directly affect organisms' health (e.g., Martin and Boruta 2014). In the case of host–vector–parasite interactions, depending on the system under study, it would be possible to observe amplification or dilution effects in response to human habitat alteration (Fig. 14.1).

As mentioned above, anthropogenic changes have facilitated the invasion and colonization of introduced species (Mack et al. 2000). When a bird species expands its distribution or is introduced to new sites, sometimes it carries with it its parasites. Host-switching of these parasites to naïve hosts can have catastrophic consequences if they are competent (i.e., novel weapon hypothesis). A very well-studied case is the introduction of avian malaria (*Plasmodium relictum*) and its vector, *Culex quinquefasciatus*, into the Hawaiian Islands. The infection of naïve competent hosts caused an alarming decrease and extinction of several populations of Hawaiian endemic forest birds (Atkinson and Samuel 2010). Fortunately, some of the endemic honeycreepers have adapted to the parasite and started to recolonize lowland areas where avian malaria has become endemic (e.g., Woodworth et al. 2005; see Chap. 15).

#### 14.2.4 Spread of Parasites with Climate Change

Understanding the key variables explaining host–parasite dynamics are crucial to predict future outcomes to specific anthropogenic changes and also to climate change. Some studies have identified temperature and precipitation (Jones et al. 2013; Gonzalez-Quevedo et al. 2014) as key variables explaining the prevalence of avian Haemosporida. With climate change, temperatures are expected to increase at rates never presented before. Higher temperatures would promote the development of Haemosporida within the vector in sites that are now too cold to allow completion of sexual stages. Likewise, areas that are currently too dry might become ripe for avian haemosporidian invasion if precipitation increases. On the other hand, regions that are presently ideal for vectors may in the future become inhospitable for parasite transmission (Lafferty and Mordecai 2016). Overall, however, we could expect a geographical expansion and/or relocation of the distribution of avian Haemosporida from the tropics into temperate regions, and the colonization of higher elevations and areas that are currently arid (see Chap. 9 and 10 for an introduction to macroecology and a synthesis on environmental gradients in relation to avian haemosporidians).

Several studies have begun to interpret how climate change will affect avian haemosporidians. For example, one work modelled prevalence data from 70 years and reported that avian *Plasmodium* prevalence mirrors the recent increases in temperature associated with global climate change (Garamszegi 2011). Pérez-Rodríguez et al. (2014) investigated how climate change may affect the three major genera of avian haemosporidians. The authors modelled that, with climate change, the overall diversity of parasite lineages will decrease, with an overall homogenization of

parasite diversity. A more recent study predicts that host specialization will also be affected by climate change, given that at present, host specialists are generally found in areas that exhibit more pronounced rainfall seasonality and wetter dry seasons (Fecchio et al. 2019). Thus, with increased temperatures, the ratios of generalists to specialists are likely to increase, which could impact bird populations that have not previously been exposed to certain lineages of parasites.

Two examples of areas of concern for bird populations are Hawaii, where endemic birds suffer severely from avian malaria, and also the high latitudes, where birds may never have been exposed to avian haemosporidians. In the islands of Hawaii, the mosquito *Culex quinquefasciatus* populations are expected to reach higher elevations, thus threatening the remaining honeycreepers (Fortini et al. 2015). Current research has focused on predicting and mitigating the impact of climate change on the remaining birds, possibly by translocating threatened populations, releasing sterile male mosquitoes, and allowing for the evolution of tolerance (Fortini et al. 2017; Liao et al. 2017). In addition to populating higher elevations, avian malaria will likely spread to higher latitudes. Models have shown that in Alaska, and also in France, avian malaria will expand northwards with climate change (Loiseau et al. 2012, 2013). Regarding climate change, it will be important to recognize that each bird species, insect vector, and parasite may respond differently and have differing thermal tolerances. Thus, although predictive models are useful, it is likely that the rapid changes will have unpredictable consequences in terms of changes in overall haemosporidian diversity and prevalence.

### 14.2.5 Conclusion

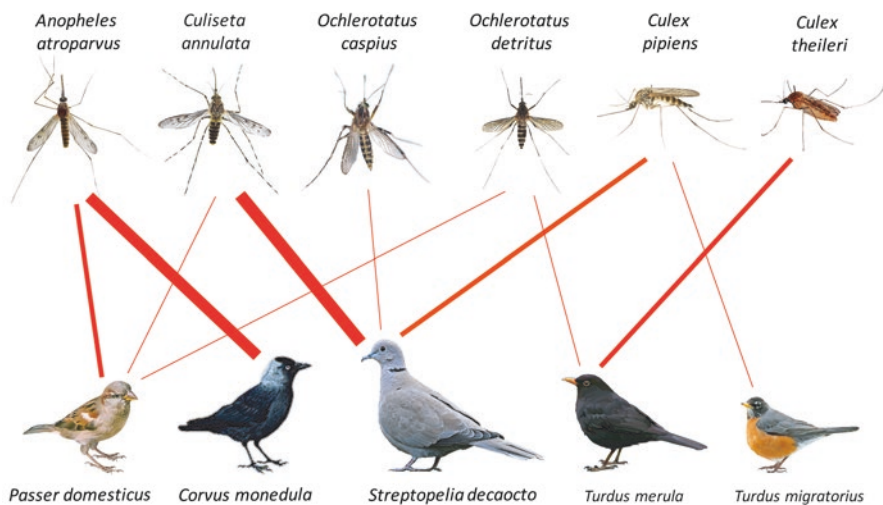
Habitat destruction and transformation into agricultural lands and urban areas pose a threat to biodiversity and will affect host–parasite interactions, leading to a homogenization in the diversity of hosts, vectors, and parasites. Also, more frequent contact between native and introduced fauna could lead to parasite host switches and disease emergence. It should be noted that not all bird species respond equally to habitat disturbance. Therefore, a specific disturbance could have a negative effect on the prevalence, parasitemia, and diversity of haemosporidians for one species, but others could benefit from the same disturbance or even have no response at all. Within habitat transformation classifications, urbanization is the most drastic of them, given that only a few species can thrive in the typical city landscape (i.e., urban exploiters). However, preserving well-connected forest patches and other green spaces (e.g., parks) within cities can preserve an important amount of native bird and parasite diversity. Increases in temperature and precipitation due to global warming would favor the development of vectors and haemosporidians (*Plasmodium* spp.) within them, increasing the probability of transmission. Increases in temperature and precipitation could also expand the distribution of parasites and vectors, affecting bird populations that are not currently exposed to specific parasite lineages. Therefore, in order to take successful conservation actions for birds and other



fauna, it is imperative to understand the processes driving parasite transmission and host susceptibility that could help predict and mitigate possible disease outbreaks.

### 14.3 An Integrative Approach for the Study of Vector-Borne Diseases

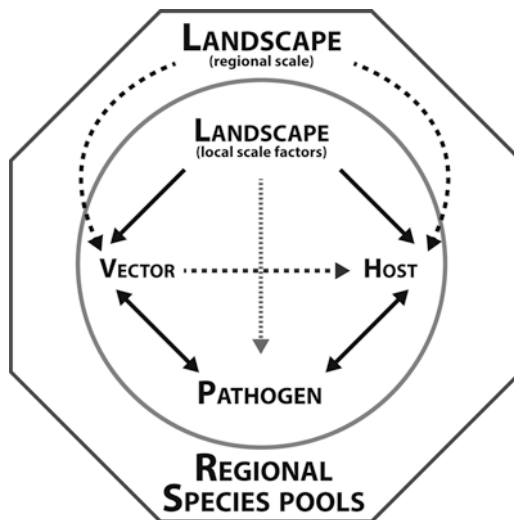
In recent years, the number of emerging and re-emerging diseases, many of them caused by vector-borne pathogens, has dramatically increased. The emergence of most of these diseases has been associated with factors of global change such as habitat alteration, growing human densities, biodiversity loss, invasion of alien species, and climate warming operating on a global scale (Jones et al. 2008). Approximately 75% of emerging infectious diseases affecting humans are of zoonotic origin (i.e., wildlife diseases that spillover from animal populations into humans) and circulate in the wild in populations of non-human vertebrates (Vorou et al. 2007). Many of these zoonotic pathogens require vectors, like mosquitoes or ticks, to be transferred from one host to another (Gubler 2009). Hence, vector-borne diseases have had a severe impact on human populations throughout history and represent an important public health issue with significant wide-ranging economic



**Fig. 14.2** One of the most recent emerging vector-borne pathogens is the flavivirus West Nile virus (WNV), maintained in nature in a bird–mosquito–bird transmission cycle. Birds are the main reservoirs of WNV, while other hosts like humans and horses are considered “dead-end” hosts (i.e., they become infected but do not spread the infection onwards). In the theoretical example of WNV transmission dynamics, mosquitoes (top) are micro-predators feeding on birds (bottom) as their resource. Persistence of WNV depends on the existence of sufficiently competent vectors and hosts able to maintain at least one full transmission cycle (e.g., species connected by thick red lines)

implications. Under a current globalized scenario, understanding which factors regulate pathogen transmission is of great importance for ecological, evolutionary, health, and economic reasons. Emerging vector-borne diseases are usually accompanied by a “reservoir” of many host species and many vector species (i.e., an ecological reservoir), without which they could not persist (Fig. 14.2).

Overall, a One Health integrated approach is relevant for dealing with vector-borne diseases, particularly when mosquito-borne pathogens are involved due to their great sensitivity to direct and/or indirect changes in their environmental conditions (particularly the microclimate), including habitat characteristics and land use (Dobson 2009). In these cases, details about the interface among the vertebrate hosts (both wildlife and livestock), the insect vectors, and the environment they share could be critical for understanding transmission patterns of pathogens. Traditionally, the study of pathogen transmission has been focused on just one or two of these actors, and the remaining ones have been largely ignored. However, from an ecological point of view, studying the interactions among each one of these three players (i.e., vertebrate host, insect vector, parasite), as well as understanding the environmental context in which ecological processes take place, is essential for controlling emerging diseases (see Ferraguti 2017 for a review). Thus, the study of vector-borne diseases requires an integrative approach that combines information on the pathogens circulating between the communities of both vectors (mosquitoes) and vertebrates (hosts) and the environmental characteristics potentially affecting this complex interaction (Fig. 14.3).



**Fig. 14.3** Schematic representation of the main relationships affecting the transmission dynamics of vector-borne diseases. Shown are the direct interactions among organisms and between local environmental conditions and organisms (solid lines), the indirect effect of the local environment on pathogen transmission and on interactions between vector-host, and the indirect effect of the regional landscape on pathogen transmission (dotted lines)

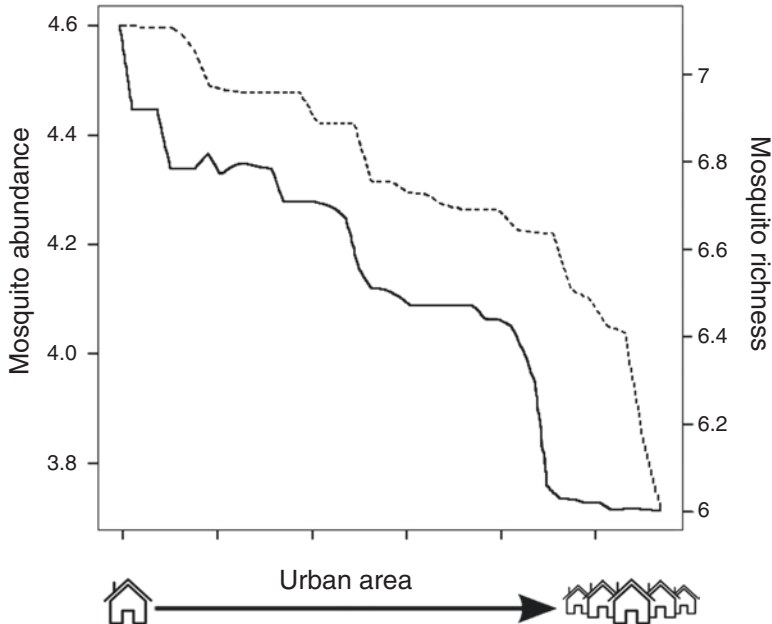
### 14.3.1 Urbanization Effects on Insect Vectors

Recent studies have shown that environmental anthropization leads to a change in distribution and abundance of mosquito species in a local community (e.g., Abella-Medrano et al. 2015; Sehgal 2015; Ferraguti et al. 2016), and hence as a by-product affects the potential spread of their dependent pathogens. With over 3500 known species described worldwide, mosquitoes are involved in a vast majority of parasite transmission, including metazoan (e.g., filarial worms), protozoan (e.g., malaria parasites), and numerous viruses (e.g., Dengue, Rift Valley and West Nile viruses; see Chaps. 5 and 6 for a thorough review of Diptera families involved in pathogen transmission and recent synthesis of research on vectors of avian haemosporidians). Mosquitoes have a wide variety of habitat requirements and feeding behaviors, which can vary greatly among closely related species (Becker et al. 2010). Consequently, environmental characteristics strongly affect the vector community composition and abundance, shaping the prevalence of vector-borne pathogens (Patz et al. 2000; Sehgal 2015; Ferraguti et al. 2016).

#### 14.3.1.1 Negative Relationship Between Urbanization and Mosquito Abundance

Generally, mosquito abundance and species richness are higher in natural and rural areas than in urban ones, as supported by studies conducted in Europe (Ibañez-Justicia et al. 2015; Ferraguti et al. 2016) and Australia (Johnston et al. 2014). In addition, anthropogenic habitats showed the lowest values of abundance and richness in comparison with natural areas, characterized by more diverse and favorable breeding environments for insects with freshwater and brackish water wetlands (but see Abella-Medrano et al. 2015, 2018, as an example of how seasonality can affect such general trends). For example, while mosquitoes of the *Mansonia* genus predominated in rural habitats, *Culex* mosquitoes are usually more common in urban sites (Johnson et al. 2008).

Also, higher richness has been found near urban environments (i.e., periurban forests) or within urban greenspaces, though abundance was higher at the better-preserved natural areas (Abella-Medrano et al. 2015, 2018). Ferraguti et al. (2016) found negative associations between mosquito abundance and richness and urbanization in southern Spain (Fig. 14.4), a temperate area of Mediterranean climate in which several pathogens affecting humans, wildlife, and livestock circulate (Figuerola et al. 2007). Also, negative relationships were found between both mosquito abundance and species richness and human population density, showing that the relationship between mosquito and human variables had a threshold at areas with approximately more than 50 inhabitants/250m<sup>2</sup> (Ferraguti et al. 2016). Previous studies have found strong support for the negative effect of human population abundance and density on the transmission of vector-borne pathogens (Padmanabha et al. 2012), which may be partially due to the detrimental impact of more densely



**Fig. 14.4** The mosquito abundance and species richness decrease as the degree of urbanization of the environment increases, although not all species are affected equally. Abundance (solid line) refers to the logarithm of the average number of mosquitoes captured at each locality, richness (dotted line) refers to the number of different mosquito species at each locality. (Adapted from Ferraguti et al. 2016)

populated areas on mosquito abundance given a reduction on the availability/suitability of breeding areas, as well as to the implementation of mosquito control programs in cities and peri-urban areas. However, such impacts will change on different cities because urban ecosystems are not homogeneous across the world, particularly in developing regions (e.g., Latin America; MacGregor-Fors and Escobar-Ibáñez 2017), having sometimes opposite trends depending on the species (e.g., Abella-Medrano et al. 2015, 2018).

Similarly, in South Australia, Johnston et al. (2014) found high abundances of different mosquito species in rural areas (further from the city center and closer to saltmarshes), and mosquito species richness was negatively correlated to factors such as the area occupied by urban land, human density, and the distance between urban areas and marshlands. Hence, the presence of salt marshes may provide a suitable environment for halophilic (salt-loving) species of mosquitoes (Leishnam and Sandoval-Mohapatra 2011; Johnston et al. 2014), strongly affecting the abundance of *Culex modestus* and *Ochlerotatus caspius*. Interestingly, in South Spain, the relationship between mosquito abundance and distance to marshlands was not linear, thereby showing a marked threshold at distances of about 2.5 km for *Cx. modestus* and 10 km for *Oc. caspius* (Ferraguti et al. 2016). These differences fit well with the estimated flying distances of mosquitoes, which range between

0.16 and 1.98 km for *Culex* (Ciota et al. 2012) and up to 12 km for *Oc. caspius* (Bogojević et al. 2011). To reduce the nuisance of mosquitoes in localities close to marshlands, larvicide treatments have been used, as in the case of treatments with *Bacillus thuringiensis isra* in urban areas from southern Spain (S. Ruiz pers. com.).

### 14.3.1.2 Adaptation to a New Environment

Regarding insects, urbanization has formed many new habitats and modified existing ones: simplification of habitat structures (Shochat et al. 2006) and the alteration of trophic interactions (Faeth et al. 2005) may lead to an increase in the abundance of a few key species that may affect species interactions (Frankie and Ehler 1978; McKinney 2008). Indeed, this anthropogenic-mediated loss of biodiversity often influences the dynamics of wildlife diseases by regulating the distribution of many mosquito species (Gilioli and Mariani 2011). Urban ecosystems can effectively act as a regulating factor of mosquito population growth, for example, residents who irrigate gardens during summer (Becker et al. 2014). Also, urban areas can have temperature and precipitation regimes that are considerably distinct from the surrounding regions, with important consequences for all organisms inhabiting them (Frankie and Ehler 1978). Here, human behaviors can alter habitat availability and ecosystem quality through changes in water sources, resource accessibility, and vegetation coverage, resulting in a severe impact on mosquito populations (Gilioli and Mariani 2011; Becker et al. 2014; Li et al. 2014), thus, affecting directly and/or indirectly their community ecology and pathogen transmission risk (for a review, see LaDeau et al. 2015). Urban characteristics, including the availability of artificial habitats such as deposits of water, gardens, and subterranean water systems, can provide alternative breeding sites for mosquitoes, therefore leading to an alteration on populations of vectors. Overall, numerous insects are associated with human waste production, and higher mosquito abundances are associated with poverty and degraded urban neighborhoods (LaDeau et al. 2013). For instance, rubbish from domestic animals, garbage dumps, sewage outfalls, and drainage ditches have provided a suitable habitat for a great variety of arthropod species for many decades (Tischler 1973; see Fig. 14.1 for a theoretical approach to tackle these multifactorial interactions in urban sites and in environments surrounding cities).

In cities, some mosquito species are favored by urbanization, especially during the dry season when surface water is otherwise scarce. From Europe to Oceania, going through Asia, some mosquito species of the genera *Culex* (Byrne and Nichols 1999), *Aedes* (Kay et al. 2000), and *Anopheles* (Overgaard et al. 2003) increased their abundance in urban areas, thus facilitating transmission success of pathogens between reservoir vertebrate hosts, or also acting as bridge vectors between infected competent-vertebrates and humans. This is particularly relevant in the case of pathogens circulating among birds that occasionally infect humans, as in the case of West Nile virus (WNV) (Hayes et al. 2005).

### 14.3.2 *Changes in Blood-Feeding Preferences*

In addition to species composition and abundance, anthropization may also affect the mosquito blood-feeding preferences, identified as a key factor modulating the amplification and transmission success of vector-borne pathogens (Kilpatrick et al. 2006). Mosquito diet represents an essential step in epidemiological studies allowing the identification of risks of transmission of vector-borne pathogens to human and other animals of both economic and conservation importance. It is known that mosquito species can feed on a large array of hosts, but they show clear feeding preferences, with some species biting mainly birds, i.e., ornithophilic species, and others preferring mammals to obtain their blood meals, i.e., mammophilic species (Santiago-Alarcon et al. 2012a; Takken and Verhulst 2013). Consequently, different feeding behaviors will determine contact rates between mosquitoes and infected/susceptible hosts, thus affecting pathogen dynamics (Kilpatrick et al. 2006; Muñoz et al. 2012). Therefore, some mosquito species may facilitate the transmission of pathogens between reservoir hosts, particularly relevant in the case of pathogens circulating among birds, which occasionally infect humans (e.g., WNV). For example, for the case of southern Spain, there was a characterization of the feeding patterns of the most common mosquito species potentially affecting the transmission dynamics of vector-borne pathogens (e.g., *Anopheles atroparvus*, *Ochlerotatus caspius*, *Culex modestus*, *Culex pipiens*, *Culex perexiguus*, and *Culex theileri*; Martínez-de la Puente et al. 2018a). In this study, there were clear interspecific differences in the feeding patterns of mosquitoes, describing the mammophilic behavior of *An. atroparvus*, *Cx. theileri*, and *Oc. caspius*; and the ornithophilic ones of *Cx. perexiguus*, *Cx. pipiens*, and *Cx. modestus*. This study revealed the importance of those species feeding mainly on birds that could disproportionally contribute to the amplification of disease such as WNV. Moreover, the mosquito species with an opportunistic behavior frequently fed on mammals and birds, such opportunistic species can play a key role in the transmission of such diseases to humans and horses. However, the differential feeding behavior of mosquito species is also dependent on the availability of potential hosts in the area, as supported by Muñoz et al. (2012) who found that differences in mosquito feeding patterns were significantly explained by both the mosquito species and the sampling locality. Furthermore, mosquitoes also showed clear feeding preferences on particular host species. Studies that integrate knowledge about the origin of mosquito blood meal with information on the host densities present in an area allows identifying both preferred and avoided vertebrate species. For instance, in a study from North Italy, by combining information between avian community with mosquito blood meal identification, authors showed how eurasian blackbirds (*Turdus merula*) and magpies (*Pica pica*) were preferred by insect vectors, while common starlings (*Sturnus vulgaris*) and rock doves (*Columba livia*) were bitten less frequently than expected according to their relative abundance (Rizzoli et al. 2015). Overall, several host variables can influence mosquito selection among species, including factors such as host phylogenetic relationships and phenotypic or behavioral traits (VanderWaal and Ezenwa 2016;

Yan et al. 2017). Obviously, temporal dynamics of host populations may affect the feeding patterns of mosquitoes and, consequently, the transmission dynamics of the pathogens that they are able to transmit. For example, the feeding patterns of *Cx. pipiens* changed seasonally in USA, with mosquitoes feeding mainly on American robins (*Turdus migratorius*) from May to June, and on humans and other mammals from July through September (Kilpatrick et al. 2006). Curiously, American robins represent less than 4% of the available hosts in the area and the disappearance from the environment of this preferred bird species due to migration coincides with the change of mosquito diet. Such changes in seasonal mosquito diet overlap with peaks of human WNV cases, determining the occurrence of epidemic outbreaks of mosquito-borne virus. Thus, knowledge on host preferences of insect vectors is essential to identifying key species and quantifying the risk of pathogen amplification and transmission by mosquitoes to humans or other species of interest. This is also the case of other insect vectors such as *Culicoides* (i.e., biting midges, Diptera: Ceratopogonidae; see Chap. 5 for an in-depth treatment of Diptera families of medical and veterinary importance) where infected vectors sucking blood from humans also feed on other vertebrate animals, thus representing a potential bridge vector of pathogens between wildlife and people (Santiago-Alarcon et al. 2012b). However, despite the importance of the availability of food resources, studies on mosquito feeding preferences, with few exceptions, suffer from the substantial limitation of not considering the availability (density and/or relative abundance) of hosts present in the local community (see Santiago-Alarcon et al. 2012a and Chap. 6 for a thorough review on current Diptera vector feeding preferences with emphasis on tropical regions).

### 14.3.3 *Habitat and Host Specificity of Culex pipiens Subspecies (pipiens and molestus)*

Differential ecological requirements have been reported within mosquito species. This is the case of *Cx. pipiens*, a worldwide spread mosquito species, which includes two different forms: the *molestus* and the *pipiens* that frequently hybridize (Vinogradova 2000; Martínez-de la Puente et al. 2016). Following their differential habitat requirements, the *molestus* biotype is able to mate in confined spaces (stenogamy) and can lay their eggs without a previous blood meal (autogeny), while mosquitoes of the *pipiens* form prefer open environments for mating and require a blood meal for oviposition (Fonseca et al. 2004). Overall, in North European countries, the *molestus* form prefers living in urban and underground environments, such as those in the London underground railway tunnels (Byrne and Nichols 1999) while mosquitoes of the *pipiens* form are mainly present in above ground and in natural large breeding habitats (Vinogradova 2003; Fonseca et al. 2004). Otherwise, in countries of the Mediterranean basin, mosquitoes of the two forms are sympatric, and hybrids are frequently found (Amraoui et al. 2012; Gomes et al. 2013; Krida et al. 2015; Di Luca et al. 2016). Hybridization has been also reported under natural

conditions in countries such as the Netherlands (Reusken et al. 2010), UK (Danabalan et al. 2012), Germany (Rudolf et al. 2013), Portugal (Osório et al. 2014), Austria (Zittra et al. 2016), Italy (Di Luca et al. 2016), Spain (Martínez-de la Puente et al. 2016), and Tunisia (Beji et al. 2017). Finally, in the United States, hybrids between these forms are ubiquitous (for a review, see Fonseca et al. 2004). Interestingly, under an epidemiological perspective, in addition to the living habitat differences between *Cx. pipiens* forms, it has been proposed that *molestus* form feeds mainly on mammals while *pipiens* prefers birds (Osório et al. 2014; Fritz et al. 2015), while hybrids may have an intermediate feeding behavior, potentially playing a role in the transmission of pathogens between humans and birds (Fritz et al. 2015). Nevertheless, a study conducted in Spain did not find significant differences in the feeding patterns of *Cx. pipiens* forms, with birds dominating the diet of the forms *molestus*, *pipiens*, and their hybrids. Consequently, a similar contact rate between mosquito forms and bird vector-borne pathogens was reported (Martínez-de la Puente et al. 2018b).

#### ***14.3.4 An Emblematic Case of an Urban Species: The Asian Tiger Mosquito***

Environmental anthropization of the landscape often impact mosquito community composition and potentially alters the transmission rate of vector-borne pathogens (Ferraguti et al. 2016). For example, the spread of invasive mosquitoes and the pathogens they transmit has become a global health concern (Kraemer et al. 2015). In this context, understanding the global invasion of the Asian tiger mosquito, *Aedes albopictus* represents an important public health challenge (Bonizzoni et al. 2013). The *Ae. albopictus* was originally considered a rural mosquito in its native distribution in Southeast Asia due to its preference to breed in natural habitats and its occurrence at forest edges (Higa 2011). However, during the last decades the species has dramatically spread its range to different continents including Africa, America, Europe, and Australia, establishing nowadays stable populations in most of the Mediterranean basin, being the most widespread species in suburban and urban environments (Bonizzoni et al. 2013). As a result, the Asian tiger mosquito has been catalogued as one of the world's 100 most invasive alien species (Lowe et al. 2000), representing one of the major threats to public health (Medlock et al. 2012).

The success of this invasive mosquitoes lies in their ability to use small temporal water reservoirs for their larvae development, which are common in urbanized areas (e.g., pots, sewers, tires). Therefore, they are easily transported by the trade of used ornamental plants and tires or by the passive transportation in cars (Roche et al. 2015; Eritja et al. 2017). In invaded areas, *Ae. albopictus* females prefer to feed on humans (Faraji et al. 2014; Martínez-de la Puente et al. 2015). Even so, domestic animals (e.g., dogs and cats) and wildlife are also common hosts of *Ae. albopictus*,



but bird blood meals are usually avoided (Martínez-de la Puente et al. 2015). However, in natural areas where a high density of birds can be found, the percentage of avian-derived blood meals could reach up to 70.0% (Hess et al. 1968). Based on preferences of *Ae. albopictus* to feed on humans, and given the low representation of bird blood in their meals, the importance of this mosquito species for the transmission of pathogens circulating between birds and mammals can be considered low (Martínez-de la Puente et al. 2015). Nevertheless, under a global change scenario, this mosquito species may represent a key potential vector for the transmission of human pathogens such as Chikungunya virus (Paupy et al. 2010), Dengue virus (La Roche et al. 2010; Paupy et al. 2010), Zika virus (Grard et al. 2014; Gutiérrez-López et al. 2019), and *Dirofilaria* worms (Cancrini et al. 2003; Gratz 2004), then requiring further studies.

### 14.3.5 Conclusion

To sum up, the study of vector feeding preferences through blood meal analyses is of great help to comprehend how the presence of invasive mosquitoes may affect the local transmission of pathogens with medical and veterinary relevance. Indeed, the presence of a highly competent vector such as *Ae. albopictus* in dense urban areas combined with its highly anthropophilic behavior can amplify its potential negative effect on public health. Moreover, it is important to remember that the establishment of an exotic vector species can create new epidemiological and epizootiological scenarios in the invaded range, with important ecological and health consequences for humans, wildlife, and domestic animals.

## 14.4 Future Research Directions

The effects of habitat disturbance on avian infections are not totally clear, since many biotic and abiotic factors are involved in parasite transmission, which create contrasting responses. Current studies in the tropics have mainly considered two contrasting habitat conditions (e.g., undisturbed vs. disturbed), leaving aside a variety of intermediate habitats (see Table 14.1 for a synthesis of studies on avian malaria and habitat disturbance in the tropics). Future research should focus on the identification of those biotic and abiotic factors explaining parasitological parameters in a gradient of disturbance, from undisturbed (or well preserved) to urban areas, considering the urbanization grade as the percentage of gray or green along the gradient.

Within cities, it is critical to conduct studies that take into account both the heterogeneity of the urban environment (e.g., greenspaces, permanent water bodies,

buildings, roads with tree lines, number of vehicles, heat islands) and the assemblage of urban species (i.e., urban dwellers, utilizers, avoiders; *sensu* Fischer et al. 2015). This will allow the understanding of how anthropogenic activities modify the ecological dynamics of host–vector–parasite interactions. Within the urban ecosystem, parks and natural reserves (greenspaces) may act as biodiversity reservoirs, mainly for native species not adapted to built areas, and (i) serve for conservation of vulnerable species at different functional levels (e.g., host, parasites, vectors, reservoirs, dead-end hosts), (ii) provide suitable habitats for urban utilizers and urban avoiders, and (iii) contribute to a better host condition and health. In addition, it is important to determine if parasite exchanges occur among the different kinds of urban organisms (i.e., urban dwellers, utilizers, avoiders) to evaluate the risk of emergent diseases from exotic species (both vertebrate hosts and insect vectors) into native ones.

Given that responses of parasite population parameters (i.e., prevalence, parasitemia, aggregation) to environmental changes largely depend on the identity of species involved in the interactions, it is essential to identify host species (i) sensitive to infections (e.g., high mortality and morbidity) in order to develop prevention and conservation actions or (ii) tolerant to infections, because they can act as reservoirs and superspreaders of virulent pathogens. Most studies that include habitats of different disturbance levels focus only on the prevalence of avian haemosporidians, leaving aside their parasitemia. Even though high parasitemia is often associated with an early infection, taking into account parasitemia would considerably improve our understanding of the host's ability to fight infections as a function of habitat types. It is important to identify those sites where higher parasitemias are expected, given that such host populations may suffer more severe consequences in terms of health, which under unfavorable habitat and climatic conditions can undergo population size reductions, and even face local extinctions.

Finally, in terms of studies of avian haemosporidians and land use changes, there is currently little research in the tropical areas of Asia and northern Australia (i.e., Queensland). Southeast Asia is undergoing high rates of habitat destruction and modification and many novel emerging diseases have derived from this region (Aguirre et al. 2012); therefore, it is of outmost importance to implement studies in the region addressing how habitat modification alters host–vector–parasite dynamics.

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