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Karen D. Mc Coy

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## 8 Community-level interactions and disease dynamics

Karen D. McCoy

### 8.1 Introduction

Understanding host and parasite ecology is crucial for inferring mechanisms of parasite transmission and for predicting its short and long-term consequences for host population dynamics (Chapter 7). This basic information becomes more challenging to obtain, and the outcome more difficult to predict, in complex communities, where hosts and non-hosts interact directly and indirectly in different ways. Current shifts in biodiversity due to global change, and the associated modifications to biotic interactions within communities, may result in profound changes in the probability of disease emergence, its dynamics over time, and its population and community-level impacts at different spatial and temporal scales. Apprehending and predicting the impacts of these changes has become increasingly important for human health, for animal production, and for conservation. Birds represent an integral part of almost all natural communities. Due to this ubiquity, and their intrinsic biological characteristics, this taxonomic group plays a major role in the ecology, evolution, and epidemiology of parasitic species at the community level.

In this chapter, I examine the role of birds as hosts to parasites in natural communities and how changes in these communities can alter disease dynamics and emergence. I start by considering the relative importance of birds and parasites in natural communities, highlighting some basic notions in community ecology. I then consider how general changes in diversity can alter disease dynamics: first, how the addition or removal of parasite diversity can alter overall community structure and function, then, how changes in host diversity can affect parasite and pathogen transmission, with a specific consideration of dilution and amplification effects. Finally, I briefly consider the importance of combining data from host and parasite communities to understand meta-community dynamics. The different elements in each section are illustrated with brief, concrete examples from the literature on avian species, when possible. Near the end of the chapter, I provide a more detailed example from my own work that examines the structure of ticks and Lyme disease bacteria in marine bird communities. The chapter finishes with a brief discussion of diverse human impacts on avian communities and the feedback effects they can have on public health and disease risk. Throughout the chapter, I refer to parasitic organisms as “**parasites**” which includes both **microparasites** and **macroparasites**. The term “**pathogen**” is reserved for micro-organisms that cause disease, the debilitating manifestations of infection.

### 8.2 Community structure and function

#### 8.2.1 Community ecology and the place of birds

An **ecological community** comprises all individuals of all species that potentially interact within a single patch or local area of habitat (Lawton, 1999; Leibold et al., 2004; Wiens, 1992). These interactions can take different forms: antagonistic (predation or parasitism), competitive, or mutualistic, but all can ultimately affect individual fitness and local species persistence. **Community ecology** is the study of these interactions and attempts to understand how they lead

to the patterns of diversity we observe at different spatial and temporal scales. It considers aspects such as variation in species richness, evenness of abundance, and productivity, as well as food web structure and community assembly rules. Birds not only make up a significant part of most natural communities, but studies of avian communities have also been of primary importance in the development of general theories in community ecology (Wiens, 1992).

Community ecology is inherently complex due to the range of species present at a given place and time, and the changing conditions from one place to another; it has been thoughtfully referred to as an ecological “mess” (Lawton, 1999). To deal with this complexity, communities are often subdivided into ‘guilds’ or assemblages of different sizes and specificities, where species are grouped by similarities in the way they exploit resources (e.g., predators), by the types of resources they use (e.g., nectar-feeding species, or granivores), by habitat units (e.g., intertidal) or by taxonomy (e.g., Class Aves). While this results in more manageable units for study, important interactions can be missed and calls for caution have been made when trying to understand community dynamics based solely on restricted criteria, particularly taxonomic (Wiens, 1983). Vellend (2010) argued that patterns of species diversity, abundance, and composition within a community can be understood via four key organizing processes: selection, drift, speciation, and dispersal. The impacts on community assembly and function of processes like drift (i.e., stochastic changes in species population sizes), speciation (i.e., addition of novel species to a community) and dispersal (i.e., species connections from outside the community) are relatively straightforward to understand. The last, more enigmatic process, selection, encompasses all the varied and complex interactions within and among species within a community that will ultimately lead to fitness differences among individuals and species.

Two major questions in community ecology have been the focus of debate over the last 50 years. The first is, How do communities assemble? This is an essential question to answer if we are to understand how quickly communities may reassemble after perturbation or how readily novel species can invade (Pearson et al., 2018). Community assembly rules actually originated as a biogeographic approach to explain island bird assemblages (Diamond, 1975). They were then later adapted as a general framework for understanding the structure of all natural communities (Weiher and Keddy, 2001). Traditional community assembly theory was niche-based, postulating that the composition and relative abundance of species within a community is determined by a series of hierarchical biotic and abiotic filters related to the functional traits of each species (Weiher and Keddy, 2001). In contrast, Hubbell’s (2001) neutral theory assumed that all individuals at a particular trophic level in a community are essentially equivalent regarding their chance of survival and reproduction and thus accumulate locally through random processes – drift, speciation, and immigration – from the global species pool (Rosindell et al., 2011). More recent syntheses have highlighted the complementarity of the two theories for explaining assembly patterns at different spatial scales (Chave, 2004; Pearson et al., 2018; Rosindell et al., 2011; Seabloom et al., 2015). For example, species arrive by random dispersal from the general species pool and then only establish if they pass local environmental filters.

The second question asks, What characterizes community stability (e.g., Lawton, 1999;

Loreau and de Mazancourt, 2013; Mougi and Kondoh, 2012; Wiens, 1983) ? Communities are considered to have a dynamic stability that leads assemblages towards an equilibrium composition (Wiens 1992). Maintaining stability is then thought to depend both on the distribution and strength of interactions (May, 2006), and on the level of biodiversity, with higher diversity increasing community stability (Loreau and de Mazancourt, 2013). This latter relationship occurs via several complementary mechanisms: asynchrony in species' phenologies, interspecific differences in temporal responses to perturbations, reductions in the strength of competition, and the occurrence of multiple types of biotic interactions within and across trophic levels (Loreau and de Mazancourt, 2013; Mougi and Kondoh, 2012). Dispersal across communities is also a stabilizing force, replacing lost individuals and species and maintaining community function (Mouquet and Loreau, 2003). Birds are particularly important in this sense, both via their own dispersal and by transporting other species during movement. **Keystone species** are thought to occur in most systems, species whose presence is crucial for maintaining organization and community diversity (Mills et al., 1993). These species can act via bottom-up effects, where changes in resources alter competition intensity and thus community structure, or top-down effects, where predation impacts prey population sizes, for example. The role of keystone species can also be more subtle, modifying habitats to create new niches or linking trophic systems by maintaining key resources. Birds may participate in many of these functions. Although few avian species have been identified as keystones *per se*, their role in community function as a whole is substantial (Şekercioğlu, 2006). For example, Daily et al. (1993) studied the keystone role of the red-naped sapsucker (*Sphyrapicus nuchalis*) within subalpine Rocky Mountain communities and found that these birds are an integral part of a keystone complex, playing a dual role in which they both create food resources for numerous other sap feeding species and produce breeding habitats for secondary cavity nesters.

Community theory has traditionally focused on a single spatial scale, assuming that local communities were closed and isolated, and that populations interacted directly to alter each other's birth and death rates (Leibold et al., 2004). However, some species interactions are indirect and occur across a network of local communities such that they can affect large scale colonization and/or extinction probabilities (e.g., source-sink effects). For example, individual lakes in a region might be considered to have fairly independent and isolated local fish communities, but some of their avian predators may have demographic rates that are regulated over larger spatial scales, involving sets of lakes; the community dynamics of fish within a single lake may thus depend on the presence and abundance of a piscivorous bird species, but the reverse may not be true (Leibold et al., 2004). Such observations led scientists to develop the concept of the “metacommunity”, that is, a set of local communities linked by the dispersal of potentially interacting species (Wilson 1992). Birds, with their capacity to move quickly over long distances, are essential components of these metacommunities, connecting local communities across different spatial scales (Figure 8.1).

[Insert FIGURE 8.1 here]

## 8.2.2 Parasites in communities

Although often overlooked, parasites are ubiquitous and active members of all natural communities, playing a major role in shaping community structure and function at different spatial scales (Freeland, 1983; Minchella and Scott, 1991; Poulin, 1999; Price et al., 1986). By definition, a **parasite** has a negative impact on the host individual. However, it is the relative virulence and transmissibility of a parasite that will define its overall impact on other members of the community (e.g., McMahon et al., 2016).

Parasites can have direct, debilitating effects on a host (Chapter 6) resulting in its extinction from a community, or changing its phenotype and thereby modifying the nature of local interactions (Poulin, 1999; Thomas et al., 2000). Raptors infected with avian poxvirus may, for instance, exhibit reduced activity and/or food intake due to the weakening effects of infection, releasing predation pressure on the prey community (Morishita et al., 1997). Infected prey may, in contrast, become more readily available to predators, improving predator fitness. Pacific killifish *Fundulus parvipinnis* infected by the trematode *Euhaplorchis californiensis* are, for example, more susceptible to predation by piscivorous birds than uninfected fish (Lafferty and Morris, 1996). However, in this case, the fitness advantage afforded by reduced foraging costs could be offset by the costs of parasitism because increasing the susceptibility of parasitized fish will result in higher infection loads in the avian predator, the parasite's definitive host. Parasites can also alter the dispersal propensity of their hosts, either reducing it due to poor body condition (Sánchez et al., 2018) or increasing it to escape parasitism. Indeed, parasites that lower the reproductive success of their hosts can provoke host dispersal to new locations for subsequent reproduction, drastically changing immigration and emigration rates within the metacommunity; this type of dynamic has been documented in several bird species (Boulinier et al., 2001; Brown and Brown, 1996; Heeb et al., 1999). For example, high infestation levels of nest ectoparasites have been suggested to cause colony abandonment in several colonially breeding bird species (Duffy, 1983; Feare, 1976; King et al., 1977). Brown and Brown (1992) used monitoring data to show that fledgling cliff swallows (*Petrochelidon pyrrhonota*) from nests with heavy infestations of hematophagous nest parasites (fleas - *Ceratophyllus celsus* and swallow bugs - *Oeciacus vicarius*) had a lower probability of recruiting to the natal colony than fledglings from uninfested nests. Similarly, in black-legged kittiwakes (*Rissa tridactyla*), reproductive success and breeding philopatry were found to be significantly lower when nests were heavily infested by the seabird tick *Ixodes uriae* (Boulinier et al. 2001).

Interspecific differences in infection and virulence can also mediate outcomes of interspecific competition among species sharing similar ecological niches within a community. Early experimental studies on competing species of flour beetles (*Tribolium* spp.) demonstrated, for example, how the presence of a shared pathogen (*Adelina tribolii*) could invert the results of resource competition leading to the extinction of the competitive dominant species (Park, 1948). **Apparent competition** can also occur in communities, where indirect interactions between host species that do not directly compete arise because of a shared parasite (Holt and Bonsall, 2017). In such cases, an overall increase in parasite abundance can cause shifts in community structure and function because of asymmetrical effects of the parasite on different host species (Bonsall and

Hassell, 1997). Tompkins et al. (2000) found, for example, that declines in grey partridge (*Perdix perdix*) populations in the UK were associated with parasite-mediated apparent competition with the ring-necked pheasant (*Phasianus colchicus*). Pheasants carry heavy loads of the intestinal nematode *Heterakis gallinarum* whose eggs are released into the environment. Partridge that become infected with these parasites while feeding the next season suffer high negative fitness consequences (Tompkins et al. 2000). The observed negative correlation in the abundance of the two avian species in this case was not due to direct competition for resources, but rather to the shared enemy that had stronger virulence in partridge compared to pheasants.

Pathogens can also promote species coexistence by regulating the relative abundance of dominant species. This has been experimentally demonstrated in plant communities where parasite removal can result in reduced community diversity, both in terms of evenness and species richness (e.g., Grewell, 2008). While community-level impacts of infection of an avian species remain undocumented, birds and the entire community can be directly impacted by the cascading effects of an infected keystone species (Getz, 2009; Selakovic et al., 2014). For example, the Spanish Imperial eagle *Aquila adalberti*, an apex predator, has suffered severe fecundity declines since 2011 (-45.5%) due to the emergence of a novel variant of the rabbit hemorrhagic disease virus (RHDV) in southern Europe that drastically reduced the population size of European rabbits (*Oryctolagus cuniculus*), a keystone species of Iberian-Mediterranean ecosystems. Changes in the demographics of this avian predator is now, in turn, expected to alter the top-down regulation of other members of this trophic community (Monterroso et al., 2016).

As is evident throughout this book, birds host a rich diversity of parasites that can be more or less shared with different community members depending on their host range (strict specialists to broad generalists) and life cycle (from direct one-host to complex 3-4 host transmission cycles). Given this diversity and the ubiquity of avian species in natural communities, birds can play a major role in determining the presence, persistence, and impact of parasites and pathogens on overall community structure and function (Figure 8.1).

## 8.3 Community diversity and parasite/pathogen circulation

### 8.3.1 Interspecific host heterogeneity

Some hosts are better than others. Indeed, we know that only a few individuals within a population typically give rise to the majority of secondary infections; these individuals are sometimes referred to as **superspreaders** (Lloyd-Smith et al., 2005; Woolhouse et al., 1997) (see Chapters 3, 4, and 7). The same notion can be applied at the community level, where different species are more or less competent reservoirs or transmitters of a given parasite. Some species may be completely resistant to infection, whereas others are highly susceptible and infectious. A parasite may be highly virulent for one host species, potentially eliminating it from the community before transmission can take place, whereas another host may be highly tolerant to infection, even at high infection intensities, maintaining the infection locally (i.e., **reservoir hosts**). This interspecific variation will greatly modify local disease dynamics in the community.

In the presence of a highly competent host species for the parasite, amplification should occur. The overall prevalence of infection will increase either because the parasite is better able to exploit this host species and produce more secondary infections (i.e., amplifying hosts), or because this host species contributes to the overall pool of competent individuals such that the threshold density of hosts for parasite persistence is reached (i.e., the critical community size: Bartlett, 1960; Begon, 2008). In contrast, a low-competent host species (i.e., one that cannot maintain an infection when exposed to a parasite) can reduce overall parasite prevalence by reducing the density of susceptible hosts below the persistence threshold, and/or by absorbing transmission events (i.e., **dilution hosts**). This latter effect has been termed the “dilution effect” and was primarily conceived to understand the epidemiology of vector-borne diseases, such as Lyme disease (Ostfeld and Keesing, 2000; Ostfeld and Keesing, 2000). The dilution effect hypothesis (DEH) has received much attention over the last decade and is still considered controversial with respect to its generality (see **Box 8.1**).

The circulation of West Nile virus (WNV) provides an excellent example of the importance of interspecific host heterogeneity within avian communities for determining disease risk. West Nile Virus is a mosquito-borne pathogen for which birds are the primary reservoir hosts. Humans, or other incidental host groups, become infected via **spillover** when they come in contact with an infected vector, different species of *Culex* mosquitos. Field studies that have examined infection rates in relation to avian diversity have found a negative correlation between the species richness of non-passerine birds in the avian community and the prevalence and density of infected *Culex* mosquitos (Ezenwa et al., 2006). This correlation did not occur for passerine species, suggesting that non-passerines, poor hosts for the virus, act as alternative bloodmeal sources for mosquitos, reducing contact rates with highly competent passerine hosts and thus densities of infected vectors (DIV). The reduced DIV then translates to lower global disease risk for humans; areas with a high diversity of non-passerine species had lower human WNV disease incidence (Ezenwa et al., 2006). Other studies have identified specific passerine species whose presence significantly amplifies DIV due to both high competence for the virus and a high rate of exploitation by mosquitos (Kilpatrick et al., 2006; Simpson et al., 2012). For example, American robins (*Turdus migratorius*) have been shown to feed a disproportionate number of mosquitos compared to other avian species within a given community (Apperson et al., 2004; Montgomery et al., 2011) and to increase DIV (Kilpatrick et al., 2006; Hamer et al. 2009, and see Figure 8.2). In regions where robins are less common, other passerine species are more likely to be used as bloodmeal sources, such as the Northern mockingbird (*Mimus polyglottos*) in south-eastern USA (Apperson et al., 2004) or the House finch (*Haemorhous mexicanus*) in western USA (Molaei et al., 2010; Montgomery et al., 2011).

[Insert FIGURE 8.2 here]

When attempting to predict changes in parasite prevalence or disease emergence within communities, additional complexity arises from heterogeneities in the environment, among

individuals within a host and/or vector species, and from the level of host specificity and heterogeneity in the parasites themselves (Jones et al., 2018). Unravelling the intricacies of these systems thus demands careful comparative analyses across a wide range of systems and spatial-temporal scales (Tompkins et al., 2011) and has become a pressing challenge given ongoing rapid changes in natural communities.

### **Box 8.1. The Dilution Effect Hypothesis**

The Dilution Effect Hypothesis (DEH) was initially conceived to explain the link between biodiversity and human disease risk of vector-borne zoonoses, particularly Lyme disease (Ostfeld and Keesing, 2000), but then was extended more generally across disease systems (Johnson and Thielges, 2010; Keesing et al., 2006). Under this model, high biodiversity is good because it results in lower disease prevalence. The idea is logical: if there is variation in pathogen reservoir competence among species within a community, competent hosts will be diluted among non-competent hosts when biodiversity is high, reducing transmission success of the pathogen and thus the overall density of infected individuals (Ostfeld and Keesing, 2000; Ostfeld and Keesing, 2000).

However, to work, this hypothesis relies on several key assumptions: 1) variation in competence for a pathogen occurs among species within the community, 2) the most competent species are present in low diversity communities, and 3) transmission is only horizontal. In the specific case of vector-borne disease, vectors are also assumed to be generalists in terms of the host species they exploit with no vertical transmission of the pathogen.

Some empirical evidence for this model exists (e.g., Allan et al., 2003; Civitello et al., 2015; Ezenwa et al., 2006; Haas et al., 2011; Johnson et al., 2013; LoGiudice et al., 2003), but criticisms to its universality are numerous (Randolph and Dobson, 2012; Salkeld et al., 2013). For example, it remains difficult to distinguish between true dilution and a simple reduction in reservoir density when additional species are added to a community (Begon, 2008); the end result is the same, but the mechanism is different (Keesing et al., 2006). Likewise, with vector-borne pathogens, the DEH assumes that vector abundance remains the same with increases in host biodiversity (i.e., there is no vector amplification) (Randolph and Dobson, 2012). If vector abundance increases, the number of infected vectors in the community may remain the same, even if infection prevalence *per se* is lower. Finally, several studies have now shown that host species are not used indiscriminately by vectors and that some species within communities contribute disproportionately to vector-blood meals (e.g., Kilpatrick et al., 2006; Montgomery et al., 2011 and see section 8.4). If strong host preferences occur within a community, the applicability of DEH is reduced because, regardless of local species diversity, vectors will use the preferred host (McCoy et al., 2013). A recent meta-analysis suggests that DEH may be strongly scale-dependent, working well at local spatial scales, but becoming weaker over larger areas (Halliday and Rohr, 2019).

### **8.3.2 Changing biodiversity**

We are living in a period of rapid and unprecedented changes to biodiversity (Tittensor et al., 2014). *What predictions can we make for the circulation of parasitic organisms if community diversity increases or decreases? What kinds of impacts can we expect from invasive species in terms of disease emergence? What role might non-host species have within communities? What are the mechanisms underlying the link between biodiversity and disease prevalence?* These



diverse questions have been the focus of some research effort, but much is left to do (Halsey, 2019; Gibb et al. 2020).

Due to the complex nature of interactions within natural communities, and the high diversity of parasitic species and life cycles (see 8.2.2), the relationship between host diversity and disease risk can vary in both intensity and direction. At a global scale, we expect that increased host biodiversity will increase parasite diversity and exposure (Jones et al., 2008). However, at more local scales, the effect of adding biodiversity can be more variable (Salkeld et al., 2013) and will depend on the nature of ecological interactions within the community (Roche et al., 2012). If a highly competent host for either an existing pathogen or vector is added to a community, transmission risk may increase (Ogden and Tsao, 2009; Roche et al., 2013) and disease amplification occurs. Although intuitive, examples of this phenomenon in the literature remain surprisingly scarce. The closest example in birds comes from cliff swallow colonies in the American Midwest invaded by the European house sparrow (*Passer domesticus*). In the presence of house sparrows, both infestation levels by swallow bugs and the prevalence of Buggy Creek virus (Togaviridae: Alphavirus), a pathogen transmitted by the bugs, increases (O'Brien et al., 2011). This increase is seemingly due to changes in prevalence and infection intensity in house sparrows as these novel hosts are more susceptible to both the vector and the pathogen than native cliff swallows (Fassbinder-Orth et al., 2013). More detailed studies are now required to assess the impact of the invading host for infection levels in other native hosts within these communities.

In the case that a weakly competent species is added to a community, rates of transmission may be reduced via different 'dilution' mechanisms (see Box 8.1). For example, amphibian host diversity has been shown to inhibit transmission of the trematode *Ribeiroia ondatrae*, a parasite that uses aquatic snails as first intermediate hosts, fish or amphibians as second immediate hosts, and mammals or birds as final hosts (Johnson et al., 2013). In species-rich communities, realized transmission can be reduced by almost 80% due to the addition of less competent amphibian species. Few examples of a dilution effect have been demonstrated with respect to avian diversity within communities, with the exception of West Nile Virus. As outlined above, the presence of incompetent non-passerine species reduces the density of infectious mosquitos within an area (Ezenwa et al., 2006). Swaddle and Calos (2008) analysed data on avian species richness and human incidence of WNV disease from a series of paired counties in eastern US and demonstrated that higher avian diversity was clearly associated with a lower incidence of human cases. However, these authors did not identify the precise mechanism at play. Examples of the impact of adding weakly competent or incompetent hosts to a community at still lacking for other avian disease/parasite systems.

Even species that do not participate directly in transmission may alter infection rates within communities. Non-host species can, for example, prey directly on free-living parasite stages or can destroy them during their normal activities. For instance, free-swimming cercariae are readily consumed by non-host predators such as shrimp, crabs, barnacles and oysters (Welsh et al., 2017) affecting trematode transmission to final avian hosts (e.g., bivalve consuming species such as gulls *Larus* spp. or common eiders *Somateria mollissima*). Likewise, snails can kill encysted

metacercariae while grazing on aquatic vegetation, removing them from the transmission cycle (Vielma et al., 2019). Other species may alter habitat conditions for competent host species, and thus may increase or decrease parasite prevalence; for example, introduced aquatic plants can alter habitat suitability for foraging shorebirds, final hosts for many parasites with complex life cycles (Crooks, 2002).

With increasing global movements of flora and fauna, the number of invasive species in natural communities is also increasing. Not only can these novel species have major impacts on community structure and function through direct competitive and trophic interactions as outlined above, but they frequently arrive in the invaded zone with their cortege of parasites and pathogens from the native range (Dunn and Hatcher, 2015). These parasites may then spillover to native community members, directly affecting their survival and reproduction, and/or altering community level interactions. Indeed, by modifying host–host interactions (including competition and predation), these parasites may be key factors determining the success of an invasion. Martin-Albarracin et al. (2015) carried out a global scale meta-analysis on the ecological impacts of invasions by non-native bird species and found that disease transmission to native fauna had one of the highest impacts on native community structure. Surprisingly, disease transmission has been relatively less studied than other effects of invasive species. The introduction of non-native birds to the Hawaiian Islands demonstrates well how invasive species, in interaction with parasites, can impact native fauna. During the last century, over 50% of the native avifauna has been lost from this archipelago due to a variety of anthropogenic causes (Atkinson et al., 2005). Exotic birds started to be introduced to the Hawaiian islands in the 1800s, and the bird-associated mosquito *Culex quinquefasciatus* arrived shortly thereafter (Warner, 1968). Avian malaria (*Plasmodium relictum*), a blood parasite transmitted by mosquitoes, likely arrived at the same time, but was not considered a factor in declines until the late 1920s when a sufficient number of introduced avian species were established to maintain the pathogen locally (Van Riper III et al., 1986). This parasite is particularly virulent for endemic bird species causing acute mortality, but is relatively well-tolerated by many of the introduced species (Van Riper III et al., 1986). Avian malaria has been identified as a major cause of mortality in low to mid- altitude regions where mosquitoes are present (Atkinson et al., 2000). Current climate-related changes are now enabling the expansion of the mosquito vector to higher altitudes, and thus the spread of the parasite to zones previously exempt of disease (Atkinson et al., 2005), threatening the last refuges for certain native species, and notably Hawaiian honeycreepers, an emblematic clade of endemic finches.

### 8.3.3 Parasite communities within avian communities

Within any local community, there exists a series of hierarchical parasite communities that can impact other community component species through diverse effects. These parasite communities start at the scale of the host individual – the parasite infra-community – affecting individual host fitness, and go all the way up to the level of the global metacommunity, composed of distinct parasite communities linked through dispersal (Figure 8.1). I outline these different nested communities and their impacts below.

#### 8.3.3.1 Parasite infra-community

The individual is increasingly recognized as being its own ecosystem, hosting a range of parasitic, commensal, and mutualistic micro-organisms. These internal communities, or infra-communities, which include all infecting organisms (or coinfections), can have an array of important effects on the host via the nature of their interactions - facilitative, neutral, or antagonistic. Indeed, this internal community has the same basic traits as the broader community in which it is nested, including resources (from the host), consumers (different types of parasites), competitors (different parasites using the same resource) and predators (host immune responses) (Pedersen and Fenton, 2007). The diversity and composition of the infra-community will affect how a host responds to other biotic and abiotic factors in the environment, whether infection (invasion) by other parasitic organisms is successful and, ultimately, will determine individual host fitness (e.g., Seabloom et al., 2015; Telfer et al., 2010). The key difference with the broader free-living community is that, in infra-communities, resources are directly linked to predation because the host supplies both ends of the trophic chain (resources and predation). By considering the within-host environment as a community, the mechanisms defining interactions can be elucidated, variation among individuals can be better explained and *a priori* hypotheses on the response of individuals to different factors can be predicted (Graham, 2008). Likewise, as individual hosts represent well-defined and self-contained habitats, they can be considered as suitable replicate units for testing general theories in community ecology (Poulin, 1999; Rynkiewicz et al., 2015). Although, several studies have examined interactions among ectoparasites infecting individual avian hosts (Choe and Kim, 1988; Clayton et al., 2015; Matthews et al., 2018; Stefan et al., 2015), for logistical reasons, relatively few have focused on internal parasites (but see Biard et al., 2015; Leung and Koprivnikar, 2016; Stock and Holmes, 1988). Likewise, the link between diversity at the infra-community level and broader community dynamics still requires specific consideration.

#### 8.3.3.2 Parasite component community

Moving up a level of biological organization, the parasite component community includes all infra-communities, that is, all parasite species found within a subset of host species, or within a particular abiotic microhabitat (Bush et al., 1997). When researchers consider parasite communities, studies are often focused at this scale, examining prevalence of diverse parasites and pathogens at a given place and time for a focal host species/group. For example, a component community would include all parasites infesting/infecting black-legged kittiwakes (*Rissa tridactyla*) within a specific seabird colony (see 8.4.1).

As outlined above, the infra-community of each individual host can dictate the host's relative quality and life history traits. In contrast, it is the component community which will define host exposure potential to a given parasite. The evenness of the parasite component community among hosts will depend on the exposure rate, the nature of parasite-parasite interactions (i.e., whether current infections facilitate or constraint infection by other parasites; Telfer et al., 2010), and the degree of host susceptibility to infection. For example, similarity in helminth communities of ring-billed gulls (*Larus delawarensis*) shows strong age structure, with high similarity among chicks within populations that declines with age (Locke et al., 2012). In addition to host associated factors

such habitat use and diet (Gutiérrez et al., 2017; Leung and Koprivnikar, 2016), host exposure rates will also depend on the parasite life cycle (Poulin, 1997). For example, parasites with environmental stages or active intermediate life stages should have more even distributions within the host population than parasites that rely on direct contact of territorial species. The evenness of the parasite community will condition its stability and the efficacy of control measures. Indeed, component communities of helminthes in gulls were found to be highly conserved among years, after accounting for seasonal changes (Levy, 1997). As for all communities, the removal of a single parasite species can destabilize relationships within a community (Ives and Cardinale, 2004), potentially increasing the virulence and dissemination of existing parasites, or facilitating invasion by novel parasites from outside the component community (Johnson et al., 2013).

#### 8.3.3.3 Parasite meta-community (or supra-community)

A pressing question in disease ecology concerns how host and parasite assemblages interact to determine transmission and disease severity within ecological communities (Rigaud et al., 2010). To address these aspects, we need to increase the scale of biological organization to the meta-community level or parasite supra-community (Bush et al., 1997). The parasite meta-community includes all parasites from all hosts (or microhabitats) at a defined spatial scale, such as all parasite species (including microparasites, helminths, and ectoparasites) from different passerine birds within a farm. A complete understanding of transmission dynamics often demands detailed information on both host and parasite communities. However, to be tractable, studies at this level of biological organization need to specify the spatial scale and the limits of the host community being considered. For example, a parasite meta-community could include all parasites infecting different avian species present within a single seabird colony (see 8.4.1). This could also be extended to include all potential intermediate hosts and free-living stages within the same geographic region. At this level of biological organization, it is important to keep in mind that parasite richness is not directly equivalent to disease risk, because parasites vary in virulence and relative abundance, hosts vary in competence, and the presence of one parasite may alter the propensity for subsequent infections (Telfer et al., 2010). Thus, key aspects to consider at the parasite meta-community scale are the degree to which parasites are shared among local host types, such as the degree of host specialization, the potential for host shifts, and the trophic links that occur within the host community.

#### 8.3.4 Modified communities

Urbanization can be defined as concentrated human presence in residential and industrial settings and its associated effects (Crangan and Horak, 1989; Marzluff, 1997). For the purpose of ecological studies, urban centers have been quantified as containing more than 2500 people (Dumouchel, 1975). Urbanization of the landscape has had, and is continuing to have, a dramatic effect on the floral and faunal communities that previously occupied these spaces (see Chapter XX). It is generally associated with a reduction in overall species richness and diversity (Beissinger and Osborne, 1982; Marzluff, 2001) due to direct habitat loss or fragmentation of intact habitat such that sufficient breeding habitat or food resources are no longer available for some species. For example, in a review of studies on bird responses to human settlement, Marzluff (2001) showed

that, although bird density increased in response to urbanization, species richness and evenness decreased, largely due to the loss of cavity and interior-nesting species, and raptors. Reduced diversity can also be associated with the increased presence of a few species preadapted to exploit human-associated resources; these are species that outcompete and/or dominate urbanized areas. Several factors determine which species can coexist and flourish with humans: for example, the presence and patch size of remnant (native) habitat, the presence of exotics – competitors, predators, or parasites – the structure and composition of the vegetation, supplementary feeding by humans, or the presence of pollutants (reviewed in Chace and Walsh, 2006).

In urbanized communities, several avian species are known to thrive, particularly omnivores, granivores, and artificial cavity-nesting species like house sparrows (*Passer domesticus*), European starlings (*Sturnus vulgaris*), Canada geese (*Branta canadensis*), or yellow-legged gulls (*Larus michahellis*). These birds can reach very high artificial densities, increasing the transmission potential for parasites and maintaining them within the community. If virulence is sufficiently low in these common host species, the hosted parasites can spillover into other less well-adapted species, potentially impacting their population sizes and viability, and thus altering community structure. Urbanized communities also are typically more homogeneous geographically (Chace and Walsh, 2006), meaning that parasites present in one locality may rapidly disseminate and establish in new areas with bird dispersal and migration. In addition to the risk posed to more vulnerable species in the community, the presence of certain parasites may be of concern for human and domestic animal health. For example, high densities of birds at backyard feeders can lead to increased transmission of diverse pathogens (Brobey et al., 2017), including *Mycoplasma gallisepticum*, a bacterium responsible for severe conjunctivitis in some avian species (Adelman et al., 2015; Dhondt et al., 2007, and [see Chapters 3, 4, 5, and 7](#)). This bacterium emerged in songbirds in the 1990s after a host switch from domestic poultry (Fischer et al., 1997). It causes substantial mortality in its primary wild host, the house finch (*Haemorhous mexicanus*), but is also carried by other birds with variable clinical symptoms (Farmer et al., 2005). Results of winter disease surveys from backyard feeders in northeastern North America found that higher disease prevalence in house finches correlated with the increased presence of alternative host species, suggesting that community composition in urban zones plays a direct role in disease risk for finches (States et al., 2009) and that this enlarged community may be a source of infection for poultry farms (Sawicka et al. 2020).

Wild birds have also been directly implicated in the dissemination of agents such as influenza viruses, *Salmonella*, *Campylobacter* and West Nile virus to domesticated animals (e.g., Brobey et al., 2017; Craven et al., 2000; Ezenwa et al., 2006; Lycett et al., 2016, and [see Chapter 11](#)). Artificial feeding stations used in animal production may act in the same way as backyard feeders, attracting a high diversity of wild birds and increasing pathogen transmission both within the wild bird community, but also at the wild-domestic interface (Caron et al., 2010). Bird droppings left in urbanized areas can also contain pathogenic bacteria or viruses that may be of public health concern (Feare et al., 1999). Indeed, reviews of available literature have implicated birds in the global epidemiology of numerous pathogenic bacterial species for humans and have documented

cases in which certain species maintain and disseminate antibiotic-resistant strains (e.g., Benskin et al., 2009; Tsiodras et al., 2008; Vittecoq et al., 2017; Zurfluh et al., 2019; **Chapter 11**). Finally, landscape modifications that change the vegetation structure and composition can cascade down to the local community. For example, floristic changes due to modifications in agricultural practices in Northern England resulted in an increase in local tick populations, and an associated increase in the transmission of the tick-borne virus that causes louping ill disease in wild birds. The presence of this pathogen contributed to declines of a dominant avian species in the landscape and one of particular human interest, the red grouse (*Lagopus lagopus scoticus*), and thus to a shift in the structure of the local avian community (Dobson and Hudson, 1986).

## 8.4 An example of Lyme borreliosis in seabird communities

Many of the aspects related to community level interactions and disease ecology mentioned above, and in other chapters of this book, can be illustrated by the example of Lyme disease bacteria that circulate naturally in polar seabird communities.

### 8.4.1 The biological system

#### 8.4.1.1 Seabird communities

Seabirds are the most numerous, diverse, and widespread of marine megafauna (Hoekstra et al., 2010). Although they include an eclectic group from an evolutionary perspective, all species are adapted to life within the marine environment, typically feeding at sea. This group includes gulls, terns, skimmers, skuas, auks, and selected phalaropes (Charadriiformes), tropicbirds (Phaethontiformes), penguins (Sphenisciformes), tubenoses like albatrosses and shearwaters (Procellariiformes), cormorants, frigatebirds, boobies, gannets (Suliformes), and pelicans (Pelecaniformes). Species distributions vary considerably, with some species found across the globe (e.g., great cormorant, *Phalacrocorax carbo*) and others limited to a single island archipelago (e.g., Balearic shearwater, *Puffinus mauretanicus*). Seabirds are also among the most threatened groups of birds (Croxall et al. 2012), and many populations are in decline (Paleczny et al., 2015), making this group particularly important to consider when examining marine ecosystem structure and the potential implications of disease in seabird communities (Provencher et al., 2019).

The greatest majority of seabirds are colonial breeders, meaning that they aggregate in large numbers (hundreds to hundreds of thousands of pairs) for several months per year in order to reproduce. The location of these colonies tends to be stable over long periods and birds often return to the same colony (and sometimes to the exact same nest site) year after year to breed (i.e., breeding site fidelity; Furness and Monaghan, 1987). The high density of individuals within colonies and their predictable seasonal occurrence provide excellent conditions for the maintenance and transmission of parasites and pathogens (McCoy et al., 2016). In addition to colonial breeding, seabirds are also long-lived; once reaching maturity at 3 to 6 years old, these birds can breed for decades (Furness and Monaghan, 1987). Given this longevity, chronic

infections of non-lethal parasites may be maintained and transmitted over long periods (e.g., *Borrelia* spp. bacteria; Gylfe et al., 2000). Similarly, with the regular reuse of nesting sites, temporary ectoparasites, such as fleas, ticks, and flies, can build up large local populations. Indeed, infestation levels can increase over time until bird reproductive success becomes so low that birds abandon the colony (e.g., Danchin, 1992; Duffy, 1983) and prospect for new breeding locations (Boulinier et al., 2016).

From a community ecology perspective, marine birds are interesting biological models because both breeding colonies and foraging hotspots at sea are frequently heterospecific (Figure 8.3), with different species breeding or feeding in complete sympatry. Indeed, seabirds use a variety of terrestrial habitats, with some species nesting in trees (if available), others on the ground (with or without nests) or on cliff ledges, and still others using underground burrows or rock crevices. Seabirds also frequently interact at sea while foraging in response to the aggregated, but temporally variable, position of their marine prey (Fauchald et al., 2000). Although each species can occupy specific habitat niches and/or specialize on particular prey items, intra- and interspecific competition for breeding sites and food can be fierce (Ballance et al., 1997; Kokko et al., 2004; Oro et al., 2009). The presence of multiple interacting species can result in the interspecific transmission of parasites and pathogens that can then favor host shifts, alter the outcome of interspecific interactions (e.g., competition, predation) and ultimately modify the circulation of parasitic agents at different spatial scales (e.g., Dabert et al., 2015; Dietrich et al., 2014a; Gomez-Diaz et al., 2007; Gómez-Díaz et al., 2010; Stefan et al., 2018). These modifications can then trickle down to alter the dynamics and composition of species at different levels of community organization, from the parasite infra-community to the global meta-community (Figure 8.1). Finally, in response to their particular life history traits, seabirds host an extremely wide array of parasites and pathogens – temporary and permanent ectoparasites, macroparasites obtained via trophic transmission, and diverse viral, bacterial, and protozoan pathogens transmitted both directly and indirectly by different vector organisms. A broad list of these infecting organisms can be found in Khan et al. (2019).

[Insert FIGURE 8.3 here]

#### 8.4.1.2 Ticks and the circulation of Lyme borreliosis-causing agents

Among seabird ectoparasites, ticks are among the most common and have the greatest impact on seabird body condition and reproductive success (Boulinier and Danchin, 1996; Duffy, 1983; Feare, 1976). These ticks can include both hard (Ixodidae) and soft (Argasidae) tick species (Figure 8.3). Hard ticks are found in colonies across the globe, from continental Antarctica to the high Arctic, whereas soft ticks are limited to tropical and temperate regions (Dietrich et al., 2011). The greatest part of the tick life cycle takes place in the substrate of the host colony, with host contact being limited to the time required for the bloodmeal. In the case of hard ticks, infestation occurs during seabird reproduction when birds remain in the same general location for prolonged periods of time. A single long bloodmeal of several days is taken in each of the three active life stages of

these ticks (larva, nymph, and adult female). In the case of soft ticks, bloodmeals are short (minutes to a few hours) and thus can be taken any time a host is available locally, but generally happen at night when the host is immobile (Vial, 2009). To compensate for the limited size of the bloodmeal, soft ticks feed several times in each life stage and nymphs will undergo several moults before developing into the adult life stage. Both groups of ticks are known to carry diverse microorganisms, including human pathogens (e.g., Dietrich et al., 2014, 2011; Wilkinson et al., 2014), but the full diversity and pathogenicity of these infectious agents for the birds, are largely unknown.

In the polar regions of the world, seabird colonies are frequently infested by hard ticks of the genus *Ixodes*, such as *I. kergulensis*, *I. kohlsi*, *I. eudyptidis*, *I. philipi*, *I. auritulus* and *I. uriae*. Among these species, *I. uriae* is the most widely distributed, found in polar colonies of both hemispheres and on a range of over 50 different seabird species (Dietrich et al., 2011). Different infectious agents have been described circulating via this tick species (e.g., Great Island Virus: Nunn et al., 2006; *Rickettsia*, *Rickettsiella*, *Coxiella* and *Spiroplasma* bacteria: Duron et al., 2017, 2016), but among the most prevalent and widespread are bacteria of the *Borrelia burgdorferi* sensu lato (Bbsl) complex responsible for human Lyme disease (Dietrich et al., 2008; Duneau et al., 2008; Gómez-Díaz et al., 2011; Munro et al., 2019; Olsen et al., 1993).

Lyme disease is the most common vector-borne zoonosis in temperate regions of the Northern hemisphere (Centers for Disease Control and Prevention, 2019; Sykes and Makiello, 2017). The Bbsl complex currently includes over 20 genospecies, seven of which are thought to be pathogenic for humans (Margos et al., 2011; Stanek and Reiter, 2011). The obligate enzootic life cycle of these bacteria involves *Ixodes* ticks and a variety of vertebrate hosts, including mammals, reptiles, and birds (Gray et al., 2002). Despite a wide host/vector spectrum, some degree of ecological specialization exists among the different species of the complex, particularly towards the vertebrate host (Kurtenbach et al., 2006). Although rarely considered in the global epidemiology of the disease, at least 4 genospecies have been reported circulating in seabirds via the tick *I. uriae* (Dietrich et al., 2008; Duneau et al., 2008), the most prevalent by far being *B. garinii*, a pathogenic species generally associated with forest birds (Hanincova et al., 2003). Indeed, this genospecies represents >80% of tick infections in the marine system (Duneau et al., 2008; Gylfe et al., 1999; Munro et al., 2019). Serological studies on diverse seabird species show that exposure rates can be high within colonies (> 90%), but can vary strongly among seabird species (Lobato et al., 2011; Staszewski et al., 2008). Direct genetic typing of bacteria in sampled ticks confirms high prevalence in the vector populations (up to 40% on average in some colonies: Gómez-Díaz et al., 2010). Although difficult to test directly in natural populations, studies combining exposure rates and capture-recapture modeling have suggested that infection has little impact on adult survival (Chambert et al., 2012). However, as yet, potential effects of infection on juvenile seabirds have not been assessed. Understanding the epidemiology of Lyme disease in seabird communities, and more globally the potential role of seabirds as disease reservoirs for terrestrial systems, requires a clear comprehension of the infection dynamics within and among colonies in both the different seabird host species and their respective tick populations.



### 8.4.2 Population structure of *Ixodes uriae* within and among seabird communities

As outlined above, *I. uriae* is a widespread generalist tick of marine birds, found in polar seabird communities of both hemispheres and on a wide range of seabird species from across different avian families (Dietrich et al., 2011). As seabird colonies are often heterospecific in nature (Figure 8.3), one would expect that sympatrically breeding species should share the same tick population. Likewise, as this tick only exploits the seabird host during the breeding season, when bird movement is largely limited to the nest site and the foraging area at sea, we would expect the probability of tick dispersal among colonies to be low. Population genetic studies carried out on this tick species at different spatial and temporal scales have falsified these general predictions and can help us better understand the circulation of infectious agents in this system.

Initial field observations of tick infestation dynamics on sympatrically breeding black-legged kittiwakes (*Rissa tridactyla*) and Atlantic puffins (*Fratercula arctica*) suggested that two distinct tick populations, one associated with each seabird species, occurred within colonies (McCoy et al., 1999). Later population genetic studies employing highly polymorphic microsatellite markers demonstrated that this was indeed the case (McCoy et al., 2001); *I. uriae* structures locally into distinct host races recurrently across the globe (Dietrich et al., 2012; McCoy et al., 2005; Figure 8.4). Experimental studies have since demonstrated that this divergence is not a simple consequence of genetic isolation, but that different races are adapted to exploit their particular host type (Dietrich et al., 2014c) and have different morphologies (Dietrich et al., 2013). The formation of these host races is temporally dynamic; distinct races are not present in all colonies, and can vary in their degree of divergence in different isolated regions. Interestingly, initial divergence into host races does not seem to lead to full speciation in this system (Dietrich et al., 2014a); more ancient areas of the tick distribution do not show stronger patterns of host-associated divergence than more recently colonized zones (Figure 8.4). The reason for this is currently unknown, but may be linked to the relative long-term stability of host populations and/or genetic constraints on adaptation.

[Insert FIGURE 8.4 here]

In addition to host-associated genetic structure, *I. uriae* populations also show variable patterns of geographic structure, patterns which depend on the host species being exploited. For example, ticks exploiting Atlantic puffins in the North Atlantic start to show signatures of population structure when colonies are separated by more than 700km, that is, it is only when breeding colonies are greater than 700km apart that tick gene flow is low enough for genetic divergence by drift to occur. For ticks exploiting black-legged kittiwakes or common murres (*Uria aalge*), population genetic structure occurs at a smaller spatial scale, when colonies are approximately 200km apart (McCoy et al., 2003a). Given the limited movement of birds during the breeding season, when ticks actively feed on birds, tick dispersal likely occurs with juveniles or failed breeders that prospect for new breeding locations (Boulinier et al., 2016). Tracking data from kittiwakes match these predictions: successfully breeding kittiwakes only move between the

nest site and foraging areas, whereas failed breeders tend to visit different colonies within an approximate 200km radius around the initial breeding site (Ponchon et al., 2014). From these results, we expect that the composition and relative stability of parasite component communities will differ across spatial scales according to the seabird host species; that is, parasite communities of puffins should be more homogeneous at large spatial scales compared to those exploiting kittiwakes or murre.

### **8.4.3 Understanding spatial patterns of Lyme borreliosis within and among avian communities**

In the marine cycle of Lyme borreliosis, we know that vector populations are at least partially isolated among different component species of the seabird community, and that tick dispersal across colonies varies depending on the seabird species exploited. When a parasite is also a vector, host use conditions not only the parasite's own population dynamics and evolutionary trajectory, but also that of the associated microparasite. We now examine patterns of Bbsl structure in marine communities at different spatial scales in light of our knowledge of tick population structure and other heterogeneities that may be present in these communities.

#### **8.4.3.1 Within and among seabird colonies**

As outlined above (see 8.3.1), heterogeneity within the host community can mean that different species contribute more or less to the maintenance and transmission of an infectious agent. In the case of Bbsl spirochaetes circulating in marine birds, this also seems to be the case, although placing the mechanism in the correct biological compartment is not yet obvious.

Studies that have examined both prevalence of Bbsl in vector populations and exposure rates of kittiwakes have shown that pathogen presence varies at both within and among colony scales (Dietrich et al., 2008; Staszewski et al., 2008). Exposure rates in kittiwakes have been shown to depend on local levels of tick infestation (Gasparini et al., 2001), which may vary due to both heterogeneity in individual host susceptibility (Boulinier et al., 1997), the quality and/or topology of the breeding area (McCoy et al., 2003b), and colony history (Danchin, 1992). The overall dynamic of a particular breeding area will also alter infection risk. Seabirds such as kittiwakes use public information on local breeding success to select future breeding locations (Boulinier et al., 2008). When success is high, new individuals, with their infra-community of parasites, will arrive more readily than in patches where breeding success is low.

These patterns become even stronger at the level of the seabird community. As outlined above (see 8.4.2), the tick vector in the marine system has diverged locally into distinct seabird-specific host races. This means that Bbsl harboured by one tick host race will not necessarily be shared with another tick host race, even if these races occur sympatrically (Figure 8.5). Thus, we could expect distinct infection dynamics among different members of the seabird community. Ticks of different sympatric races examined for Bbsl infection have shown that this is indeed the case. Data from three colonies in Iceland and one colony in Norway indicated that prevalence and infection intensities of Bbsl varies significantly among tick host races at the colony scale, with ticks from Atlantic puffins showing higher prevalence and greater infection intensities compared to kittiwake

and murre races (Gómez-Díaz et al., 2010). This suggests that puffins, and/or their specific ticks, are more competent hosts for Bbsl than the other seabird species/tick races in the community. Genetic analyses of the most prevalent bacterial species of the complex, *B. garinii*, further demonstrated that bacterial strains were locally isolated among seabird species/tick host races; at the colony level, Bbsl strains do not circulate freely among the different component species of the community (Figure 8.5). This structure does not seem to be due to adaptation of the infectious agent to different seabird species, as no pattern of divergence could be found in genes thought to be related to host use (OSPs genes), and host-specific patterns of strain divergence at the colony level were not repeatable at larger spatial scales, that is, a strain infecting a puffin tick in one colony could be found in a murre tick in a different isolated location (Gómez-Díaz et al., 2011). Patterns of pathogen structure at the colony level therefore seem to be due to isolation by vector host use rather than adaptation *per se*. Because of this, increasing or decreasing seabird diversity within a given seabird community would not be expected to alter the infection dynamics of Bbsl, that is no dilution effect would be expected in this system. The question now is the degree to which the patterns found for ticks and Bbsl bacteria hold for other parasites of the meta-community. Evidence from another tick-borne pathogen, Great Island Virus (Orbivirus), supports results from Bbsl, that parasite component communities may not be readily shared among sympatric seabirds. Indeed, viral prevalence in the one colony was found to be high in both murre ticks and their ticks, but low in kittiwake ticks and absent in kittiwakes themselves (Nunn et al., 2006). Too few studies currently exist for other types of parasites to examine this question more generally.

[Insert FIGURE 8.5 here]

#### 8.4.3.2 Linking marine and terrestrial enzootic cycles

Results from several studies have suggested that Bbsl bacteria are shared between marine and terrestrial systems (Bunikis et al., 1996; Gómez-Díaz et al., 2011; Munro et al., 2019). This link leads to several important questions about the epidemiology of Lyme disease and the evolutionary trajectory of these infectious agents. *How important are seabirds as reservoirs for Lyme disease spirochaetes? At what frequency do seabirds disperse these infectious agents over large spatial scales? And where are the contact points between terrestrial and marine ecosystems?*

The importance of the first two questions depends on the answer to the third. Indeed, from the patterns described above, we know that Bbsl circulates in a natural enzootic transmission cycle in marine bird communities and that seabirds could be excellent reservoirs (and potential generators) of pathogen diversity. We also know that seabirds can travel rapidly over substantial distances, taking Bbsl, and the rest of their parasite infra-community, with them. Dispersal propensity in colonial seabirds depends both on individual reproductive success and overall colony dynamics, with failed individuals leaving unsuccessful colonies to find better locations for future reproduction. This dynamic means that any extrinsic factor affecting seabird reproductive success, including anthropogenic effects such as reductions in food resources due to overfishing, or colony disturbance due to ecotourism, may increase pathogen dispersal to alternative colony locations.

However, to understand the importance of marine Bbsl for human health, there needs to be a link between ecosystems. When present in seabird colonies, humans can be bitten by *I. uriae* ticks, and cases of Bbsl transmission have occurred under these circumstances (pers. obs.). The increasing presence of humans in seabird colonies with the rise in eco-tourism therefore poses a substantiated risk for Bbsl exposure. However, as humans are accidental and dead-end hosts for Bbsl, infective strains received from seabirds can not be transmitted to the terrestrial cycle. The bridge between systems may thus lie in the presence of other alternative host species within colonies. For example, other animals, such as rodents or passerine birds can sometimes be present in seabird colonies and may serve as accidental hosts to *I. uriae*. In such cases, ticks may transmit seabird-derived Bbsl strains to these animals which may then circulate outside the colony location. In more temperate zones, it is also possible to have additional tick species within seabird colonies, ticks that can feed successfully on a wider range of host species than *I. uriae*, including seabirds, mammals and passerine birds. These links still require specific testing, but suggest that transmission dynamics within the marine cycle of Bbsl should be considered more explicitly for understanding the global epidemiology of Lyme disease. More generally, the detailed work on Bbsl circulation within seabird communities highlights the importance of accounting for different spatial scales for understanding pathogen transmission dynamics and parasite community composition. It has also identified the key role of parasite specialization (here, host race formation in ticks) in determining local exposure rates and infra-community composition within host communities.

## 8.5 Avian communities and One Health

We are currently experiencing a period of rapid global change that will have strong impacts on natural communities and their dynamics. Organisms are shifting their geographic distributions and phenologies in relation to climate change (Gorman et al. 2010; Jaenson et al., 2012; Matthysen et al., 2011), species are going extinct due to changes in food resources (Grémillet et al., 2019), and natural habitats are becoming more and more fragmented with expanding human populations (Chace and Walsh, 2006). These different effects may alter overall community structure and function, including avian diversity and that of their associated parasites and infectious agents.

Parasites are fundamental components of all natural communities. This diversity is structured at different biological scales and can define individual host fitness and lead to increases or decreases in overall community diversity. However, in order to determine the functional role of a parasite at the level of the free-living community, it is necessary to first understand how it impacts the parasite infra-community, because it is this community that will alter individual host fitness. Studies on within-host interactions in coinfecting parasites are becoming more frequent (e.g., Graham, 2008; Telfer et al., 2010), but work at the level of the infra-community is still missing. The possibility that a parasite species simultaneously affects structure at all levels of a community, from the parasite community up to the community of free-living animals (Poulin, 1999), has also not yet been evaluated for avian communities, but may be interesting to explore more explicitly in zones of recent parasite invasion (e.g., the spread of *P. relictum* to high altitude zones of the

Hawaiian Islands).

Throughout this chapter, examples have highlighted the direct relationship between avian community structure and parasite diversity. Adding host biodiversity to communities can shift parasite community structure and stability, in some cases amplifying parasite presence in the community, in other cases reducing transmission and lowering overall infection prevalence. The direction this takes is thought to be associated with the spatial scale of the community being considered (Halliday and Rohr, 2019), with higher biodiversity at local scales often being associated with reduced disease risk, and amplification occurring at broader spatial scales. More rigorous tests of this hypothesis are now required, as well as a consideration of the temporal stability of such changes for both parasite and host community dynamics.

Much of our understanding of the links between avian community structure and function and parasite and pathogen diversity have come from field studies of natural populations, but data are still limited. For example, the generality of the dilution effect model requires data demonstrating that shifts in diversity and community composition directly affect vector infection rates. Surveillance data from communities undergoing rapid changes in community structure, such as island populations following the removal of an invasive species (Le Corre et al., 2015), or communities found in forested areas with planned logging activities (e.g., Schmiegelow et al., 1997), may be particularly useful in this respect. Similarly, the spatial scale at which parasites might alter host community functioning will depend on relative dispersal rates and distances. Such information is now becoming more readily available for avian species with recent technical advances in animal tracking (Kays et al., 2015) and rapid genetic typing of infectious agents (e.g., Michelet et al., 2014).

Finally, although the notion of spatial variation is often explicit in analyses of community structure in relation to pathogen transmission and disease risk, temporal variation in species presence and activity within the community are less frequently considered, but are essential to estimate contact rates, particularly in seasonal species (Caron et al., 2010). Thus, to better predict risk, surveillance data on the activity of different species within a community over time are required. When combined with data on pathogen competence, this spatial and temporal data can then be combined to estimate parasite spillover within natural communities, or to human and domestic animals.

More generally, one thing is evident, if biodiversity buffers ecosystems against environmental variation, its loss, be it avian or parasitic, can destabilize natural communities, potentially altering transmission cycles and leading to disease emergence. Although the mechanisms underlying such changes are diverse and difficult to pinpoint (e.g., dilution effects, threshold density effects, parasite-parasite interactions, or other idiosyncratic effects), maintaining high diversity within natural communities should be a priority to help retain their stability and may reduce disease risk for humans and their domestic animals under the One Health paradigm (Zinsstag et al., 2012). This aim will be challenging to meet in the near future.

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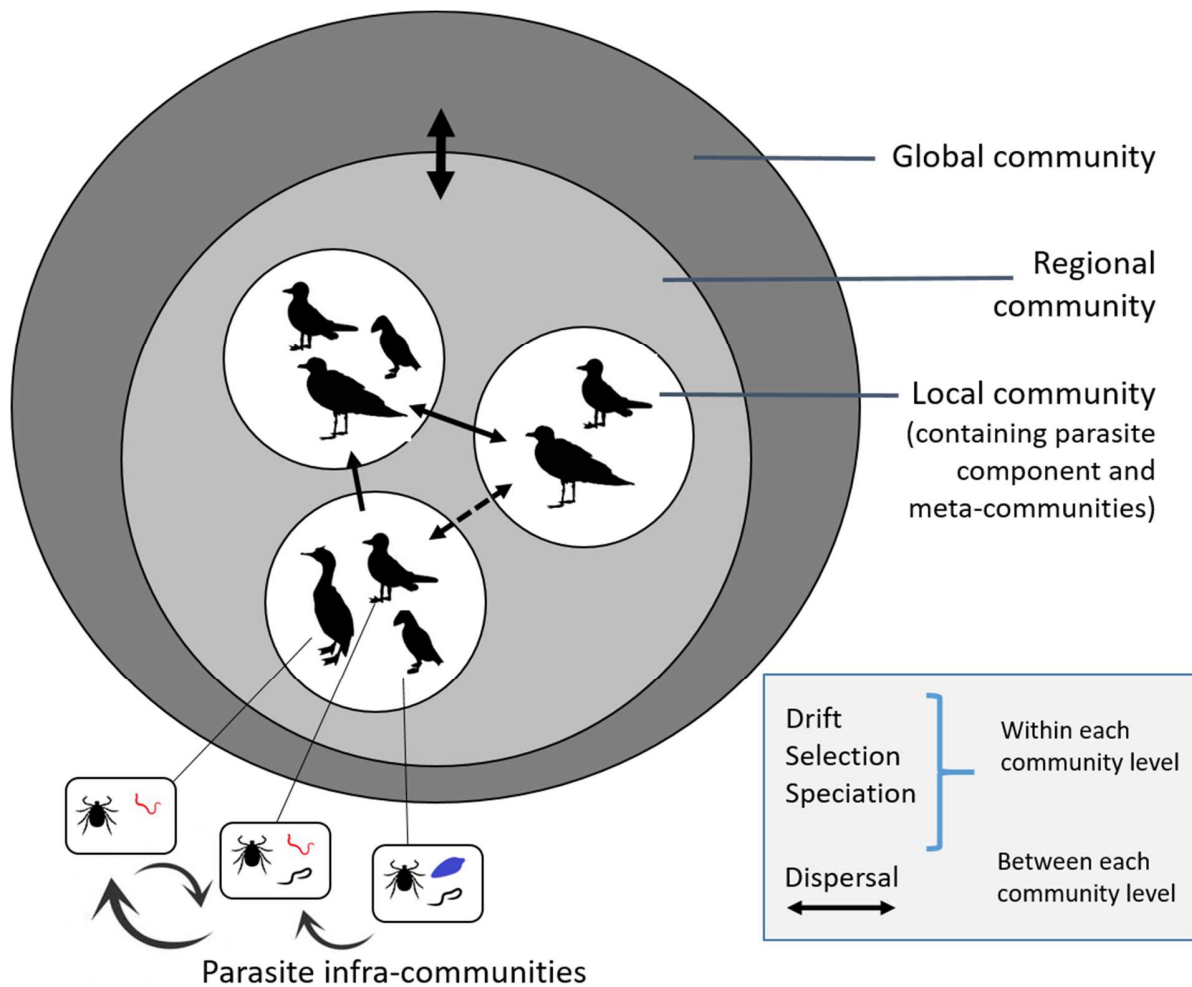
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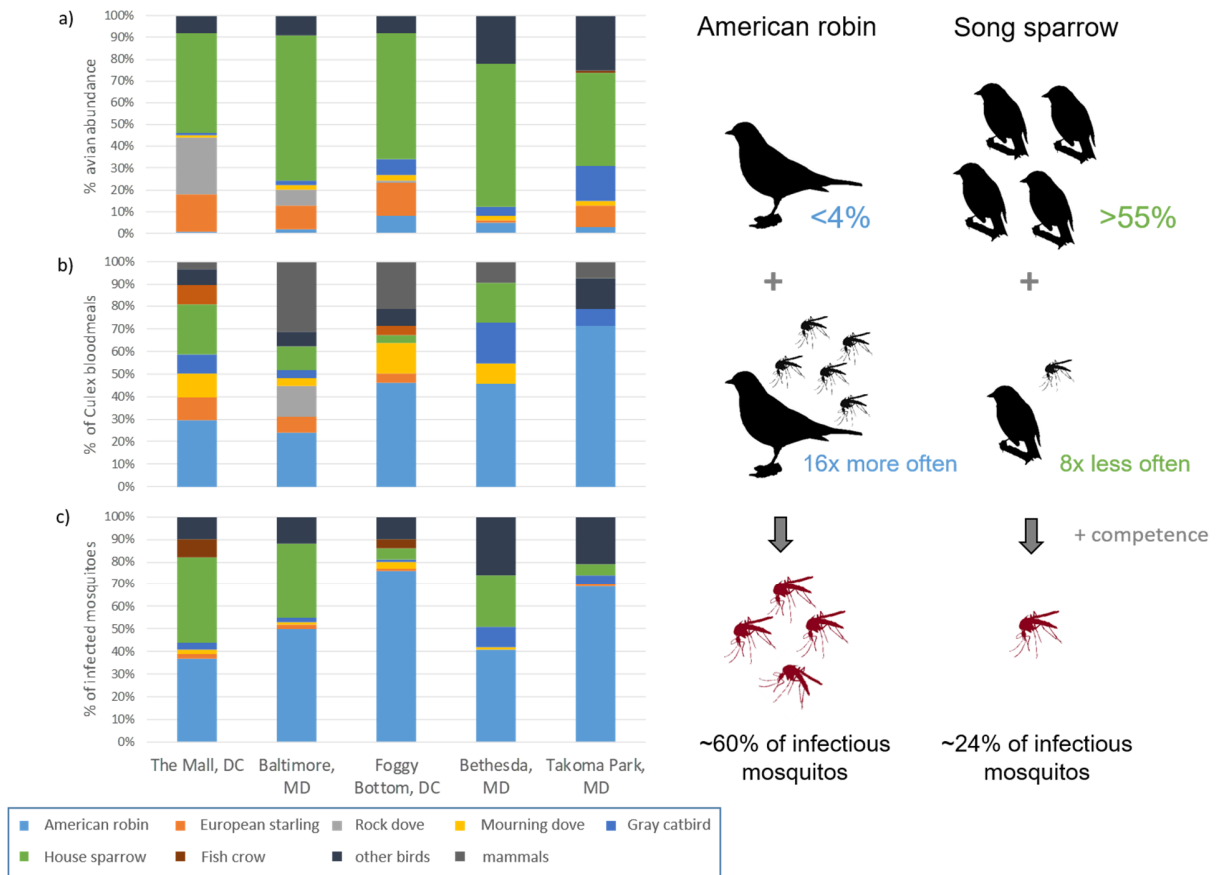
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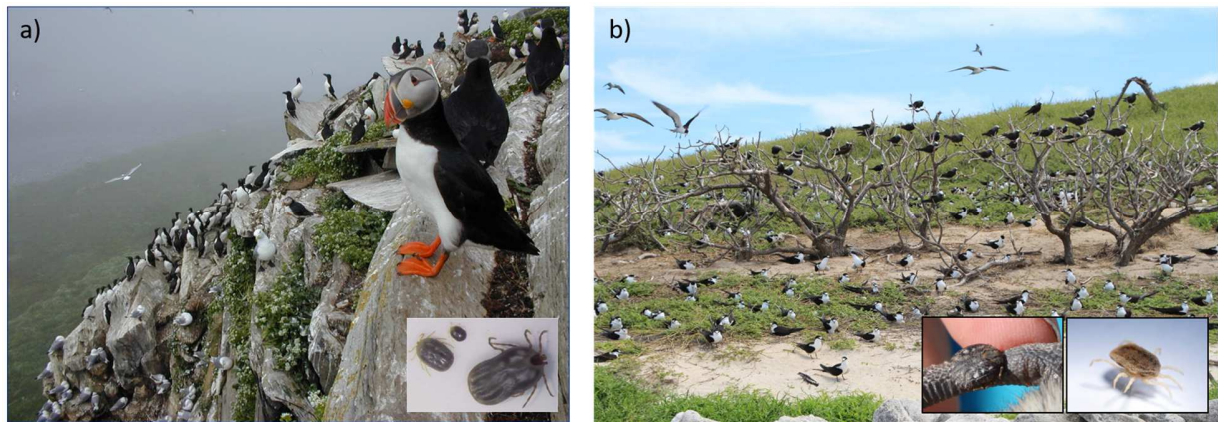
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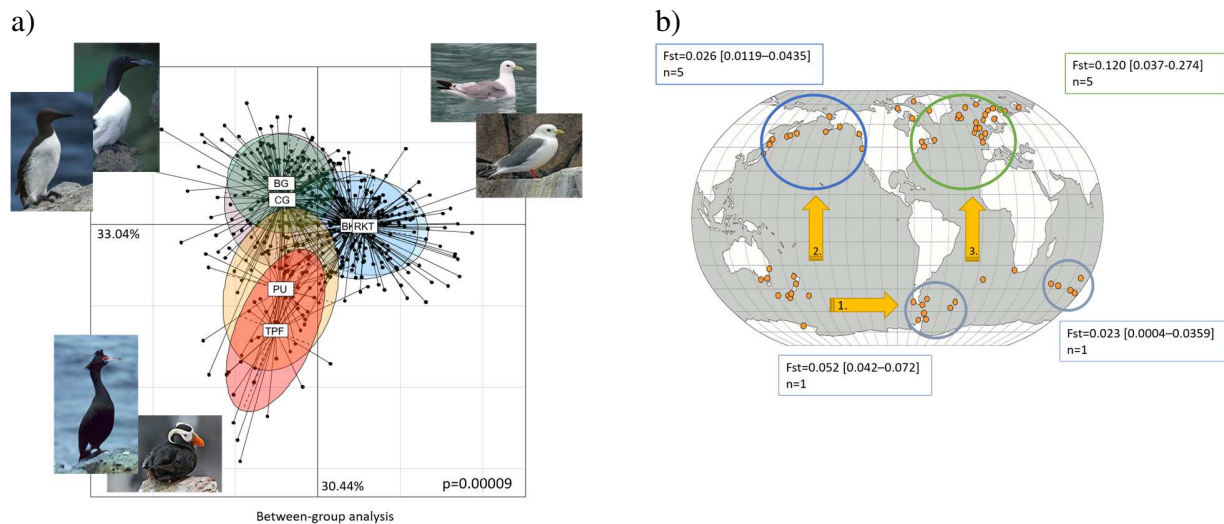
**Figure 8.1:** The structure of natural communities and the general processes that characterize different levels of biological organisation (after Vellend, 2010). Communities can form at different levels of biological organisation, starting with the community of parasites found within a single host individual (the infra-community) and extending to regional and global communities (or metacommunities) of different interacting species. At each level, the processes of ecological drift, selection and speciation will occur. Dispersal links communities across scales, defining their distinctness, and can vary in intensity and direction. The global species pool and the nature of dispersal will determine which biological units arrive at local scales, where intrinsic biotic and abiotic processes will then act to determine the final community composition (Pearson et al., 2018).



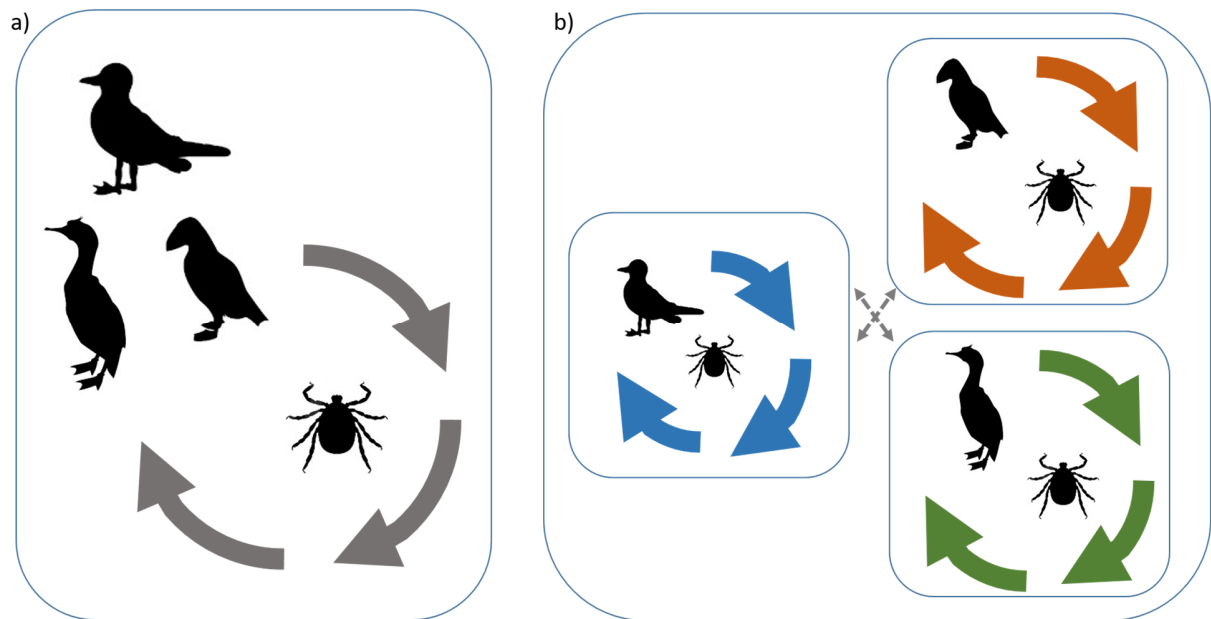
**Figure 8.2.** Relationship between avian community composition, mosquito feeding preference and amplification fraction of West Nile Virus infections. Among the five studied sites (x-axis), American robins made up less than 4% of the avian community (a), but accounted for over 40% of mosquito blood meals (b) such that mosquitoes fed on robins 16x more often than expected if they fed randomly. Taken together with species-specific competence estimated from the lab, viraemic robins were estimated to produce approx 60% of infected mosquitoes, compared to only about 24% in dominate song sparrows (c), if initial infection rates were similar among avian species within the community. From Kilpatrick et al. (2006).



**Figure 8.3.** Community level interactions among seabird communities and their ectoparasites. a) A heterospecific colony of seabirds on Hornoya, an isolated island in northern Norway (photo. T. Boulinier). Five different species breed in sympatry at this site and are all exploited by the hard tick *Ixodes uriae* (inset: photo K.D. McCoy). b) Two different seabird species found on the small island of Ile de Lys (Scattered Islands) in the western Indian Ocean: sooty terns *Onychoprion fuscatus* and lesser noddies *Anous tenuirostris* (photo: K.D. McCoy). In colonies of this region, seabirds are frequently exploited by both hard (*Amblyomma loculosum*, left inset, photo: K.D. McCoy) and soft ticks (*Ornithodoros capensis*, right inset, photo; P. Landmann).



**Figure 8.4.** The tick *Ixodes uriae* is a regular member of seabird communities in polar regions of both hemispheres. These communities commonly include multiple seabird species. (a) Population genetic studies have shown that ticks have evolved distinct local populations associated with each type of seabird in the local community: tick host races. Here, ticks were sampled from six seabird species in nine heterospecific colonies of the North Pacific and were typed at a series of microsatellite markers (figure modified from Dietrich et al., 2012). (b) At broader spatial and temporal scales, it was found that divergence levels between tick host races varied across the different regions of its distribution (orange dots indicate colony locations), but not in relation to the time since tick colonisation. On the figure, the colonisation order is shown based on 37 tick populations from 18 colony locations across the globe: *I. uriae* first evolved in the southern hemisphere where it expanded along with its seabird hosts approximately 22myr (1.). Ticks then invaded the northern hemisphere independently via the two oceans, first in the Pacific (2.) and then latter in the Atlantic (3.). Although populations in the North Atlantic were among the last colonised, host-associated divergence among sympatric tick populations is strongest, as shown by average estimates of  $F_{ST}$  ( $\pm$  SE) between host-associated tick populations within colonies (figure modified from Dietrich et al., 2014a).



**Figure 8.5.** The circulation of vector-borne pathogens within host communities depends on vector host use. (a) All available species in the community are used by the vector (i.e., the vector is a true host generalist). Pathogen transmission will depend on the relative abundance of each host species in the community and their competence for the pathogen. (b) Each vertebrate host species is exploited by a distinct vector population resulting in the presence of locally independent or semi-independent disease cycles. Pathogen transmission in this case will depend on the degree of vector specificity (dotted arrows indicate potential contacts). After McCoy (2008) and McCoy et al (2013).