

Wildlife Research Monographs 3

Joaquín Vicente
Kurt C. Vercauteren
Christian Gortázar *Editors*

Diseases at the Wildlife - Livestock Interface

Research and Perspectives
in a Changing World



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Volume 3

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Editors

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Preface

Wildlife have coexisted with livestock in dynamic systems over thousands of years. The overall picture we can see today is that about one-fourth of the planet's ice-free land (or over half of the agricultural land) is used for livestock grazing, and production from approximately one-third of croplands is used to feed livestock (<http://www.fao.org/3/ar591e/ar591e.pdf>, Tilman et al. 2001). Worldwide today there are almost 1.5 billion cattle, 2.2 billion small ruminants, over 25 billion chickens, and almost 1 billion pigs (FAOSTAT 2018). If we combine pastures used for grazing with land used to grow crops for animal feed (mostly intensive systems), livestock accounts for about three-fourths of global agricultural land, with a highly unequal distribution over the planet. Livestock produces almost 20% of the world's calories and approximately one-third of total protein (Poore and Nemecek 2018). The coexistence of livestock and wildlife occurs across a wide variety of contexts and is constantly changing, varying from interfaces along the borders of pristine areas to those in highly anthropogenic environments, where in certain cases, wildlife adapt well to new niches.

Human interests and needs have determined the distribution of livestock and farming practices throughout history. In recent decades, several factors, such as changes in wildlife management, land uses, farming practices, and the human demography, have led to an expansion and increased abundance of some species of wildlife (Massei et al. 2015), facilitating the interaction between the wild and domestic compartments at common niches by other mechanisms (Walsh and Wiethoelter 2017). The former especially applies to developed countries in the Northern Hemisphere and, particularly for many ungulates and certain carnivores. In extensive systems, such as in semiarid regions and certain tropical and arctic areas of the world, the coexistence between wildlife and livestock has probably been facilitated by relatively low human densities (du Toit et al. 2017). However, in many developing countries or in certain regions with a relatively small human footprint, human activities, including farming practices, increasingly encroach natural areas (i.e., deforestation, forest fragmentation, land degradation, urbanization, fencing), and subsequently, new opportunities for the wildlife and livestock interaction

emerge as they cohabit and/or compete for the same resources (Foufopoulos et al. 2002). These local changes in human ecology produce alterations of the ecological niches of natural wild hosts and may modulate spillover risk of pathogens to humans and livestock in regions where a risk for potential transmission naturally exists (Han et al. 2016). This situation leads to increased risks and also contributes to the loss of wildlife populations, such as many wild herbivores, carnivores, and marsupials which are endangered or even close to extinction (Knight-Jones and Rushton 2013). Overall, scientists monitoring changes in the populations of thousands of animal species around the world concluded that the variety of life on Earth and associated wildlife populations are disappearing fast (Grooten and Almond 2018), by an overall decline of 60% in population sizes between 1970 and 2014. Species population declines are especially pronounced in the tropics, with South and Central America suffering the most dramatic declines. It is forecasted that humans will cause so many mammal species to go extinct in the next 50 years that the evolutionary diversity of the planet will not recover for 3–5 million years (Davis et al. 2018). Many wildlife/livestock interfaces will probably become simpler, and presumably, higher quality hosts will probably tend to occur in species-poor communities. Interestingly, current host communities show that lower quality hosts tend to occur in more diverse communities and may regulate abundance of high-quality hosts or vectors and thus reduce encounter rates between these hosts, vectors, and associated pathogens (Otsfeld and Keesing 2012).

The presence of wildlife is sometimes considered incompatible with agricultural production, particularly livestock farming, because the costs associated with conserving wildlife and mitigating its impacts on conservation are perceived by humans as unaffordable in most situations; this may be less apparent in semiarid rangelands (du Toit et al. 2017). Among other conflicts, interactions between wildlife and livestock have historically hindered agriculture practices and livestock farming, often justified by the need to protect livestock from disease spillover and spill-back from wildlife reservoirs. Shared diseases between wildlife and livestock, often transboundary, are relevant to public health, global economy, game production, wildlife management, and the conservation of biodiversity (e.g., Caron et al 2013; Rhyan et al. 2010). Disease-related morbidity and mortality of livestock negatively affects production, which is especially negative to livelihoods of small producers in developing countries. For instance, production losses due to foot and mouth disease (FMD) have a large impact on the world's poorest areas, where more people are directly dependent on livestock (Knight-Jones and Rushton 2013). In addition, and more important for developed farming, just the presence of pathogens can result in economic and trade consequences (e.g., the current outbreak of African swine fever (SF) in domestic and wild pigs; Costard et al. 2013) resulting in reduced access to international markets. Diseases of great economic importance may have global impacts, and, normally in countries with ongoing control programs for disease prevention, create large costs. In addition, sporadic outbreaks result in substantial effort and costs to regain disease-free status. Diseases among wildlife populations, especially emerging diseases, can negatively impact conservation, and

a cascade of ecological effects may appear (e.g., wild rabbit viruses and Iberian lynx *Lynx pardinus*; Lozano et al. 2014), sometimes altering the ecosystem's functionality and even impacting economies linked to ecosystem services and human-related activities (e.g., hunting and tourism). These ecological losses may be consequences of invasive or domestic animals and their associated pathogens (e.g., TB and brushtail possum in New Zealand, or canine distemper virus and domestic dogs in Africa; Nugent et al. 2015; Viana et al. 2015). Finally, human zoonotic disease risk exists for most pathogens shared at the wildlife/livestock interface, which rely on several factors underlying the frequency of transmissible contacts at the human/animal and the wildlife/livestock interfaces (Han et al. 2016).

We define livestock, broadly, as all domestic, nonaquatic vertebrate animals that are farmed in agricultural systems and holdings (individuals of various genera or families are being aggregated into a single group; e.g., the term "poultry" covers domestic fowls, guinea fowl, ducks, geese, and turkeys (FAO, Robinson et al. 2011). Depending on the degree of human influence and supervision, wildlife can comprise free-ranging, captive, wild and feral domestic animals. We do not differentiate among these groups; all feral and nondomestic animals whether free-ranging, captive, or semi-captive are included.

The main motives of this book, as a comprehensive new contribution to the study of the wildlife/livestock interface, are:

- The study of animal interfaces, especially those involving wildlife, requires *multidisciplinary approaches*, for which we identify the need for a comprehensive and transversal text reviewing and evaluating current understanding and research approaches.
- *The historical interaction between wildlife and livestock* has shaped the distribution of diseases into what we know today and our current range of ecological effects on both sides of the interface. In turn, we can understand part of the history of the wildlife/livestock interface by observing current events. Particularly, the domestication of livestock played a crucial role in transmission of pathogens at the newly created interfaces, and subsequent human actions have led to unprecedented animal and pathogen distribution, spread, and evolution.
- Today, global patterns in spillover risk reflect close contact interactions among wildlife, livestock, and humans that occur in the context of complex, diverse, and numerous circumstances all over the world. Focusing on one of the current animal interfaces offers only a partial view of the whole. A given interface is a narrow window through which we see one of the multiple "edges" or interfaces that each compartment has potential to contribute. Therefore, *the drivers of the wildlife/livestock interfaces must be integrally considered* (the One Health concept). The chapters of this book consider the human side to always be present as the driver, involved in and affecting every compartment.
- Chapters herein *review and analyze the different ecological, epidemiological, cultural, and socioeconomic drivers of the interface*. Since the study of the interface has a relatively short trajectory (Box 1), the explosion of recent

contributions required a synthesis of the progress to date and new directions needed, expanding the review to related disciplines, topics, and research areas.

- There is a need to *evaluate a range of ecological, epidemiological, and analytical tools to design best approaches to understand the animal interfaces*; this is also important from a practical perspective.
- There is a need to compare how in such complex systems different factors related to host communities, pathogens, environments, and human-based social and economic contexts operate. *Analyzing the regional situations and diversity of contexts and characteristics of the interfaces can therefore help to draw an integrative perspective*. This is not a complete compilation of studies but an exercise to evidence similarities and differences on specific patterns and cases.

As for the *organization of the book*, an introductory chapter (Chapter “Host Community Interfaces: The Wildlife-Livestock”) approaches the epidemiological interface among communities as a barrier among hosts where pathogens “find” opportunities to emerge. We raise some questions which have arisen to us in the present times, characterized by a global human health crisis. The wildlife/livestock interface is a complex ecological and epidemiological feature that requires in-depth characterization in a dynamic space of transition and contact among host compartments. We basically introduce theoretical frameworks, from a multidisciplinary point of view, to understand and initiate the study of dynamic processes, drivers, and outcomes we observe at the animal interfaces, with particular references to those established between wildlife and livestock.

The interfaces have changed over the last millennia due to human domestication of animals in terms of distribution, extension, composition, pathogen flow, inter-relationships among hosts, relative contribution of specific risks, opportunities for pathogens to breach barriers, and potential for spread all over the world; local spillover at multiple interfaces and global (animal or human) emergences are now omnipresent. Today, though the human capacity to disseminate pathogens worldwide is greater than ever, we also now have greater knowledge and tools to counteract and contain pathogens. Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface” compiles the history (natural and human) of the multi-host multi-pathogen systems, subsequent interfaces, and what drivers have operated. This look at the history of animal interfaces also aims forward, providing the necessary perspective to focus on current questions, better understand what is going on at present, and how we can best approach the future.

The transmission of pathogens at wildlife/livestock interfaces is a complex mechanism involving interspecific interactions occurring at multiple scales in time and space. Some major factors determining the frequency and intensity of direct and indirect contacts among potential hosts at the interface are the access to resources, interspecific competition, and predation. Chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health” addresses the ecology of pathogen transmission at the wildlife/livestock interface with an approach toward socio-ecological system health. It is illustrated with various examples of how the processes of pathogen

transmission among interacting wild and domestic host populations may be analyzed using tools and concepts drawn from population, landscape, and evolutionary ecology. This chapter highlights the importance of the interdisciplinary integration of ecological, biomedical, and social sciences into a single discipline of “disease socio-ecology,” which remains a major research frontier for improved management of wildlife/livestock interfaces and emergence of pathogens at animal interfaces with humans.

Today, interfaces occur at multiple spatial scales, ranging from natural scenarios to human-generated conditions for host interactions. In subsequent chapters (Chapters “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Europe”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Asia”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Africa”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Oceania”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in North America”, and “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Central and South America”), authors with deep understanding of the wildlife/livestock interfaces in their respective regions describe the specific nature and drivers of the interface for each continent. The approach is to present, for each region, (1) a brief history of the wildlife/livestock interface; (2) the socioeconomic and geographical circumstances, (indicating differences between areas within the continent); (3) the characteristics of wildlife, livestock, farm typologies, management strategies, and veterinary services; (4) wildlife/livestock coexistence (problems and opportunities, implications for conservation and development); (5) the holistic perspective and One Health context applied to the region; (6) what the main features of the identified interfaces are, including types of interfaces and relevant diseases; (7) ongoing research of diseases at the wildlife/livestock interface: main topics addressed, methods, and gaps; and (8) a summary of management practices (ranging from traditional grazing systems to modern techniques) at the interfaces.

The methods selected to study the wildlife/livestock interface have to adapt to the objectives of the study, logistical constraints, target host species and pathogens, and the routes of transmission at the wildlife/livestock interface. Chapters “Collecting Data to Assess the Interactions Between Livestock and Wildlife” and “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field” focus on methodological aspects employed to study the wildlife/livestock interface, using an applied approach. Chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife” describes multiple methodologies for collecting data for assessing the interactions between livestock and wildlife, both to quantify and to detect the potential of interaction, evidencing specific pros and cons. It is illustrated with a specific case study of animal tuberculosis in the Iberian Peninsula of Spain. The study of the wildlife/livestock interfaces has particular characteristics and implications in disease ecology which justifies the need for a dedicated field of scientific endeavor devoted to the topic. Chapter “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field” emphasizes the

need for interdisciplinary approaches and a dedicated thematic field to approach the wildlife/livestock interfaces. Following recent events, bridges have been developed between sectors and different disciplines, especially between the fields of epidemiology and ecology and more recently of molecular biology and social sciences. This chapter provides case studies in the context of disease ecology illustrating how the characterization of the wildlife/livestock interface can inform disease ecology studies and guide surveillance and control of infectious diseases.

The previous chapters showed different types of approaches extensively used in epidemiology to evaluate pathogen transmission among individuals in one or more populations, which rarely consider multi-host approaches at the wildlife/livestock or wildlife/livestock/human interface. The quantification of transmission at these interfaces is key to not only understand disease dynamics and identify high-risk areas/time periods but also to be able to more cost-effectively allocate preventive and control interventions. Chapter “Quantifying Transmission Between Wild and Domestic Populations” aims to provide a brief overview of the main modeling approaches available to quantify the multi-host disease transmission at the wildlife/livestock interface, illustrated with specific case studies. The main approaches are discussed in order to respond to specific research questions as well as the benefits, uses and limitations of each method, and recommendations and future directions (Chapter “Synthesis and Future Perspectives of the Study and Management of Diseases at the Wildlife-Livestock Interface”) to better understand disease dynamics at the wildlife/livestock interface.

Overall, this book not only provides an introduction to readers new to the topic, but also reviews and synthesizes historical and recent insights in a global and transdisciplinary context, detailing specificities to each continent. The contents will also be of value to professionals and policymakers working in the field, and our aim is to address the management of the wildlife/livestock interface in a further volume.

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Part I
Introduction

Host Community Interfaces: The Wildlife-Livestock



Kurt C. Vercauteren, Christian Gortázar, Daniel Beltrán-Alcrudo, and Joaquín Vicente

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Barriers Among Hosts as Opportunities for Pathogens

Living host organisms are part of biological communities, and there are boundaries, i.e., epidemiological interfaces, across which pathogens can be transmitted among these communities (Hassell et al. 2017). For instance, some pathogens are shared between wild and domestic animals, many others are maintained by wildlife reservoirs, or in other cases by livestock and other domestic species causing major outbreaks in wildlife, e.g., ungulates and carnivores. The different epidemiological

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interfaces are characterized by the community of species on both sides of boundaries (or compartments; human, domestic animals, and wildlife), and the habitats and resources where these communities live and interact (Huyvaert et al. 2018). Most disease-causing organisms in nature are capable of infecting multiple hosts (Cleaveland et al. 2001; Haydon et al. 2002) and are thus referred to as multi-host pathogens. Some multi-host pathogens are maintained solely in multiple wildlife species. It is, however, remarkable that among domesticated animal species, roughly 77% of pathogens of livestock and 90% of pathogens of domestic carnivores are known to be multi-host pathogens (Cleaveland et al. 2001).

An epidemiological interface is therefore established among wildlife, domestic animals, and human compartments in an abiotic environment (a potential reservoir itself) (Haydon et al. 2002). *These “barriers” between compartments constitute opportunities for horizontal transmission between species and a new space for evolution, emergence, and maintenance of pathogens.* The epidemiological and ecological connections among host species are dynamic, and new edges and paths continuously break host species barriers (Han et al. 2016). Pathogens must evade their potential new host’s immune system to successfully infect it and, therefore, they normally infect more readily host species whose internal environment is similar to that of the original carrier (Pepin et al. 2010). Subsequently, shared pathogens have the opportunity to expand in the newfound compartment. Some pathogens benefit from the existing conditions at the interface and become endemic, spilling easily back, and forth between compartments, e.g., bovine tuberculosis at the wildlife livestock interface (Barasona et al. 2017).

A recent event in geological times over the natural history of Earth (see Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”) has determined the various animal interfaces we see today. The livestock compartment only appeared after human domestication gave rise to three new animal interfaces: human–domestic, wildlife–domestic, and their juxtapositions as human–domestic–wildlife. More recently, anthropogenic effects, especially during the last century, and the subsequent changes in urban areas, farming, food systems, and natural ecosystems, have led to increased exposure of human and animal populations to novel pathogens and the establishment of newly shared diseases, which are considered emergent (Lindahl and Grace 2015). Some examples are swine and avian influenza or African swine fever (ASF) (Gavier-Widen et al. 2015), and more recently, Coronavirus (CoVs) disease 2019 (COVID-19), which likely jumped from infected wild animals to humans resulting in millions of infected people worldwide in just a few months (Morens et al. 2020). Humans, animals (both domestic and wild), and ecosystems are tightly linked, more than ever, and this also affects global health. This vision is increasingly evident and widely accepted by the scientific community. However, the implementation of certain practices (e.g., surveillance) and actions (ranging from local to holistic) under this principle across the animal health, human health, and environment sectors remain a challenge (Berezowski et al. 2019; Savory 2016). From the disease perspective, the risk of unexpected spillover events resulting from interactions between wildlife and

domestic populations (in all their varieties and conditions) trying to adapt to a changing world has never been so real.

In modern times, epidemiology and preventive medicine, as medical disciplines of human and animal health, have provided information and a better understanding of how diseases have changed the history of humanity and helped to shape the world. However, they are mostly biased toward the human component. Some examples of such diseases include bubonic plague, cholera, tuberculosis, smallpox, and coronaviruses, which have induced humans to develop and implement control measures to mitigate their spread. The focus of researchers and animal and public health policymakers at the interfaces involving animal compartments is relatively recent, particularly for wild species, and is an area of increasing concern (Fig. 1). Medicine, veterinary science, conservation biology, and other disciplines now converge because *these interfaces are hotspots for pathogen transmission, maintenance, and emergence*. We cannot look at any compartment in isolation from others, as they are ineludibly and functionally linked through ecological and evolutionary processes underlying host jumps by pathogens. Broadly, the factors causing emergence can be defined as ecological or adaptive (Pepin et al. 2010). If the main factor causing emergence is ecological, and adaptation is not required for the jump to occur, the cause of the host jump is known as an ecological driver. An adaptive driver requires a genetic change in the pathogen for its emergence in a new host, although an ecological driver is likely to be involved in this situation as well. An adaptive driver occurs when a selective pressure operates in the new host population after cross-species transmission has occurred, and consequently, pathogen genotypes capable of successful spread and maintenance in the new host species are selected over other genotypes that fail. The adaptive genetic changes leading to adaptation after a host jump can originate either in the new host or in the reservoir host. For instance, surveillance, molecular epidemiology, bioinformatics, and microbiology have shown that SARS-CoV host jumps require viral adaptation. During the early spread of SARS-CoV in humans in 2003, although numerous independent cases of SARS-CoV transmission from reservoir hosts occurred, most died out after just a few human cases, indicating that the introduced strain was not fit for human-to-human transmission (Zhao 2007; Li 2008; Sheahan et al. 2008). Unfortunately, a different outcome is obviously occurring with the present COVID-19 pandemic.

Regardless of transmission mode, the process by which a pathogen moves from one host population (or environmental reservoir) to another is referred to as spill-over. This phenomenon depends on complex bidirectional interactions among hosts, pathogen communities, and environments (Alexander et al. 2018). Spillback consists of transmitting infection back to a potential host, which may occasionally play a crucial epidemiological role, for example, serving as maintenance hosts (Haydon et al. 2002, Fig. 6). Disease spread and patterns of transmission at the wildlife-livestock interface are largely due to the effect of the increase in global human population and demand for protein and other commodities. This has led to habitat destruction, bringing livestock closer to wild populations, favoring conditions for interaction among compartments and disease transmission (Chua 2003). Today, increasing globalization has brought additional risk factors that add

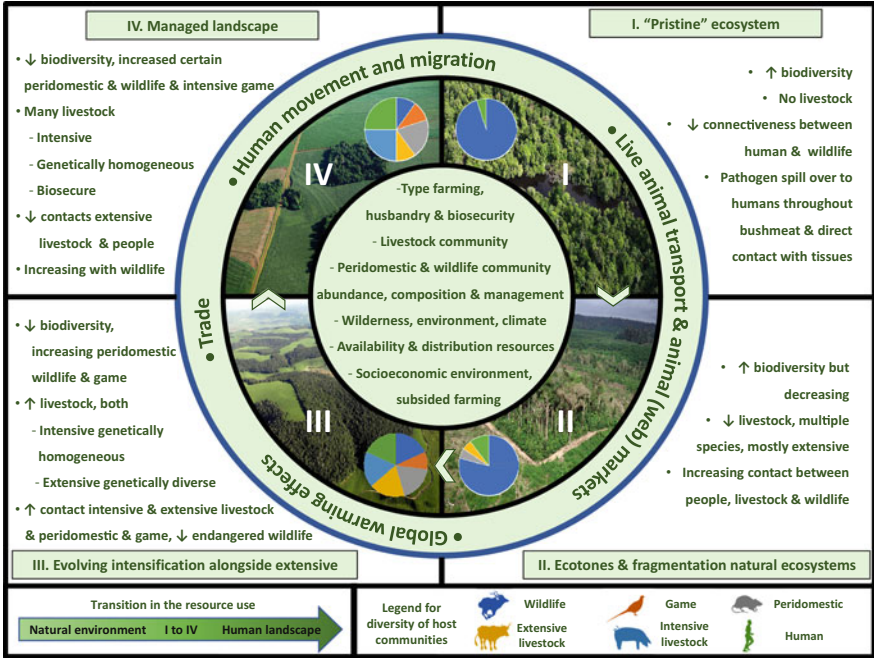


Fig. 1 Increasing human population growth, the subsequent increasing demand for food production (including increased meat and animal product consumption), and the conversion of natural habitats to agricultural land use have all altered interactions between domestic and wild animal populations. This figure depicts the wildlife-livestock-human interface characteristics according to the transition from pristine natural continuous habitats to highly human-modified landscapes (level of biodiversity, livestock farming, connectedness between communities at the interface, based on Jones et al. 2013). The characteristics of the wildlife-livestock interface (inner circle) are fundamentally responsible for local patterns of distribution of hosts, vectors, pathogens, and risks for interaction among these elements and subsequent disease spillover at the interface, with subsequent emergence and/or establishment. The sectorial graphs inside each interface typology indicate the relative abundance of host communities. The outer circle denotes regional and global drivers associated with risk for regional or global expansion, connecting elements from situations characterized by pathogens exclusive to wildlife in the absence of livestock and local pastoral systems with transcontinental-global circulation of pathogens

complexity and allow for very distant spread very quickly, i.e., human movements (such as tourism, refugees, and international workforce), legal and illegal transportation of live animals and animal products, both domestic and wild (e.g., bushmeat), increasing complexity of live animal markets, and the impacts of climate change (Beltran-Alcrudo et al. 2019). This has resulted in an unprecedented emergence and spread of many diseases that in livestock have spilled over to wild populations and have spilled back to livestock. The consequences of pathogen transmission at the interfaces vary from local to global, from affecting livelihoods in a limited region to worldwide pandemics and economic crises (Rhyan and Spraker 2010; Costard et al. 2017). Our planet is changing quickly, with natural habitats transforming into

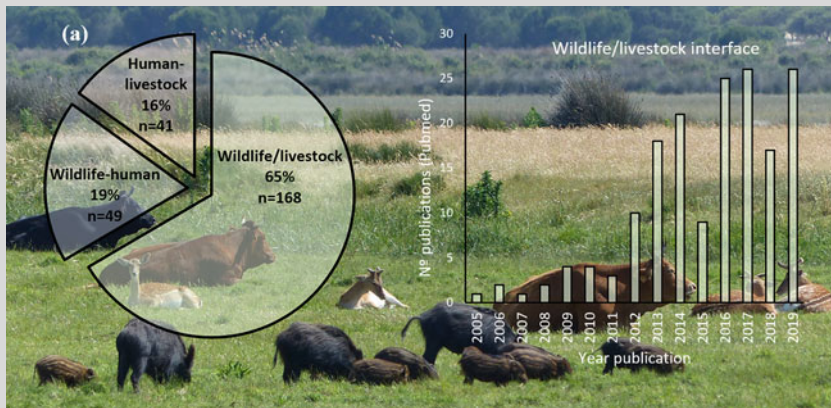
agricultural land, increasing competition of wildlife and livestock for natural resources, and huge biodiversity loss that threatens the contribution of nature to human livelihoods (Jori et al. 2019). The ever-increasing role of these drivers of change suggests future exponential growth in the interactions among wildlife, domestic animals, and humans, which has important implications including additional disease emergence at the interfaces.

“Transboundary,” “shared,” “emergent,” “pandemic,” these worrying words are increasingly adjectivizing the term “disease” if we read recent press, scientific literature and reports from international organizations dealing with the control of infectious diseases in humans and animals. This reinforces the increasing concern being given to emergent public health pathogens, followed by those impacting economy and trade, with those thought to only affect ecology or wildlife conservation coming third in importance. By April 2020, the global spread of African Swine Fever had reached well over half of the world’s pork markets (China alone is half), causing great economic losses due to pig mortality, control measures, and trade disruptions. Not long ago, this virus was confined to wild suids in Africa. While drafting this introductory chapter, the COVID-19 virus emerged, quickly turning into a pandemic with unprecedented economic and social consequences. The causative agent, named as severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) is closely related to two major previous zoonotic epidemics: SARS (severe acute respiratory syndrome coronavirus, SARS-CoV or SARS-CoV-1) and MERS (Middle East respiratory syndrome-related coronavirus or MERS-CoV). COVID-19, likely of bat origin, emerged at the animal–human interface found at live animal markets in Wuhan, China. Research has concluded that the lineage from which COVID-19 came has been circulating among bats for decades and is likely to include other viruses with the ability to infect humans (Boni et al. 2020). The magnitude of this pandemic, while certainly huge in proportions, remains to be estimated under its multiple angles, i.e., not just purely from the public health perspective, but in terms of its mounting economic and social impacts. What is clear is that humanity did not learn the lessons from previous disease emergencies. The current pandemic increases our certainty that a systems-wide holistic perspective on pathogen dynamics at the wildlife-livestock-human interface based on interdisciplinary approaches to the examination of biological, ecological, economic, and social drivers of pathogen emergence is required (Jones et al. 2013; Baum et al. 2017; Harrison et al. 2019). It stresses the need to understand, predict, prevent, and control disease emergence at their main origin, the animal interfaces. Unfortunately, historically, One Health international interventions have been the exception. While the world is now directly responding to counteract the effects of COVID-19 on human health and the economy, the international community must apply previous valuable lessons and act in advance to prevent or address future disease emergencies. This snapshot of human history will be remembered because, maybe, it could have been prevented.

In summary, *human activities have created new interfaces and opportunities for pathogen emergence and spread, and therefore, the holistic understanding of ecological, epidemiological, social, cultural, and economic mechanisms that operate at animal interfaces must contribute to transdisciplinary integrative approaches*

to prevent and control disease. Thus, we must step up research cooperation to ensure we can make the best coordinated decisions for similar future challenges in the interest of humanity. Recent disease emergence at animal interfaces, and their spread around the world, also illustrate shortcomings in the monitoring of current wildlife diseases and the surveillance of wildlife populations. We need to detect early warning signs at the origin of pathogen emergence so they can be halted before they lead to dramatic local, regional or global consequences. The increasing risk of pathogen emergence demands we anticipate as far ahead as possible when and where pathogen spillover could occur, which is likely to be more cost effective than adaptation (Pike et al. 2014; Wu et al. 2017) to mitigate consequences at the wildlife-livestock-human interfaces. As we write, most of humanity is trying to reduce contact rates through social distancing and implementing drastic trade and travel restrictions in an effort to contain the spread of COVID-19. This sudden appearance, the third significant coronavirus to emerge in 17 years, together with the high prevalence and virus diversity in bats, suggests that these viruses will likely cross species boundaries again.

Box 1 Bibliographical Analysis of Indexed Publications Referring to Different Animal Interfaces



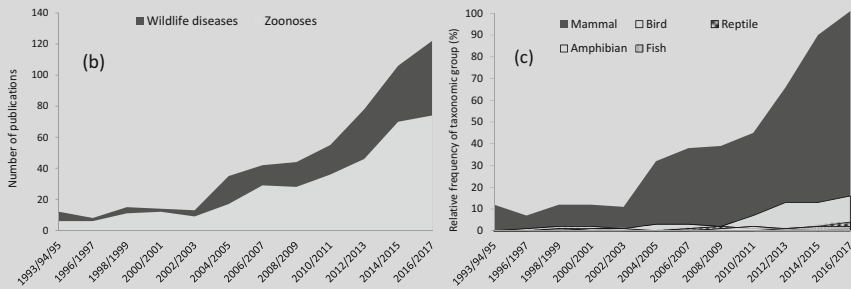
(a) Bibliographical analysis of publications indexed in PubMed (n° retrieved and proportion of the total) published during the last 15 years. The search terms were “human–wildlife interface”; “human–livestock interface”, and “wildlife–livestock interface” (in both orders, PubMed accessed on Mar 25, 2020). The temporal trend (2015–2019) for the wildlife–livestock interface (n° publications year) is shown on top right. Image: J.J. Negro ©. Next (b–d) we reviewed research works retrieved through a search in Scopus, PubMed, and Web of Science platforms (1b, c and d) using a combination of the search terms “wildlife,” “disease,” and “long-term” by the Boolean operator “AND” to obtain only the intersection. Selected articles dated from Jan 1993 to Dec

(continued)

Box 1 (continued)

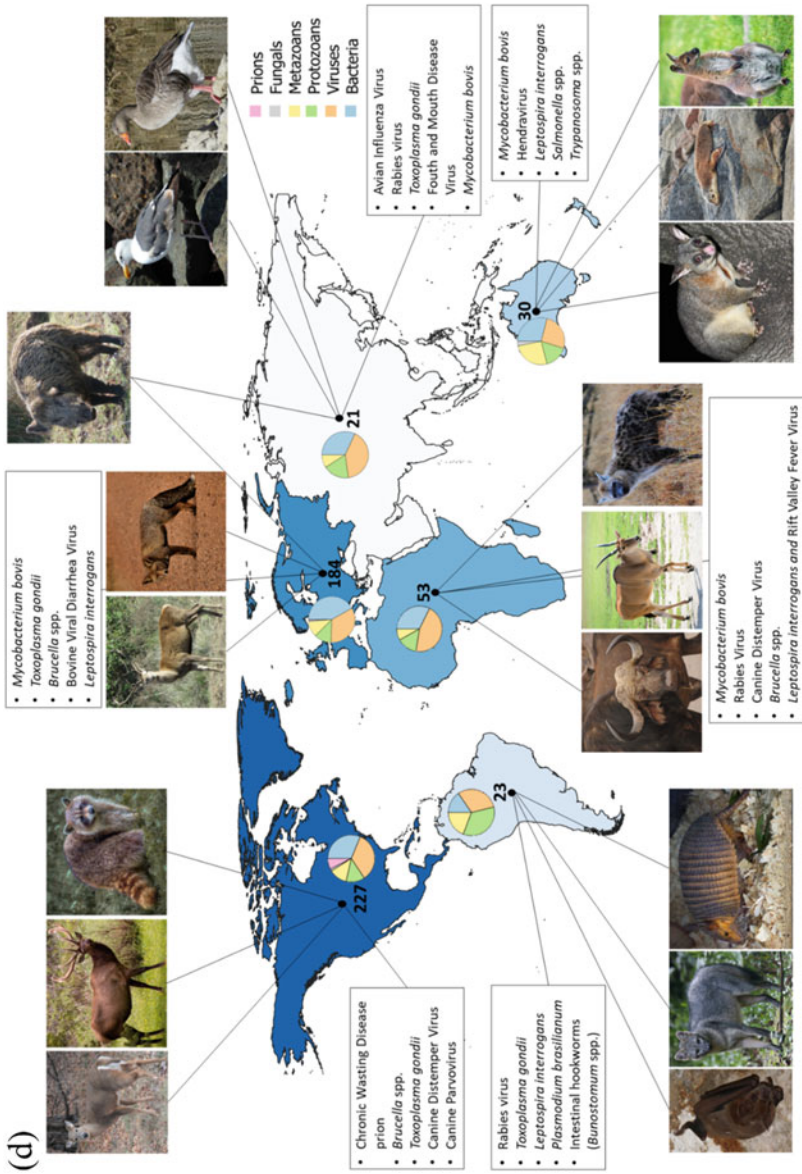
2017 with a study period ≥ 4 consecutive years and sampling a minimum of 10 individuals per year (studies based on passive surveillance, clinical trials, or which selected for the study experimental animals or captive wildlife populations were excluded). **(b)** Temporal trend of long-term publications (numbers, 1993–2017) on wildlife diseases ($n = 544$), indicating which diseases are zoonoses ($n = 344$) and disease shared only at the wildlife-livestock interface. **(c)** Temporal trend of long-term publications on wildlife diseases ($n = 544$), indicating which host taxa were addressed. **(d)** Representativeness of pathogen agents and host species addressed by long-term studies (period 1993–2017) by continent. The research productivity of each continent (n° of papers) is shown.

Source of graphs and analysis: The authors of the chapter and Patricia Barroso (see Barroso et al. 2020).



The bibliographical analysis of papers published during the last 20 years **(a)** revealed a bias toward more studies assessing or referring to the interface established between wildlife and livestock (Box 1a). The number of long-term publications dated from 1993 to 2017 showed a marked growing temporal trend, which reflects both the overall increased scientific production, but also the increased awareness about wildlife relevant to the epidemiology of shared pathogens, which may have consequences on public health or other aspects. From 2002 to 2003 is when the increase became more obvious, and zoonoses were acquiring importance. Several significant zoonotic events took place around these years. In 2003, a new strain of highly pathogenic avian influenza (HPAI-H5N1) spread throughout Asia, Africa, and Europe (Ellis et al. 2004; Sturm-Ramirez et al. 2004) and at the same time, the first Coronavirus outbreak in humans, SARS, emerged in China (Anderson et al. 2004). In addition, during these years there was a greater economic outlay in veterinary measures for the control of animal disease outbreaks such as foot and mouth disease and influenza viruses (OIE and FAO 2012). The impact of these events on human health and the global economy gave rise to the promotion of

(continued)



Box 1 (continued)

research on animal diseases through greater availability of funding for research.

Approximately 25% of total publications referred to more than one pathogen. Figure c indicates that viruses were the most frequently addressed pathogens (40.4%), followed by bacteria (33.3%) and parasites (23%, protozoan and metazoan), whereas prions and fungi were less frequently studied (3% of the articles). Interestingly, most of the pathogens included in the ranking are zoonotic, evidencing that the wildlife reservoir constitutes a major public health problem, leading to increased awareness of governments on the role of wildlife in the epidemiology of shared infections. Mammals (91.4%), followed by birds (6.1%), and reptiles (1.2%), were the most studied hosts. Amphibians (0.8%) and fish (0.5%), though, were scarcely represented in the literature. Ungulates were the most investigated group (40%) due to their role as reservoir hosts of more than 250 species of zoonotic pathogens (Woolhouse and Gowtage-Sequeria 2005), and their increasing expansion and numbers mainly in developed countries. Carnivores were the next most studied group (31%) due to conservation reasons.

Cervids (including red deer, white-tailed deer, roe deer, fallow deer, and elk, all native to the Northern Hemisphere) and wild boar were addressed in more than half of the studies. Research production of long-term studies on wildlife diseases was mainly located in developed countries in the North Hemisphere; North America (41.2%; $n = 229$) and Europe (34.9%; $n = 190$). However, in Africa, Oceania, South America, and Asia long-term studies were far less common (less than 20%, $n = 125$ of the total reviewed publications). The largest proportion of the retrieved articles in North America, Europe, Africa, and Asia addressed viruses, whereas in Oceania and South America it was metazoan and protozoan parasites, respectively. It is worth noting the limited number of long-term studies addressing the epidemiological role of wildlife species, such as bat, as reservoirs of Coronaviruses.

The Wildlife-Livestock Interface

The livestock compartment only appeared after human domestication of wildlife occurred, which gave rise to three new animal interfaces, human–domestic, wildlife–domestic, and human–domestic–wildlife (Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”). Since then, the wildlife-livestock interfaces are the physical space in which wild and livestock species overlap in range and potentially interact, a continuum of direct and indirect contact between free-ranging wildlife and domestic livestock (Huyvaert et al. 2018). Indirect contact can occur through exposure to infected materials (such as aerosols or any excretion product such as feces, urine, saliva, or ocular or nasal discharge) or through

environmental reservoirs (such as soil, water, or forage). Actually, the disease interface between wildlife and livestock is usually through indirect contacts (Kock 2005; Kukielka et al. 2013). However, as we will elaborate below, the delocalization of such interfaces is becoming a common characteristic in modern times. *For shared infections at the wildlife-livestock interface, at least one wild and one livestock host species are infected, and at least one of them maintains the infection.*

The wildlife-livestock interface in all its dimensions is complex and susceptible to changing along with natural landscapes, but especially with increasing human intervention (Jori et al. 2019). The characteristics of the interface are the result of a complex interplay between natural ecosystems within which livestock production takes place (Ostrom 2009). Thus, the wildlife-livestock interface is synonymous with the wildlife-livestock-human interface because the focus is on the interaction between “natural” and “human-influenced” sub-systems (Chapter “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”). The description of prevalent pathogens in a range of hosts is still a necessary first step in many epidemiological systems (for instance, identifying new viruses in animals and quickly determining their emergent potential is a key way to assess global health threats). However, understanding ecological, epidemiological, and socioeconomic complexity requires an in-depth characterization of underlying processes at this dynamic space of transition and contact between wild and domestic compartments. As an ecological and epidemiological entity, the wildlife-livestock interface has a proper ecosystem with its specific niches, which allows for the emerging, maintaining, and sharing of pathogens (Chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). This interface often defines the suitability for risk distribution of shared pathogens, for instance, the map of anthrax suitability is strongly associated with the elephant–livestock interface (Walsh et al. 2019). The nature and potential for interaction among wildlife, livestock, and human compartments and their characteristics are schematized in Fig. 1 in terms of biodiversity, livestock farming, and connectedness between communities at the interface (based on Jones et al. 2013). It evolves from complex continuous habitats with rich trophic structure and wild host communities throughout a gradient of forest loss. Many human intervened landscapes consist of a mosaic of crops, pasture, and urban areas with natural islands, which has resulted in extremely modified trophic structures, land degradation, and simplified host communities, with increasing presence of peridomestic (e.g., Abrahão et al. 2009) and managed wildlife (Gortazar et al. 2006). Host communities across gradients, though, are difficult to classify (see Fig. 2) relative to the degree of human impact on wildlife. For instance, peridomestic and more anthropic wildlife have adapted to human environments and can promote the transmission of pathogens between other wildlife and livestock or humans, since they circulate both in and around farms. We note (see preface) that we also differentiate between livestock and pets, and this book focuses on the former. There are relevant differences on how the interfaces with wildlife are established, respectively. However, pets are often involved in epidemiological cycles or relevance to livestock and humans, and they are mentioned in different

examples throughout this book (e.g., dogs). In the case of livestock, the transition from free ranging, extensive, backyards, outdoor, and intensive is also a gradient. The four main scenarios (consider this as a simplification) indicative of a gradient of the wildlife-livestock-human interfaces where pathogens emerge or are shared include (1) “pristine” ecosystems with human incursion to harvest wildlife and other resources; (2) ecotones and fragmentation of natural ecosystems (farming edges, human incursion to harvest natural resources, i.e., wood); (3) evolving landscapes characterized by rapid intensification of agriculture and livestock, alongside extensive and backyard farming; and (4) managed landscapes that consist of islands of intensive farming, highly regulated, and farmland converted to recreational and conservancy uses (Jones et al. 2013). Urban and periurban areas are increasingly present in these scenarios. Local and regional drivers associated with risk for emergence of pathogens are connected worldwide, ranging from situations characterized by wildlife exclusive pathogens in the absence of livestock and local pastoral systems to transcontinental-global circulation of pathogens to transcontinental-global interconnected food animal production systems and markets. For instance, much of the meat from the wildlife trade is sold through online platforms (Nijman et al. 2019). Illegally imported wildlife products in passengers’ luggage, particularly meat, must also be considered. Wildlife, which provides essential services, and pathogens, are both indisputably essential components of ecosystems. However, the importance of wildlife to ecosystems and human communities, while being the natural reservoirs of many relevant economic and zoonotic pathogens, presents a challenge for disease control. Particular attention is needed in developing regions with high biodiversity, where emerging infectious diseases (EIDs) are most likely to arise, and where substantial losses to agricultural production greatly impact national economies. The interplay of ecological and human factors (socioeconomic and anthropogenic) increases opportunities for pathogen spillover, such as with neglected tropical diseases.

During recent decades there has been an increasing amount of research on animal interfaces (Box 1). An extensive literature search looking at infectious diseases shared at the *wildlife-livestock interface* was performed by Wiethoelter et al. (2015). By combining wildlife, livestock, disease, and geographic search terminology they assessed the interest by the scientific community in infectious diseases at the interface, characterizing animal species, regions involved, and trends over time. Results should not be confused with incidence of diseases or absolute occurrence of interfaces. Their analysis of almost 16,000 publications dated from 1912 to 2013 showed an increasing trend over time, a progressive shift from parasitic to viral diseases, and a majority being zoonoses. Most importantly, authors identified and characterized the major wildlife-livestock interfaces, showing that relatively few interfaces have been considered important from a disease ecology perspective. Of those, the bird–poultry interface was the most frequently cited worldwide, followed by the Artiodactyls–cattle and Carnivorans–cattle interfaces. However, the relative importance of interfaces varied among regions, reflecting local circumstances. As expected, the most frequent livestock species worldwide are represented in the top interfaces, i.e., the higher their abundance, the more they will contribute to disease

transmission. Results also showed that interfaces between closely phylogenetically related and/or potentially cohabitant species were most frequent. The perceived importance of the order Chiroptera in emerging infectious diseases is not reflected yet in the number of publications on their interface with livestock. Funding plays a key role in shaping these results, with zoonoses and major disease epidemics, e.g., avian influenza, largely driving scientific interest. Wild animal hosts for shared pathogens have been vastly under-recognized because the majority of species have not been sampled at the level needed to detect shared pathogens, and many geographic regions lack adequate data. More basic research is needed at interfaces, to further characterize transmission pathways and specific roles of the involved species.

The *domestic* side of animal interfaces can be found on every continent on Earth. Even sled dogs have been used in Antarctica. Great diversity can be observed within and among livestock, environments, and management systems. Livestock producers living within the wildlife-livestock interface in many regions mostly practice pastoral farming as a sustainable management system. In *rangelands and other extensive production systems*, livestock are integrated into the ecosystem, and they have a variety of positive and negative impacts on soil, vegetation, biodiversity of plants, nutrient recycling, and native wildlife. Livestock have influenced the environment through coevolutionary history with plants and wildlife. Livestock and wildlife ecologically and epidemiologically interact because they share and/or compete for resources (water, food, cover). Often, livestock are relevant and sometimes even the most important source of food for wild carnivores and scavengers, with subsequent ecological and epidemiological connections (Vicente and Vercauteren 2019). On such livestock extensive systems, problems, or what humans sometimes call wildlife conflicts, arise in relation to competition, disease, and depredation. These conflicts stimulate subsequent human intervention at the livestock-wildlife interface. From the producer's perspective, in most cases, preserving wildlife communities (especially large vertebrate species) is incompatible with livestock farming and other agricultural activities because the associated costs are considered nonviable. Livestock husbandry, the provision of supplementary food and water, together with the persecution or prevention of wildlife occurrence, helps livestock to proliferate and/or be economically profitable. However, as they have similar needs, some of these resources are points of attraction for the remaining wildlife. Pathogens can become endemic at the interface ecosystem and especially once endemic free-ranging wildlife they can be difficult to eradicate, and spillover to livestock continues (Gortazar et al. 2007). Managers usually focus on separating livestock from wildlife, which, normally, can only be partially achieved (Barasona et al. 2013). Rangelands are integrated into natural ecosystems (see major particularities for each continent in the subsequent chapters), and the ecological and epidemiological consequences of management are not always direct and easily measurable. The effects of rangeland management on wildlife and ecosystems may vary depending on the composition of ecological communities but may produce cascading effects in terms of community composition, trophic relationships, and pathogen dynamics (Ostfeld et al. 2008; Becker et al. 2015; De Vos et al. 2016).

In recent decades, there has been an enormous expansion of livestock production, driven by increasing demand for animal source foods from a large part of the world's population. This has been linked with a change in livestock production systems. For instance, it is estimated that more than half of current global pork production and three-fourths of poultry meat is produced in *intensive systems* (Steinfeld et al. 2006). Developing countries especially, have accounted for the majority of this increase (Thornton 2010). The driving forces behind this growth have principally been human population growth and changes in dietary preferences associated mostly with increasing income and urbanization. There is increasing evidence (Jones et al. 2013) of the large effect of agricultural intensification and environmental changes on the risk of pathogen emergence, many zoonotic and/or for which there are epidemiological interactions between wildlife and livestock. There are two main paths associated with the increased risk of disease emergence at animal interfaces and subsequent zoonotic events. First, the most intensive production conditions involve crowding tens of thousands of animals in very close contact. Such intensive systems constitute the perfect breeding ground for pathogens to emerge, with high-density populations of generally low genetic diversity, which may favor increased transmission and adaptation in a given species (i.e., avian influenza in poultry). While intensive farms are associated with a lower number of people exposed to zoonoses (per animal unit) compared with extensive systems (e.g., mixed farming systems, which numerically dominate over the world), workers in intensive farms may be more exposed to animal pathogens compared with other people. In contrast to more extensive systems, and in spite of being more isolated from the external ecosystem, intensively produced animals live in closer contact with each other and the humans taking care of them. Intensification is also accompanied by more frequent movement of people and vehicles between farms, which further increases the risk of pathogen transmission. This risk can be reduced by employing effective sanitary management and biosecurity. In addition, it is also common that different production systems for a given livestock species, ranging from extensive to intensive, are connected. For instance, reproduction can be centralized and intensive with young stock then being shipped elsewhere to be reared or fattened in open-door or completely outdoors where wildlife is present (see Fig. 2 for the case of pigs). This provides human-mediated epidemiological links between different animal production systems and wildlife. The risks of pathogen spread from wildlife diseases also occur in chaotic scenarios such as in wet or live animal markets, which become an interface itself among living animals. This risk is exacerbated in such markets by the concentration and interconnectedness of recently trapped wildlife, wildlife that was reared in captivity, semi-domesticated wildlife, domestic animals, and humans. For instance, wet markets in urban areas of Asia are now recognized to be the primary locus of infection for highly pathogenic avian influenza (HPAI) H7N9, H5N1, SARS (Gilbert et al. 2014), and COVID-19.

On the other hand, the agricultural intensification and environmental change driven by expanding human activities stimulate the creation of new wildlife-livestock-human interfaces, sharing emergent pathogens. Anthropogenic environmental change and subsequent encroachment of human settlements and agriculture on

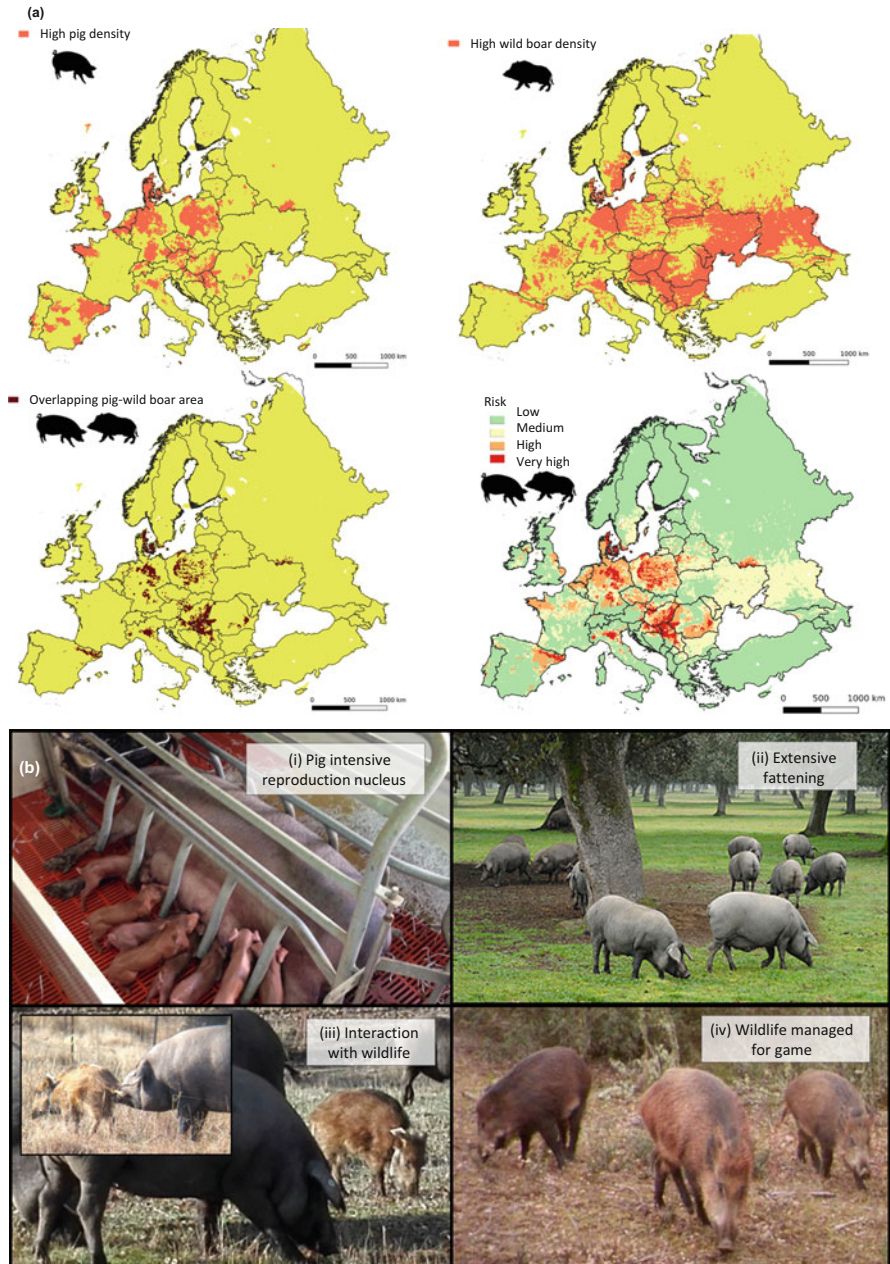


Fig. 2 (a) Predicted spatial wild boar–pig interface (irrespective of farming type) at the European scale (Enetwild consortium 2020 for more details). Top: Areas of high wild boar and domestic pig densities (ENETWILD 2020; Robinson et al. 2014). Bottom: Wild boar–domestic pig interface risk maps. Four risk categories that are defined from low to very high risk. (b) Example of interconnections between pig farming systems (intensive and extensive are linked) and the interface with wildlife (wild boar)

natural ecosystems have resulted in the expansion of ecotones (transition zones between adjacent ecological systems), where species and communities mix. This provides new opportunities for pathogen spillover, genetic diversification, and adaptation. Most recent emergent zoonoses involve both wildlife and livestock in their epidemiology, such as Nipah virus encephalitis. Growing demand for animal source foods has important implications for agricultural production systems and for producers in poor rural areas, where mostly mixed farming is practiced, i.e., intermediate, semi-intensive production systems, usually mid-sized family farms. As they need to adapt continuously to the changing environmental, social, economic, market and trade circumstances, farmers expand cultivated areas, encroach natural areas, intensify production and close integration of crops and livestock (Jones et al. 2013), often in proximity to wildlife. The two reported paths for pathogen emergence at animal interfaces indicate that assessing the complexity of risk at animal interfaces requires not only addressing different hosts and communities locally or interconnected throughout a given region, but also the more delocalized, scattered, and sparse risk factors that operate at long distances. The animal interfaces are not merely physical spaces where pathogens are passed between communities, but they are built of a number of linked epidemiological scenarios, which are highly determined by human ecology and socio-economy and their intricate complexity is increasing due to globalization. Not only pathogens, but also their associated burdens, such as antimicrobial resistance, are disseminated across interfaces (Ramey and Ahlstrom 2020). This reflection reinforces that the focus is on the interaction between “natural” and “human” sub-systems (Chapter “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”), and we cannot disregard wildlife-livestock and wildlife-livestock-human interfaces.

The characterization of pathogen transmission events among animals and humans (the *human–animal interface*) remains an important scientific challenge. A recent review of the connections between human, animal, and environmental health revealed that at least 142 viral pathogens of mammalian origin cause disease in humans, i.e., animal to human direction (Johnson et al. 2020, Fig. 3). This list would grow if we considered other pathogens, such as parasites, bacteria, fungi, and prions. Even though livestock represent a small proportion of the total mammal biodiversity and their diseases are more commonly reported relative to wildlife, reports suggest that domesticated species are responsible for half of viral zoonoses. However, no data exist for most wild species. Overall, domesticated species, primates, rodents, and bats were identified as harboring more zoonotic viruses than other species groups. The highest proportion of zoonotic viruses were found among species in the orders Rodentia (61%), Chiroptera (30%), Primates (23%), Artiodactyla (21%), and Carnivora (18%). The only wild animals among the top 10 species in terms of detected zoonotic viruses were the house mouse (*Mus musculus*) and the black rat (*Rattus rattus*), both of which are comparable to domestic species since they most frequently occur in close association with humans.

As a group, domesticated mammals may host 50% of the zoonotic virus richness but represent only 12 species (Johnson et al. 2020). These figures reflect the

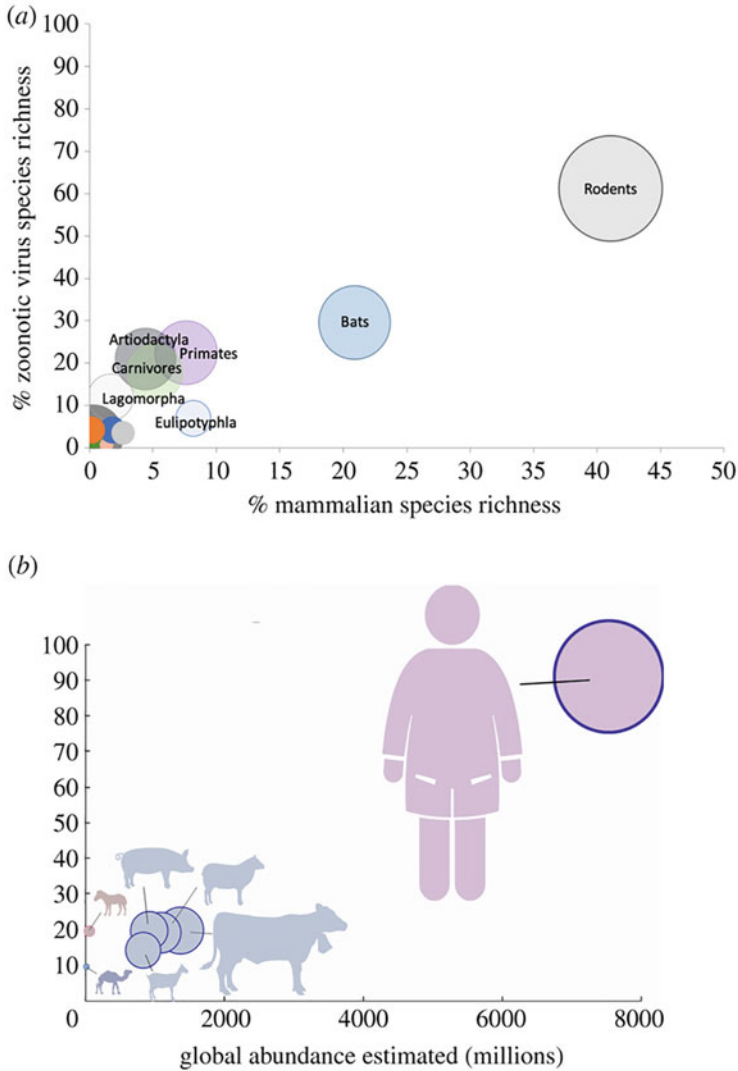


Fig. 3 Richness of zoonotic viruses found in mammalian hosts, by taxonomic order for wildlife and by species for domesticated animals and humans (reproduced from Johnson et al. 2020, under common creation license). **(a)** Zoonotic virus richness corresponding to species richness among wild mammalian orders. Area of the circles represents the proportion of zoonotic viruses found in species in each order out of the total number of zoonotic viruses among all mammalian species. **(b)** Zoonotic virus richness corresponding to estimated global abundance (in millions) for humans and domestic species. Species in **(a)** are colored according to the order in which they belong. Area of the circles reflects the estimated population size for that species relative to the other species shown

relevance of the wildlife-livestock interface (*stricto sensu*) to amplify and mediate as bridge host in the transmission of animal diseases from wildlife to humans, as has unfortunately been confirmed in recent emergences of zoonotic HCoVs. Domestic animals not only can suffer disease caused by wildlife-borne pathogens but may have important roles as intermediate hosts that enable pathogen transmission from natural wild hosts to humans or other animals. For instance, after spilling over from bats, swine acute diarrhea syndrome caused by coronavirus SADS-CoV (Zhou et al. 2018) caused a large-scale outbreak of fatal disease in pigs in China across four farms. Although there is no evidence of infection in humans, this case reveals the continuous threat to animal and human health and food production of wildlife diseases at the interface with livestock. Focusing on terrestrial mammals, the most species-rich orders contain the greatest diversity of zoonoses (Han et al. 2016). Groups with more zoonotic host species than expected for the richness of the clade include the ungulates (Artiodactyla and Perissodactyla), which comprise the majority of domesticated mammal species. Many more wild ungulates are closely related to domesticated livestock species with which humans are in regular close contact, which could facilitate successful transmission. Ungulate reservoirs of zoonotic pathogens have also been of particular interest because of high human contact rates through hunting and consumption over history. Recent work also shows that the time since domestication correlates positively with the number of zoonotic infections shared between ungulates and humans, and that species with the longest history of domestication not only carry more zoonotic pathogens, but may also transmit infection to a greater diversity of alternative host species (Morand et al. 2014). Wild ungulates cover a greater spatial range, for instance, than bats, and other orders of mammals, and a large proportion of species overlap in certain areas, such as Africa and Asia, establishing high levels of mixing with livestock. Some specific features of ungulate species are relevant to the wildlife-livestock interface, since they normally live in spatially discrete small family groups or in larger herds (up to many thousands), with intraspecific fusion-fission herd dynamics (e.g., Pays et al. 2007), which has epidemiological implications, i.e., opportunities for contact and transmission of infection between herds of a given species. Also, mixing or contact between animals or herds of different species and with livestock occurs (illustrated in Fig. 1), but less often. Under certain conditions of food scarceness, such as droughts or hard winters, indirect and direct contact increases at watering points or food locations, leading to increased pathogen transmission. Carnivores have regular contact with domestic species (e.g., dogs), providing an opportunity for human exposure (e.g., Packer et al. 1999). As for birds, particularly migratory, a relevant characteristic is their potential role as bridge hosts at wildlife-livestock-human interfaces, including emerging infections such as avian influenza viruses across wild bird–poultry interfaces (Chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”).

While addressing the study of diseases in domestic animals is relatively straightforward, it may be hampered in wildlife by pathogen detection limitations. Beyond the methodological limitations, the wildlife-livestock interface has often been neglected. This interface is an essential interplay among host species where disease

spillover is largely under-reported, often even for zoonosis, such as in regions where people have limited access to healthcare. Monitoring trends in wildlife populations, large-scale surveillance efforts, and addressing the ecological and epidemiological study of the wildlife-livestock interface to identify epidemiologically relevant animal reservoirs are warranted to understand and prevent diseases of animal relevance, but also those potentially spreading to humans. Also, improved monitoring of livestock and large-scale trends are needed to depict interfaces and evaluate broad-scale risks, for which high-resolution data and discriminating among farming systems would be required. As illustrative of the need for better, harmonized, and standardized data in the livestock compartment, Fig. 2 suggests low reliability when predicting the wild boar-pig interface (irrespective of farming type) at European scale (Enetwild consortium 2020, www.enetwild.com).

Interfaces Among Host Communities: Questions, Theoretical Frameworks, and Approaches

Some questions that also concern the wildlife-livestock interface have, especially arisen in the present times characterized by a global health crisis that is mainly perceived as wildlife-human interface: what will be the next emergent pathogen at the interfaces? a virus? an RNA virus? what will be the role for pathogen emergence, maintenance, and spread within wildlife and livestock? can we predict and prevent pathogen emergence? how will human-induced rapid changes impact the capacity of host communities to adapt to pathogens and vice versa? We are challenged because our understanding of patterns, trends, and drivers associated with disease emergence at interfaces is in its infancy. The same is true about the persistence and transmission of pathogens.

There are essential knowledge gaps, which prevent us from better understanding and managing the dynamics of diseases at the wildlife-livestock interface. Primarily, the first step in many interfaces is to describe the hosts and their pathogens, their distributions and behavioral characteristics, and ultimately their epidemiological consequences. We must then work to comprehend the pathways and transmission rates among these compartments, and which effects pathogens exert at both population and community levels. Subsequently, we must recognize the effect of disease management efforts at the interface, and understand the prevalent socioeconomic and cultural environment, which is crucial to determine the success of disease mitigation strategies.

Some of the abovementioned questions are unfortunately in vogue as we are drafting this book because of the current COVID-19 global pandemic. However, general theoretical frameworks have been developed to understand the ecology, epidemiology, and response to the main drivers for multi-host multi-pathogen systems. Below we approach multi-host pathogen systems simply, though they are intrinsically complex, shaped by pathogen and host dynamics as well as

evolutionary and environmental interactions. This basic approach can contribute to the necessary background for understanding ecological and epidemiological networks. For in-depth reading on the subject, several seminar books are available (e.g., Hudson et al. 2002; Ostfeld et al. 2010; Wilson et al. 2019). We also aim to project our current understanding to past scenarios (see Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”), since the main drivers and mechanisms of wildlife disease ecology also apply. Retrospectively learning from the past will also provide a necessary perspective to address current questions, better understand contemporary circumstances, and inform how we approach the future.

Wildlife Disease Meets Ecology

One of the characteristics of the wildlife-livestock interface is the integration of ecological, agricultural, and human systems, which requires considering multiple and diverse disciplines and solutions. The study of the wildlife-livestock interface is principally and primarily addressed by *disease ecology*, a primary field of interest to us (see Chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). From a “health” perspective, *epidemiology*, applied to the study of the wildlife-livestock-human interfaces has provided a basic understanding on how most infectious agents circulate in communities composed of hosts that are infected by multiple pathogens, and pathogens that can infect a variable diversity of hosts. In turn, ecology has addressed how changes in host and pathogen communities (e.g., within-host competition, host population and community dynamics; this is closely linked to the discipline of disease ecology) result in consequences for the epidemiology of single- or multi-host pathogens. There has been, to date, a tremendous bias toward studies in zoonotic disease systems (e.g., cowpox, Lyme disease, and Nipah and Hendra virus infections). The empirical characterization of disease reservoirs also involves a conceptual ecological approach. The functions of different disease reservoirs and connectivity between source and target populations are challenging to comprehend for current multi-host systems (Haydon et al. 2002), even more so for past scenarios. The current ranges of hosts of many pathogens of wildlife shared at the interface still remain poorly defined, partially because of a relatively low number of isolates and wild species studied to date. Subsequently, there is an incomplete understanding of their roles as disease reservoirs in many systems. The conceptualization of disease reservoirs by Haydon et al. (2002) identifies the elements that determine disease maintenance (i.e., reservoir capacity), and how they are connected: “A *‘reservoir of infection’* is defined with respect to a target population as *‘one or more epidemiologically connected populations or environments in which a pathogen can be permanently maintained and from which infection is transmitted to the target population. Some reservoirs can be simple and comprise a single nontarget host population. However, they can comprise a more structured set of connected host subpopulations termed ‘maintenance community’.* Individually,

some of these populations can maintain the pathogen ('maintenance populations'), whereas others cannot ('non-maintenance populations')." An interface, including all its elements, can be a reservoir itself. Pathogens evolve and adapt to one or various hosts; wildlife, domestic animals, or humans. The capacity of a pathogen to successfully infect, cause, and transmit disease within the primary (or maintenance) host species by itself makes it a true or maintenance reservoir. This is in contrast to occasional spillover events into their host species in which the full life cycle, in particular the transmission to secondary hosts, is not maintained. When pathogens never spillback, we have a dead-end host. From the point of view of the wildlife-livestock interface, the dynamics of a pathogen in the host community involve the transmission between maintenance and/or non-maintenance host species. Studying the role of wildlife in multi-host disease systems is more complicated, apart from their ecological and behavioral specificities defaulting the application of conceptual models of disease transmission, they are more difficult to observe, monitor, sample, and diagnose. The most basic parameter, prevalence of infection, is often unknown in potential animal reservoirs. In a multi-host pathogen system, wildlife may contribute within the maintenance community (as a maintenance host or non-maintenance host) but also from outside the maintenance community as a bridge host (Table 1, Viana et al. 2014; Caron et al. 2015; see Chapter "The Ecology

Table 1 Definitions of hosts and relevant epidemiological parameters (based on Caron et al. 2015; Hartfield and Alizon 2013; and Faust et al. 2017)

Maintenance host population: Hosts in which the pathogen persists even in complete absence of transmission from other hosts. Population larger than the critical community size (i.e., size under which the pathogen cannot be maintained in the community) in which the pathogen persists.

Maintenance host community/maintenance host complex: One or more epidemiologically connected populations or environments in which the pathogen can be permanently maintained. Any host complex in which disease persists indefinitely is a reservoir. Host for which cross-species transmission and interspecies transmission are high.

Bridge host: Non-maintenance host population able to transmit a pathogen from a maintenance host/complex to the target population, otherwise not or loosely connected to the maintenance complex.

The basic reproductive ratio (R_0): Number of secondary infections caused by a single infected individual, in a susceptible population. It is classically used to measure the rate of pathogen spread. In infinite-population models, a pathogen can emerge if $R_0 > 1$. In a finite population, the pathogen can emerge from a single infection with probability $1-1/R_0$ if $R_0 > 1$, otherwise, extinction is certain.

The critical community size (CCS): Total population size (of susceptible and infected individuals, or others) needed to sustain an outbreak once it has appeared. This idea was classically applied to determining what towns were most likely to maintain measles epidemics, so that there would always be some infected individuals present, unless intervention measures were taken.

Force of infection FOI: Number of infections acquired over time.

Dilution effect: Occurs when the addition of one or more host species to a community makes a pathogen less abundant and less likely to persist than in the presence of one or less highly competent reservoir host species. Increased biodiversity should lead to reduced pathogen abundance. When increased host diversity leads to increased infection prevalence the opposite occurs:

Amplification effect.

of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). The study of bridge hosts, often birds, is obviously complicated, especially for migratory species. In basic epidemiological models, the persistence required for hosts to maintain a pathogen and thus act as a maintenance community is determined by the basic reproductive number (R_0 : the transmission potential of a pathogen for a totally susceptible population) and critical community size, and subsequent risk for spillover transmission out of the maintenance community is defined by the force of infection. R_0 is therefore closely linked to the rate of contact between susceptible and infectious individuals, as are the recovery or mortality rates of infected individuals.

The force of infection is a function of the number of contacts, the transmission rate per contact and the frequency of infectious individuals. Contact is therefore a key feature of both reservoir and disease emergence dynamics. Disease spillover is determined by the prevalence of infection in the maintenance population and/or bridge hosts, the rate of contact between infected individuals, and the probability that infection occurs upon contact. Host ecological traits, such as life-history characteristics (seasonality, aggregation, sociability, sympatry with other species), local population dynamics, and land use are key parameters to determine pathogen transmission and persistence at the wildlife livestock interface. These factors, whose study is mainly addressed by *ecology*, determine the contact between wildlife, livestock, and humans. Further, ecology has provided understanding into many other fundamental aspects relevant to reservoir dynamics and disease emergence in changing landscapes. *Wildlife disease ecology* brings together evolutionary and population biology with epidemiology, and is essential to understand the causes, consequences, and management of wildlife diseases. It aims to answer questions like; How do hosts and parasites co-evolve? What determines how a pathogen spreads through a population and community? How do co-infecting pathogens interact? Why do hosts vary in parasite burden, or risk of exposure and susceptibility against infectious diseases? Which factors determine parasite virulence and host resistance? How do pathogens influence the spread of invasive species? How do we control infectious diseases in wildlife and at the interfaces? (Wilson et al. 2019).

Ecological Hierarchies of Host–Pathogen Interactions

The range of scales of host–pathogen interactions includes within-host (“pathogen infracommunity,” i.e., pathogen–pathogen and pathogen–immune system interactions); between-host (“pathogen component community,” population biology); among species (“pathogen supracommunity,” community ecology); and across regions (macroecology and disease biogeography) (Johnson et al. 2015a). With the emergence of high-profile pathogens that exhibit wide host plasticity (such as Ebola), some of relevance at the wildlife-livestock interface (e.g., avian influenza viruses), a community approach is being increasingly embraced for studying the multi-host ecology of pathogens. A common factor underlying emerging diseases is

the involvement of multiple hosts, vectors, or parasite species in complex ecological communities. However, it is difficult to forecast the outcome of the host community. In recent decades, epidemiological theory and empirical research have contributed to a better understanding of inter- and intra-specific interactions among hosts, and between hosts and pathogens. This research can account for the impact of a wide range of complexities on host ecology and transmission dynamics (Roche et al. 2012). Most of what we know relative to multi-host communities is normally based on simplified scenarios and specially focused on infectious diseases of humans and livestock. *Community ecology* aims to identify the factors that determine the structure, assembly, and dynamics of ecological communities (Johnson et al. 2015a, Becker et al. 2019). This discipline integrates processes at the fine-scale of individuals and populations, and the ecological and evolutionary drivers of species distributions at coarser scales. It therefore can be adopted to address the ecological complexity of multihost–multipathogen assemblages to understand multilevel infection processes, identifying the drivers of heterogeneities among individuals, species, and regions, and quantifying how processes link across multiple scales of biological organization to drive disease dynamics. The disciplines of epidemiology and community ecology have developed largely independently of one another. Recently though these disciplines are being integrated into a new discipline known as *disease community ecology*. A theoretical framework for disease community ecology considers the complete set of species that influence infection dynamics (e.g., Roche et al. 2012 for directly transmitted pathogens). Relevant concepts, such as the dilution effect or the amplification effect, occurring when biodiversity increases disease risk, are hot topics of discussion among researchers, in many cases with controversy due to differing observations (Table 1, Norman et al. 1999; Ostfeld and Keesing 2012; Faust et al. 2017). Theoretical frameworks under the umbrella of these disciplines provide support to answer, for instance, if variations in community composition affected the diversity and intensity of pathogen transmission in past assemblages of hosts (see Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”).

The research focused on one scale of the above-mentioned scales may not consider what is going on at other scales, which are interconnected. Today, our understanding about the global distribution of most infectious diseases is still very limited, even for humans. Global-scale analysis of multi-host pathogens reveals structured variation among host species implicated as a potential source of pathogen spillover (Johnson et al. 2020). Particularly, a review found that there is disproportionate representation in research of mammal-borne zoonoses among emerging human diseases (Han et al. 2016). As an illustration (Johnson et al. 2020, Fig. 3 left), it has been reported that zoonotic virus species richness highly correlates with mammalian species richness, evidencing that the more diverse mammalian taxa are the source of more zoonotic viruses (e.g., of total mammal species on earth, bats account for about 25% and rodents for almost 50%). Interestingly, from the point of view of wildlife-livestock-human interface, zoonotic virus richness in domesticated mammalian species correlates with global abundance estimates for humans and

domesticated species. This has been evidenced by recent research on the connection between human, animal, and environmental health (Fig. 3 right).

Analytical Approaches

Quantifying transmission between wild and domestic populations at the interface requires knowledge of epidemiology, ecology (community, see below), and mathematics. *Mathematical models are being applied with increasing frequency to improve our understanding of complex multi-host disease systems. Mathematical models of infectious diseases* use a body of developing theory to construct simplified and dynamic representations of epidemiological systems (e.g. Keeling and Rohani 2008; Lloyd-Smith et al. 2009; Huyvaert et al. 2018, Chapter “Quantifying Transmission Between Wild and Domestic Populations”). Many modern quantitative techniques are currently applied to correlation analysis and risk biogeography, longitudinal sentinel surveillance data, or network analysis. The application of mathematical models to infectious diseases can be used to address both scientific hypotheses and develop disease-control policy, for example, identifying when to intervene to achieve effective disease control (Grassly and Fraser 2008). For such purposes, mathematical models represent the key individuals, groups, populations and communities, and the essential mechanisms determining pathogen transmission (Chapter “Quantifying Transmission Between Wild and Domestic Populations”). Although simplifications, a certain level of complexity is ineludibly required since interactions among individual groups and among populations are complex. Therefore, in order to link the biology of infectious diseases and appropriate mathematic tools, a multidisciplinary approach and solid background information from the field are required. Basically, the fundamental susceptible-infected-recovered (SIR) model (see Chapter “Quantifying Transmission Between Wild and Domestic Populations”) classifies groups of individuals within the host population as “susceptible” to infection, “infected” and able to transmit the pathogen, or “recovered” and immune to re-infection. Transmission of infection to new cases is driven by contacts between susceptible and infectious individuals. These models reproduce the classic epidemic curve, and have been remarkably successful in elucidating fundamental principles, such as the threshold for epidemics to take off if the basic reproduction number R_0 is greater than 1, and the potential to achieve natural or artificial “herd immunity.”

One of the most useful applications of dynamic network theory and modelling in epidemiology is the possibility to simulate and explore the transmission of pathogens on the basis of the different parameters that characterize them (e.g., Farine 2018). Dynamic network models can simulate the transmission of pathogens transmitted through both direct and indirect pathways, according to spatiotemporal definitions of direct and indirect interaction, and to explore the potential role of wild species in transmission, for example, at the wildlife-livestock interface. The probability of infection given interactions in field conditions is a difficult parameter

to estimate (Chapter “Quantifying Transmission Between Wild and Domestic Populations”). Network analysis can simulate different probabilities of infection, according to the species that initiated the transmission, conditions such as seasonal variations in contact rates and probability of transmissions, or include the environmental reservoir. Simplifying, networks are a connected matrix consisting of nodes representing individuals within a population (or population within a community of metapopulation), and edges (links) that represent interactions between individuals (or whatever nodes they represent). In an epidemiological context, this provides a framework for visualizing potential pathways of transmission within populations, metapopulation, or communities. Network analyses are useful to capture the complexities of multi-host pathogens, which allow us to estimate and compare the potential effectiveness of management actions for mitigating or suppressing disease in wildlife and/or livestock host populations.

Huyvaert et al. (2018) (see also Chapter “Quantifying Transmission Between Wild and Domestic Populations”) recently reviewed the gaps and challenges in modelling pathogen transmission at the wildlife-livestock interface, and the available quantitative methods and approaches to complete gaps, concluding that modelling diseases across the wildlife-livestock interface involves many challenges and only transdisciplinary approaches are able to integrate modern quantitative techniques to produce robust, powerful and, most importantly, useful multi-host dynamic transmission models. They identified four key components necessary for effectively modelling disease at the wildlife-livestock interface: (1) host and pathogen distributions and movement patterns, (2) transmission rates and pathways, and (3) estimates of disease effects. Interestingly, they noted (4) the need for effective communication among wildlife biologists, mathematical modelers, veterinary medicine professionals, producers, and other stakeholders concerned with the consequences of pathogen transmission.

The Evolutionary Perspective

What were the specific barriers to the flow of pathogens among hosts operating along natural history of host communities–species? (Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”). What have the relative contribution of ecological scales been to host–parasite interactions, parasite emergence, maintenance, and spread (i.e., before and after anthropogenic impacts appeared)? In which scenarios? Can we identify the paths that permitted pathogens to breach host barriers and spillover to other species? Summarizing, a general flow proposed for present communities (Becker et al. 2019; Plowright et al. 2017) can look like this: (1) *pathogen pressure* is determined by interactions among reservoir host distribution, pathogen prevalence, pathogen excretion by the reservoir host, subsequent pathogen survival, development, and dissemination outside of the reservoir hosts; (2) vector behavior and human factors modulate *pathogen exposure*

(likelihood, route, and dose) and (3) *genetic, physiological, and immunological attributes of the recipient host* determine host invasion for a given pathogen.

Host–pathogen coevolution has shaped both their relationships and the diversity and population structure of hosts and their pathogens (Morgan and Koskella 2011). Coevolution has been demonstrated in a diverse set of host–pathogen systems; it is ubiquitous across ecosystems. In particular, it has probably had a key role in animal and human diseases after domestication, once the wildlife-livestock-human interface appeared (Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”). Pathogens and hosts exhibit remarkable abilities to adapt to each other (convergent evolution), which is driven by evolution, either as a direct relatively short response or through long-term coevolution generating host or parasite traits that interact. *Evolutionary biology* provides the scientific basis to understanding disease from the standpoint of adaptation, but also improves our understanding of the mechanisms underlying current infectious disease transmission dynamics, context-dependent virulence, and more effective treatment and control strategies (Stearns and Koella 2008). For instance, the bacterial pathogen *Mycoplasma gallisepticum* has relatively recently and successfully jumped from poultry, its original host, to house finches (Hochachka et al. 2013). Evolutionary biology has integrated with traditional approaches to immunology and pathogen biology to address how new pathogens keep emerging as a result of evolution, driven by human activity, including ecological changes related to modern agricultural practices. Evolutionary biology and applied epidemiology can be used to detect adaptation in the case of pathogen emergence, such as host jumps. The increasing ease of large-scale genomic sequencing, together with advances in bioinformatics, molecular evolutionary theory, and new statistical tools for linking viral genetic variation with epidemiology and phylogeography (Pepin et al. 2010), is providing valuable means to visualize viral emergence and generate hypotheses about evolutionary mechanisms. This requires interdisciplinary teams (including field ecologists, microbiologists, immunologists, epidemiologists, bioinformaticians, and evolutionary biologists) using multiple approaches (field sampling, laboratory experiments, data analysis, and theoretical modelling).

In summary, a large body of developing theoretical frameworks have increased our understanding of transmission processes in complex host communities, especially relative to zoonotic situations but less so for the wildlife-livestock interface. The geographic diversity and complexity of the wildlife-livestock interface and any multi-host system require conducting local interdisciplinary research to find the best appropriate management. Also, research must adopt a holistic perspective to interpret pathogen dynamics at the wildlife-livestock-human interface considering biological, ecological, economic, and social drivers of pathogen emergence. What is the frequency and risks of pathogen flow between species at the wildlife-livestock interface? What mechanisms of amplification and persistence operate? What is the influence of different livestock production systems, socioeconomic context, and wildlife management? What possible interventions and more effective strategies can lead to reduced pathogen emergence and maintenance at the interfaces?

Final Remarks

- The different interfaces are “barriers” among human and animal (livestock and wildlife) compartments, which constitute opportunities for horizontal transmission between species, a new space for evolution, emergence, and maintenance of pathogens. The wildlife-livestock interface or ecotone often constitutes a proper ecological and epidemiological entity, with specific niches and epidemiological roles for wild, domestic, and environmental reservoirs, representing an important feature of pathogen transmission in the landscape. This allows for delineating the suitability for risk distribution of shared pathogens to identify a target for ecological and disease surveillance in these areas and allocating limited resources to improve and better understand and manage both human and animal health.
- Human activities have determined the appearance of new interfaces and opportunities for pathogen emergence and spread. Only the integrated understanding of ecological, epidemiological, social, cultural, and economic mechanisms that operate at wildlife-livestock-human interfaces will allow transdisciplinary integrative approaches to prevent and control disease. The wildlife-livestock interface term should equally be used for the term wildlife-livestock-human interface. This means different disciplines should increase their level of research cooperation and collaborative surveillance of animal and human pathogens to make the best coordinated decisions for similar problems of global concern.
- Recent disease emergence at wildlife-livestock-human interfaces, and their global spread, as exemplified in recent pandemics, illustrate the weaknesses of current wildlife disease and population monitoring and early warning systems acting at the origin of pathogen emergence, which need to be capable of detecting what is going on at the interface before pathogens spread and it becomes too late to prevent their impacts.
- These interfaces are interconnected centers for pathogen transmission giving rise not only to temporal, but spatial disease emergence. Local and regional drivers associated with risk for emergence of pathogens are connected worldwide, ranging from wildlife exclusive pathogens in the absence of livestock and local pastoralism systems to transcontinental-global interconnected food animal production systems and markets. Particular attention to the neglected wildlife-livestock interface is needed in complex ecosystems in developing regions, characterized by high biodiversity, a complex interplay of ecological and human factors, and increased opportunities for EIDs to arise and pathogen spillover to occur.
- The wildlife-livestock interface has been often neglected, and, consequently, disease spillover is largely underreported, even for zoonoses. Monitoring trends in wildlife populations, large-scale surveillance efforts, and addressing the ecological and epidemiological study of the wildlife-livestock interface to identify epidemiologically relevant animal reservoirs are warranted to understand and prevent diseases of animal relevance, but also those potentially spreading to

humans. Also, improved monitoring of livestock and large-scale trends are needed to depict interfaces and evaluate broad-scale risks.

- There are essential gaps, which prevent us from better understanding and managing disease dynamics at the wildlife-livestock interface. As the first step in many interfaces, it is necessary to describe the hosts and their pathogens, their distributions and behavioral characteristics with epidemiological consequences; and then, what the pathways and transmission rates are among these compartments, and which effects pathogens exert at both population and community levels. Also, the effect of disease management at the interface in given socio-economic and cultural environments needs to be understood to develop successful mitigation strategies.

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Natural and Historical Overview of the Animal Wildlife-Livestock Interface



Joaquín Vicente, Vidal Montoro, and Kurt C. Vercauteren

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Introduction

Epidemiological and ecological connections among host species and pathogens are continuously evolving as host contact rates and ecological interactions drive cross-species transmission of pathogens. The previous chapter discussed that in such communities, epidemiological ecotones, or interfaces are spaces of transition and contact among different compartments, becoming “experimental scenarios” where

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pathogens have evolved to adapt, taking the opportunity to jump to new hosts. In more recent geological times, domestication of animals led to an epidemiological transition from human–wildlife interactions to human-wildlife-livestock interactions. Since then, humans have served as the key drivers of pathogen spillover at these interfaces, influencing their distribution, intensity, and subsequent consequences. The observation of contemporaneous events indicates that the outcomes of interspecies transmission vary widely, from single-infection spillover transient outbreak events with no consequence in life history of hosts, to long-lasting outbreaks maintained in new hosts which greatly impact communities (e.g., the introduction of rinderpest virus in sub-Saharan Africa at the wildlife-livestock interface the late 1800s, Roeder et al. 2013). The complex nature of ecological, epidemiological, and socioeconomic factors that determined past events, though, are ineludibly interconnected and difficult to disentangle.

Over the last millennia, and accelerated in contemporaneous times, industry and urbanization have progressed exponentially and wild habitats have been dramatically altered into agricultural land, threatening biodiversity and provoking profound changes to interfaces among animals and humans. Only 1000 years ago, less than 4% of the world's ice-free (four million km²) and non-barren land area was used for farming (Ellis et al. 2010), compared to this day, where half of all habitable area (70% of global land area) is used for agriculture. Livestock uses most of the world's agricultural land. However, the distribution of land use between livestock and crops for human consumption, and specific farming and husbandry practices are contextualized in very different environments and socioeconomic realities. *Human intervention, including cultural, political, and economic dimensions, has resulted in epidemiological interactions at the interfaces as human impact progressively intensified and expanded the wildlife-livestock interface over the world*, which is reviewed in this chapter. The pathogen communities shared by wild and domestic populations and the dynamics of these complex host–pathogen systems reflect the historical epidemiological interactions between them (Caron et al. 2020). We present how humans have coexisted in complex interdependent relationships, first with wildlife and later also with domestic animals, in a wide range of natural and human-impacted environments. This chapter illustrates how, from domestication, the interface has been a socio-ecological system where economies have influenced agricultural practices and the relationship with wildlife (management and use).

Human population growth, increasing demand for food and other goods, globalization, associated environmental changes (e.g., habitat alteration, urbanization, agricultural expansion, and intensification), and climate change are seriously impacting overall world health. We are experiencing a new epidemiological transitional period, characterized by emerging diseases and a globalization of disease ecology, reflected by the impacts of rapid changes in demographic, environmental, social, and technological aspects. *Our capacity to modify and connect the interfaces has increased to the extent that improving health at the human, animal, and ecosystem interfaces (One Health approach, a recent term for an old concept) is the only option to successfully address the main global health challenges (Godfroid et al. 2014; Cassidy 2015). What we do during the next decades at ecosystem interfaces will determine our common future.*

Many questions arise from historical, ecological, and epidemiological perspectives. Which host interaction networks, composition, relative abundances occurred in past contexts, and how they interacted with and within their environment? What were the impacts of pathogens in past community assemblages and diversity? When and how did pathogens emerge in past multi-host systems, and particularly at wildlife-livestock-human interfaces? What were the consequences on transmission of novel species entering new host communities? How did virulence evolve after pathogens crossed to new host species? What were the interactions in the host assemblage? Host–pathogen–environment interactions have changed, but we can presume that the theoretical ecological framework that operated in the past is supported by the processes observed today (see Chapter “Host Community Interfaces: The Wildlife-Livestock”). We can probably identify parallels between the process of change of the wildlife-livestock interface over human history and the current gradient of characteristics of the interface from pristine to highly anthropized ecosystems (Fig. 1 of Chapter “Host Community Interfaces: The Wildlife-Livestock”).

Understanding Previous Ecological and Epidemiological Contexts

Theoretical frameworks and technical advances (see Chapters “Host Community Interfaces: The Wildlife-Livestock”, “Collecting Data to Assess the Interactions Between Livestock and Wildlife”, “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”, and “Quantifying Transmission Between Wild and Domestic Populations”) developed by different disciplines provide support to address the dynamics of current multi-host multi-pathogen systems, such as what the risks are for pathogen interspecific transmission and emergence. This scientific background can be applied to past assemblages of hosts, which have changed in terms of host community composition, the specific ecological relationships of their components, and the relative importance of the main drivers such as anthropogenic factors. As it happens for present systems, describing cross-species transmission processes that occur at varying levels of biological organization, especially in the past, is complicated by the many scales and data required (Becker et al. 2019), which are almost systematically absent for most past scenarios. Fortunately, research is providing clues on the characteristics and evolution of ecological animal networks and the prevalent interfaces of the past.

Unfortunately, our capacity to understand the ecology of past, often extinct, communities and their pathogens attenuates rapidly with time because the evidence for their functional characteristics become harder to discover and reconstruct. However, especially for recent communities in geological times, there may be some data, for instance, based on preserved fossil information (e.g., Poinar 2018) and evidence of habitat and climate conditions (Woodburne 2010). Different disciplines can help

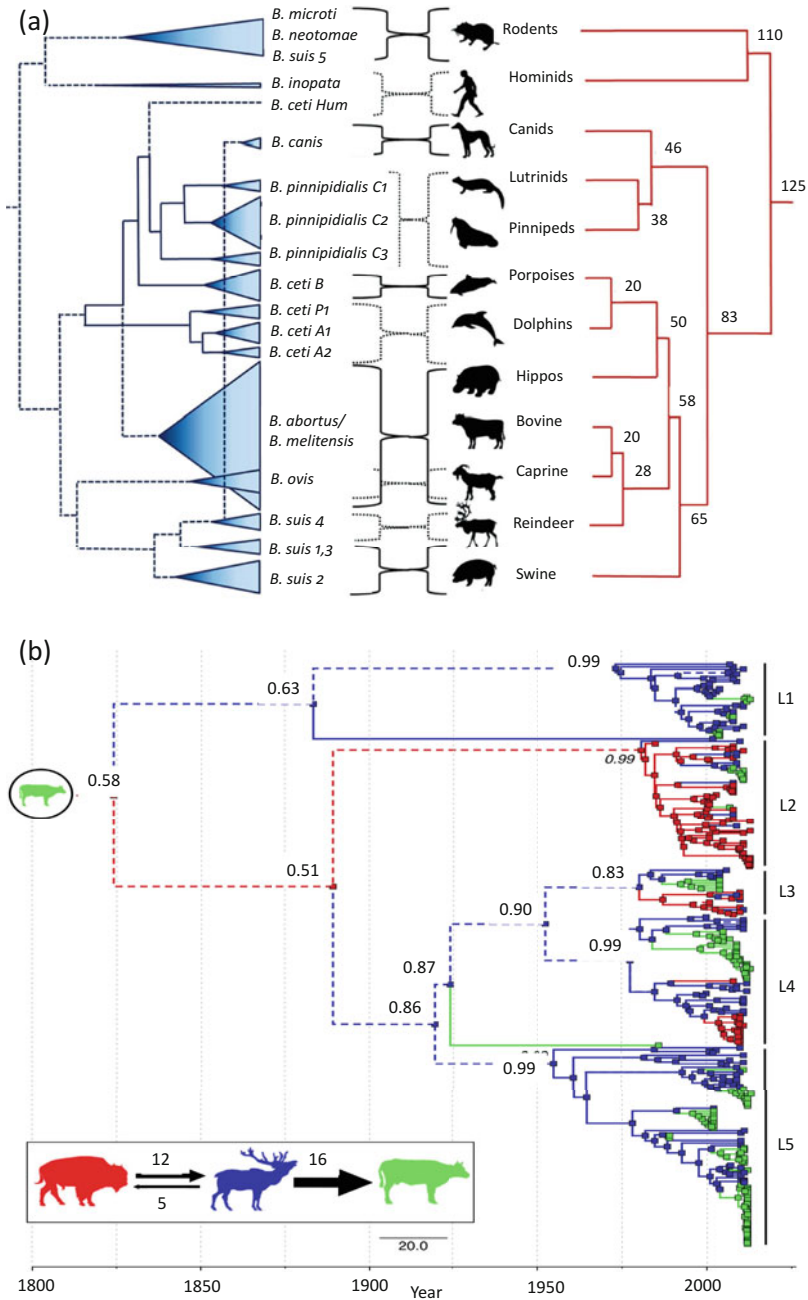


Fig. 1 The copyphylogeny of hosts and *Brucella* pathogens. **(a)** The dispersion of *Brucella* species is confronted to the phylogeny of their preferred host mammal (cones proportional to the number of strains analyzed, modified from Moreno 2014 after Guzmán-Verri et al. 2012). Numbers in the mammal phylogenetic tree represent millions of years. **(b)** Shows a more contemporaneous approach, a reconstruction of *Brucella abortus* genealogies by Whole-genome sequencing for at the wildlife-livestock interface in the Greater Yellowstone Ecosystem (GYE, Kamath et al. 2016). It

Table 1 Comparison of disciplines potentially studying determinants of pathogen spillover in present and past host communities (inspired in Plowright et al. 2017)

Determinants for transmission	Disciplines studying past determinants of transmission	Disciplines studying current determinants of transmission
Reservoir host distribution, relative abundance, interactions between species	Paleontology, paleoecology, paleogeography, paleoclimatology, paleoethology, paleophilogenetics	Animal ecology, population biology, biogeography, behavioral ecology, landscape ecology, agricultural science
Pathogen prevalence	Paleogenetics, paleomicrobiology, paleoparasitology, paleopathology, paleoepidemiology, paleogenetics	Disease ecology, animal epidemiology, infectious disease dynamics, immunology, microbiology, veterinary medicine
Infection intensity		
Pathogen excretion from reservoir		
Pathogen survival and/or spread	Paleomicrobiology, paleoepidemiology	Microbiology, disease ecology, vector ecology, epidemiology, spatial ecology
Human factors	Archaeology, anthropology	Human epidemiology, medical anthropology, vector ecology, social sciences, behavioral ecology
Host–pathogen interaction	Paleomicrobiology, paleopathology, paleoepidemiology, evolutionary biology, paleogenetics	Microbiology, innate adaptive immunology, cell biology, pathology, genetics, evolutionary biology

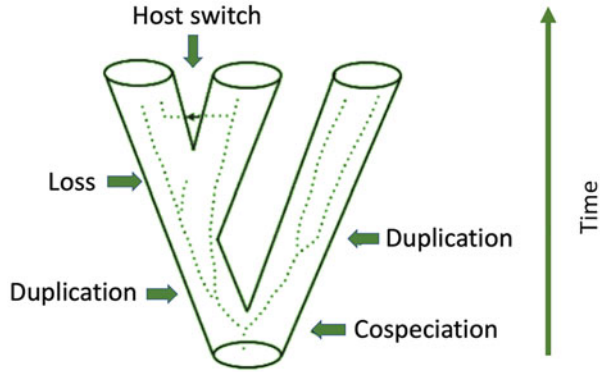
to understand the structure of interaction networks in these preterit communities, such as paleoecology, paleoepidemiology, pathology, and genetics (Table 1). They address unknown ecological and historical contexts, can infer and speculate about the past based on (1) what the prevalent composition of host communities and their interactions were, (2) evidence of pathogens, and (3) evolutionary and phylogenetic studies of host and pathogens based on current and old samples. The introduction of improved molecular tools allowed the extraction of ancient DNA (aDNA, Marciniak 2016) and subsequent massive application of next-generation sequencing technologies. Paleogenetics and phylogenetic methods can be applied to situations where direct knowledge of the past is absent by the analysis of molecular sequences. In contrast to genetics, which studies individual genes and their roles in inheritance, paleogenomics aims at the collective characterization and quantification of all genes of an organism, their interrelations and influence on the organism. For instance, it is now possible to detect genetic drift, ancient population migrations and

←
Fig. 1 (continued) evidences cross-species transmission, and that brucellosis was introduced into wildlife in this region at least five times (authors estimated 12 host transitions from bison to elk, and 5 from elk to bison). These results support that free-ranging elk is currently a self-sustaining brucellosis reservoir and the source of livestock infections. The predicted date of the ancestral root of the tree was approximately 1769 (the time to most recent common ancestor for all GYE isolates)

interrelationships, their association with pathogen spread and evolution, the evolutionary history of extinct species, and even the identification of phenotypic features across geographic regions (e.g., Huerta-Sánchez et al. 2014; Barlow et al. 2018). Scientists can also use paleogenomics to compare ancient ancestors (wildlife, domestic species, and their ancestors, pathogens) against modern-day species and provide insights as to when and by what means traits evolved, and how extinct organisms are related to living species and populations.

The *genomics revolution* (population genomics and paleogenomics) has increasingly provided insight regarding patterns of pathogen evolution and spatiotemporal epidemiological dynamics (Dearlove and Wilson 2013; Orton et al. 2013) and is continually developing. New findings and hypotheses continually arise, which are supported or rejected, and therefore examples must be considered in that context. Bacterial microbiomes (the genetic component of a microbiota) have been partially reconstructed from ancient remains in prehistoric humans using coprolites (Tito et al. 2008, 2020), and from Mammoth *Mammuthus primigenius* and woolly rhinoceros *Coelodonta antiquitatis* from frozen preserved intestinal contents (Mardanov et al. 2012). The evolutionary history of pathogens is closely linked with that of their hosts (Clayton and Moore 1997). Researchers, by using phylogenetic trees and networks of evolutionary relationships, can explain evolutionary paths (e.g., using pathogen samples from different times), how closely organisms are related to each other (e.g., samples from current pathogens so distance is a proxy to time of evolutive separation), and the study of cophylogeny (concordance between the phylogenies and interactions of different groups of species) of hosts and pathogens. Fig. 1 shows the case of bacteria *Brucella* (Moreno and Moriyón 2002), a monophyletic genus with high DNA similarity (Verger et al. 1985). *Brucella* species can be distinguished by single nucleotide polymorphism analysis and host preference (Foster et al. 2012). *Brucella* divergence seems linked to the evolution of the host (Moreno 2014), but these organisms are also able to breakdown the species barrier and “jump” from one mammal order to a very different one (Figs. 1a and 2). The fine spatial and temporal dynamics of pathogens, such as the transmission among wildlife and livestock of *Brucella abortus* (Fig. 1b) can also be approached by highly resolved time-calibrated phylogenies, evidencing cross-species transmission and the introduction history as well as identifying current maintenance reservoirs as source of infection to livestock hosts (Kamath et al. 2016). An interesting case is that of the *Mycobacterium tuberculosis* complex (MTBC). *M. tuberculosis, stricto sensu*, is the causative agent of tuberculosis (TB) and has caused more deaths in humans than any other infectious disease, likely infecting more people than any pathogen has at any other time in human history (Gagneux 2018). Most evidence to date supports an African origin for the human-adapted MTBC (the closest living relatives of the common ancestor of the MTBC are almost exclusively found in the Horn of Africa). *M. bovis*, which has a broader host range than *M. tuberculosis*, and humans were originally thought to have acquired TB from domestic animals during the Neolithic period. Later, the availability of the first full bacterial genome sequences revealed that *M. bovis* contains a smaller genome than *M. tuberculosis*, and this may indicate that the latter was unlikely to have evolved from *M. bovis* (Brosch et al. 2002).

Fig. 2 Schematic representation of the possible different coevolutionary events among host and pathogens (modified from Baudet et al. 2015). The tube represents the host tree and the dotted lines the pathogen tree



Several studies showed that the order of gene loss across the various members of the MTBC supported an evolutionary scenario in which humans transmitted TB to animals (Mostowy et al. 2002; Dippenaar et al. 2015). In addition, multiple host jumps might have occurred in the evolution of certain MCT lineages, both from humans to animals and back. Another interesting example is the old lineage of protozoan parasites. Molecular paleoparasitology on mammalian trypanosomes has clarified that *Trypanosomatid* divergences can be dated prior to the origins of both current insect vectors (30–60 million year ago, Ma, for tse-tse fly), and placental mammalian hosts (<85 Ma) (Fernandes et al. 1993). Finally, as for viruses (Tao et al. 2017), phylogenetics provides evidence for natural recombination between distantly related African bat coronaviruses that resulted in ancestor viruses of certain Human Coronaviruses (HCoV), suggesting that past interspecies recombination played an important role in CoV evolution and the emergence of novel CoVs with zoonotic potential. As indicative, close correlations between Italian bat CoVs belonging to the genus *Betacoronavirus* and SARS-related CoV that emerged far in Asia have been shown (Balboni et al. 2010).

Pathogens, Host Communities, and the Time Scale of Evolution

Pathogens have been ubiquitous in ecosystems, affect evolutive forces upon populations, and are commonly regarded as factors that co-participate in fluctuations or declines in wild populations with consequences at the wildlife-livestock interface (Dobson and Hudson 1992; Kilpatrick and Altizer 2010; Pybus et al. 2013). Pathogens and host communities (wild and domestic) evolve in response to one another and changing environments, leading to co-evolutionary dynamics that modulate their genetic composition and diversity, and even co-speciation events. The immense diversity of hosts in natural communities, including domestic animals and humans has resulted in a large diversity of current pathogens, where *evolutive processes have shaped the biology of hosts and pathogens*. However, outcomes of pathogen–host relationships, such as immune escape and changes in virulence, are diverse and

system-specific. Today, evolutionary questions underlying the emergence of pathogens in novel hosts are particularly challenging. The extent to which *pathogens have evolved toward generalists or specialists* following transmission into a novel host depends on their level of adaptation to dealing with different environments, their rates of molecular evolution and their ability to recombine (Bonneaud et al. 2019). Crucial mutations may also occur in reservoir or novel environments (Pepin et al. 2010). An *evolutionary arms race between hosts and pathogens* begins when pathogens impose a selective process in hosts, which leads to a strong selection pressure for a pathogen to evade the host immune response (Meyerson and Sawyer 2011). The evolutionary dynamics of pathogens and hosts is characterized by a *trade-off between transmission rate and virulence* (i.e., transmission time prior to host death limits pathogen adaptation). Current research on how pathogens are able to breach species barriers and evolve as emergent is providing insight on how pathogen strains arise in response to selective pressures from past environments (e.g., the role of adaptation in host jumps of viruses such as CoVs at the interfaces; Park et al. 2013) and why some pathogens (e.g., influenza) constantly evolve to evade antigenic recognition (Restif and Graham 2015) or adapt to new hosts (e.g., CoVs and host cell receptors; Park et al. 2013).

Viruses illustrate the strong selection pressures exerted by pathogens on hosts, which has led to the development of effective responses against pathogens. Viruses present high mutation rates (especially RNA viruses) and have been subject to selection pressure for millions of years, acting on virus proteins by amino acid changes (Demogines et al. 2013). However, successful evolutionary pathways for viruses are limited, as evidenced by convergent evolution of different viruses (Stern et al. 2017). In turn, host alleles in genes participating in antiviral response have a major selective benefit that spreads rapidly through host populations (Fernández-de-Mera et al. 2009). However, this spread can be disrupted by various factors, including biogeographical reasons (see Chapter “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”).

Viruses also offer good examples of evolutionary transitions leading to emergence of relevant pathogens at the wildlife-livestock interface, which can be seen when extrapolating from genetic diversity among extant viral species. They can inform us about the long-term “arms races” between hosts and viruses, characterized by events of selection and counterselection, and increasing depths of ancient viral lineages. In this respect, endogenous virus elements (EVEs) are a common component of the eukaryotic genome (Holmes 2011), there are even sequences from RNA viruses that have no DNA stage in their life cycle. The discovery and research of EVEs have contributed to a better understanding of the time scale of virus evolution (Emerman and Malik 2010) in contrast to molecular clock studies using “heterochronous” samples (sampled at different time points during epidemiological history) from a single virus (Gilbert and Feschotte 2010). The presence of EVEs in related host species integrated into the same genomic position (like “fossilized” genetic prints within host DNA) indicates that this integration event occurred prior to the divergence of these species. If it is known when species diverged, then the minimum age of the insertion event can also be estimated (Katzourakis and Gifford (2010). Although there are different dating estimates, recent reconstruction of the

evolutionary history of retroviruses indicates they likely emerged between 450 and 550 Ma in the early Palaeozoic Era, coinciding with the origin of jawed vertebrates (Aiewsakun and Katzourakis 2017). This is currently the oldest inferred date estimate for any virus group and indicates that these viruses evolved within the marine environment. Other pathogens, such as bacteria, may display key differences in processes underlying their evolutive history. For instance, the jump of a pathogen into a novel host species followed by the specialization on that host and the loss of infectivity of previous host(s) is commonly observed in viruses but less often in bacteria. Bacterial pathogens typically exhibit high levels of phenotypic plasticity, low rates of evolution, and decreased ability to recombine, which should reduce their propensity to specialize on novel hosts. Thus, bacterial infections could be more likely to result in transient spillovers or increased host ranges than in host shifts.

Coevolution occurs when two or more species exert a reciprocal influence on one another's evolutionary trajectories (Vermeij 1994), and synchronous development of pathogen lineages with those of their hosts occurs. Cophylogeny is the reconstruction of ancient relationships among ecologically linked groups of organisms from their phylogenetic information. Cophylogenetic reconstructions for tracking host-parasite pathways normally use event-based models, including cospeciation, duplication (divergence), loss, and host switch (Fig. 2), and approaches that identify lateral gene transfers for the gene tree(s)/species tree problem (Hallett and Lagergren 2001). Pathogens that do not show complete fit with the phylogeny of their hosts are also interesting and may evidence their ability to jump between host species and establish on novel hosts. In fact, most pathogens seem to be able to switch hosts (Kossida et al. 2000). For instance, co-phylogenetic analyses revealed that cross-species transmission (host switch) may have been more common than co-divergence across coronavirus evolution, and cross-species transmission events were more likely between sympatric bat hosts (Leopardi et al. 2018).

The extent to which pathogens and their hosts codiverge remains an open question in most systems. However, cases of both cospeciation and horizontal switching have recently been documented, especially for RNA viruses (e.g., phylogeny for Hantavirus is significantly similar to its host trees, whereas Lyssavirus seems to display no significant congruence; Jackson and Charleston 2004). Numerous examples illustrate different cophylogenies where the timing, evolutionary mechanisms, nature of the pathogen, involved host compartments, and directional relationships vary:

- Herpesviridae, a large family of DNA viruses (McGeoch et al. 2000), have mammals and other vertebrates as their natural hosts (and in one described case, an invertebrate). Phylogenetic analysis of herpesviruses (HV) found in mammals and birds clearly evidence descent from a common ancestor. Each of the subfamilies of the Herpesviridae shows tree-branching features that can be explained by coevolution of HV lineages, as well as other features that require non-coevolutionary explanations. For instance, herpesviruses show weak correlations with the phylogenies of primates, rodents, ungulates, and carnivores. There are cases representing clear recent interspecies transfer of viruses, such as certain herpesvirus of wallaby (macropodid marsupials) and bovine.

- The Hepadnaviridae family of DNA viruses comprises two genera: Orthohepadnaviruses (including the Human Hepatitis B virus HBV that infect mammals), and Avihepadnaviruses (that infect avian species). Hepadnaviruses also have the ability of endogenization into the host genome (Gilbert and Feschotte 2010; Littlejohn et al. 2016) and phylogenetic analysis suggests that the integration events occurred at least 19 Ma (and a more recent study estimated to have occurred during a period of bird evolution from 12 to 82 Ma, Suh et al. 2013). Comparative phylogenetic analysis on endogenous and existing exogenous avian hepadnaviruses indicates multiple genomic integration events, and birds have been proposed as the ancestral hosts of Hepadnaviridae, while mammalian HBVs probably emerged after a bird–mammal host switch (Suh et al. 2013). Frequent cross-species transmissions have resulted in their widespread distribution in the animal kingdom and, as a result of a series of recombination events with other HBVs, for instance, both primate and human, resulted in at least 10 genotypes of human HBVs that are recognized today. Several theories (reviewed by Littlejohn et al. 2016) have been proposed to explain the origins of HBV, including cospeciation, coevolution, and cross-species transmission (even a bat origin). However, HBV evolution probably involved cospecies evolution within birds, rodents, and bats, followed by a series of cross-species transmission events to explain the close relationship between human and nonhuman primate HBVs observed today.
- In the particular case of adeno-associated virus (AAV)-derived endogenous viral element (mAAV-EVE1; Smith et al. 2016), a time-scaled cladogram using previously published estimates of divergence among marsupials represents a speciation history spanning an estimated 30 million years. This possibly suggests that the exogenous ancestor of mAAV-EVE1 could have been introduced to the island continent of Australia by migratory birds, evidencing a host jump (which probably was a complex process) among very different hosts.
- The Hepeviridae family (RNA viruses) includes two genera, *Orthohepevirus* and *Piscihepevirus* (Kelly et al. 2016; Cagliani et al. 2019). The *Orthohepevirus* genus is divided into four species of viruses infecting mammals and birds (*Orthohepevirus A–D*). Hepatitis E virus (HEV, an *Orthohepevirus A*) is a common cause of hepatitis worldwide. Human-infecting HEV strains are genetically heterogeneous. HEV-1 and HEV-2 only infect humans, primarily in tropical and subtropical regions. Genotypes 3 and 4 account for the majority of HEV human cases in industrialized countries and infect several domestic (mainly swine) and wild animals (e.g., ungulates and small carnivores). Phylogenetic analyses (Fig. 3; Cagliani et al. 2019) showed that HEV-3 and HEV-4 sequences derived from human cases are interspersed within those isolated from swine, indicating that pig-infecting HEV-3 and HEV-4 can easily cross the species barrier and infect humans. The wild boar *Sus scrofa*–domestic pig–human interfaces are interesting ecological, epidemiological, and evolutionary scenarios to study HEV-3, -4, -5, and -6. The remaining genotypes HEV-5/HEV-6 and HEV-7/HEV-8 have been detected in wild boars and camels, respectively. Phylogeny approaches have revealed that humans were the most likely hosts of the

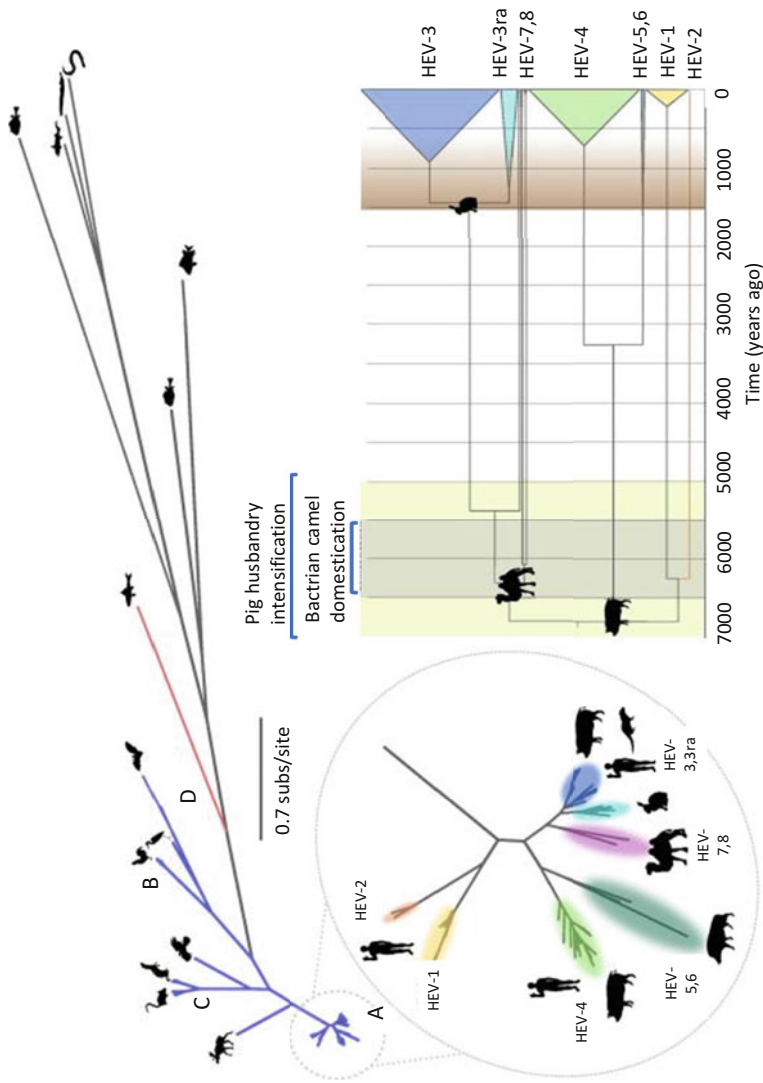


Fig. 3 Hepevirus phylogeny and time-scaled phylogenetic tree (modified from Cagliani et al. 2019, see reference for more details). Left: a maximum-likelihood phylogeny of the RdRp domain of known hepeviruses. The Psicthepevirus branch is in red, Orthohepevirus branches are in blue. The enlargement below shows phylogenetic relationships for viruses belonging to the Orthohepevirus A species (HEV), with representative hosts. Branch lengths represent evolutionary time. The timeframes of historical events mentioned in the text are reported. The rabbit and camel silhouettes mark the split of the rabbit- and camel/dromedary-infecting genotypes. The pig silhouette marks the human-restricted/enzootic genotype split

ancestor of extant orthohepeviruses, which is in concordance with the observation that most HEV genotypes can infect humans, whereas other animals are differentially susceptible to distinct HEV genotypes. Origins of the *Orthohepevirus* genus was recently dated to be at least 21 Ma. The Orthohepevirus A species originated in Asia, most likely from a human-infecting ancestor that existed approximately 4500 to 6800 years ago (Fig. 3 right), coinciding with the appearance of large human settlements that probably facilitated HEV emergence and spread (see below). The earliest events involved the separation of the enzootic (animal) and human-restricted genotypes, as well as the split of the camel-infecting genotypes occurring during the timeframe of camel domestication (Fig. 3 right). More recently, the place and timing of HEV-3ra divergence also corresponded to the period of rabbit domestication (Fig. 3 right). Today, humans may have acquired HEV through cross-species transmission from other animals, and the wildlife-livestock interface is crucial as a bridge for transmission.

- Species in the genus *Plasmodium* cause malaria in humans and infect a variety of mammals and other vertebrates. Mammalian *Plasmodium* parasites may have originated over 64 Ma (Silva et al. 2015). Cophylogeny reconstruction at the human-wildlife-livestock interface ecologically was applied to clarify the relationships for the most virulent human malaria, caused by the protozoan parasite *Plasmodium falciparum*. This parasite was at once thought to have arisen as a result of a host switch from birds to humans, at the time of the domestication of chickens (e.g., Waters et al. 1991). However, more recent work has shown that there is a close evolutionary relationship between *P. falciparum* and *P. reichenowi*, the chimpanzee malaria parasite, indicating codivergence events with respect to primate and *Plasmodium* evolution (Rich and Ayala 2010). Research supports the hypothesis that the last common ancestor of *P. falciparum* and *P. reichenowi* occurred around the time of the human–chimpanzee divergence and that current *P. falciparum* infections of African apes are most likely derived from humans and not the other way around, although *P. falciparum*-related pathogens can naturally circulate in some monkey populations in Africa (Prugnolle et al. 2011; Silva et al. 2011). On the other hand, *P. vivax*, split from the monkey parasite *P. knowlesi* in the much more distant past, during the time that encompasses the separation of the Great apes and Old-World monkeys. Overall, mammalian-infecting *Plasmodium* evolved contemporaneously with their hosts, with little evidence for parasite host-switching on an evolutionary scale, as evidenced by research on the timeframe within which to place the evolution of *Plasmodium* species (Silva et al. 2015).
- Different *Brucella* species (Fig. 1) cause brucellosis in domestic animals, terrestrial wildland animals, and sea mammals (dolphin, whales, seals, and walrus; Guzmán-Verri et al. 2012). The only species that are linked to human brucellosis are *B. melitensis*, *B. suis*, *B. abortus*, and to a minor extent *Brucella canis* (Moreno and Moriyón 2002). As mentioned above, *Brucella* divergence appears to be linked to the evolution of the host. One interesting feature of the genus is the absence of plasmids and lysogenic phages, which prevent horizontal transference of genes (Moreno 1998). It has been proposed that the extant *Brucella* species

expand clonally within the host environment and that genetic drift depends almost exclusively on mutation and internal genetic rearrangements (Moreno 1998). *Brucella* divergence seems linked to selective forces within the host environment, and consequently, to the evolution of the host (Moreno 1998). However, these organisms are capable of breaking down the species barrier and moving from one mammal order to a very different one (Fig. 1), which might favor the persistence of a distinct *Brucella* clone in a different “preferred” host.

- Changes in complex life cycles and pathogenicity of pathogens can occur rapidly, and this can be tracked by phylogeny and biogeographical approaches. The parasite *Toxoplasma gondii* protozoan infects warm-blooded vertebrates and also causes zoonotic disease in humans (Dubey 2010). There is a global predominance of three clonal *T. gondii* lineages, which suggests they have exceptional characteristics responsible for their current parasitism of nearly all warm-blooded vertebrates. The study of its genetic polymorphism analyses indicates that these clonal lineages emerged within the last 10,000 years after a single genetic cross. Comparison with ancient strains (approximately one million years) suggests that the success of the clonal lineages resulted from the concurrent acquisition of direct oral infectivity (Su et al. 2003). This key adaptation bypassed sexual recombination (only occurring in Felid species) and promoted transmission through successive hosts, thereby leading to clonal expansion. This radiation to transmission emergence through carnivorousism (i.e., oral infectivity of tissue cysts) between intermediate hosts manifested itself in clonal strains 10,000 years ago (Su et al. 2003). It is hypothesized that such oral infectivity may have developed previously in South America where it was shown to be a trait of many *Toxoplasma* species before migrating to North America and then further north along the Bering Strait to colonize Asia, Europe, and Africa. The original genetic diversity of Old-World *T. gondii* may have been larger and the recent expansion of the domestic cat, an Old-World species until the sixteenth century, may have favored a specific subset of preadapted genotypes.
- It is thought that about 2 Ma, African hominids who scavenged for food or consumed bovids were exposed to tapeworm colonization (see Box 1). Supporting evidence was inferred from an examination of host and parasite evolutionary histories and evidence for the rate of molecular evolution between species of *Taenia* (Michelet and Dauga 2012). Humans probably transferred tapeworms to cattle and swine because the association between *Taenia* and hominids was established before livestock domestication. Only after the development of agriculture about 10,000 years ago, did cattle, swine, and domestic carnivores become intermediate hosts. Today, cysticercosis and echinococcosis due to tapeworm infection are relevant issues at the wildlife-livestock interface in developing countries (e.g., Miran et al. 2017).

From a biogeographical perspective, Brooks and Ferrao (2005) expressed that emerging infectious diseases are “evolutionary accidents waiting to happen.” During periods of biotic expansion and exchange, pathogens and hosts may disperse from their areas of origin (Reullier et al. 2006; Hoberg and Brooks 2015). This, in

conjunction with other ecological processes, may allow for host switching without evolving new host utilization capabilities. In fact, most of the recent host switches of emergent infectious diseases (EIDs) have been associated with events of biotic expansion (Hoberg and Brooks 2015). Over the course of natural history, either new hosts have moved into the area of origin of given pathogens, or the pathogen has moved out of its area of origin into an area where susceptible hosts live (Engering et al. 2013). Isolation of host populations, upon geographical or behavioral separation, likely resulted in isolation of pathogen populations and pathogen population bottlenecks, leading the way to further diversification (Van Blerkom 2003). Pathogens have probably been shared most commonly between species that are closely related and inhabited and/or used the same geographical region, habitats, and/or resources. However, this is challenged by globalization, which characterizes the ecological, epidemiological, social, political, and economic relationships of the modern world.

Pre-Domestication History

Pathogens rarely survive in the fossil record. Viruses could have originated 4 Ma, or “only” 2 billion years ago according to different theories and sources (Domingo 2016), and Bacteria probably arose on the planet more than 3.5 years ago (Schopf et al. 2018). Mutualism is probably as old as first life, however, the earliest fossil record of mutualism between microorganisms and animals are protists and bacteria from a fossil termite entombed in amber during the Mesozoic (by Poinar 2009, 2018). One of the oldest known instances of infectious agents is the case of spirochete cells that looked like the *Borrelia* genus (named *Palaeoborrelia dominicana*; genus *Borrelia* is today associated to Lyme disease) and were found in ticks that were also entombed in amber at least 15 Ma. This suggests Lyme disease-like and other tick-borne diseases may have been infecting animals long before humans were present on Earth (the oldest documented case of Lyme disease bacteria presence in humans comes from the famous 5300-year-old [ice mummy](#) discovered in the Eastern Alps; Keller et al. 2012). Additionally, the history of pathogen change (for adaptability within host populations and communities) from the behavior of current systems (Chapter “Host community Interfaces: The Wildlife-Livestock”), with continuous emergences (re-emergences) and extinctions also needs to be inferred.

Ecological and Environmental Changes Determining Host Diversity, Distribution, and Communities During the Pleistocene

Through processes of evolution, migration, colonization, and later, trade and travel, humans have impacted landscapes, other species, and the ways in which species have co-evolved, including pathogens. The very early origins of these processes, although accelerated during the last millennia and decades, were primarily forged during the Pleistocene. This is the geological epoch that approximately corresponds to the Paleolithic period in human prehistory (Toth and Schick 2007) and extends from the earliest known use of stone tools by hominins c. 3.3 Ma, to the end of the Pleistocene c. 11,650 years before present (BP). It is characterized by glaciations, relevant animal and human migrations, and colonizations. During the Pleistocene, key ecological and environmental changes determined the distribution and assemblages of animal communities (hosts) that later determined those giving rise to domestic species, and the evolution of anatomically modern humans. The appearance of *Homo sapiens* occurred about 200,000 years ago. This epoch is a key anteroom to a crucial change in human, animal, and pathogen history: domestication.

During the Pleistocene, climatic and environmental fluctuations resulted in successive events of north-south migration of animals, affected human dispersion, and produced the geographic shifting of many species, probably in many cases accompanied by absorption of part of the gene pools of local related species dispersing and sharing pathogens. Paleogenomics has demonstrated ancient gene flow between genomes of extinct species and existing recipient species (Huerta-Sánchez et al. 2014; Barlow et al. 2018), which probably also determined the flow of their respective guilds of pathogens. The case of wild boar during its expansion from Asia to Europe illustrates this (Liu et al. 2019), as a species that is widely distributed today and plays relevant epidemiological roles for animal- and human-shared pathogens. The genus *Sus* differentiated about 3 Ma and *S. scrofa* subsequently spread throughout Asia, Europe, and North Africa. This expansion (Schiffels and Durbin 2014; Fistani 1996) was highly efficient and similar to the great human expansion during the late Pleistocene (Frantz et al. 2013). It is thought that wild boar expansion could cause the disappearance of most suid species across Eurasia (wild boar appeared in Europe 1.5 to 0.4 Ma, depending on whether estimates are based on archaeological or molecular data. However, it is hypothesized that wild boar did not replace the other suid species it encountered, but instead exchanged genetic materials with them through admixture. These inter-specific/inter-generic admixtures likely led to the transfer of pathogens. Another example is the great American biotic interchange when the Neotropic (roughly South America) and Nearctic (roughly North America) ecozones joined, which resulted in land (its most evident effect was on the zoogeography of mammals) and freshwater fauna migrating from North America via Central America to South America and vice versa (accelerated about 2.7 Ma). This interchange ultimately determined the wildlife that humans would later discover and even domesticate during their expansion across the Americas.

Further (see above), it is hypothesized that an ancestral form of *T. gondii* was introduced in South America through the migration of Felidae after the emergence of the Panama isthmus and that the evolution of oral infectivity through carnivorism and the radiation of felids in this region enabled a new strain to outcompete the ancestral lineage and undergo a pandemic radiation (Webb 2006; Bertranpetit et al. 2017).

Pleistocene terrestrial ecosystems included a much greater diversity of megaherbivores (e.g., mammoths, mastodons, and giant ground sloths) and thus a greater potential for widespread habitat degradation if population sizes were not limited. The last ice age ended about 11,000 years ago, coinciding with the beginning of the Neolithic period. At this time, wild mammals on all continents underwent major changes, with a great impact in North and South America, where 33 (73%) and 46 (80%) genera of mammals became extinct, respectively. Australia also lost 55 species, but losses in Europe were not as severe, and extinctions during this time in Africa and Asia were similarly mild. Scientists attribute these extinctions to numerous causes, which primarily included climatic changes and overhunting by humans. What is clear is that humans during the Pleistocene were extremely efficient in exploiting natural resources and influenced animal community compositions, which probably conformed an intimate epidemiological human–wildlife interface until domestication.

Origins, Evolution, and Dispersal of Humanity and New Interfaces

No other living organism has influenced the current ecological and epidemiological scenarios on Earth like humans have. The genus *Homo* evolved during the lower Paleolithic age. Populations expanded and retreated due to glacial and interglacial periods, alternating fragmentation, and contiguous interbreeding, experiencing both bottlenecks and considerable intrapopulation divergence. These phenomena also increased the rate of diversification of many organisms (Lovette 2005). The superfamily Hominoid (including the ancestors of *Homo* species and Great apes) history dates up to 30 Ma in Africa and Eurasia and is characterized by many extinct genera and species. The evolutive history of humans begins at the end of the Miocene (approx. 6 Ma), a period characterized by a large diversity of primates inhabiting tropical forests of Africa. The common antecessor of humans and chimpanzees is still controversial (*Orrorin tugenensis*, Senut et al. 2001; *Sahelanthropus tchadensis*, one million older, Brunet et al. 2002). Australopithecines, which are supposed to be the bipedal ancestors (approximately 4–1 Ma) of the *Homo* branch, expanded their range from woodland to more open grassland savannah-like environments in East and South Africa. This scenario was probably the first actual human–animal interface and entailed changes in exposures to new vectors and risks associated with eating meat. However, most hominin evolution in eastern

Africa transpired in the context of faunal communities unlike any known today (large-bodied mammalian herbivores differed markedly from those today until ~700,000 years ago). Therefore, there is controversy whether what we observe at present is a sufficient analog for much of the past (Faith et al. 2019). The genus *Homo*, academically termed “human,” emerged in Africa around 3 Ma and comprises a highly diverse group, which is still not completely disentangled. The earliest *Homo* found outside of Africa seems to be *Homo erectus* around 2 Ma, and when interpreted in the broad sense (there is some dispute over which fossils should be included within the species), spanned a very large geographical range in Eurasia. The subsequent expansion of such hunter-gatherers into unfamiliar environments would have exposed them to various new pathogens.

The first hominins were omnivorous (Thompson et al. 2019) and consumed meat and marrow from bones (first tools date back from at least 3.4 Ma). *Homo* probably accessed large mammal carcasses mainly through scavenging (Blumenshine and Pobiner 2006). However, evidence also suggests primary access to ungulate carcasses through hunting for those Early Pleistocene human populations (Domínguez Rodrigo et al. 2010) and replaced active scavenging. The carnivore guild composition and food web structure present as *Homo* expanded probably influenced their expansion and access to meat resources, especially large herbivores, for the earliest European hominins (Croitor and Brugal 2010). Interestingly, the transition from a predominantly herbivorous diet to an omnivorous diet and then eventually toward a strongly carnivorous diet shaped a *predator–prey interface*, with epidemiological consequences for the rest of human natural history (Michelet and Dauga 2012). The consumption of wild animals that also were prey to a variety of predators could be a relevant path of pathogen interspecific transmission in a natural environment. For example, it is thought that about 2 Ma, hominids who scavenged for food or preyed on bovids were exposed to *Taenia* infections (a cestode whose adult forms are intestinal tapeworms; Box 1). These worms were using hyena and large cats as definitive hosts and bovids as intermediate hosts. It is speculated that there may have been a role for anthropophagy during the middle and late Pleistocene in maintaining cross infections in humans, providing a possible disease transmission route for taeniids and allowing parasites to survive when animal hosts were rare (Rudolf and Antonovics 2007). The descendants of the African hominids spread and diversified tapeworms cysticercosis (the intermediate cyst is present in human tissues) and taeniasis (intestinal tapeworms present in humans) around the world through migrations, and later, following the development of farming and animal movement and trade. Another interesting example is *Trichinella* nematodes. The current species diversified during the age of modern placental mammals, and early hominids may have first acquired *Trichinella* on the African savannah several million years before swine domestication as their diets shifted from herbivory to facultative carnivory (Zarlenga et al. 2006). Transmission of *Trichinella* depended on carnivory and scavenging of carrion among Eurasian and African paleoguilds. Particularly, *Trichinella spiralis* appears to have commenced its independent evolutionary trajectory several million years before pigs were first domesticated, thus, the ecological setting in which hominids first acquired *trichinellosis* may parallel that of *Taenia* tapeworms.

The migration of *Homo* spp. out of Africa started as early as approximately 1.8 Ma, with evidence of the presence of *H. erectus* in the Middle East and as far as South-East Asia (Dennell and Roebroeks 2006). An ancient cultural shift much earlier than agriculture first appeared might have affected human evolution dramatically: the controlled use of fire. Early hominins may have used fire in an ad hoc manner by at least 1 Ma, but the controlled use of fire arose more recently (only 300,000–400,000 years ago; Gowlett 2016), or about 790,000 years ago (Goren-Inbar et al. 2004). This had a major effect on human host–pathogen relationships in sterilizing food (Wrangham et al. 1999). However, concomitant cultural changes associated with fire use by early humans exposed to smoke at campfires, which could contribute to the emergence of the *M. tuberculosis* complex (MTBC), the etiologic agent of tuberculosis (TB; Chisholm et al. 2016).

Homo sapiens appear in the Upper Palaeolithic (300–200,000 years ago) in Africa, together with relevant technological advances. The fact that a recently discovered species, *Homo naledi*, lived at the same time and in the same region as *H. sapiens* in Africa reveals the diversity of human forms that existed during the late Pleistocene (including *Homo rhodesiensis*), and therefore, epidemiological relationships. Neanderthals and modern humans both occupied the same areas in Europe for thousands of years prior to the spread of modern humans into the rest of Eurasia. The cause of Neanderthal extinction remains unknown as they were diverse and complex. Interestingly, it has been proposed that infectious-disease dynamics can explain the localization and persistence of the interspecies boundary during this time period and that modern human could overcome disease burden earlier than Neanderthals, giving them an advantage in their subsequent spread into Eurasia (Greenbaum et al. 2019).

Box 1 Shaping a New Predator–Prey Epidemiological Interface: The Origin of the Taeniasis/Cysticercosis Complex at Human–Wildlife Interface

A new predator–prey interface and ancient human migrations promoted the emergence and spread of pathogens around the world, creating new opportunities for pathogen transmission at the human–wildlife interface, some of which later found a niche at the wildlife–livestock interface. The taeniasis/cysticercosis complex are zoonotic diseases still endemic in many regions of the developing world and well established at the human–livestock interface, with secondary roles of the wildlife component today (wild bovids and wild boar). Based on the hypothesis that *Taenia* spp. and their hosts share a common history (Michelet and Dauga 2012; Wang et al. 2016), molecular and computational tools have enabled reconstruction an evolutionary history of the three species of *Taenia* currently known to parasitize humans, causing taeniasis and cysticercosis: *T. solium*, *T. saginata*, and *T. asiatica*. Pork and beef tapeworms are globally distributed, each infecting approximately 50–60 million people around the world. It is likely that two independent host switches

(continued)

Box 1 (continued)

from carnivorous species led to the occurrence of taeniids in human hosts. The emergence of *T. saginata* and *T. asiatica* is consistent with shifts from a felid host. The emergence of *T. solium* implies a shift from hyaenids (Hoberg 2006). The diversification of *T. asiatica* is estimated to have occurred 41,000 years ago (34,000–98,000), during the late Pleistocene. Thus, ancestors of modern-day human tapeworms emerged during the early to late Pleistocene, an epoch during which significant climatic fluctuations occurred. The arrival of *H. sapiens* in Asia coincided with the estimated time of emergence of *T. asiatica*, suggesting that new populations of wild boar and/or new breeding and husbandry practices imported by humans into Asia contributed to the emergence of this new species. Molecular chronologies also highlight correlations between evolutionary events and biotic factors, including secondary host switches and human migrations, long before the true development of agriculture and animal husbandry. Later, the development of animal husbandry, making livestock preferential intermediate hosts, led to the worldwide distribution of these parasites, where both domestic and sylvatic cycles were able to meet at the wildlife-livestock interface. A recent comparative genomics study reveals that high rates of gene duplications and functional diversifications might have partially driven the divergence between *T. asiatica* and *T. saginata* already during the expansion of *H. erectus* in Asia.

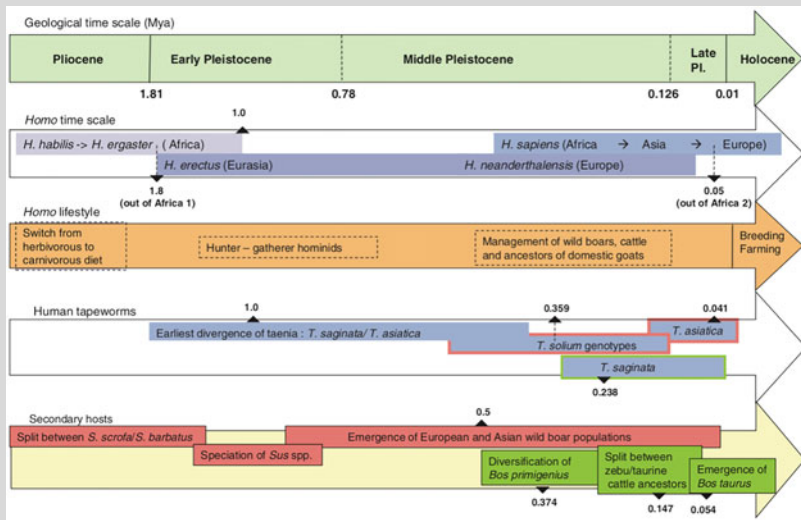


Figure Geological, human, and *Taenia* time scales (modified from Michelet and Dauga 2012). The length of the boxes for the time scale provides the 95% confident intervals. The arrow points represent the date of emergence.

During the Late Pleistocene (approx. 200,000 years ago), modern *H. sapiens* began dispersing out of Africa and into the rest of the world. The timing of the arrival of humans on each continent parallels the disappearance of many megafaunal genera (see above, the quaternary extinctions occurred 50,000–7000 years ago) and the extinction of larger carnivorans may also have provided niche space for dispersing humans. Interestingly, the late quaternary extinctions likely reduced the dispersal of pathogens by megafauna (Doughty et al. 2020). The migration of *Homo* spp. out of their African homeland similarly led to contact with new species and opportunities for cross-species transmission of zoonotic pathogens (Barrett et al. 1998). At this time, carrying capacity greatly depended on natural resources as the main driver of human and wildlife population sizes, and resource availability and distribution, and interspecific relationships (predation, competence, commensalism, etc.) determined community composition and interspecific opportunities for different species to interact and share pathogens. The influence of predators (e.g., lions) or prey (e.g., aurochs) on early humans was a force that caused humans to form cooperative groups or “tribes.” These small nomadic groups of hunter-gatherers, probably no more than 30–50 individuals, were highly mobile. These groups were likely too small and dispersed to support many of the acute pathogens that are/were typical of more densely populated sedentary communities (such as upper respiratory infections, and smallpox, measles, or mumps; Burnet 1962; Barrett et al. 1998; Dux et al. 2020).

Domestication: Origins and Diversity of Infectious Diseases at Animal Interfaces

Since the domestication process, human activities have promoted the emergence of new epidemiological spaces due to new interfaces created between domestic animals, wildlife, and humans. Animal domestication was a gradual process of intensification of the relationships between humans and animals over time, which culminated in relevant biological modifications observed in domesticates (Zeder 2015). This process was probably prompted by the demographic pressure of increasing human populations. Increased dependence of Neolithic humans on domesticated animals and plants led to semipermanent settlements, which later became permanent villages. Neolithic agriculture was independently developed several times and provided a new source of food and other goods to humans, which made increases in population density possible, and most habitable areas of the world were colonized around 12,000-years ago. Correspondingly, the human-livestock-wildlife interface plausibly started to serve a role as an epidemiological amplifier and source of pathogen emergence (Morand et al. 2014). New interfaces between domestic animals, wildlife, and humans were also introduced into new geographical areas or new host species during human travel and migrations. For example, rabies virus (Rhabdoviridae family) could be disseminated as dogs were brought to new continents long before the domestication of other species (Reperant et al. 2012).

Wildlife were the original hosts for most livestock pathogens, sharing them with domesticated species over centuries of coevolution and domestication. Domesticated animals then served as the source for many novel human pathogens, such as measles and smallpox (Pearce-Duvel 2006). However, domestication led to greater pathogen transmission between humans and domestic animals than other pairs of the complex human-wildlife-livestock interface, and many present-day human infections originated from zoonoses of domesticated animals (Wolfe et al. 2007). Additionally, the frequency of contact between humans (within and between communities), and the accumulation of infective material from human and animal waste increased. This favored denominated crowd diseases, which are now caused by more virulent and shorter lived infections predominate in large and densely settled populations (Zuckerman et al. 2014). Vectors also developed dependent relationships with human habitats. During the expansion of farming into new regions, the transmission of diseases such as malaria and yellow fever was favored (e.g., the yellow and dengue fever-carrying mosquito *Aedes aegypti* breeds preferentially in artificial containers; Thompson and O’Leary 1997).

Domestication and First Pastoralism

Over thousands of years (for most relevant species in Eurasia and Africa for 5000–12,000 years), animal domestication occurred following a sequence from the control of captive wildlife, to extensive livestock breeding, and finally, leading to intensive breeding (including pets). It is now clear that dogs were the first domesticated animal and originated from gray wolf (*Canis lupus*) before the development of agriculture (Larson and Fuller 2014). The intrusion of carnivores as secondary consumers of carcass remains (both cooked and raw) at abandoned human camps was a source of hominin–animal interactions and could have favored the domestication of wolves (Arilla et al. 2020). Apart from dogs, the earliest domestication of animals and plants most likely occurred in the Near East when hunting and gathering tribes began to domesticate goats and sheep at least 12,000 years ago. However, questions about the timing, location, and number of domestication centers remain unknown and recent genetic findings have proposed earlier domestication, up to 40,000 years ago (Freedman et al. 2014; Germonpré et al. 2017). The process of early domestication occurred in separate locations, including the Near East, Southeast Asia, eastern North America, highland Mexico, and Peru (Diamond 1987). For example, sheep (*Ovis aries*) were probably domesticated at least three separate times in the Fertile Crescent approximately 10,500 years ago and involved at least three different subspecies of the wild mouflon (*Ovis gmelini*). Genetic evidence suggests chickens were domesticated multiple times in Southeast Asia, China, and perhaps India (Liu et al. 2006; Kanginakudru et al. 2008).

Livestock and other domesticated animals have interacted with their wild counterparts and other wildlife since domestication began. Long-term contact and gene flow between wild and domestic stocks was common during the process of animal

domestication and selective breeding of females was probably absent during the early phases of animal domestication (Marshall et al. 2014). In many cases, gene flow has not ceased until recent historic times. For instance, *Sus scrofa* exhibited significant introgression and gene flow between wild boar and domestic pig populations after domestication, indicating that initial domestication was probably not limited to a reduction of the number of wild boar from some local populations and subsequent genetic isolation, and new local wild boar lineages could rapidly replace “founding” lineages (e.g., Dzialuk et al. 2018). Another example of genetic flow, even hybridization, with potential epidemiological consequences at the first wildlife-livestock interfaces, or even before, is that of the European bison (or wisent, *Bison bonasus*; Fig. 4a, b), which is thought to be the result of hybridization between extinct bison and ancestors of modern cattle (aurochs, *Bos primigenius*) before 12,000 years ago (Węcek et al. 2017). Up to 10% of genomic ancestry in European bison today is from aurochs. Nuclear DNA sequences and morphology of wisent show close similarities to American bison (*B. bison*), but wisent mitochondrial DNA (mtDNA) indicates a closer relationship with cattle. This suggests some form of introgression from cattle or a related *Bos* species. The precise identity of the introgressor (aurochs or domestic cattle) is less certain, given the lack of knowledge of population structure in aurochs. Additionally, the European bison has no recognized Pleistocene fossil record and seems to suddenly appear in the early Holocene (<11,700 years ago). Taurine and zebu cattle from Asia also contain domestic cattle genes, descending from other bovine species with many combinations of mixed-species origin.

There is overall agreement on the common ancestors of domestic species. However, many details on the domestication process (beyond the scope of this book) and its consequences are still missing. The transition to domestication was a complex gradual process leading to the intensification in the relationship between wildlife and human societies (Vigne 2011), rather than an intentionally directed strategy. For each species, there were time periods of significant pre-domestication human–animal interactions (McHugo et al. 2019). However, multiple origins and the domestication process is relevant to the epidemiological role of the first wildlife-livestock interfaces. Vigne (2011) and Zeder (2012) grouped the phases of domestication into three general scenarios that seem to account for the full spectrum of animal domesticates: (1) commensal pathway, (2) prey pathway, and (3) directed pathway. The commensal pathway applies to animals, like dogs, that had initial contact with humans to feed on refuse or to prey on other animals attracted to human settlements. It is also possible that wild boar were drawn to human settlements to scavenge off refuse dumps and waste about 12,000 years ago (Ervynck et al. 2001). Epidemiological consequences of the commensal pathway included shared parasites. The prey pathway was probably followed by major livestock species because they were primary species that humans had hunted for thousands of years. Humans developed hunting strategies designed to increase prey availability when they became scarce over hundreds or thousands of years. The initial management of animals would consist in the rational control of animal resources which developed into herd management and finally, the controlled breeding of managed animals. For

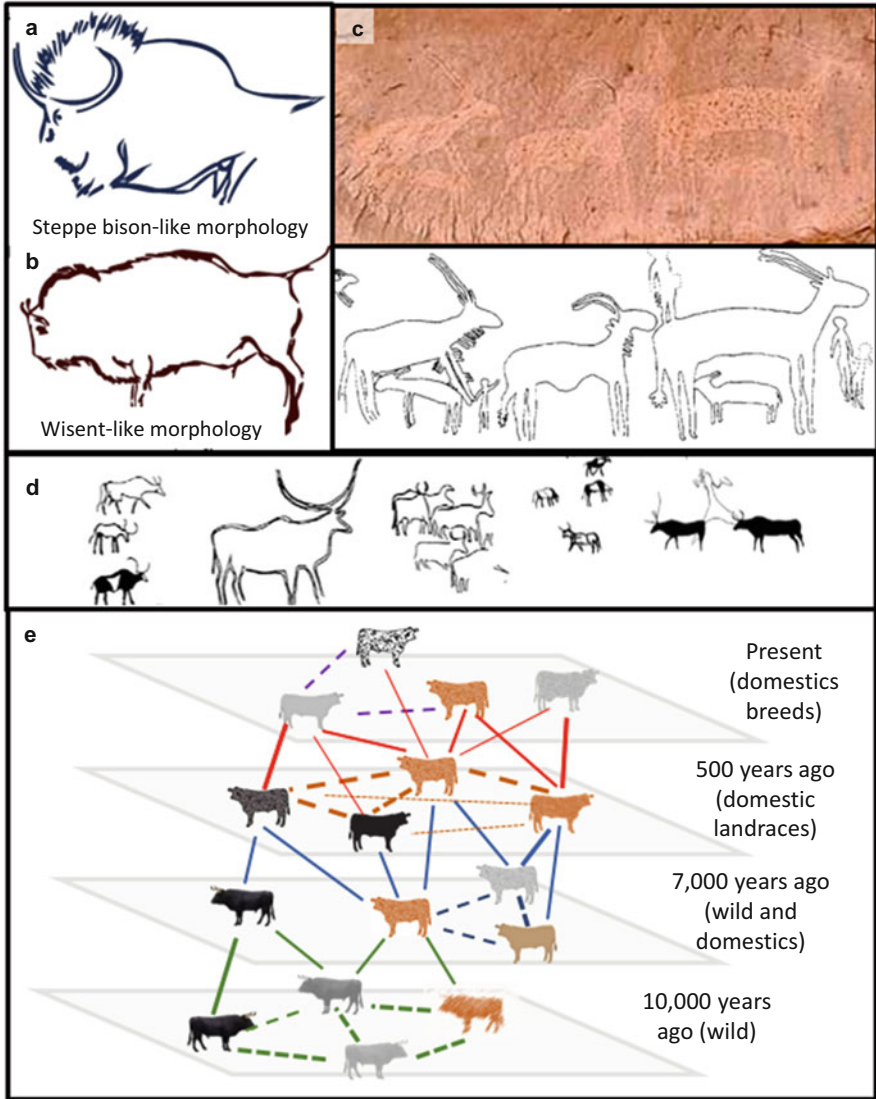


Fig. 4 Early cave artists recorded distinct morphological of ancient bison indicative of the replacement of the steppe bison (a) by the hybrid form (b) in Western Europe: reproductions (a) from Lascaux (France approximately 20,000 years ago) and Pergouset (wisent type, France <17,000 years ago, adapted from Lorblanchet 2001 and Soubrier et al. 2016). The combination of genomic, paleoenvironmental reconstructions, and cave paintings suggest that the hybridization of steppe bison with an ancient aurochs lineage during the late Pleistocene could have led to morphologically and ecologically distinct forms of bison (b). (c) Paintings at In-Taharin (central Tadrart Acacus) (After Sansoni 1994). This species was never actually domesticated but archeological remains suggest an intermediate domestication stage process occurred (Di Lernia and Cremaschi 1996). (d) Rock paintings from Tassili n'Ajjer in southwest Algeria showing putative domesticated cattle and a human figure, possibly a herder (Reproduced from

instance, baiting by means of the cultivation of wild plants in food plots was one of the first strategies. Reindeer (*Rangifer tarandus*) may be the most recent species to follow a prey pathway to domestication, and there is evidence for multiple independent reindeer domestication events (Røed et al. 2008). Interestingly, Barbary sheep (*Ammotragus lervia*) were never actually domesticated. However, archeological remains suggest an intermediate stage where “wild livestock” were kept, as an intermediate and necessary step to domestication, but fully domesticated sheep and goats arriving from the near East in the Neolithic probably interrupted the domestication process (Di Lernia and Cremaschi 1996; Fig. 4c). Finally, the directed pathway (fast track) to domestication begins when humans use the knowledge gained from the management of already domesticated animals to domesticate the next desirable wild species. This is likely the pathway followed in the domestication of the horse (*Equus caballus*) from wild horses (*E. ferus*) or donkeys (*E. asinus*) from wild Nubian ass (*E. a. africanus*; Rossel et al. 2008).

During the first transitional period, the Neolithic foraging economy still relied on hunting, while farming and pastoralism were progressively adopted. For example, between 12,000 and 11,000 years ago, goats were heavily exploited in the highlands of Lebanon and Syria, while Nubian ibex (*Capra nubiana*) was the target of intensive hunting. Over time, a primarily agropastoralist economy evolved (the change was appreciated mainly in the mid-10 millennium before present) where hunting was steadily “replaced” by herding. This facilitated a more constant and recurrent exposure to pathogens and possibly, the expansion and emergence of pathogens at the new interfaces. As Neolithization progressed, domesticated animals were introduced to other areas. The movement of managed herds outside the range of wild populations increased contact with other wild species and/or pathogen guilds, which furthered pathogen spread at the wildlife-livestock interface. As livestock became more globally distributed, the contact with close phylogenetic related wildlife and the opportunities for cross-species pathogen transmission intensified. Some ancestors during the expansion of domestic species become extinct, for example, aurochs, some wild Bactrian camel populations and wild horses. Predation, disease, competition for space and resources, and hybridization were inherent to the first wildlife-livestock interfaces. These interactions were not necessarily considered as conflicts by first pastoral societies, and there are regions where livestock and wildlife have coexisted for hundreds, even thousands of years with relatively few problems (e.g., some parts of Africa; Bourn and Blench 1999).

Early animal management involved herding, building shelters, and pens and the collection of fodder. Since these first steps, maintaining healthy animals and problems associated with inbreeding were recurrent. Herds were small and retained wild phenotypes due to regular restocking from the wild population, which probably resulted in significant disease issues. However, as a result of increased technical

Fig. 4 (continued) Grigson 1991). (e) Spatiotemporal model of historical admixture and gene flow in European cattle populations (McHugo et al. 2019, reproduced under the terms of the Creative Commons Attribution 4.0 International License, <http://creativecommons.org/licenses/by/4.0>)

competence and the availability of large, regional populations of domestic stock, and productivity progressively increased. The gradual development of systems of animal husbandry took place over several millennia and followed markedly different trajectories in different regions (Zeder 2012; Makarewicz and Tuross 2012; Vigne 2011; Arbuckle and Atici 2013). The Neolithic, Chalcolithic, and Bronze Age (c. 11,000–3200 years ago) periods encompass the major innovations in pastoral technologies in the ancient Near East, including:

- The earliest forms of pastoralism were characterized by a wide array of local, diverse, experimental pastoral economies, and relatively low herd productivity that evolved over a period of several millennia. Prehistoric pastoral nomads in southwest Asia were strongly associated with sedentary communities that practiced intensive plant cultivation, but there is no evidence to support the notion of a “dimorphic society” characterized by separate and specialized agriculturists and mobile pastoralists.
- By mid-to-late 8500–9000 BP, the organization of pastoralism shifted toward increased pastoral mobility, dispersed settlements, and greater emphasis on the exploitation of livestock for secondary products (dairy and fiber), and probable importation of new pathogens from other regions.
- During the late Chalcolithic (6000–5000 BP) period, changes in the pastoral economy are thought to have played an important role in the rise of the first complex urban societies in Mesopotamia, including increasing use of secondary products (wool and animal traction). Appearance of the domestic donkey and horse, as well as wheeled vehicles in southwest Asia, increased pastoral mobility, the expansion of sheep pastoralism into interior grasslands, and the development of mobile steppe regions, which intensified contact with new wildlife, pathogens, and vectors.
- A westward expansion of agricultural societies brought domestic taurine cattle, together with other livestock and crops, to central Anatolia around 10,000 BP. An eastward migration reached northern China or Mongolia between 5000 and 4000 BP. Cattle remains from Egypt and green Sahara have been dated from 5000 BP, and the earliest signs of livestock in Europe were found in Thessaly, Greece around 8500 BP.
- The fifth millennium BP is characterized by the proliferation of urban societies based on complex agropastoral economies. Pastoralists were highly integrated with cities, which intensified contact among animals (also peri-domestic) and with humans. Presence of urban markets for both primary and secondary animal products emerged. In the fourth and third millennia, BP mobile forms of pastoralism became more widespread, including specialized mobile pastoralists supplying settlements with animal products.

Consequences of Domestication and First Pastoralism at Wildlife-Livestock-Human Interfaces

Domestication created a new scenario for emergent pathogens, which adapted well to new conditions of multiple human–livestock–wildlife interfaces. This transition from human–wildlife to human–wildlife–domestic interactions was characterized by the maintenance of “crowd diseases” (both by humans and/or animals), the continuous presence of a domestic reservoir, and anthrophilic animals and vectors, which not only increased contact and exposure to pathogens, but provided space (interfaces) for evolution and adaption of pathogens to specific conditions. During the first stages of pastoralism, animals were reared in lower densities than today, and they could even be less prone to disease epidemics than those in high-density wild populations. However, wildlife and livestock cohabited and environmental or direct exposure to wildlife pathogens was common. Wildlife contacted escaped domestic animals, which already had developed more or less resistance to given pathogens, as still occurs today. Increased crowding without significant intervention measures to control disease during millennia of coexistence could select pathogens favored by high transmission rates, pathogenicity, or zoonotic potentials, both in livestock and in humans. Progressively, the development of husbandry practices created animal colonies or herds that were generally isolated from other wildlife but contained in crowded facilities. These conditions may have favored the spread of preexisting animal viruses and their divergence into specific genotypes, which later could spill over to wildlife. The history that accompanied the emergence of camel-infecting genotypes of hepatitis E viruses (Cagliani et al. 2019; Fig. 3) is an informative example. Authors dated the split of HEV-7 and HEV-8 from other genotypes ranging from 6300 BP to 3400 BP.

The development of animal husbandry also made livestock preferential intermediate hosts for many parasites capable of infecting humans (e.g., *Taenia*; Box 1) and led to their subsequent spread and worldwide distribution. For example, *Brucella* seems to have evolved through selection during the domestication of animals. The most virulent *Brucella* species with higher zoonotic spectrum are those from domesticated animals, while those that display lower pathogenicity and zoonotic potential are from wild animals (Moreno 2014; Fig. 1). The exception is *B. ovis*, which remains non-pathogenic for humans or for other animals (Blasco 1990) and it is speculated to be an earlier adaptation of *B. ovis* to sheep because it was already selected toward a higher affinity for venereal transmission in sheep before domestication of ovine (Moreno 1992).

Human migrations and trade favored the increase of livestock spatial ranges and the expansion of pathogens at the wildlife interface across the world. This first occurred within the domestic and/or human compartment, creating subsequent opportunities for pathogen transfer to wildlife. Many spillover events have probably occurred in which pathogens were eventually lost from the host without repeated

reintroductions via cross-species transmission. However, the pathogen could be maintained at the wildlife-livestock-human interface and lead to the emergence of the disease in the new host species. In tropical areas, shared diseases at the wildlife-livestock interface prevented the expansion of pastoralism (e.g., gammaherpesviruses in ruminants, such as malignant catarrhal fever viruses) that keep certain regions seasonally off-limits for livestock. The opposite could also be possible because wild ungulates would be absent from human settlements due to diseases. For example, locally domesticated species (e.g., tropical bovids such as the mithan (*Bos frontalis*) of South Asia and the Bali cattle) performed better than ruminant species first domesticated in the Fertile Crescent (Felius et al. 2014).

As the final desiccation of the Sahara set in about 4500 BP, pastoralists gradually abandoned the Saharan region, shifting southward to the Sahelian biome, which were most suitable for their herds. However, they entered areas that exposed their herds to new disease challenges in more closed habitats of western Africa, where endemic tsetse flies transmitted trypanosomes from wild hoofed animals. Indigenous wild bovids are tolerant to this protozoan as the result of their long coevolution with the infection, but domestic livestock develops acute symptoms that often result in death. Similarly, African buffalo (*Syncerus caffer*) was probably the original host of the protozoan parasite *Theileria parva parva* (causing theileriosis or East coast fever transmitted by ticks), that infected cattle as pastoralists moved their herds into eastern Africa and zones of theileriosis for the first time (Gifford-Gonzalez 2000). This slow spread of domesticated animals south between 4000 and 3000 BP could also be attributed to diseases such as malignant catarrhal fever, Rift Valley fever, or foot-and-mouth disease. Even when agriculture and animal farming became more relevant, the ecological, cultural, and epidemiological relationship of humans and wildlife still were largely mediated by hunting. Hunter-gatherer societies persisted, even when increasingly confined to marginal areas. Within agricultural systems, farmers hunted in response to conflicts caused by predation upon domestic animals and to reduce competition for resources, such as water or pasture. Wild animals and their products could also be a source of pathogen entrance in livestock systems. However, as societies evolved, the balance of the wildlife-livestock interface progressively fell on the domestic side as the predominant host reservoir community, which continued and geographically expanded in the ages to come, where spillback and spillover roles have often changed.

The Neolithic transition toward an agricultural and pastoralist economy also facilitated the emergence of human-adapted pathogens due to the abovementioned factors (increased and closer contact between humans and animals, higher populations, higher densities in settlements, and mobility). For instance, when humans began to farm and live with their livestock, the evolution of a more virulent form of *Salmonella* was fostered. The analysis of the genetic material of old *Salmonella enterica* genomes (Key et al. 2020) provides evidence in support of the hypothesis that the cultural transition from foraging to farming facilitated the emergence of human-adapted pathogens that still persist today. The reconstruction

of ancient *S. enterica* genomes from western Eurasia reveals how this bacterial pathogen evolved over a period of 6500 years. All *Salmonella* genomes recovered from foragers, pastoralists, and agropastoralists are progenitors to the strain *Paratyphi C* that specifically infects humans but is rare today. Those ancient *Salmonella*, however, probably did not display host specificity and instead infected humans and animals alike. It was previously suggested that old strains of *Salmonella* spread from domesticated pigs to humans around 4000 years ago, but the discovery of progenitor strains in humans more than 5000 years ago suggests they might have spread from humans to pigs. However, a possibility is that both human- and pig-specific *Salmonella* evolved independently from unspecific progenitors. Measles is another example of how pathogens crossed over to humans (Düx et al. 2020). There is controversy about when measles emerged in humans, because the historical descriptions of measles are relatively recent (late ninth century CE). However, recent research evidenced that measles virus diverged from rinderpest virus in the sixth century BCE, indicating an early origin for measles possibly associated with the coinciding rise of large cities (Düx et al. 2020). Düx et al. (2020) postulate that a bovine virus, the common ancestor of modern strains of rinderpest and measles, circulated in large populations of cattle (and possibly wild ungulates) since its divergence from peste des petit ruminants virus around the fourth millennium BCE. As a typically fast-evolving RNA virus, it may have produced variants that were able to cross the species barrier on several occasions, but small human populations could only serve as dead-end hosts. Then, as contiguous settlements reached adequate sizes to maintain the virus' continuous transmission, it emerged as a human pathogen.

The (1) establishment of local settlements, agriculture, and domestication of livestock spurred a large epidemiological change for human and animal health, which, during different times over the world, continued with (2) an intensification of regional contacts through trade and their epidemiological consequences. From a human perspective, the (3) first intercontinental explorations, imperialism and industrialization and more recently, (4) globalization, rapid urbanization, and climate, are primary transitional events determining changes in the wildlife-livestock-human interfaces.

Domination of the Land by First Civilizations and Regional Spread of Animal Epidemics

Over the course of human history, our impact on the natural environment has magnified, including our ability to alter, shape, and reshape nature. One notable effect was the creation of local interfaces established among domestic animals, wildlife, and humans. The alteration of environments and landscapes, such as clearing of trees to plant cereals, began from early Neolithics, and from the first

civilizations, humans accelerated the decline of natural resources and wildlife. The development and expansion of trade with other regions, and the rapid growth of populations and concentrations of humans and animals in towns and cities permitted the spread of human and animal pathogens. This process, very relevant from the perspective of shared diseases at the livestock-wildlife interface, can be historically encompassed from the first civilizations that emerged in the Eastern Crescent to the development of intercontinental exploration, which provided the first glimpse of current globalization.

The earliest civilizations were characterized by complex divisions of labor and increasingly depended on trade with subsequent exploration and conflict. As a consequence, there was an increase in regional (continental) contact through trade and movement of livestock during approximately 5000 to 3000 BP (the first long-distance trade would occur between Mesopotamia and the Indus Valley in Pakistan around 5000 BP; McMichael 2004), promoting human and animal interactions. For instance, trade and animal movement fostered contact between domestic and wild Bactrian camels due to immigration of domestics from Iran (where wild camels were extinct) eastward to Mongolia, where native wild Bactrian camels still roam (Ming et al. 2020). Human actions significantly increased dispersal of hosts, pathogens, and vector species, enabling host switches (Rogalski et al. 2017). However, trade and movement effects on the history of animal disease dispersion were complex, as indicated by recent genomics and paleogenomics. For instance, after substantial evolutionary divergence between *B. taurus* (taurine) and *B. indicus* (zebu) cattle, it is evident that extensive zebu-taurine admixture occurred in African and Middle Eastern cattle populations (see Fig. 4d, e); which also may also be applicable to other areas or domestic livestock as they and their pathogens migrated, first with early agriculturalists, and later with traders and conquerors as they encountered related domestic or wild species.

Ancient civilizations had an impact on wildlife abundance, diversity, and distribution as wildland habitats were converted to agriculture (Angelakis et al. 2020). Since then, many species have shown relatively high tolerance to humans and have adapted well to anthropized environments (e.g., roe deer and wild boar in Europe). Some species have greatly benefitted from peri-domestic habitats (urban or agricultural environments), even becoming pests in some localities. The dependence on natural resources made it such that the depletion of natural resources accompanied the decline in the power of old civilizations (e.g., Eastern Crescent, northern Africa, Mediterranean basin). Later, human civilizations progressively accelerated the transformation of landscapes over other regions of Eurasia and the rest of the inhabited world (Kaplan et al. 2009). The most important initial anthropogenic alterations of the natural environment that impacted wildlife-livestock interfaces was forest clearing to establish cropland and pasture, and the exploitation of forests for fuelwood and construction materials (Kaplan et al. 2010).

Following the case of Europe, the first detailed reports on livestock husbandry came from Greek and Roman civilization, with detailed contemporary accounts.

Transhumance, the seasonal migration of humans to provide pasture to their herds, was well established during the Classic period. This mobile pastoralism was associated with well-defined spatiotemporal interfaces occurring between livestock in wintering (e.g., lowlands in Mediterranean areas) and estivation (mountainous areas where open pastures were shared with wildlife and maintained with fire) quarters, where pathogens were also transported. Cattle from ancient Greece could be exported to several regions of western Europe, and Roman conquest further expanded the social, economic, and agricultural organization, including animal farming strategies (Colominas et al. 2014). The collapse of the Roman Empire was followed by periods of large-scale migration of Germanic and eastern European peoples and their livestock during the fifth and sixth century AD (Trentacoste et al. 2018). The migrations probably led to a considerable mixing of livestock, particularly cattle and horse populations from various European regions and their pathogens. It has been suggested that numerous concurrent human–bovine epidemics in the early medieval period (sixth to tenth centuries AC) were caused by an immediate ancestor (now extinct) of measles and rinderpest that was pathogenic to both cattle and humans (Newfield 2015), and even earlier concurrent human–bovine mortality events may have occurred before in Rome (Spinage 2003). During the following centuries, introduction of measles into naive human populations and/or flare-ups of the disease might have caused some ancient epidemics whose etiology remains uncertain.

About half of western European forests are estimated to have been cleared prior to the Middle Ages and deforestation increased gradually but steadily during 1000 years of medieval European history, alternating periods of increase and decrease due to historical and climatic contexts (Kaplan et al. 2009). For instance, collapse of the European human population due to the bubonic plague in the mid-fourteenth century may have resulted in the abandonment of up to 25% of all croplands (Yeloff and van Geel 2007). Forests returned in many areas, some to their previous levels within a hundred years.

Livestock diseases affected local populations in the Middle ages and importing animals from neighboring regions for restocking is likely to have caused both intensive gene and pathogen flow (Feliuss et al. 2014). There were also remarkable cultural and technological developments produced by the renaissance society and increasing urbanization. Fencing of pastures and cultivation of animal feed became common and storage methods improved, allowing for the survival of larger numbers of livestock during the winter. The export of animal products was of considerable importance and large numbers of animals were exported to surrounding countries (Feliuss et al. 2014). In most of western Europe, cattle were still kept as part of a mixed farming system (for the purpose of traction and dairying), but a thriving and highly organized cattle ranching economy developed in Spain where large herds of 1000–15,000 work and beef cattle were kept under extensive management and in close interaction with wildlife.

Worldwide Expansion of Wildlife-Livestock-Human Interfaces, Industrialization and First Glimpses of Globalization

The growing interdependence of the world's economies, cultures, and populations brought not only by regional, but also intercontinental trade and transportation, included animals, their pathogens, and vectors, which impacted current interfaces and created new ones. This period is characterized by *intercontinental exploration, colonization/imperialism, and the agriculture and industrial revolutions*. All these events provided opportunities for animal pathogens to cross considerable geographic boundaries and influenced modern agricultural practices and the characteristics of modern wildlife-livestock interfaces.

In general, agriculture inevitably transformed the land. Removal of natural vegetation impacted wildlife abundance, distribution, and behavior. Concurrently, the number of livestock husbandry practices have been increasing ever since pre-industrial times and have determined wildlife-livestock interfaces. Overall, wildlife is becoming less abundant, and populations are more fragmented and isolated (Kaplan et al. 2009). As for most large mammals, the cumulative impact of human activities had driven most species into severe declines and regional extinctions by the end of the Holocene (i.e., late nineteenth and early twentieth centuries), a trend that has continued for many of the planet's wild ungulates (Ripple et al. 2015). As landscape changes progress, the interface has become more local and occurs at smaller spatial and more fragmented scales. From the Old-World perspective, transformation of the natural landscape of Europe by deforestation continued from the Middle Ages until the nineteenth century. The rate of deforestation remained high during the early decades of the industrial revolution so that by 1800 AD most European countries were largely deforested. This habitat change influenced an important regression of the wildlife component of the interface. By the seventeenth century, growing human populations resulted in an ever-increasing demand for animal products (meat and dairy) and the expansion of cultivation has greatly reduced the forests which once covered so much of medieval Europe. When changes in agricultural practices improved productivity and slowed the clearing of forests for crops, and later, when fossil fuels replaced wood as the main source of industrial energy, wildlife populations, mainly ungulates and later carnivores, slowly recovered. We are still witnessing this recovery process and during the last several decades some wildlife populations in developed countries, such as ungulates, have adapted and are thriving and creating serious concerns at the interface (Gortazar et al. 2006).

In other regions, China's population reached 413 million and forest cover was 17% by 1840 (Liu and Tian 2010). The forests of southern Asia were cleared to provide cropland to support the rapidly expanding human population (FAO 2016). In 1500, the population of India was 100 million, more than twice that of Europe. It is probable that more than half of southern Asia's historic forest area has been lost in the last 500 years. Unfortunately, deforestation and forest degradation are still

increasing in our globalized world (see below). Latin America was probably about 75% forested before European settlement (Sponsel et al. 1996), but today it is about 50% forested. European livestock occupied the space and replaced the role of native wild herbivores (e.g., big rodents in Llanos of Venezuela) in introduced ranching practices. In North America, as populations increased and settlers pushed westward in the nineteenth century, the rate of forest clearing and opportunities for interfaces with wildlife increased rapidly. By the early twentieth century, however, deforestation had largely stopped in North America (McCleery 1992). Forests in Africa are extremely diverse and over the centuries, in sub-Saharan Africa, deforestation and human populations have gradually increased together, with the greatest forest losses coming in areas where wood is needed for fuel or where forest land is needed for growing crops (FAO 2012b).

In Europe, the export of local livestock from areas characterized for their production to neighboring countries was well established during the sixteenth century. Movement of large herds of livestock to big cities for consumption occurred within and among countries. Livestock production increased in response to the demand of urban populations and the higher density of animals fostered the dissemination of infectious diseases such as the cattle plague, which in the eighteenth century devastated continental Europe. Livestock types that existed in Europe were regionally adapted and only since the late eighteenth century has selection for certain traits began to be practiced. Overall, the history of livestock on other continents during this period is not as dynamic as it was in Europe. However, on the Indian subcontinent, several zebu breeds have a history dating back to the late 16th century.

At the end of the nineteenth century, a devastating rinderpest (a morbillivirus, family Paramyxoviridae) epidemic spread throughout the African continent. The epidemic started in Eritrea in 1887, possibly introduced by Indian cattle brought by the Italians, and reached the Atlantic Ocean in 1893 and South Africa in 1898. According to some accounts, it killed 90% of all African cattle and devastated wild ungulates (i.e., buffalo, giraffe, and wildebeest). Rinderpest probably had their origins in an environment where cattle and humans were living in close proximity, likely from the cattle herds of Central or South Asia some 10,000 years ago at the time of domestication of the wild aurochs. Although rinderpest was eliminated from southern Africa shortly after the turn of the twentieth century, it became enzootic in other parts of the continent, often in wildlife, until eradicated globally in 2011. The partial resistance of zebu to rinderpest with a mortality of only 10–30% led to a drastic replacement of many taurine populations, and zebu is now the dominant species in West and East Africa. They are not, however, kept in the coastal regions infested with tsetse flies, where the trypanotolerant African taurine cattle have remained the primary domestic cattle breed.

Domestic animals, particularly ruminants and swine, were essential components of European colonial projects around the globe during this period of expansion. The exploration and colonization of North and South America resulted from the so-called Columbian exchange, i.e., the respective introduction of crops, livestock, and their associated pathogens into Europe and America. American domesticated animals (like llamas and guinea pigs), compared with European livestock, had a reduced

potential for zoonotic disease. Therefore, Americans lived relatively free of animal-borne diseases. However, they faced severe risk when novel Old-World pathogens were introduced. It is estimated that livestock-derived zoonotic diseases contributed to the loss of as much as 90% of the native American population of humans (Jones 2004). For example, in 1493, an outbreak of what is now thought to have been swine influenza struck Native Americans in Hispaniola. There is some evidence to suggest that the infection source was pigs from Columbus's ships. Europeans also took measles and smallpox to the New World, where it caused devastating epidemics in the early sixteenth century. Native Americans were not exposed to smallpox or measles until the arrival of Europeans to North America and their genome had not experienced selection pressure by these pathogens. There is evidence that the immune-related genes of the ancient American were well-adapted to local diseases but not to novel infections (Lindo et al. 2016). On the other hand, the exchange resulted in the introduction of treponemal infections to Europe (Baker and Armelagos 1988). Horses, pigs, cattle, goats, sheep, and several other species adapted readily to conditions in the Americas, where broad expanses of grassland were available. By 1525, more than 1000 Spanish cattle populated the Caribbean colonies, from where they spread to Spanish colonies in America (Feliuss et al. 2014); bringing along their associated pathogens, including Texas fever, caused by *Babesia*. In South America, wild camelids (vicunas and guanacos rapidly following the Spanish conquest due to hunting and competition with sheep and cattle (Acebes et al. 2012; FAO 1996). Today remaining wild camelid populations are either endangered or extremely threatened (Wheeler 2012). The spread of European settlers and their domestic animals throughout northern Europe and North America during the past four centuries was followed by the deliberate extermination of large predators, including seven subspecies of wolf (*Canis lupus*; Day 1981). Livestock also caused serious damage to inland ecosystems (e.g., New Zealand and Pacific). Some introduced livestock or domestic animals, like pigs, horses, and ferrets, easily became feral and constitute part of the present wildlife-livestock interface (Long 2003). For instance, in North America a large proportion of wild ungulates in the Great Plains were exterminated. An estimated 30–60 million plains bison (*Bison bison*) roamed North America in 1500 and were reduced to their lowest point in 1884 (425 bison; Lott 2002). Today, there are thousands of woods and plains bison, however, bovine tuberculosis and brucellosis are of serious concern in some populations that interface with livestock (Shury et al. 2015).

Agriculture and Industrial Revolutions

The agricultural revolution, initiated in Britain, led to modern farming, and stimulated an increase in agricultural production between the mid-17th and late 19th centuries. Advancements were attributed to new agricultural practices such as crop rotation, selective breeding, and a more productive use of arable land (Williamson 2002). Selective breeding for desired traits was established as a scientific practice

(mating of related animals with similar traits) to fix certain characteristics in animals, including cattle breeds used primarily for beef (Molne 2010). Certain practices displaced the wildlife-livestock interface in newly industrialized countries, such as by converting some pastureland into arable land and increasing habitat more appropriate for wildlife, such as fenlands.

Almost in parallel, the industrial revolution started in England in the second half of eighteenth century and led to further urbanization and increased demand from cities for agricultural products (Molne 2010). Since then, developed countries of the world have all gone through the process of industrialization, with important consequences for agriculture. First, industrialization was always accompanied by rapid population growth, which increased the demand for food and subsequent need for crops and livestock. This encouraged the decline of subsistence farming and increased use of machinery, which decreased the demand for farm workers and influenced others to move to industrial cities. The industrial revolution marks a historical transition in late modern history that eventually led to the globalization we know today. It is considered the second epidemiological transition from the human perspective since pandemics receded and resulted in a shift in patterns of disease and mortality from primarily infectious diseases to what are referred to as “chronic” diseases (McKeown 2010). The massive growth of livestock production was possible due to increased farming intensification and trade of animals. A new model of dimorphic wildlife-livestock interfaces began to emerge in developed countries, characterized by significant encroachment of natural habitats by agriculture (especially from the late nineteenth century). This caused more complex disease dynamics and compartmentation of the relationships between domestic animals and wildlife. Options for disease control are more difficult, for example, when wild reservoirs are present. Phylogenetic analyses indicate that the emergence of human metapneumonia ancestors some 150–200 years ago coincides with the industrialization of the poultry industry (de Graaf et al. 2008), and the massive expansion of strain diversity of influenza viruses in swine and poultry correlates with the increase in industrial populations of swine and poultry worldwide. In the second half of the nineteenth century, a highly infectious respiratory disease with a high mortality rate affected cattle herds around the world, though it is difficult to distinguish the exact cause by just clinical symptoms it was likely a contagious bovine pleuropneumonia caused by *Mycoplasma mycoides mycoides* (Caswell and Williams 2016). Interestingly, the dating of the most recent common ancestor of bovine coronavirus BCoV and human coronavirus HCoV-OC43 is around 1890 (based on the spike of gene sequences; Vijgen et al. 2005; Bidokhti et al. 2013). During the slaughtering of affected herds, there was ample opportunity for culling personnel to contact bovine respiratory secretions, which could have contained BCoV, either as the causal agent or as a coinfecting agent. It can be hypothesized that the bovine respiratory disease in the second half of the nineteenth century might have been similar to the coronavirus-associated shipping fever disease.

One World, One Interface

The total number of livestock declined dramatically during the First and Second World War in most countries involved, especially in developed regions. However, the numbers of pigs, cattle, and poultry have increased considerably since. Food animal production in much of the world, beginning in the USA, has been transformed from traditional small-scale methods to industrial-scale operations that are vertically integrated, in which most aspects of production are controlled by a single entity (Graham et al. 2008). Industrial animal production includes high-tech animal husbandry, increased veterinary oversight, and formulated feeding, often with the addition of antibiotics to increase growth rates and feed conversion efficiency. About 60% of all mammals on Earth are livestock, mostly cattle and pigs, and 36% are human (globally, livestock and people constitute 97% of the world's mammal biomass; Thomas 2017; Berger et al. 2020). Wild mammals account for just over 4% of mammal biomass on Earth today. For example, the biomass of chickens is approximately over double the total mass of all other birds combined on Earth. The destruction of wild habitat for farming, logging, and development has resulted in the start of what many scientists consider the sixth mass extinction of life to occur in the Earth's four-billion-year history. However, some pastoral systems are biodiverse (e.g., savannah-like habitats in Spain called Dehesas; Gaspar et al. 2009). Humans represent just a hundredth of a percent of the Earth's biomass but have driven down the biomass of land animals by 85% and marine mammals by about 80% since the beginning of the last major extinction approximately 50,000 years ago. Wildlife on Earth have overall been reduced by humans to their lowest level in history. This impact is variable based on taxa, capacity of wild species to adapt to perturbed (anthropized) environments, geographical region, and recent history. However, disease issues at the wildlife-livestock-human interfaces are of increasing concern and far from being solved, but why?

During the twentieth century, significant epizootics of diseases at the wildlife-livestock interface occurred worldwide, such as foot-and-mouth disease, rinderpest, avian influenza, and African and classical swine fever. In certain cases, such as cattle rinderpest, measures that included vaccination were able to progressively reduce the prevalence of disease. Rinderpest reached the Americas in the nineteenth century by imported livestock and was eradicated in 1929 in the USA. In 1994, the Food and Agriculture Organization (FAO) launched a Global Rinderpest Eradication Programme and it was announced that rinderpest had been eliminated from the world in May 2011 (FAO 2012a). Another example is influenza viruses, which have evolved into numerous strains, posing threats to their natural hosts, pigs and birds, and jumping to humans (Taubenberger and Kash 2010). Migratory patterns of numerous wild bird species have spread influenza across continents throughout the ages, and in recent outbreaks has also affected the interface with poultry. Pandemic influenza viruses have caused significant mortality in humans. In the twentieth century, 3 influenza viruses caused major pandemics: the 1918 H₁N₁ virus, the 1957 H₂N₂ virus, and the 1968 H₃N₂ virus. These pandemics were initiated by the

introduction and successful adaptation of a novel hemagglutinin subtype to humans from an animal source, resulting in antigenic shift (Smith et al. 2009). There is no empirical evidence that swine played a role in the emergence of human influenza pandemics in 1918, 1957, or 1968, but swine-to-human transmission occurs periodically and can trigger pandemics, as in 2009. Swine are not the only species capable of mediating the establishment of avian viruses in humans (Nelson and Worobey 2018). The virus that caused the 1918 influenza pandemic probably emerged from North American domestic and wild birds. While this last topic remains a point of discussion (Worobey et al. 2014), the message, as Rudolf Virchow stated in 1856, is that “between animal and human medicine there are no dividing lines,” nor should there be. The wildlife-livestock interface term should equally be used for the term wildlife-livestock-human interface. Today, we estimate that almost 77% of livestock pathogens infect multiple host species, including wildlife (Cleaveland et al. 2001). This final section of the chapter offers a general perspective of the globalization of the wildlife-livestock-human interface. We note that brief introductions to current situations and specific characteristics of the interfaces in different regions are provided in successive chapters.

The Globalization of the Wildlife-Livestock-Human Interfaces

After numerous historical events (world wars, protectionism periods, and economic depressions), a definitive wave of globalization has occurred, with enormous consequences for the interfaces and their connections. Globalization has resulted in enhanced trade in livestock, other animals and their products, the relocation of farming centers, industrialization of farming, and unprecedented speed, volume, and reach of global air travel. Altogether, leading to increased risk for diseases to emerge at the wildlife-livestock-human interfaces, and spill back to wildlife (e.g., foot-and-mouth disease, peste des petits ruminants, African swine fever, Newcastle disease, highly pathogenic avian influenza, and zoonotic diseases like Ebola, West Nile fever, severe acute respiratory syndromes caused by coronaviruses, Nipah, Hendra, swine flu). From the human perspective, it has been proposed that this is a new epidemiologic transition (third), which combines the effects of globalization and ecological disruption (McKeown 2010). This transition is characterized by the emergence and re-emergence of an unprecedented number of diseases, most of which include a wildlife and/or domestic component, such as Ebola virus, Hantavirus, leishmaniasis, West Nile virus, Lyme disease, and human pathogenic coronaviruses. Although most of the global population now lives in urban environments, globalization has linked the health problems of impoverished communities with other populations throughout the globe (Neiderud 2015). Correspondingly, all humans and animals tend to be more frequently share a common global infectious disease ecology.

Over the last century, livestock evolved from highly localized production, often in mixed systems, where animals were typically born, fattened, and slaughtered in

the same region, to *relocated intensive animal production*, where the number of live animals traded for food among regions and countries has exponentially increased. This long-distance live animal or product transportation amplifies risks derived from the concentrated and intensive nature of current industrial farming practices. In the past, pathogens would have simply emerged and died out; instead of being transmitted to livestock and amplified. For example, outbreaks of the highly pathogenic avian influenza virus H₅N₁ were reported across eight countries in Southeast Asia nearly simultaneously in 2004 (Tiensin et al. 2005). The pattern and timing of outbreaks suggested that the transport of live birds reared for human consumption was the primary cause in the rapid spread (FAO 2007). The long-distance transport of live animals was also related to the spread of swine influenza viruses in the USA, a large country where livestock may travel hundreds or thousands of miles (Greger 2007). The possibility of fast spread is a relevant concern for human and animal health. During the last several decades, sequencing of viral genomes evidenced triple reassortment of human, avian, and porcine influenza virus gene segments (Zhou et al. 1999). Apart from livestock, animals translocated for other human uses, such as exotic pets captured in the jungles have also been implicated in the spread of diseases affecting human and other animals (Chomel et al. 2007). For instance, pet bird shipments have likely been involved in the introduction of West Nile virus from the Middle East (Lanciotti et al. 1999) into the Western hemisphere (Rappole et al. 2000). Another example is the movement of hares from central and eastern Europe for hunting purposes that led to several outbreaks of tularemia (Godfroid et al. 2005).

The so-called “Livestock Revolution” initiated in the 1970s, in response to world population increase, urbanization, higher incomes, and demand for animal products expanded rapidly to developing countries. The world’s meat production nearly doubled from 1980 to 2004 (FAO 2006). This revolution implied a progressive replacement of traditional systems by intensive systems, where large numbers of genotypically similar animals are farmed under concentrated confinement with rapid population turnover (Pearson et al. 2005). Efficient and productive industrial animal production poses environmental concerns due to the large amount of waste, gas emissions, and elevated need for feed (e.g., soy and alfalfa), most of which is produced far away from industrial farms. There are also associated disease risks for animals and humans. High concentrations of genetically homogeneous animals kept indoors allows for the rapid selection, amplification, and dissemination of pathogens (Delgado and Narrod 2003; Pearson et al. 2005). Crowding of increasingly greater numbers of animals into increasingly smaller spaces has been identified as a critical factor in the spread of disease (Delgado and Narrod 2003). In the USA, the average number of animals in each chicken, pig, and cattle operation approximately doubled between 1978 and 1992 (Tilman et al. 2002), and a small proportion of farms produce most of the pigs or poultry.

The wildlife-livestock-human interface is more interconnected than ever. Wildlife-livestock-human interface is increasing as a result of human encroachment into wilderness, especially in tropical ecosystems (see Chapter “Host community Interfaces: The Wildlife-Livestock”). This increased population pressure on land use is also mediated by hunting and consumption of “bush meat,” capture of wildlife that

is shipped to live animal markets (e.g., wet markets), and farming of game animals in proximity to traditional livestock and humans, which increases cross exposure to new pathogens originating from wildlife (e.g., bat coronaviruses). Mix farming, or the integration of crop and animal production, is well developed in developing countries, together with small-scale agriculture. There are a vast range of modalities and practices (Devendra and Thomas 2002) and opportunities for interaction with wildlife and there is increased exposure to new pathogens often in areas recently encroached. Additionally, the intensification of animal production favors increasing livestock-to-human contact, and in certain cases, with peri-domestic animals. Design and operational requirements of large-scale farming often result in compromises of biosecurity, and multiple pathways are available for exchange among wildlife (e.g., birds), other livestock, and other animals, as well as humans. Certain bridge hosts, such as “peri-domestic animals” (rodents, pets, birds) commonly associated with industrial animal agriculture (Slingenbergh et al. 2004), may vector pathogens from the outdoors to indoors. For instance, wild birds in proximity to farms and backyard productive systems with low biosecurity measures and close contact among several animal species are considered risk factors for the emergence and spread of influenza A virus. The confinement of thousands of animals requires controls to reduce heat and regulate humidity, and high-volume fans that result in a considerable movement of materials into the external environment. Waste and manure may also become a pathogen transmission route, particularly transmission of food-borne pathogens such as verotoxigenic *E. coli* and *Salmonella* (Newell et al. 2010; Fig. 5). Intensification also requires greater frequency of movement of people and vehicles on and off farms, which further increases the risk of pathogen transmission. Effective management and biosecurity measures can mitigate between-herd and wildlife interactions (see Fig. 6). Due to increased poverty, the proximity of increasingly concentrated smallholder farming communities to intensified, industrial farming systems is growing, creating conditions conducive for disease emergence and entrenchment. Often, diverse types of production, ranging from free-range to outdoor paddocks and finally, intensive production, are epidemiologically connected, which make it difficult to control pathogens within compartments and at the interfaces established between livestock, wildlife, and humans (see Fig. 2b of Chapter “Host community Interfaces: The Wildlife-Livestock”).

Antimicrobials are often used in industrial systems for growth promotion, disease prevention, or therapeutically, but can promote the evolution of antimicrobial-resistant pathogens that later can be transmitted to humans and wildlife. Paradoxically, 10,000 years ago, domestication of animals gave human populations zoonotic infections, but interactions with domesticated animals are now conferring drug-resistant infections. Drug resistance is even a growing concern in wildlife populations.

As a common determinant at the global level, climate change, particularly global warming, has changed ecosystems in many regions and has subsequently extended the distribution of several vectors that transmit diseases such as Rift Valley Fever, West Nile Fever, and Bluetongue. The, establishment, development, phenology, survival, and transmission of many pathogens depend on environmental conditions

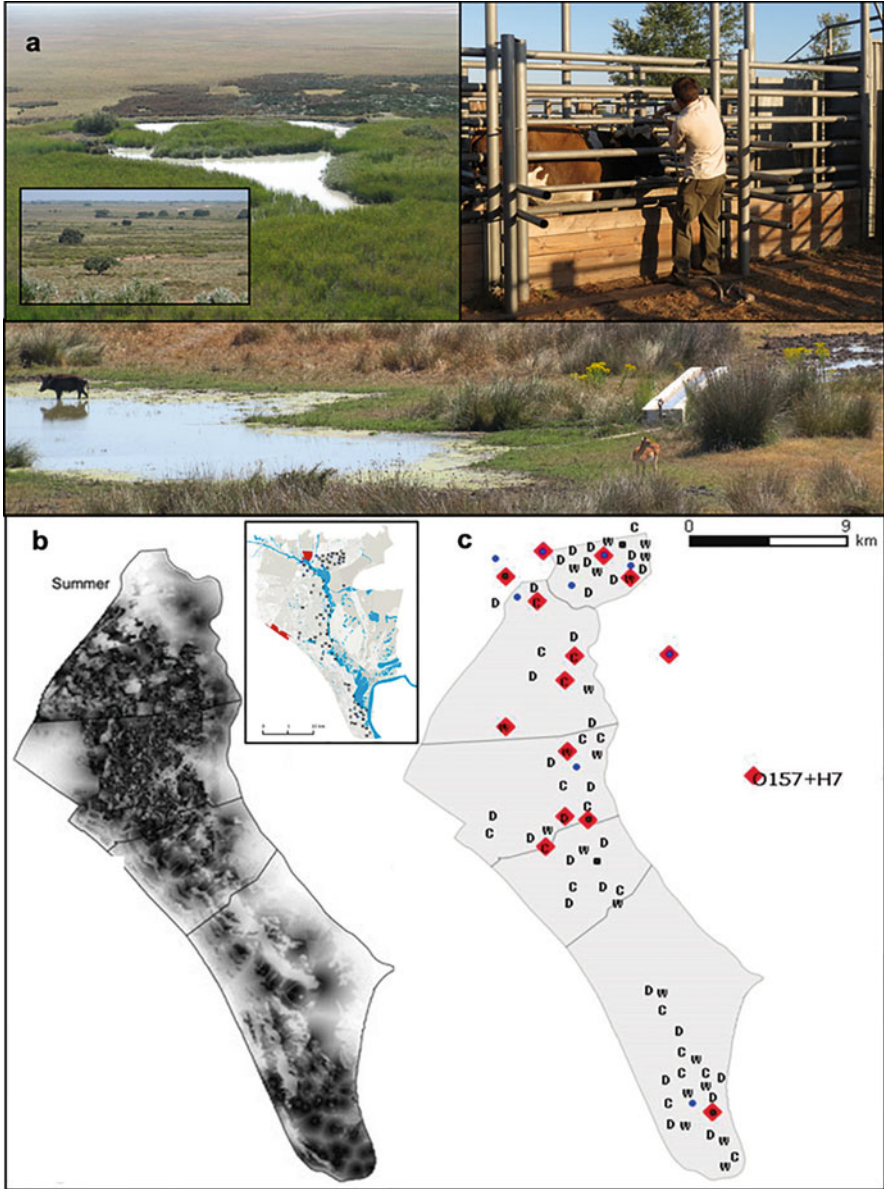


Fig. 5 Representation of the biotic homogenization at the wildlife-livestock-human interfaces. In relation to the distribution of *Escherichia coli* virulence genes in natural habitats (reproduced from Cabal et al. 2017). (a) Doñana National Park (South Spain) is considered one of the most important European wetlands in terms of biodiversity where extensive livestock (cattle, horses) and wild ungulates (red deer, fallow deer, and wild boar) share habitat. (b) As indicative, it represents the map of interactions (in gray tones) between wild boar and cattle based on telemetry (Barasona et al. 2014). (c) Spatial distribution (positive samples in red) of selected *E. coli* genes (rfb_{O157} + fli_{C_{H7}}) detected in pooled fecal samples (C cattle, D deer, W wild boar), surface water (blue dots), and septic tanks (black squares) collected in DNP, Spain. The small map in between indicates urban nucleus (red) and surface waters (blue)

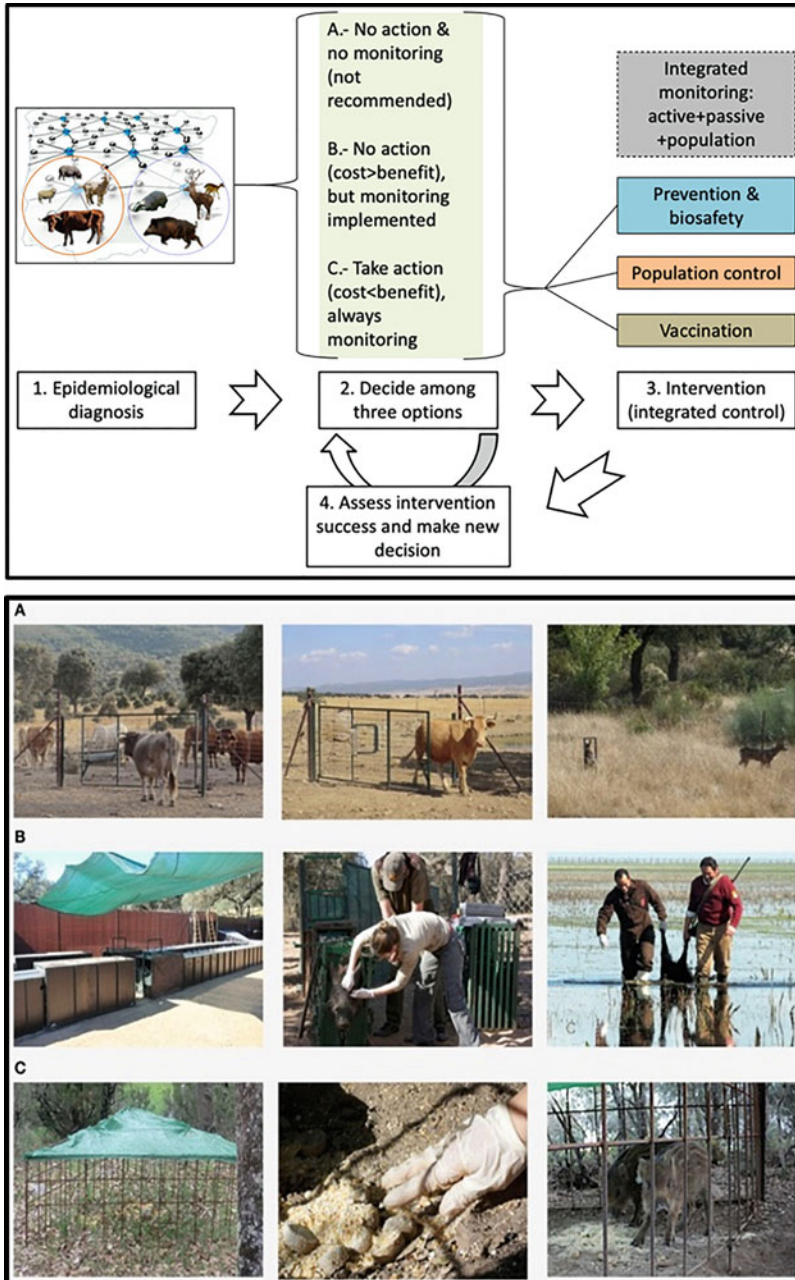


Fig. 6 The recent impacts of diseases on the wildlife-livestock interface have contributed significantly to shaping the current patterns of pathogen emergence, and therefore a better scientific understanding is essential to identify and manage risks. Top: Flowchart of the available disease control options and result assessment in diseases shared with wildlife. Bottom: Examples of some disease control options currently applied: (a) Farm biosecurity by segregating wildlife and cattle

(e.g., Rose et al. 2014). As a consequence of the environmental perturbations caused by climate (and associated anthropogenic change), the distribution, abundance, behavior, and population dynamics of pathogens and hosts have been impacted, so as transmission dynamics (Altizer et al. 2013; Molnár et al. 2014). “Warming of the climate system is unequivocal, and since the 1950s, many of the observed changes are unprecedented over decades to millennia” (concluded by the Intergovernmental Panel on Climate Change, IPCC 2013). However, the pattern of global warming is not spatially homogeneous, and therefore, the impacts we will observe at the wildlife-livestock interface. For, instance, the reduction of a population of moose (*Alces alces andersoni*) between 1960 and 2000s in Minnesota occurred in parallel to an increase in temperatures and lengthening of the annual growing season, which could interact with nutritionally deficient habitat at the edge of the species range (Murray et al. 2006). Multiple factors may participate together with climate change to determine epidemiological impacts at the wildlife-livestock interface, particularly in multiple host/vector systems, and we are just starting to understand the interactions between climate and host/pathogen responses (Rohr et al. 2011; Altizer et al. 2013).

Increasing biotic homogenization, including the spread of pathogens across interfaces, is likely a process that is increasingly characterizing many current ecosystems, and is anchored in processes driven by humans over recent history. Biotic homogenization consists of invasions and extinctions increasing the taxonomic, genetic, or functional similarity of multiple locations over a specified time interval (Olden 2006). As an example, Fig. 5 represents a process currently taking place on the *Escherichia coli* community in Doñana National Park (South Spain). This is a natural area that has been influenced by humans since the Paleolithic, with an old history of extensive farming (cattle and horses), while also being a hotspot of biodiversity in western Europe. This research has identified the effects of anthropic pressure and wild and domestic ungulate abundance on the distribution and diversity of the main human *E. coli* pathotypes and 9 of their representative virulence genes (VGs). One example has shown, *E. coli* was detected everywhere and there were no big differences among host species or among DNP zones. However, the distribution of genes characteristic of the described pathotypes was not random and VGs were more diverse and abundant where surface waters are more contaminated by human waste and farms. This exemplifies that human influence, in this case, was more relevant than host species in shaping the *E. coli* VGs spatial pattern and diversity in DNP.



Fig. 6 (continued) using fences [Source: Barasona et al. (2013); (b) Facilities for selective and random culling; (c) Vaccination against TB in wild boar using oral baits. Reproduced from Gortazar et al. (2014)]

Scientifically Based Management of the Interface in Modern Times

Species distributions and community structures have fluctuated dramatically during the Holocene, which has been accelerated during the so-called Anthropocene (the twentieth century's transition) and driven by climate, human exploitation, and human land use (Boivin et al. 2016). While a negative trend has continued for many wildlife species in most parts of the planet, the status of most wild ungulates and carnivores in developed countries has improved during the Anthropocene (Linnell and Zacos 2010). In some cases, species such as the Alpine (*Capra ibex*) and Iberian (*Capra pyrenaica*) ibexes were reduced to a few individuals but have now expanded over large areas (Stüwe and Nievergelt 1991), even causing conflicts in some cases as disease reservoirs (i.e., *Brucella*). Overall, the complete domination of the landscape by humans has contributed to the collapse of wildlife populations in most parts of the world and unprecedented biodiversity loss is a reality. Environmental problems arising from livestock production are particularly severe in developing nations, like deforestation for rearing livestock, overgrazing, land degradation, and particularly, diseases. Fences and other barriers interfere with wildlife migrations or natural movements and impede access to ephemeral resources. Modern wildlife management is an essential component of current interfaces with livestock and humans. While we are addressing in some cases catastrophic species extinction periods, wildlife use is increasingly regulated, and wildlife are managed and appreciated for their ecological, economic, social, and cultural value. Wildlife management must balance the needs of wildlife with the needs of people using the best available science (Leopold 1933). The apparent increase in severity of what we call conflict (from the human perspective) has a complex nature and is due to a number of factors (expansion of human activities into wildlife habitats, recovery, and expansion of some wildlife populations and large-scale environmental changes; Treves 2008). While human–wildlife conflict was previously considered a “rural or agricultural problem” (Messmer 2000) that mainly affects communities in proximity to forests, conflicts are now common both in urban and in suburban areas (Soulsbury and White 2015), as well as in remote areas newly encroached by humans. Urban/suburban human conflict incidents typically involve wildlife species that have a history of coexistence with humans or the ability to survive in human-dominated environments, where infectious diseases are also involved. For example, *Leishmania* in wild lagomorphs has been recognized as the origin of a leishmaniasis outbreak in humans and domestic animals in central Spain in peri-urban environments (de Paixão Sevá et al. 2017).

There is currently much discussion regarding models of wildlife management and conservation, considering human–nature interactions, which will surely affect the wildlife–livestock–human interface. These include questions about land protection vs. land sharing (Fischer et al. 2014), what the role of protected areas is and how multiuse landscapes must be managed (including farming; Sayer 2009), and sustainable use vs. protectionist ideals (Cretois et al. 2019). Contrary to the

science of spared landscapes (i.e., protected areas) the science of coexistence promotes the presence of wildlife in multiuse landscapes, remains ad hoc and fragmented, but the strategic utility and practicality of the whole approach are being contested (Linnell et al. 2020). Definitively, shared diseases at the wildlife-livestock-human interfaces are a crucial component to be included in the formulation of modern wildlife management. Today, human connections with ecological and epidemiological systems are increasingly driven by expanded and intensified agriculture, the use of environmental resources (e.g., forestry and mining in developing countries and remote areas) and impacts on climate. The subsequent alteration in habitats, changes in host communities, diversity, and functional interactions are favoring increased contact rates, susceptibility, and/or exposure of pathogens at the interfaces with wildlife, many of which are shared with livestock and/or zoonotic. The subsequent spread and maintenance of emergent pathogens are favored by the growing worldwide human population, global trade and ease of travel, and the existence of altered host communities (involving interfaces) that provide ecological niches. Consequently, as discussed earlier, the wildlife-livestock interface is becoming global. More than ever, today it is challenging to analyze the complex ways with which wildlife interact with livestock and humans and how those interactions are relevant to emerging diseases at the interfaces.

Comprehensive and continuing epidemiological studies at the wildlife-livestock-human interface are required in different scenarios (e.g., countries, farming systems, pathogens, degree of anthropization) to better understand the infection and transmission dynamics in wildlife and domestic components. It is essential to understand local, regional, and international social, economic, and cultural systems to better focus strategic control programs. Population and disease monitoring will improve the overall understanding of the role of wild hosts and the mode of transmission and emergence of new infections. This must enable countries and international organizations to better target their disease control programs and move toward eradication. Strategic research in collaboration with the medical sector is also needed to better understand the factors that contribute to interspecies pathogen transmission among all species. African swine fever (ASF) in Europe provides an interesting example. ASF was eradicated in domestic pig populations in Europe (except Sardinia) after decades of significant effort (Gavier-Widen et al. 2015). In 2007, the current outbreak of ASF, which severely affects wild boar and domestic pig populations, reached the Caucasus region via contaminated waste arriving in ships from Africa. Since then, the virus has spread into eastern Europe and some places in central and western Europe through wild boar, domestic pigs, and human activities. The virus has raised serious concerns in countries with large pork industries, which may suffer economic losses due to trade restrictions. To control the outbreak, national authorities have taken drastic, but not always effective measures, which disregard the science of wildlife management (Vicente et al. 2019). Poland, for example, has massively increased the culling of wild boar to minimize ASF spread and the risk of transmission to domestic pigs, despite opposition by experts, because the policy does not include population monitoring that could evaluate its effectiveness. It also does not limit wild boar access to agricultural crops and game feed, which is a key driver

of population growth. Meanwhile, countries are building large border fence to exclude cross-border migration of wild boar, which will disrupt wildlife habitats, but it will not stop the virus from spreading through the transportation of live pigs, wild boar, or pig- and wild boar-derived tissues and products or through the movement of other objects carrying the virus, such as human clothing. Instead of haphazard policies, efforts coordinated by governments that adhere to the principles of modern wildlife management are required. Adaptive wildlife management strategies consider the human dimension and prevent unsound reactive management. Improved wildlife population monitoring and analysis are the best ways to determine which approaches to wildlife management are successful ecologically, economically, and socially. Sustainable management will depend on local circumstances and national wildlife management regulations, but science-based strategies can be implemented at the continental scale. Legislators should consult scientists and wildlife and animal health agencies before making decisions about wildlife policy. Countries should coordinate population monitoring and management. Shared responsibility for wildlife management among countries should also enable funding for research that can critically evaluate its success. The crisis associated with disease emergence at the wildlife-livestock interface, including zoonotic diseases, can serve as a chance to develop a science-based wildlife management plan.

Finally, we remark that establishing a proper surveillance and monitoring scheme (for disease and population) is the absolute priority before deciding whether or not to intervene. Disease control can be achieved by different means, including: (1) preventive actions, (2) arthropod vector control, (3) host population control through random or selective culling, habitat management or reproductive control, and (4) vaccination. Alternative options of zoning or no-action should also be considered, particularly in view of a cost-benefit assessment. Ideally, tools from several fields should be combined in an integrated control strategy. The success of disease control in wildlife depends on many factors, including disease ecology, natural history, characteristics of the pathogen, availability of suitable diagnostic tools, characteristics of the domestic and wildlife host(s) and vectors, geographical spread of the problem, and scale of the control effort and stakeholders' attitudes. The control of wildlife disease often consists of an intervention in natural ecosystems and is, as such, often controversial. Figure 6 schematizes the options that are available for disease control at the wildlife-livestock-human interface, including preventive measures, population control, and vaccination, with some examples provided.

Final Remarks

- Through processes of evolution, migration, domestication, colonization, trade, travel, harvest, erasure, and fragmentation of habitat, disease, introduction of alien species, humans have greatly and irreversibly impacted the planet and most life forms on it. This includes pathogens of humans and animals. As the human

population approaches eight billion today, human impact is continuously shaping, creating, expanding, and interconnecting new wildlife-livestock-human and their subsequent epidemiological interactions all over the world.

- Pathogen communities and the dynamics of complex multiple host multiple pathogen systems (interfaces) reflect this history of epidemiological interactions among them, where evolutive processes in this human-driven system have influenced the biology of both hosts and pathogens.
- Wildlife were the original hosts for most pathogens of livestock, sharing them with domesticated species over centuries of coevolution and domestication. Domestic animals subsequently transmit pathogens to humans and today many human infections originated from zoonoses of domesticated animals.
- The initial stages of animal domestication were probably characterized by frequent interaction of first forms of livestock with their wild counterparts and constant and/or recurrent exposure to pathogens. The gradual development of animal husbandry took place over several millennia and followed markedly different trajectories in different regions. Domestication determined a new scenario for emergent pathogens that adapted well to the new conditions of the multiple human–livestock–wildlife interface, characterized by the maintenance of “crowd diseases” (both by humans and/or by animals), the continuous presence of domestic reservoirs, anthropophilic animals and vectors. This provided niches for the evolution and adaption of pathogens to specific conditions.
- Agricultural activities by humans inevitably transformed different parts of the world at different rates, varying by epochs, civilizations, and regions. The removal and change of natural vegetation, the impacts on the abundance, type, distribution, and behavior of wildlife, the number of livestock and husbandry practices have been increasing and expanding since pre-industrial times and have determined the wide diversity of wildlife-livestock interfaces. Overall, wildlife is becoming less abundant and distributed and more fragmented and isolated, but interfaces have become more interconnected.
- The growing interdependence of world economies, human population growth, intercontinental trade, and transportation (including animals, their pathogens, and vectors) has provided opportunities for animal pathogens to cross considerable geographic boundaries and determined modern agricultural practices and characteristics of wildlife-livestock interfaces.
- The wildlife-livestock interface is more interconnected than ever. On the one hand, the wildlife-livestock-human interface is increasing as a result of human encroachment into wilderness, especially in tropical ecosystems. On the other hand, the intensification of animal production also favors increasing livestock-to-human contact, and occasionally, with other animals.
- Overall, wildlife has been reduced by humans to their lowest levels ever. Disease issues at the wildlife-livestock-human interfaces, though, are of increasing concern as they are leading to global pandemics and are far from being efficiently controlled or managed. The capacity to modify and connect the interfaces that characterize humans has increased to the extent that improving health at the

human, animal, and ecosystem interfaces is required to successfully address the main global health challenges.

- Climate and associated anthropogenic and environmental change impact the distribution, abundance, behavior, and population dynamics of pathogens and hosts, determining transmission dynamics, and threats to human health and livelihoods. The global warming impacts on the wildlife-livestock-human interface will be diverse, and the pattern not spatially homogeneous. However, multiple factors may participate together with climate change to determine epidemiological impacts at the interface, particularly in complex host/pathogen/vector systems. This context requires a better understanding of the interactions between climate change and host/pathogen responses.
- More than ever, it is challenging to analyze the complex ways in which wildlife interact with livestock and humans, and how it is relevant to emerging diseases. Comprehensive and continuing epidemiological studies at the wildlife-livestock-human interface are required in different scenarios (e.g., countries, farming systems, pathogens, and degree of anthropization) to better understand the infection and transmission dynamics in wildlife and domestic components. Population and disease monitoring of wildlife will improve the overall understanding of the roles of wild hosts, modes of transmission, and emergence of new infections. This would enable countries and international organizations to better target their disease control programs and move toward eradication. Legislators and animal and human health policy makers must base decisions on wildlife and animal health science and countries should coordinate responsibility and management.

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The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health



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Introduction

The past decades have been marked by infectious disease pandemics in humans and livestock whose origins were traced back to wildlife hosts (Cunningham et al. 2017; Jones et al. 2008) in areas where wildlife interacts directly or indirectly with domestic animals and humans: the “wildlife-livestock-human interface” areas. Wildlife reservoirs harbored microbial organisms or parasites that were mostly commensals or non-pathogenic in the wild reservoir species but became pathogenic for domestic species and eventually humans. Some of these organisms adapted to human hosts by chance through secondary epidemiological cycles via vectors or bridge species such as domesticated animals or peridomestic wildlife (i.e., living in and around human habitations), and now circulate among humans (see hereafter the definition and discussions for pathogen spill-over/spill-back events). Direct infection by pathogens from animals to humans (zoonosis) is a relatively rare event, and the proportion coming directly from wildlife is even more exceptional. However, when it occurs, it can be very serious as dramatically illustrated by the COVID-19 pandemic. Previous recent pandemics also had devastating impacts, claiming numerous lives and shaking entire communities, such as the Ebola outbreak that occurred in West Africa from 2014 to 2016 (Shiwani et al. 2017), which is presumed to originate from a wildlife reservoir (Coltart et al. 2017), possibly frugivorous bats (Leroy et al. 2005; Pourrut et al. 2005).

Infection of humans from wildlife has historically been related to occupational hazards, such as bushmeat hunting or consumption for Ebola virus on exposure to bat excreta through agricultural practices for Nipah virus. Pathogen spill-over seems to be associated with long-term practices that provide opportunity for the establishment and spread of infection in human communities through changing human landscapes and contact networks. What is more, anthropogenic impacts on ecological systems largely dictate the risk of spill-over and spread at the interface between humans and animals (Hassell et al. 2017). Biodiversity losses that affect pathogen maintenance and spill-over at wildlife-livestock-human interface often result from anthropogenic interventions (Keesing et al. 2006; Morand et al. 2014a). Changes in agricultural practices, domestic animal husbandry infrastructures, especially transportation networks, and artificial habitats as well as specific stressors, such as climate change, play important roles in triggering pathogen spill-overs at wildlife-livestock-human interfaces. The emergence of diseases in humans and domestic animals is therefore often linked to anthropogenic alterations of the structure of landscapes and species communities (e.g., Lambin et al. 2010). Current evidence also indicates that the same drivers are also responsible for the emergence of disease in wildlife, mostly due to direct exposure to domestic sources of infection and exposure to a wild source via human intervention such as the translocation of hosts (Tompkins et al. 2015).

The efficient management of epidemic events requires early detection and control of outbreaks where the initial transmission events occur, at the wildlife-livestock interface. The precise mechanisms and pathways of emergence of pathogens in humans and domestic animals from wild organisms are still poorly understood

except in some well-studied cases such as Yellow Fever. Each emergence appears as an idiosyncratic event (Caron et al. 2012). The current reductionist approaches adopted to analyze the mechanisms at stake are unlikely to provide holistic and generic insights, because they only focus on parts of the system and fail to encompass all the complex interactions of very different nature (ecological, evolutionary, sociocultural) that are at play among wildlife, livestock, and humans in order to generate a “successful” disease emergence (Plowright et al. 2017). Mass pathogen discovery from wildlife species around the globe (Morse et al. 2012) will certainly lead to the discovery of “new” pathogens, the immense majority of which do not, and will probably never, represent a threat to humans, livestock, or even wildlife from which they originate. Even focusing on the “usual culprit” bat reservoir (Han et al. 2015) is of little predictive value for future emergence, unless we adopt a fully integrated approach to understand the infection dynamics within the hosts and the impacts of humans on the environment that change the likelihood for virus spill-over (Plowright et al. 2017; Smith and Wang 2013). Large-scale retrospective analysis of disease emergence events over the past decades highlighted regions of the world that have been disproportionately hit by disease emergence (e.g., “hotspots” (Jones et al. 2008)). They listed a number of correlative variables potentially associated with these greater odds of emergence, but this cannot be truly representative of all situations even if corrected for bias. Indeed, we are still far from understanding the mechanisms at stake and forecasting the next pandemic of emerging diseases will require more integrative social-ecological-evolutionary studies focusing on where the initial transmission events occur, the wildlife-livestock interface.

The transmission of pathogens from a wildlife source to domestic hosts involves complex mechanisms operating within diverse ecological communities, which are best analyzed through an ecological lens. Disease ecology is the study of host–pathogen interactions within the context of their environment and evolution. It is concerned with how interactions between species and with the abiotic components of their environment affect patterns and processes of infectious diseases. Several books are now considered as landmarks of the theoretical and empirical developments associating ecology and epidemiology in order to study and manage diseases in wildlife-livestock interface systems. Grenfell and Dobson (1995) offered the foundations for the ecological approach of infectious diseases in natural populations. Collinge and Ray (2006) proposed a community epidemiology perspective of disease transmission between wildlife and livestock. Disease–ecosystem relationships analyzed in Ostfeld et al. (2010) encompass both the role played by parasites in ecosystems, and vice versa. They have paved the way for further applications of ecological theories to disease management and policies. Since then, the emerging discipline of disease ecology has continued to develop, integrating different ecological perspectives: spatial and landscape, functional, community, evolutionary, and molecular ecology. Simultaneously, the human component of wildlife-livestock interfaces has received increasing attention. As we have entered the Era of Human-Induced Diseases (Chaber 2017), it is increasingly acknowledged that human activities (e.g., agricultural, industrial, recreational, and conservation) are largely shaping these interfaces, as will be illustrated below.

Local, regional, and even global processes affect the community of hosts composing the wildlife-livestock interface and their network of interactions, both of which impact pathogen transmission and persistence. The ecology of disease transmission at the wildlife/livestock interface addresses crucial questions such as (1) the effect of community composition, landscape, and human management on pathogen transmission, regulation, and maintenance at this interface; (2) the ecological interactions among host species and interspecies transmission rates, and (3) the impacts of infectious diseases on host populations, communities, humans ecosystems, and subsequently, sustainable land management and conservation. This chapter reviews the current evidence for pathogen transmission in wildlife-livestock interface areas. We use examples drawn from the experience of the co-authors to illustrate how advances in ecology have improved our ability to analyze the patterns of pathogen transmission among wildlife, livestock, and humans. We then analyze the mechanisms at stake, emphasizing the importance of ecological drivers, such as access to resources, competition, and predation, and the increasing evidence for the importance of anthropogenic drivers, such as agricultural and conservation practices. We conclude by emphasizing the necessity for an integrative socio-ecological approach for research and management of wildlife-livestock interfaces and discuss some opportunities and challenges.

The Transmission of Pathogens at Wildlife-Livestock-Human Interfaces

Direct and indirect interactions may result in the transmission of pathogens from wildlife to livestock, and from livestock to wildlife. The transmission of pathogens from livestock to wildlife, i.e., “spill-over” as defined here following Nugent (2011), or back from wildlife to livestock (i.e., “spill-back”; Nugent 2011) represents a series of epidemiological events at wildlife-livestock interfaces that are difficult to demonstrate empirically. Detecting pathogens in the putative hosts is not sufficient, as the epidemiological evidence for spill-over and spill-back should document the temporal sequence of infections: presence in initial host, subsequent transmission to the spill-over host, and transmission back to the initial host. This requires diagnostic and analytic tools that have been only recently available (e.g., phylogenetics) and in the absence of routine surveillance data for poorly known (wildlife) species, most spill-over events remain undetected, and even when they are, it is rarely possible to determine accurately when they have happened (Voyles et al. 2015). This section reviews and illustrates with several examples the epidemiological evidence for pathogen spill-over between wildlife-livestock and livestock-wildlife, and to/from humans.

Wildlife-to-Livestock

Historically, protecting livestock from wildlife diseases has been used as a prime justification for confining and extirpating wildlife reservoirs from rangelands that they shared with livestock. For instance, the control of trypanosomiasis in Southern Africa during the first half of the twentieth century resulted in the culling of over one million wild ungulates, most of them in vain from an epidemiological point of view as they belonged to species such as the African Elephant (*Loxodonta africana*), Sable Antelope (*Hippotragus niger*), or Common Ostrich (*Struthio camelus*) that do not play a significant role in maintaining the parasite (Matthiessen and Douthwaite 1985).

However, there are a number of well-documented cases for which wildlife populations have been demonstrated to act as maintenance hosts (sensu Haydon et al. 2002) of diseases affecting livestock (Bengis et al. 2002). Foot-and-mouth disease (FMD) provides an appropriate model to illustrate the complexity and the need for integrated ecological studies at wildlife-livestock interfaces mainly in Southern Africa (Brahmbhatt et al. 2012). This disease has important economic impacts and constrains exporting countries to implement massive control programs (e.g., through culling or vaccination (Paton et al. 2009)). It is widespread worldwide and has been earmarked by the World Organization for Animal Health (OIE) as a target for eradication from the globe.

In Africa, several strains of FMD virus are circulating within a community of host species, including African buffalo (*Syncerus caffer*), impala (*Aepyceros melampus*), greater kudu (*Tragelaphus strepsiceros*), common warthog (*Phacochoerus africanus*), cattle (*Bos taurus* and *Bos indicus*), and small domestic ruminants. All can be involved in the circulation of FMD (Lefèvre et al. 2010). The respective roles and relative importance of each species in a system associating wildlife and livestock are difficult to quantify and disentangle. The African buffalo is assumed to be the natural reservoir of the virus, as it can be infected without apparent symptoms and maintain the virus within populations, whereas cattle can also maintain the virus, and develop clinical signs including mouth ulcers and foot wounds and a decrease in milk production (OIE 2009). However, because the host communities include very diverse species and wildlife-livestock interactions are very complex and dynamic, several aspects of FMD in interface areas in Africa still remain unclear (seasonal dynamics, strains circulating, virulence according to the inter-specific contacts) (Miguel 2012; Teklehiorghis et al. 2016).

In 2010–2011, a study was carried out in Zimbabwe at different interfaces to quantify the frequency of contacts between African buffalo and cattle (Miguel et al. 2013) in relation to the availability of natural resources (vegetation and water), anthropogenic activities (crop fields and settlements) (Miguel 2012) and predation pressure (Miguel et al. 2017b). A total of 36 GPS collars were deployed on African buffalo and cattle at 3 sites to assess contact patterns at the periphery of 3 protected areas in Zimbabwe. Simultaneously, a longitudinal survey of 300 cattle with five repeated sampling sessions on known individuals during 16 months was undertaken.

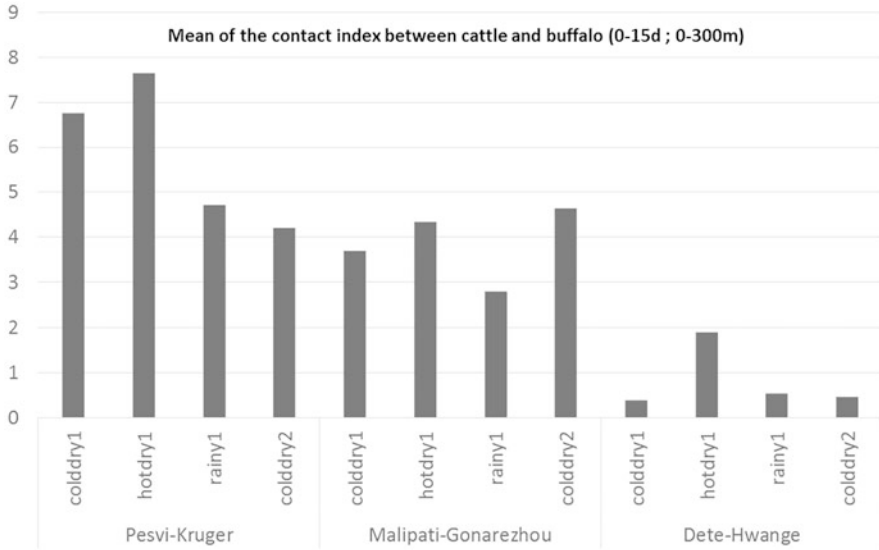


Fig. 1 Seasonal variations in indirect contact rates between African buffalo and cattle in three different interfaces between rural/protected areas in Zimbabwe. Potentially infective contacts were defined when a cattle location was recorded within 300 m of a buffalo location and less than 15 days after the buffalo location had been recorded. More details in Miguel et al. (2013)

Immunological assays (ELISAs), that allowed tracking the production of antibodies following infection or vaccination, were used to assess serological transitions (i.e., incidence and reversion) in the surveyed cattle.

Simultaneous GPS tracking of sympatric cattle and buffalo revealed significant differences in contact patterns across areas (Fig. 1). Although the permeability of the boundaries was similar in the 3 interface sites (unfenced or extensively damaged fence) and the animal densities almost equivalent (Miguel 2012), very different contact rates were observed in terms of frequency. However, the seasonal patterns of contacts were similar among sites with the lowest contacts during the rainy season, and usually reaching a maximum during the hot (or cold) -dry season. This seasonality suggests that contacts between cattle and buffalo are driven by resource availability, as will be explored further in paragraph 3.3.

The results also demonstrated that the probability of cattle FMD serological incidence (antibodies acquisition) was positively associated to the frequency of contacts with buffalos (Fig. 2). On the contrary, serological reversion (i.e., loss of antibodies) was negatively associated to the frequency of buffalo–cattle contacts (Fig. 1b). As direct contacts (i.e., at the same time, at the same place) were almost never recorded, the results suggest that the survival of FMD viruses in the environment is high enough for delayed contacts to generate virus spill-over from buffalo to cattle, or that transmission occurred by unrecorded individuals and/or species. Furthermore, in spite of strong serological evidence for infection events, no clinical signs for FMD were detected in the monitored cattle populations during the course of

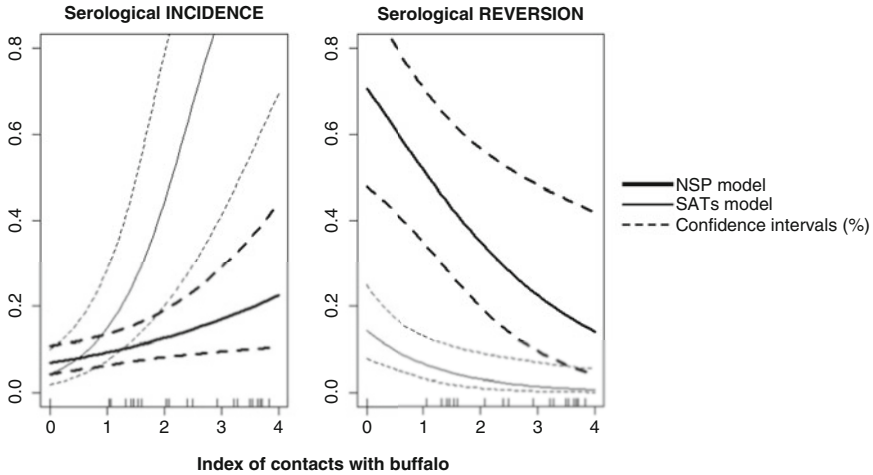


Fig. 2 Serological incidence and reversion probabilities of foot and mouth antibodies in cattle populations depending on the buffalo–cattle contact rate. Non Structural Proteins (NSP) for “natural antibodies” and SATs (South African Territories) for “natural” and “vaccinal” antibodies. The lines at the bottom of the figure represent the data used from GPS devices to estimate the index of contact among cattle and buffalo (For more details see (Miguel et al. 2013))

the study, which tends to support the idea of a silent virus circulation in some areas of southern Africa.

Livestock-to-Wildlife

Until the 1970s, the impact of parasites and pathogens on wildlife populations was largely overlooked (Grenfell and Gulland 1995), and academics, managers, and even the general public perceived wildlife as being resistant to the parasites and pathogens they have coevolved with (de Garine-Wichatitsky et al. 2014). It is only recently that the impact of diseases on biodiversity conservation has been recognized and has gained attention from researchers and conservation organizations (Smith et al. 2009). According to the IUCN Red List of Threatened Species™ (Version 5.2 downloaded 2 March 2018), up to 20.7% of the 1.424 terrestrial mammal species classified as threatened may be impacted to some level by diseases, although Threat Category 8 which accounts for disease risks also includes “invasive and other problematic species.” Nevertheless, there is no doubt that interactions between wildlife and livestock are an avenue for pathogen transmission in both directions, and that domesticated animals do also play the role of reservoir for a number of infections that have had significant and detrimental effects on wildlife species, populations, and ecosystems.



Fig. 3 Saiga antelope (*Saiga tatarica*) carcasses after mass mortality event in Kazakhstan in 2017. (photo@ Association for the Conservation of Biodiversity, Kazakhstan, Biosafety Institute, Gvardeskiy RK, Royal Veterinary College, London, UK)

The most well-documented of these are the morbillivirus infections: rinderpest, peste des petits ruminants, and distemper. The first two are pertinent to artiodactyls and food animals. Rinderpest caused massive mortalities in cattle over 5 centuries across Eurasia and in the 19th–20th centuries in Africa. Cattle populations were the maintenance hosts. This occurred alongside colonization and introduction of infected cattle from Eurasia. The Great Pandemic as it was called, spread the virus across the whole continent and entire ecosystems like the Serengeti changed. Key stone species, such as African Buffalo and Blue Wildebeest (*Connochaetes taurinus*) declined, and the removal of bulk grazers from African savannah ecosystems resulted in a dramatic vegetation shift. This change in vegetation composition and structure, and its reversal when the disease was eliminated, have been well documented (Dobson et al. 2011; Holdo et al. 2009). After the eradication of rinderpest, around 2003 (officially declared globally absent in nature in 2011), the less well-known virus Peste des petits ruminants emerged in ruminants and spread widely from West Africa to East and southern Africa. The virus perhaps partly filled the ecological niche emptied by the eradication of rinderpest and eventually spilled from domestic small ruminants into wildlife. To date, it has caused little harm in wildlife in Africa, but in Asia in 2017 it nearly destroyed the last remaining population of the Saiga Antelope (Mongolian subspecies, *Saiga tatarica mongolica*) when over 60% of the remaining 10,000 antelope died (Kock et al. 2018) (Fig. 3). Prior to this event, an effort to eliminate the virus from livestock involved some 11 million vaccinations. But little consideration was given to the risks to wildlife over this period by national or international agencies. This lack of consideration

contributed to its spill-over to the saiga antelope as no extra precautions were taken to buffer these populations more intensively.

Livestock-to-Wildlife, and Back?

As discussed earlier, interface areas may lead to the transmission of pathogens and parasites from wildlife to livestock, as documented for several diseases of economic importance a long time ago, and also from livestock to wildlife, which was only acknowledged more recently. This was partly due to technical difficulties in collecting ecological and epidemiological data from free-roaming wild animals. However, despite recent significant methodological and technical advances (molecular ecology, spatial ecology; see Chapter “Collecting data to assess the interactions between livestock and wildlife”), little attention has been given to successive spill-over and spill-back events between sympatric hosts over time.

Bovine tuberculosis (bTB) at the wildlife-livestock interface provides a good case study of this complexity (Fig. 4). First globally, the disease has spread and spilled-

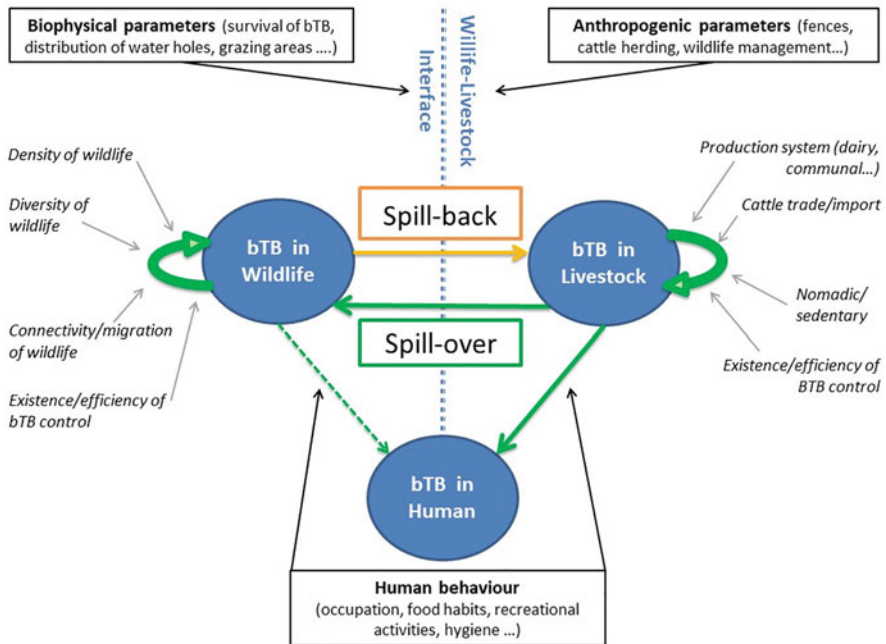


Fig. 4 Biophysical and anthropogenic drivers of bTB spill-over and spill-back across wildlife-livestock interfaces (adapted from de Garine-Wichatitsky et al. 2013c). Green and orange arrows indicate the direction and the width is proportional to the frequency of pathogen transmission (dotted arrow indicates that spill-over from wildlife is suspected but not documented to our knowledge)

over to wildlife through intercontinental cattle movements, mainly using primary and secondary colonial routes (Smith 2011). In southern Africa, the introduction of multiple strains in the ecosystem through cattle importation is a typical example (Michel et al. 2008). The subsequent spread and spill-over to wildlife are not fully understood in the region. However, it is estimated that bTB spilled-over from cattle populations to the buffalo population in Kruger National Park (KNP) in the early 1960s in the southern part of the park, across the unfenced Crocodile River (Bengis et al. 1996; De Vos et al. 2001). The main hypothesis points to a single bTB spill-over event from cattle to buffalo (Michel et al. 2009). Subsequently, the disease spread across the KNP buffalo population and to buffalo populations across countries within the Great Limpopo TransFrontier Conservation Area (Caron et al. 2016; de Garine-Wichatitsky et al. 2010). Until recently, no spill-back events to cattle were detected despite investigations in several cattle populations separated physically or not from infected buffalo populations in South Africa and Zimbabwe (de Garine-Wichatitsky et al. 2013c). However, in 2015, Musoke et al. (2015) reported the first description of bTB in cattle on the periphery of KNP across a hard fence, with a wildlife, mostly probably buffalo strain of bTB, indicating a spill-back event. Buffalo straying from the KNP boundary into the communal land across African elephant- or flood-made breaks in the fence provide a good hypothesis to explain this spill-back event (van Schalkwyk et al. 2016). The pathogen and subsequent disease transmission risk across this wildlife-livestock interface in the Great Limpopo TFCA is, therefore, real both ways and threatens bTB naïve cattle and wildlife populations, notably in Zimbabwe (Caron et al. 2016; Kock et al. 2014).

These two-way exchanges of bTB across wildlife-livestock interfaces have been described in other contexts: Eurasian Badger (*Meles meles*) in England and probably other continental European countries (Payne et al. 2012); Wild Boar (*Sus scrofa*) and Red Deer (*Cervus elaphus*) in Spain (Gortázar et al. 2010); White-tailed Deer (*Odocoileus virginianus*) in the USA (Palmer et al. 2012); brushtail possum in New Zealand (Coleman and Cooke 2001). In each of these cases, it is assumed that bTB was introduced by cattle into wildlife and the subsequent control of bTB in cattle reversed the risk of pathogen transmission across the interface. Gortázar et al. (2010) documented in details the succession of management options taken that led to the current situation in Southern Spain, where bTB is emerging in overabundant wild ungulates and spilling-back into cattle, which could apply in very similar situations for most of continental Europe and North America.

Wildlife-to-Livestock-to-Humans

Following the Nipah, Hendra, and Severe Acute Respiratory Syndrome (SARS) epidemics, and various publications on the subject of zoonoses (Jones et al. 2008), the general public and nonspecialist members of the research and academic world have come to realize that most human pathogens and parasites originate from animals, especially from wildlife in the case of emerging infectious diseases. This was not a surprise for evolutionary biologists, as humans have evolved in proximity

to animals for a long time, especially with domestic animals with whom they may exchange pathogens and parasites frequently and through diverse transmission modes (Cleaveland et al. 2001). Morand et al. (2014b) have demonstrated the importance of time since domestication in determining the number of pathogens and parasites that have spilled-over to humans. Humans, of course, engage in direct physical or indirect contact with their livestock in a variety of ways, from husbandry to consumption, providing continuous opportunities for pathogen spill-over. Although such direct and indirect interactions between humans and wildlife are less common, there is circumstantial evidence that wildlife represent a direct source of human pathogens or spill-over of organisms which can lead to what is described as a pathogen jump, with the organism establishing in its new host. This can occur with or without any livestock species playing the role of “bridge” (Caron et al. 2015). However, documenting the circumstances that lead to the emergence in humans of a new pathogen and identifying the animal source of the pathogen is a difficult task. It necessitates a combination of efficient laboratory and field investigations, which may prove problematic when the suspected emergence occurs in countries with limited resources or areas difficult to access.

The latest pandemic threat, the Middle East Respiratory Syndrome Coronavirus (MERS-CoV), provides an illustration of the challenges encountered to elucidate the role played by putative livestock and wildlife species in the transmission of a zoonotic pathogen. In September 2012, a novel coronavirus, MERS-CoV was identified from a patient with a fatal viral pneumonia in Saudi Arabia. This coronavirus was genetically related to the SARS coronavirus that emerged in southern China in 2002 (Hilgenfeld and Peiris 2013). As of February 19, 2018, 2143 human cases had been reported to the World Health Organization with at least 750 deaths (WHO World Health Organization. 2018). Most zoonotic infections have occurred in the Arabian Peninsula, particularly in Saudi Arabia, although nosocomial outbreaks arising from returning travellers have been reported from Europe, North America, Africa, and Asia.

Dromedary camels (*Camelus dromedaries*) have been confirmed to be the source of human infection (Al-Tawfiq and Memish 2014) of MERS-CoV (Chu et al. 2014). Alraddadi et al. (2016) showed that direct exposure to dromedary camels and particularly milking camels were associated with MERS-CoV human illness in Saudi Arabia (Alraddadi et al. 2016). Secondary infections in humans have been reported, especially within nosocomial settings or to a smaller extent, within households (Assiri et al. 2013). The genetic analyses confirmed that the long-term MERS-CoV evolution occurs exclusively in camels, whereas humans act as a transient, and ultimately terminal host. Spill-over events are frequent and the virus has been introduced into humans several hundreds of times in Saudi Arabia leading to occasional outbreak amplification according to specific “environmental” conditions, which are still unknown (Dudas et al. 2018).

So far MERS-CoV has not been detected in wild animals, such as birds (Perera et al. 2013) or feral camels (Cramer et al. 2015). Some short fragments of the virus genome almost identical to MERS-CoV were found in bats (Kim et al. 2016; Memish et al. 2013) but the role that these hosts may play in the epidemiology of the disease, if any, is not confirmed. In domestic hosts, however, the MERS-CoV has

been investigated in numerous species (horse, cattle, pig, goat, chicken, water buffalo *Bubalus bubalis*, and bactrian camel *Camelus bactrianus*) and all specimens were negatives (Funk et al. 2016; Miguel et al. 2016b). By contrast, the virus is circulating actively in dromedary camels (Miguel et al. 2016a, 2017a). Retrospectively, collected serum samples provide evidence that this virus has been infecting camels in East Africa for many decades (Muller et al. 2014). However, so far, it is not clear whether transmission of MERS-CoV to humans is occurring in Africa or not; and the role played by the usual culprits, bats, as compared to camels and human practices are not clear either.

Ecological Drivers of Wildlife-Livestock Interactions

Whether direct or indirect, pathogen transmission between wildlife and livestock results from the use of shared areas (Miguel et al. 2013; Woodroffe et al. 2016). Understanding the ecological and anthropogenic drivers of species distribution at broad scales and animal movement at fine scales will enhance our ability to model wildlife-livestock interactions and the likelihood of disease transmission. In this section, we present evidence of bottom-up effects of resource availability (Section “Resource Availability Drives Wildlife-Livestock Interactions”) and top-down effects of predation (Section “Predation”), anthropogenic drivers are discussed in the following Section (Anthropogenic Drivers of Wildlife-Livestock Interactions).

Resource Availability Drives Wildlife-Livestock Interactions

Wildlife use of interface areas is highly idiosyncratic. Camera trap surveys of large mammals in Southeast Asian forests have shown that some species strongly avoid human disturbances, whereas others appear to select areas that have been subjected to logging and thus appear to be attracted by the human-wildlife interface (Brodie et al. 2015). Underlying these idiosyncratic responses, resource preference can be used as one of the key predictors of wildlife-livestock interactions. Foraging resources are a primary driver of habitat selection; however, multiple resource requirements must be considered to fully understand transmission patterns. The transmission of bovine tuberculosis between cattle and badgers in European pastures illustrates these complex interactions. Badgers favor pasture/forest ecotones that provide prime foraging grounds (pastures) as well as refuge areas (forest) where they can escape predation and dig safe burrows, despite behavioral avoidance of cattle by badgers, contamination may occur by the shared use of a contaminated environment (Woodroffe et al. 2016).

Domestic and wild herbivores are particularly prone to disease transmission due to their phylogenetic proximity and their similar resource requirements (Fig. 5).

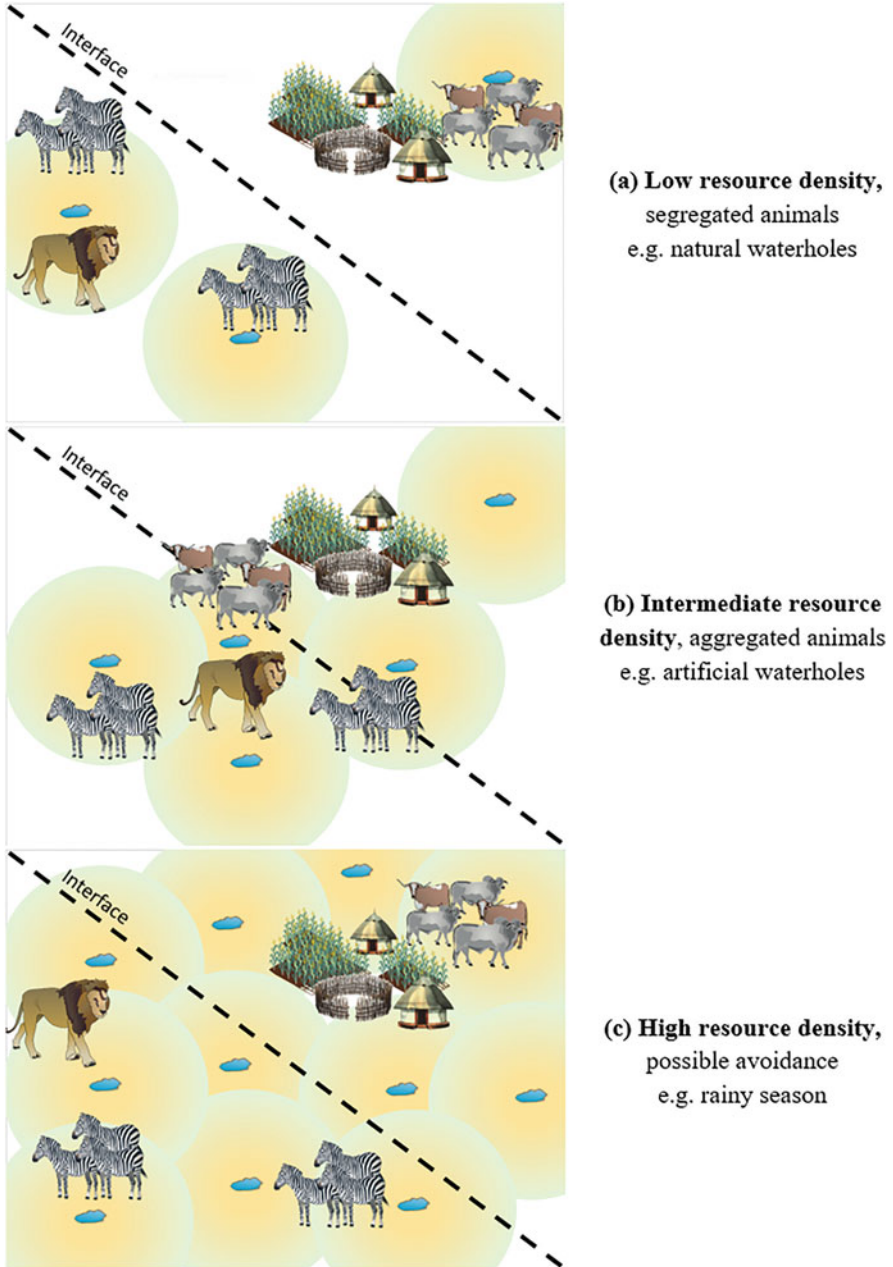


Fig. 5 Resource-driven encounters between wildlife, livestock, and predators at an African wildlife/livestock interface (adapted from Borchering et al. 2017)

Despite dietary niche partitioning, large herbivores consume a number of shared plant species. Dietary overlap is greater for species with similar body size and proportional grass consumption (Kartzinel et al. 2015). Thus, in African rangelands domestic species such as cattle are more likely to compete with similar-sized ruminant grazers such as African buffalo than browsers (e.g., Greater Kudu), nonruminant grazers (e.g., zebra, *Equus quagga*), or very large (e.g., African elephant) or very small (e.g., duikers and subfamily *Cephalophinae*) herbivore species. Grazed ecosystems are also characterized by positive feedbacks between herbivores and their resource base. Both competition and facilitation provide mechanisms that may increase or decrease the likelihood of direct (contact) or indirect (environmental) disease transmission. Competing herbivores may seek out the same resource patches or segregate into different patches due to competitive exclusion. In extensive farming systems in southern Spain, Wild Boar density is positively correlated with cattle density but negatively correlated with domestic pig density (Carrasco-Garcia et al. 2016). East-African savannas, short grass grazers such as Blue Wildebeest select areas grazed by livestock, whereas bulk grazers such as African Buffalo avoid these areas (Bhola et al. 2012; Tyrrell et al. 2017). In turn, facilitation may lead herbivores to share resource patches such as grazing lawns or use these areas in sequence due to post-grazing regeneration (Odadi et al. 2011).

Although domestic and wild herbivores can share foraging resources, when resources are abundant and widely distributed, free ranging wild herbivores generally avoid mingling with livestock due to direct competition (Riginos et al. 2012) or fear of humans. However, the behavioral response of each species differs. For instance, in a dystrophic savannah system in Zimbabwe, African Buffalo nearly completely avoid cattle at the home range scale whereas elephant bulls favor temporal niche shift, allowing their home range to overlap with cattle by avoiding direct encounters during the day and using the shared range during the night (Valls-Fox et al. 2018a, b). These differences imply that each species may play a different role in pathogen transmission networks at livestock-wildlife interfaces (VanderWaal et al. 2014).

In situations of resource limitation, key resources distributed in discrete localized patches create hotspots where animals aggregate, acting as hubs in epidemiological networks. In tropical savanna ecosystems, most herbivore species are water dependent and their distribution is constrained by access to water, particularly during the dry season (Ogutu et al. 2014). Seasonal variation in resource availability reveal similar patterns across ecosystems, resource-driven encounters increase when resources become scarce (Barasona et al. 2014; Kaszta et al. 2018; Valls-Fox et al. 2018a, b; Zengeya et al. 2015) due to the limited mobility of animals that are forced to share the remaining key resource patches. Counterintuitively, when resources are very scarce, increasing resource availability can increase spatial overlap and contacts (Borchering et al. 2017). To explain this pattern, Borchering et al. (2017) provide a mechanism based on the assumption that animals have a limited movement radius around their core home range. As a result, when resources are sparse each animal or group of animals use different resource patches that are too far apart for them to interact (Fig. 6a). When resource density increases, animals have access to multiple

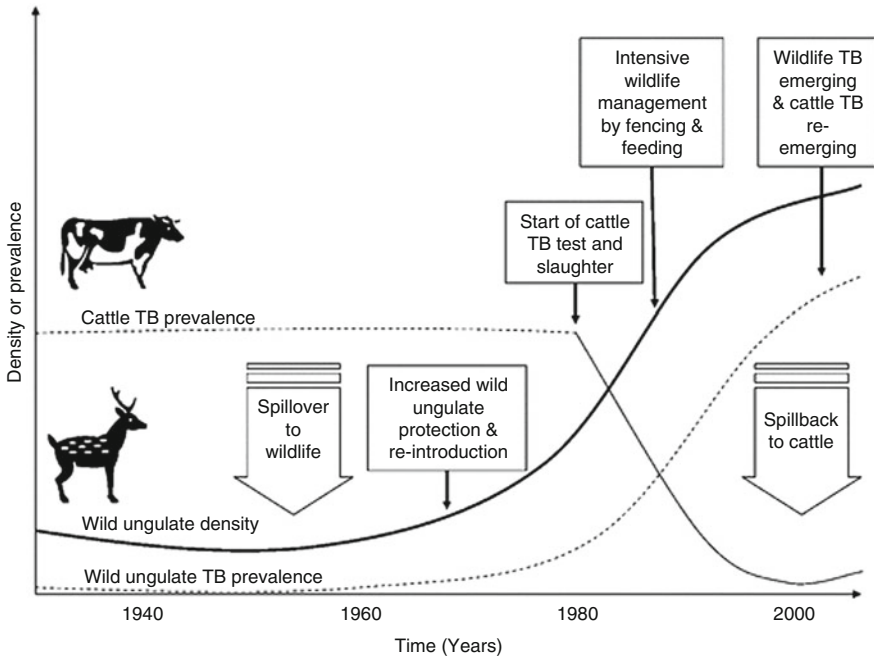


Fig. 6 Evolution of bovine tuberculosis prevalence and transmission (spill-over and spill-back), in livestock and wildlife populations in southern Spain (reproduced from Gortázar et al. 2010). The solid line represents the demographic trend of wildlife (mainly Wild Boar *Sus scrofa* and Red Deer *Cervus elaphus*). Dotted lines represent bTB prevalence in cattle and wildlife

patches and are likely to come in contact with one another particularly if these patches are located close to the interface (Fig. 6b). As resource density increases more (Fig. 6c), animals can adopt a more flexible behavior and avoid encounters. Managing key resources, such as waterholes, at domestic-wildlife interfaces may substantially reduce the probability of contact (Barasona et al. 2014; Valls-Fox et al. 2018a, b). Direct management of livestock movement patterns accounting may be used to limit contact at the most risky areas (such as forest/pasture ecotones that may be used for hay) or at critical time periods. However, top-down mechanisms such as predation risk may modify these patterns, as will be illustrated in the next paragraph.

Predation

The presence of large carnivores is likely to affect habitat use by herbivores (Valeix et al. 2009) and may indirectly influence where interactions occur (e.g., Fig. 6), and consequently disease transmission between sympatric hosts. For instance, a study in Yellowstone National Park, USA, discussed the potential for gray wolf (*Canis*

lupus) restoration to decrease the spatio-temporal overlap between bison and elk and decrease the transmission risk for brucellosis (Proffitt et al. 2010).

In Africa, where human population growth is high, especially at the edge of protected areas (Bongaarts and Sinding 2011; Wittemyer et al. 2008), and where livestock plays a key role in the livelihoods of rural families (Herrero et al. 2010), an understanding of where, when, and why livestock interact with wildlife is a priority (du Toit 2011). The use of space by cattle in African rangelands is likely to reflect the trade-offs between potential benefits (i.e., access to resources such as water and grazing) and potential costs for livestock owners, including the risk of predation by wild carnivores (Kuiper et al. 2015), disease transmission from wild reservoirs (de Garine-Wichatitsky et al. 2013b), and fines or confiscation of livestock grazing illegally inside protected areas. These potential costs may thus influence husbandry decisions, such as when and for how long livestock are allowed to graze within protected areas (Alexander and McNutt 2010). These decisions are likely to influence the different disease transmission hubs, from wild to domestic hosts or inversely, through direct interactions, the environment and/or vectors evolving in wild or anthropized areas. Further, the presence of large carnivores is likely to affect habitat use by herbivores (Valeix et al. 2009), and may indirectly influence where interactions and consequently disease transmission between sympatric hosts occur (Proffitt et al. 2010).

A recent study explored the potentially modulating influence of African Lion (*Panthera leo*) presence on interspecific interactions on cattle incursions inside a protected area and thus the risk of disease transmission (Miguel et al. 2017b). They combined a longitudinal serological cattle survey for FMD, GPS-collar data from three sympatric species (lion, buffalo, and cattle), and cattle owner interviews in Zimbabwe. No sign of significant short-term interactions (i.e., time window of 24 h) was found between cattle and lion, although they frequently used the same areas. More interestingly, the analysis of incursion frequency time series revealed that lions made frequent incursions in the buffer between rural and protected areas a few days to a few weeks after buffalo had used it, suggesting a potential attraction effect of buffalo on lions. Not only did lions use the buffer a short time after buffalo (3 days), but also after longer time lags (up to 40 days). Conversely, buffalo, the main prey for lions in this ecosystem (Davidson et al. 2013), did not use the buffer zone when it had been occupied by lions a few weeks before, which suggests avoidance of lions by buffalos, but at a temporal scale that is not traditionally considered. Under such scenarios, lions could play a role of “natural barrier” between sympatric species by reducing the spatio-temporal overlap between cattle and buffalo in the buffer zone, consequently reducing the likelihood of direct or indirect contacts and subsequent transmission risk of diseases like FMD (Miguel et al. 2013; Miguel et al. 2017b; Proffitt et al. 2010).

The results also showed that cattle entered the buffer zone of the protected area almost exclusively during the rainy season, which was also observed in a similar ecosystem in Zimbabwe (Kuiper et al. 2015). This pattern is informative at three levels. First, the rainy season coincides with the season when resources (grazing and water) are the most abundant and allow access to a larger home range (“ecological

driver”). In addition, cattle can substantially damage crops and are driven into the buffer zone away from the communal areas during the growing season (“anthropogenic driver”) (Perrotton et al. 2017). The amount of agricultural work required, and the necessity to keep cattle herds out of growing fields, encourage cattle herds to be grazed away from communal lands and hence more into the buffer zone (Murwira et al. 2013). After crop harvest, cattle are often fed with crop residues in fields during the early dry season, which constrains cattle movements to areas closer to villages and farther from protected areas as described in Perrotton et al. (2017). The availability of resources (vegetation and surface water) inside protected areas should be attractive for cattle owners during the dry season. At this time, surface water is scarce and grass is rare or trampled in the vicinity of homesteads and driving cattle inside the protected areas would represent an opportunity (Prins 1996; Zengeya et al. 2011). However, the buffer zone was not used by cattle during the dry season. This suggests that cattle owners decide to rely on lower-quality resources in the communal land, maybe in order to avoid the risks of infection with FMD virus or tick-borne diseases, and/or predation in the protected area. It has been shown that cattle are more often killed by lions during the rainy season than during the dry season. Indeed, seasonal use of protected areas during the crop-growing season increases vulnerability of cattle to lion depredation (Kuiper et al. 2015). The optimized strategy for cattle herders at the wildlife-livestock interface might be to decrease the likelihood of livestock depredation by avoiding the use of protected areas when the constraints in communal lands are acceptable (i.e., when the crop residues are available). Considering that the risk of being fined for entering the protected area is the same throughout the year, this effect alone does not explain the seasonal variations of cattle buffer use. Contrary to what was found in other similar ecosystems with less predation pressure (Caron et al. 2013; Miguel et al. 2013; Zvidzai et al. 2013), the study showed that the rainy season was the key season for pathogen transmission risk and exposure to predation (Miguel et al. 2017b).

Predator-prey-host interactions, the availability of resources driven by seasonality and human herding practices adapting or reacting to the perceived state of the system, all influence FMD transmission to cattle. The risk of pathogen spill-over between sympatric host populations is restricted to limited areas at specific seasons, and avoidance of predators could potentially be manipulated in order to mitigate interspecific disease transmission. A better picture of the patho-ecosystem would require an understanding of how cattle owners make their herding decisions and according to which clues and perceived risks: disease, predation, or risk of fines? The integration between biological and social sciences is therefore necessary to better understand and manage the risk of disease transmission at complex wildlife-livestock-human interfaces, which are hotspots in the context of emerging infectious diseases (Woolhouse and Gowtage-Sequeria 2005).

Anthropogenic Drivers of Wildlife-Livestock Interactions

In the “Era of Human-induced Diseases” (Chaber 2017), there are numerous examples of how human activities may have a profound influence on disease epidemiology in interface areas (Daszak et al. 2001; Jones et al. 2013). The management of wildlife populations, inside or outside protected areas, and the associated recreational and economic activities, have a direct or indirect impact on wildlife-livestock interactions and pathogen transmission among them. Similarly, livestock belongs to farmers, whose management practices are the results of changing demographic, economic, and socio-cultural parameters, with direct and indirect consequences for wildlife-livestock interactions and disease transmission. Livestock health policies and management have evolved over the past decades, at a different pace and with contrasting results in industrialized versus developing countries. But one general trend is the increasing recognition of the importance of integrated cross-sectoral management of animal health (Binot et al. 2015) and including environmental and wildlife conservation agencies.

The links between livestock and wildlife health, and the associated risks for public health, livestock production, and wildlife conservation have been reviewed for Europe by Gortázar et al. (2006). The evolution of bTB in cattle and wildlife populations in southern Spain over the past century (Gortázar et al. 2010) illustrates these relationships and their implications for management (Fig. 6). After an initial decrease of bTB prevalence in cattle following the test-and-slaughter control program established during the early 1980s, the prevalence reached very low levels during the early 2000s and started rising again. This trend was not completely unexpected from an epidemiological point of view, as it was partly attributed to bTB spill-back from increasingly abundant wildlife. The active conservation of game species put in place after the 1970s resulted in an increase in wild ungulate densities. High levels of bTB prevalence have thereafter been recorded in wild ungulates in central and southern Spain, maintaining a multi-host system of bTB transmission that more than likely involves the livestock populations (Gortázar et al. 2010).

Similar epidemiological situations for bTB could arise in the future in other regions, particularly in Europe and North America that experience comparable increases in wildlife populations. Beyond the particular case of this disease, the following sections will illustrate the complex and far-reaching influences of human activities on wildlife-livestock interface areas adopting two different perspectives: protected area management and pastoralism.

Management of Protected Areas

Wildlife-livestock interfaces have evolved in the last centuries under various social, economic, and demographic pressures, often driven by factors that were independent

or distantly related to biodiversity conservation (Andersson et al. 2013), and at an increasing pace in the last decades with the creation of protected areas. The next section will describe how the evolution of livestock management (e.g., pastoral activities in Africa), has profoundly transformed disease ecology at the interface. But we must also consider the other side of the coin and evaluate how the remaining “natural landscapes” kept by humans under some level of protection (e.g., national parks, hunting reserves, and conservancies) have evolved throughout the twentieth century and what were the consequences for wildlife-livestock interfaces.

The emergence of the conservation paradigm in the twentieth century, which created reserves and national parks, has impacted the remaining natural landscape in several ways. First, it created land use boundaries around the protected “natural landscape.” De facto, these land use boundaries created a virtual wildlife-livestock interface that would evolve according to the socio-ecological context. Land use boundaries lead to different regulations being applied on each side of the boundary. On the protected side, the control of human activities (from tourism only to a wider array of activities such as natural resource collection or cattle grazing) modified the wildlife-livestock-human interactions. In addition, the management of protected areas includes modifying the environment through the creation of water holes, roads, and camps, and the impacts of these on wildlife ecology and distribution as well as on the (limited) human activities within the protected area must be considered.

For example, the impact of logging roads in Central African forests on increasing wildlife trade has been demonstrated (Burivalova et al. 2014). Similarly in southern Africa, African buffalo populations are negatively impacted by the human footprint within protected areas (Naidoo et al. 2012). Therefore, the management of protected areas has consequences on wildlife-livestock interactions and on pathogen and disease transmission. In Central Africa, the great ape tourism industry that constitutes an important source of funding for conservation at the country level, has created a human/great ape interface that promotes exchange of bacterial species (Rwego et al. 2008). Ultimately this transmission of pathogens between humans and apes may threaten great ape conservation (Goldberg et al. 2008).

A classical model of land use management around protected areas to mitigate human-wildlife conflicts is to surround the core national park with other types of protected areas (e.g., controlled hunting zones) that will buffer the impact of human activities inside the protected area and conversely decrease human-wildlife conflicts negatively affecting surrounding rural areas. A more recent model, developed mostly in southern Africa and progressively expanding in East Africa, relies on the creation of “TransFrontier Conservation Areas” (TFCAs). TFCAs interconnect protected areas (under different land uses) and rural landscapes in a vision to integrate biodiversity conservation and local rural development (Cumming et al. 2013). By promoting wildlife population connectivity and a more socio-ecosystemic approach of the landscape, these initiatives should lead to a better management of wildlife-livestock interactions, and thus reduce the risk of pathogen transmission at these interfaces. These positive outcomes will take time to emerge but the health issues in TFCAs have been highlighted as important and potential threats to the TFCA initiatives (de Garine-Wichatitsky et al. 2013a; Osofsky 2005).

The proximity of protected areas impacts the risk of pathogen transmission to livestock. In fact, this risk of transmission at the wildlife-livestock interface has been a major driver for the establishment and management of protected areas, which have often been established in marginal agricultural lands for that very reason (Andersson and Cumming 2013; Cross et al. 2007). But disease management at wildlife-livestock interfaces has evolved, and elimination of wildlife is increasingly considered an unacceptable solution. The control of FMD (see Section “Wildlife-to-Livestock”) could arguably be considered one of the major constraints to the coexistence of livestock and wildlife in southern Africa (Ferguson et al. 2013). Strict land policies on animal movement controls (e.g., fencing) have sometimes locally solved the problem when they have been strictly applied (Thomson 1995). The lack of sustainability of these control options and the indirect costs they induce have raised concerns for decades among conservationists (e.g., Taylor and Martin 1987). Even the best maintained fences cannot restrain the movements of all wild animals (Dion et al. 2011; Suttmoller et al. 2000).

Evolution of Pastoralism and Consequences for Wildlife-Livestock Coexistence in Africa

With its human population exploding, the speed of change in the socioeconomic and political landscapes in Africa is hard to comprehend, with far-reaching consequences for wildlife-livestock coexistence. Predictions during the early 2000s were for an African population in 2020 of 1 billion; the figure in 2016 was already 1.2 billion, while meat consumption (livestock excluding fish) was estimated to reach ten million kg by 2020, the true figure being closer to 16 million kg by 2013 (Desiere et al. 2018). The demand for meat will rise in Sub-Saharan Africa and pending shortages cannot be taken up entirely by traditional livestock systems and rangelands, but the traditional livestock production sector will play a significant role. The ongoing “tragedy of the commons” for competitive use of disputed rangelands involves land grabbing for crop agriculture, irrigation schemes, and hydroelectric or extractive industries, usually promoted by State and private actors. Pastoral communities are squeezing into less and less land for livestock, changing water and forage dynamics, and driving socioeconomic decline.

One strategy for pastoralists in the face of this loss of open resources is to reduce livestock numbers, diversify livelihoods and practices, and inevitably sedentarise, if not permanently, at least on a more frequent basis by shifting to agro-pastoralism or mixed livestock and cropping land use. These communities have the opportunity to develop more sophisticated socioeconomic models and become part of the conservation management system, which is to match stocking densities to resource availability rather than the age old “as many as will survive” policy of traditional nomadic pastoralism. This change diversifies the livelihoods of these communities beyond herding, including settlement in market towns to process livestock rather than

relying on itinerant traders (e.g., Mangesho et al. 2017) and using mobile phone technologies to gather market information and trade directly rather than through middlemen. These new developments add much needed value to their economy. Diversification of these communities into a wider landscape and range of work activities is inevitable under these pressures and opportunities. It enables adaptation and compensation for loss of assets or resource access, including (sometimes remote and part time) employment in other sectors in both urban and rural environments, with remittance supporting at-risk family groups such as the youth and elderly in rural rangelands. To some extent, this inevitably leads to more sedentary livestock, cattle and small stock, and associated land degradation, which was uncommon in nomadic systems.

Another pressure on pastoral communities is that traders increasingly demand a different animal product than the tough “rangy” livestock of old, and this is being promoted and achieved through the introduction of “so-called improved genetics” for indigenous breeds or replacement of traditional stock altogether. The main externality of this change is increasing vulnerabilities to and expression of disease, with the trade-offs being increased milk or meat products and more marketable meat. Traditional livestock have shown considerable resilience to diseases, especially indigenous breeds. They have developed tolerances to a range of pathogens in the ecosystems they have occupied for millennia and co-evolved with. Pathogens, which can devastate imported livestock (e.g., *Bos taurus* European breeds) and often did during colonial times, include FMD, trypanosomiasis, theileriosis, bTB, and many others. These diseases are endemic in traditional livestock, but they result in relatively mild conditions with minimal impact. Examples of this include the resilience among Maasai cattle against FMD in Kenya and Tanzania, bTB resistance in Ethiopian breeds of cattle, Ankole cattle in Uganda, and resistance to trypanosome infection amongst the dwarf cattle breeds of West Africa (Ameni et al. 2007; Meunier et al. 2017). With a fundamental shift from traditional livestock, not only will there be more pathogens circulating but more virulent variants will undoubtedly emerge. This will lead to economic loss, increased costs for control, and more impacts of pathogens on wildlife.

Pathogens, which historically spilled from wildlife into indigenous livestock to little negative effect, more often promoting endemic stability and co-evolution, are no longer tolerated where economic losses from disease arise among more vulnerable breeds. This leads to a more exclusionary management of stock and wildlife typified by the emergence of the livestock and wildlife sectors in colonial southern Africa over the twentieth century, where the introduction of European breeds promoted high loads of pathogens like bTB, FMD, and other pathogens (see Section “Livestock-to-Wildlife, and Back?”). This has also led to industrialization of wildlife systems and conservation concerns over genetic manipulation of wildlife for commercial purposes. In addition, rising profiles of disease in tightly managed wildlife can increase risks to livestock systems. Changing political circumstances in the southern African countries are beginning to reverse this process to some extent, with the abandonment of fencing as a tool in some areas with full agreement from the veterinary authorities. Global agendas change and the shift to sustainability is now at

the core of development (United Nations 2016). This allows for a fresh look at pastoralism in the food system and its contribution to future food and nutrition security in Africa, with less impact on the climate and environment. Pastoralism is not an outdated agricultural system, quite the reverse, it may resolve many of the challenges currently faced by the food system, biodiversity conservation, and the environment. More attention should be given to a One Health approach considering livestock, wildlife, humans, and environment to achieve a fair balance and mutual benefits across sectors and particularly when implementing disease control measures.

Way Forward: Toward Socio-Ecological Management of Wildlife-Livestock Interfaces

As illustrated throughout this chapter, wildlife-livestock interfaces are very complex and dynamic systems, where spill-over/spill-back of pathogens is at the core of disease ecology problematics. Pathogens must overcome a hierarchical series of barriers to cause spill-over infections, as recently illustrated for zoonotic pathogens by Plowright et al. (2017). Understanding how pathogens spread among complex multi-host systems through these barriers, in time and space, and identifying the drivers of wild and domestic host movements and contacts requires multiple disciplines and approaches, a combination of ecology (behavioral, community, molecular, spatial), epidemiology, and social sciences. The fact that spill-over and spill-back events are not occurring with the same frequencies and intensities is probably a widespread phenomenon (“asymmetric interfaces”), which should be explored more thoroughly, with potentially great implications for the management of diseases in interface areas.

Understanding how these barriers are functionally and quantitatively linked, and how they interact in space and time, will substantially improve our ability to predict or prevent spill-over events (Plowright et al. 2017). And several major conceptual and methodological advances have been made in various ecological fields during recent years, which provide us with unprecedented capacities to characterize pathogens, hosts, and vectors, track their movements and dispersal from molecular to population and landscape levels, and model disease spread (see Chapters “Collecting Data to Assess the Interactions Between Livestock and Wildlife” and “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”). But there is still a need for integrated holistic models linking demographic and societal factors to land use and land cover changes whose associated ecological factors help explain disease emergence (Wilcox and Gubler 2005) and the circulation of pathogens in interface areas. Despite considerable attention given over the past decade to One Health and EcoHealth approaches (e.g., Roger et al. 2016; Zinsstag et al. 2011), the interdisciplinary integration of ecological, biomedical, and social sciences into a single discipline of “disease

socio-ecology” still remains a major research frontier relative to challenges at the wildlife-livestock interface (see Chapter “Characterization of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”).

To sum, the main challenge ahead for improved wildlife-livestock disease management is not merely technical or even conceptual. It will necessitate a radical shift in attitudes toward wildlife, which should be considered more as an asset than a problem to be controlled (du Toit et al. 2017), and the strategic use of ecological complementarities between livestock and wildlife to promote coexistence (Fynn et al. 2016). Pathogen transmission between sympatric hosts is inevitable, especially between wild and domestic species that are taxonomically related. Further, eradicating diseases from wildlife populations is very difficult, and has rarely been successful. The history of the interface, where livestock and wildlife are framed in terms of conflict only and not synergy, is full of examples where veterinary interventions have largely exacerbated disease impacts or created catastrophic externalities for biodiversity conservation across the globe. A more socio-ecological understanding of disease is vital to fulfil human ambitions for sustainable systems into the future, to sustain both culturally, economically, and ecologically valuable livestock and wildlife populations.

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Part II
Regional Perspectives of Disease at the
Wildlife-Livestock Interface

Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Europe



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Introduction

Europe is the western part of the Eurasian supercontinent. It extends from Iceland in the West to the Ural Mountains in the East and from Arctic Islands in the North to Mediterranean coastal areas in the South. Throughout Europe, habitat change has been significant during the last 3000 years, with deforestation as a historically

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dominating feature (Kaplan et al. 2009). Land-use changes are still going on at a high rate, and it is estimated that annually 0.5% of the whole European territory changes its use between categories such as pasture, agriculture, forest or urban and industrial (EEA 2017). In the last 60 years, however, deforestation has been reverted and forest surface has grown in most if not all European countries (Fuchs et al. 2015). These massive changes in habitat, along with agriculture intensification and human population growth (>742 million inhabitants in 2018, 34/km², 74% urban; <http://www.worldometers.info/world-population/europe-population/>) have had significant effects on the European wildlife communities. Today, Europe is composed of 44 countries, of which 28 (until Brexit) belong to the European Union (EU). In 1970, Europe contributed 27.5% to global agriculture added value. By 2013, this share was only 15.5% (FAO 2015).

Biodiversity loss due to human-mediated habitat change (Fig. 1) has been more intense in Europe than in other less densely or more recently populated regions of the world. However, remaining biodiversity is still significant, particularly around the Mediterranean basin, in the alpine area and in remote regions. In general terms, opportunistic species that benefit from anthropogenic habitat change such as the red fox (*Vulpes vulpes*) or some urban and coastal bird species have seized the opportunity represented by these changes and have greatly increased their numbers (e.g. Rock 2005). Rural abandonment and growing woodland and scrubland habitats, along with agricultural intensification, favour the population growth of the native Eurasian wild boar (*Sus scrofa*) and several wild ruminants (Milner et al. 2006; Massei et al. 2015), often leading to overabundance and conflicts with agriculture including sanitary risks (Gortázar et al. 2006). Large predators are recovering almost Europe-wide due to this population explosion of their prey as well (and mainly) due to protectionist policies (Chapron et al. 2014). By contrast, specialist species and lowland species that are more susceptible to modern agriculture and habitat loss are in general terms declining (Donald et al. 2001). These changes imply that a few actors, including several carnivores, most ungulates and relatively few highly adaptable bird species, become the main wildlife species to consider at the European wildlife-livestock interface and regarding some vector (ticks) overabundance. Driven by the changes in habitat and animal populations, as well as in human behaviour, there is an emergence or re-emergence of infections shared between wildlife and livestock and considering that some of them are zoonotic, an increased impact of wildlife health on human health. Given this context, the goals of this chapter are:

- Describe the main characteristics of the potential interactions between wildlife and domestic animals in the European context.
- Describe the problems related to those interactions that can facilitate disease emergence (management of environment and livestock, sharing of pastoral resources, etc.).
- Discuss the possible impact of climate, environmental or socio-economic change on our capacity to successfully mitigate the sanitary consequences of wildlife-livestock interactions.



Fig. 1 Environmental changes in Europe include new “Naturban” areas (a mix of the urban and natural environment). **(a)** As an example, in this alpine valley, the scattered presence of houses is coupled with abandoned woods and pastures that host abundant populations of wild boars, roe deer, chamois, foxes and wolves. As a consequence, at the end of the rainbow in his backyard one can find, in spite of a jar of coins, **(b)** hundreds of ticks from different genera (*Ixodes*, *Dermacentor* *Haemaphysalis* and stages) infected by several pathogens

Socio-Economical and Biogeographical Circumstances of the Wildlife-Livestock Interface in Europe

The early development of agriculture in the Fertile Crescent, including domestication of the main livestock species since around the 12th millennium B.P., spread around the Mediterranean Basin for about 6000 years. From the Mediterranean, the agricultural technologies soon expanded westwards and northwards having a huge impact on European landscapes and wildlife, as well as on the economy of European societies. Neolithic economies changed the original biotic communities and local faunas were progressively replaced by a mixture of domestic animals and adaptable wild fauna (Zeder 2008). Along history, many factors facilitated the growth and expansion of European livestock and the invention of agriculture multiplied human population growth by five (Gignoux et al. 2011), and this, in turn, generated a need for additional animal-derived commodities. In many areas forest reduction was the result of a mix of direct and indirect activities as in many cases deforestation was mainly driven by an increased wood demand for building or heating (not only for fireplace, but also for forge). Anyway, continent-wide deforestation and the development of agriculture created pastures and generated surplus feed for maintaining livestock during the limiting season. More recently, in the last centuries, growth of the mean annual temperature and further land-use change had a positive effect on densities of wild and domestic ungulates, probably through improving food supply (Jędrzejewska et al. 1997). In the last century in many areas rural abandonment has let a recovery of wooded areas with a move from initial scrubland to mature forests of coniferous or, mainly, deciduous trees. These progressive changes in soil coverage drive also the animal communities that in many areas are now represented by species that inhabit forests and benefit also by mast production and the presence of neighbour's cropland. Linked with this spatial change, the human dimension has also greatly changed with a move from the "rural approach" that considers animals as useful or pest, towards a conservationist approach and in the last decades with some fringe that shows an animalist approach. In the vast majority of European countries, the number of hunters is declining, and this can pose a problem in the control of some opportunistic species such as wild boar (Massei et al. 2015).

Because of this early development of agriculture and livestock breeding, several major livestock diseases have their roots in Europe. The change from small hunter-gatherer to large agricultural communities was associated with the emergence of contagious diseases including many food-borne and vector-borne ones, often of animal origin (Jones et al. 2013). Europe has been a historical source of animal diseases, with animal tuberculosis as an example of disease spread worldwide through cattle trade. Other cases of disease emergence were linked to the introduction of domestic animals of European origin into new regions, for instance rabbits and myxomatosis (origin South America) or sheep and bluetongue (origin South Africa). In many cases, alien pathogens have been introduced as is the case of the big liver fluke (*Fascioloides magna*) accidentally introduced from North America in some European countries that has spread in many areas with a negative

impact on some populations of deer (Novobilsky et al. 2006). By contrast, Europe is also at the forefront of disease control at the wildlife-livestock interface. For instance, fox rabies and classical swine fever in wild boar are two shared viral diseases which have been largely controlled in western Europe through oral vaccination (Müller et al. 2015), and Foot and Mouth disease has been successfully controlled in several occasions (Alexandrov et al. 2013). Even the use of baits with praziquantel for the control of *Echinococcus multilocularis* in foxes has been successfully adopted (König et al. 2019), but, as the economic crisis has driven resources towards other topics, the sustainability of the cost of such initiative may be at stake, especially true when notifiable diseases are not involved.

The Prevalent Livestock, Farm Typologies in Every Region and Opportunities for Interface

Europe is a major global dairy, beef and pork producer, and maintains also significant poultry, sheep and goat populations. In 2016 (last census), half of the EU-28 livestock units (LU, a reference unit which facilitates the aggregation of livestock from various species and age as per convention, based on nutritional requirements) consisted of cattle, one quarter of pigs and one-sixth of poultry. France, Germany, Spain and the UK had the highest number of livestock units. However, the Netherlands, Belgium and Malta had the highest livestock densities, while Balkanic and Baltic countries had the lowest ones (https://ec.europa.eu/eurostat/statistics-explained/index.php/Agri-environmental_indicator_-_livestock_patterns).

Improved monitoring of livestock and large-scale trends are needed to depict interfaces and evaluate broad-scale risks in Europe, for which high-resolution data discriminating among farming systems would be required. As illustrative of the need for better, harmonised and standardised data in the domestic compartment, Fig. 2 of Chapter ““Host Community Interfaces: The Wildlife-Livestock”” suggests low reliability when predicting the wild boar-pig interface (irrespective of farming type) at European scale (ENETWILD consortium 2020, www.enetwild.com).

Dairy cattle and beef cattle are present all over Europe, with dairy dominating in the more productive and pasture-rich rainy and flat regions and beef cattle more dominant in mountain regions, including the Alpine region and the dry Mediterranean pasturelands. Variability regarding farm size and characteristics is huge, and most cattle farms have a limited biosafety regarding the possible contact with wildlife. Beef cattle sharing communal pastures with other domestic and wild animals are probably at the highest risk, for instance regarding animal tuberculosis, but even most of the dairy cattle herds will have direct or indirect opportunities to contact wildlife such as badgers, wild boar and deer (for contrasting examples, see LaHue et al. 2016; Acevedo et al. 2019)).

While most pigs are kept in modern industrial farms where contact to wildlife is limited, millions are kept open-air or semi free-ranging due either to regional



Fig. 2 Examples of potential interactions between pigs and livestock in different habitats and husbandry regimes over Europe. Wild boar is probably one of the most relevant target species for integrated disease surveillance in Europe and, eventually, for targeted disease control interventions at the interface (e.g. Classical swine fever, African swine fever, tuberculosis). The left column represents the animals, and the right one, the habitat they inhabit, respectively. (a–b) Domestic pig foraging free on alpine pasture in the French Pyrenees close to the Spanish border. Free-range pig husbandry occurs in many European countries. This is a risk for disease transmission. (c–d) Direct contact between wild boar and pigs in South Central Spain, where Iberian pigs typically graze savanna-like habitat conformed by oaks (dehesas) during the mast season. (e–f) Indirect interaction between extensively reared pigs and wild boar in Sardinia island (image A. Pintore). (g–h) Indirect interaction between wild boar and cattle in Doñana National Park (South West Spain) in pastures associated with the marsh-woodlands ecotone

traditions based on the use of extensive grasslands such as the Mediterranean woodlands or due to the increasing consumer demand for high-quality and more animal-friendly open-air production. This creates challenges for disease control.

Moreover, backyard pigs are still common in some countries or regions such as the Danube delta and this may represent a risk for some pathogen transmission as in the case of *Trichinella spiralis* that is still a problem in the area (Pozio 2019). Even if biosecurity has been greatly increased in most intensive pig farms, some diseases, such as classical swine fever, may enter even into high-biosafety farms. On the contrary others, such as swine brucellosis, are more often linked to open-air production and contact with wild boar (<https://thepigsite.com/articles/the-role-of-outdoor-farms-in-the-spread-of-african-swine-fever-in-europe>). Recently, the ongoing African swine fever crisis has boosted research about pig farm biosafety in Europe in order to face this notifiable disease, but also to increase preparedness towards this new emerging pathogen.

The same trend observed in pigs holds for poultry: while numerically the industrial farms with generally good biosafety are dominant, open-air production is growing and backyard holdings are still prevalent in many parts of Europe (EFSA 2017). Also, in this case, the move towards more open-range production to warrant better animal welfare or the increase of backyard poultry due to the need of many people of more organic and ethical food creates new challenges. Furthermore, the economic crisis of the last years encourages many people to breed poultry for self-consumption. So, the high farm density and the presence of open-air and backyard production systems, sometimes in close link to habitats that harbour significant waterfowl populations such as for instance in southwestern France, creates ample opportunities for interactions with wildlife. Even if many pathogens may benefit from this situation surely the biggest threat is represented by avian influenza that can easily spread in some contexts (Andronico et al. 2019).

Regarding other livestock, sheep and goats are less uniformly distributed, as these species are able to use less productive habitats and are therefore more typical of extreme climates in the northwest and in the south, around the Mediterranean. The proportion of intensive sheep and goat farming has grown in recent decades, but most of the herds still have access to pasturelands and are therefore in contact with wildlife and eventually, with other livestock, particularly cattle and free-range pigs.

Minor livestock species, which can locally be abundant, include equids, gamebirds, farmed deer, South-American camelids and a diversity of other recently domesticated species even if their contribution to the wildlife-livestock interface and to infection maintenance can be locally significant. Fish-farming is also a relevant activity in some of Europe's coastal regions, but it is not addressed in this chapter.

The livestock sector contributes €168 billion annually to the European economy (45% of the total agricultural activity), helps in levelling the trade balance and creates employment for almost 30 million people, often in rural areas that are at risk of depopulation (http://www.animaltaskforce.eu/Portals/0/ATF/Downloads/Facts%20and%20figures%20sustainable%20and%20competitive%20livestock%20sector%20in%20EU_Final.pdf). While the relative contribution of Europe to the global agricultural GDP is declining, the European livestock sector is still significant and one of the most modern ones in terms of animal health and welfare. The EU has an animal health law (AHL; https://ec.europa.eu/food/animals/health/regulation_en) and modern veterinary services with common disease control strategies. The AHL

considers aspects such as climate change, disease emergence at the interface including vectors, and wildlife.

The Wildlife

European bioregions are defined by official delineations used in the Habitats Directive (92/43/EEC) and for the EMERALD Network set up under the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention). GIS data can be accessed in <https://www.eea.europa.eu/data-and-maps/data/biogeographical-regions-europe-3>. Of the 11 bioregions defined by the European Environmental Agency, the largest ones are the Continental (large parts of central and eastern Europe) and the Boreal (Baltic and northern Russia), followed by the Mediterranean (the Iberian, Italic and Balkanic peninsulas) and the Atlantic (northern Iberia and central and northern European west coasts) ones. The Alpine bioregion is split into several spots following the main mountain chains (Maiorano et al. 2013).

There are about 700 bird species in Europe, and they represent an enormous biodiversity and recreational value (http://ec.europa.eu/environment/nature/conservation/wildbirds/eu_species/index_en.htm). Most species can potentially be involved in the epidemiology of shared infections. Some species however are scarce and only locally distributed, while a few others are widespread, at least regionally abundant, and hence more commonly present at the wildlife-livestock interface (Figs. 2, 3 and 4). The following Table presents a simplistic overview of some key groups and their possible roles at the interface (Table 1).

Regarding mammals, all groups include potentially relevant species for the wildlife-livestock interface. However, a handful of more successful and widely distributed ones are at the top of the list. The following paragraphs address this by taxonomic groups.

Among the rodents, two groups are of particular relevance. Peridomestic mice and rats, for instance, are important bridge hosts regarding zoonotic bacterial pathogens such as *Salmonella* or *Leptospira*, among others, or good intermediate hosts for *Toxoplasma gondii* or *Neospora caninum* with important effects on human health in the first case and on livestock abortion storms in the second. Voles and other rodents sometimes are important in the cycle of *Mycobacterium microti*, an emerging member of the *Mycobacterium tuberculosis* complex increasingly reported from wild boar, deer and cattle, mainly in Atlantic and Alpine bioclimates. Small rodents are also the reservoir for some emerging tick-borne pathogen such as *Borrelia burgdorferi*, tick-borne encephalitis or zoonotic *Babesia microti* and *Babesia venatorum*.

Lagomorphs (hares and the European wild rabbit) has been recently demonstrated to be a maintenance host for *Leishmania infantum*. Leishmaniosis is, due to climatic changes that now let the vector to survive also in continental and climate areas (Ferroglia et al. 2005), an expanding zoonotic vector-borne disease that is also important for wild canids and domestic dogs.



Fig. 3 Examples of indirect interactions in Mediterranean livestock extensive systems (a) in a waterer and (b) a seasonal stream, involving wild boar and red deer, the most widely distributed wild ungulates over the continent (together with roe deer). Pigs, cattle and goats are observed. The need to identify interactions with the potential for pathogen transmission among the community of hosts at the wildlife-livestock interface has led to the use of multiple methodologies, such as camera trapping. The study of both direct (i.e. the simultaneous presence of two individuals at a certain point) and indirect (i.e. the sequential presence of two individuals at a certain point) interactions are addressed in Chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife”



Fig. 4 Wildlife reservoirs harbour microbial organisms or parasites that are mostly commensals or non-pathogenic in the wild reservoir but became pathogenic for domestic species and eventually humans and vice versa. Some pathogens adapted to the human, the wildlife or the domestic compartment, respectively, may be transmitted between these compartments thanks to bridge hosts species, such as domesticated animals or peridomestic wildlife. The white stork (*Ciconia ciconia*) is a traditional trans-Saharan migrant in Europe. Recently, storks have adapted to rubbish dumps (a–b) as a reliable food source and have reduced migratory distance or become sedentary. (b) White stork interacting with cattle at a water source (pond) in central Spain. (c) The cattle egret (*Bubulcus ibis*) is a cosmopolitan species of heron, originally native to parts of Asia, Africa and Europe which has undergone a rapid expansion in its distribution. The image illustrates some individuals scavenging on discarded eggs (normally broken) in the periphery of a hen farm. (d) House sparrows (*Passer domesticus*) may bring health hazards to poultry facilities. The image was taken in backyard hen holding (note the unusual presence of a semi-domesticated roe deer). Images: courtesy of U. Höfle

Generally, rabbits are locally abundant, while hare population trends are generally declining, however, wild Lagomorphs have a domestic counterpart in the domestic rabbit that is important for meat production in the Mediterranean basin so the interface risk could be high in these areas.

Many infections of dogs and cats, such as rabies, distemper or feline leukaemia, can also infect wild carnivores generating conservation concerns. Even if the risk is usually linked to uncontrolled stray dog and free-roaming cat populations, the increase of outdoor activities of urban dogs when follow their owner or suburban areas, from one side and the increase of urbanisation of wild carnivore such as the red fox from the other increase the risk of the healthy interface. At the same time, European badgers have been shown to act as relevant maintenance hosts for *Mycobacterium bovis*, the main causative agent of animal tuberculosis, complicating the

Table 1 key groups of European bird species and their possible roles at the wildlife-livestock interface in Europe

Group	Examples	Relevant links with the interface
Urban and peri-urban birds, and birds that are common on farm premises	Rock pigeons, wood pigeons, collared doves, corvids, black-bird, starlings, sparrows	Close contact with human beings and livestock. Some are migratory. Some can act as bridge hosts, crossing farm fences and other barriers (sparrow, magpie). Others are frequent hosts for mosquitoes.
Ducks, gulls and waders	Mallard, diving ducks, black-headed gull, herring gull, lapwing	Many are migratory and most are gregarious. Their adaptation to aquatic habitats makes them relevant regarding infections linked to wetlands
Gamebirds: Pheasants, quail and partridges	Ring-necked pheasant, grey partridge, red-legged and chukar partridge, common and Japanese quail	Gamebirds belong to the same order as poultry (Galliformes) and share most infections. Many gamebird species are farmed and millions (probably >100) are released yearly to re-stock for hunting. Gamebird farming and releasing create many opportunities for infection sharing at the interface.
Carion consumers: Vultures, corvids; and waste consumers: Gulls, storks, corvids	Gulls, griffon vulture, raven, carion crow, magpie, white stork, starlings	On the one hand, necrophagous birds are important allies for the destruction of carcasses, contributing to a lower environmental persistence of infected remains; on the other hand, frequent rubbish-dump visitors such as gulls or corvids can act as bridges between these sites and urban or farm sites.

eradication of this zoonotic and communicable disease in livestock. Canids such as the abundant and widespread red fox and the expanding wolf participate in the cycles of many viral, bacterial and parasitic infections as the before mentioned *Leishmania infantum* (Oleaga et al. 2018) or hydatidosis (*Echinococcus granulosus*—wolf *E. multilocularis*—fox, e.g. Sobrino et al. 2006). Hence, carnivores and their diseases at the interface are often triggers of human-wildlife conflicts in Europe.

European wild ruminants belong to two main families, cervids and bovids, and both share several infections with domestic animals, mainly ruminants (Putman and Apollonio 2010). Regarding the cervids, the most abundant one at the European scale is probably the roe deer. For several reasons, this widespread selective browser is not a very relevant host for shared infections. Instead, deer belonging to the subfamily Cervinae, such as red deer and fallow deer, do participate in the

epidemiology of many relevant shared infections including bluetongue, tuberculosis and a large list of tick-borne diseases (Gortázar et al. 2016) Regarding bovids, their distribution is patchier, but they are locally relevant for infections at the interface, sometimes as a source of infection (e.g. *Brucella melitensis* spill-over from Alpine ibex to cattle, Mick et al. 2014) and sometimes as victims of spill-over from livestock (e.g. sarcoptic mange in Iberian ibex and Cantabrian chamois). Among the wild ruminants, the locally abundant and generally widespread red deer is possibly the single most relevant species at the interface in Europe.

However, another artiodactyl, the Eurasian wild boar, is possibly the most important wild host at the interface. This is because, being the ancestor of the domestic pig, wild boar share potentially all relevant infections with their domestic counterpart, but are also implicated in other shared zoonotic infections such as hepatitis E and tuberculosis. Wild boar are expanding both in geographical range and in number throughout Europe, generating concern regarding disease maintenance and disease emergence (see boxes).

Bats, insectivores and other mammals are occasionally relevant for diseases at the interface, but in Europe generally this occurs at a local scale and so they are less relevant than the above-described groups. Of all the species mentioned in this section, rabbit, badger, fox, red deer and wild boar are probably the most relevant targets for integrated disease surveillance and, eventually, for targeted disease control interventions at the interface. A general overview of the status of transmissible diseases in European wildlife has been recently updated (Yon et al. 2019).

The Disease at the Interface: One Heath Perspective

Till now wildlife diseases have gathered authority's attention mainly when a communicable disease is involved. So, a few shared diseases have a strong impact on the European economy, with implications beyond the wildlife and livestock sectors. Tuberculosis is currently regarded in many parts of Europe as the main sanitary problem in cattle and the factor making the difference between profit and loss, especially in beef herds from TB-endemic countries (see Box 1). But beyond that, the badger TB-debate also confronts the urban and rural society, especially in the UK. A second example is wild boar population control, either for TB control in Iberia or for ASF control and prevention elsewhere in Europe (see Box 2). Among other actions, reverting the current wild boar population trends requires feeding bans, which are not popular among hunters, and increased culling, which is opposed by animalist-oriented public. In fact, Europe is the historical source of animalism, and the so-called Bambi-syndrome generates strong debate wherever wildlife is harvested for hunting purposes or culled as an intervention for disease control. Progressively, this debate is expanding to question the very existence of livestock production. More and more, interventions at the wildlife-livestock interface will require prior negotiations and involvement of stakeholders from the livestock and

the hunting sectors, and the more open-minded conservation NGOs as the animalist fringe is unlikely to enter any agreement.

However, many reports clearly highlight the new challenge played by wildlife diseases for the One Health perspective in Europe. As stated above Europe is a highly populated continent with a huge number of livestock and pet animals, but also, in the last decades, a significant increase in many wild species abundance and distribution. This is the heritage of century of human activities (practical and cultural) that is still in progress and we are facing a new era where the rewilding of many lands, with the consequent increase in many wild species, will coexist with a more fragmented landscape with an increment of suburban areas that will boost the overlapping of wild and domestic animals and of animals and humans also for pathogen transmission. Land-use and climatic changes are reshaping also vector distributions and abundance and, except for the case of sandflies and leishmaniasis, mosquito driven infections, such as West Nile Virus, has also increased in the last decades due to the introduction of new mosquito species. Ticks and tick-borne diseases are a health issue of greater concern as it has been shown that up to 75% of pathogens found in ticks collected from dogs are of sylvatic origin (Zanet et al. 2020) and that a high prevalence of zoonotic *Babesia* species, with wildlife as reservoir, has been found in ticks collected from humans (Battisti et al. 2020). The spread of *E. multilocularis* towards many new countries all across Europe up to the Scandinavian peninsula represents another example of the new scenario, to which contributed the introduction of a competent alien reservoir, the raccoon dog, the natural movement and increasing densities of red foxes, and the movement of domestic dogs that can act as the competent definitive host.

To face the challenge represented by this complex network between local and global chances, wild and domestic animals, vector and pathogen and human activities, wildlife medicine will move from the small circle of adept and embrace clearly the One Health approach, but moreover that wildlife diseases issue must be fully embedded in policymaker decisions. Europe is a crossroad and the movement of animals and goods can easily introduce new pathogens in the continent, and the fact that 24% of European wildlife EID have been introduced (Yon et al. 2019) clearly demonstrates this risk. Table 2 summarises examples of disease transmission from livestock to wildlife and vice versa.

Management Practices at the Interface (from Traditional Grazing Systems to Modern Techniques)

The European livestock sector is extremely varied regarding the management systems, ranging from backyard holdings and traditional pastureland use to ultramodern high-biosafety pig or poultry farming. However, all farming systems and all habitats are prone to the emergence of relevant shared infections. Avian influenza outbreaks have taken place in modern aviculture facilities, and both CSF and ASF eventually

Table 2 examples of disease transmission from livestock to wildlife and vice versa in Europe

Identified interface	Area/Region	Specific /Major diseases at the interface	Main characteristics and relevance
Birds	Widespread	Avian influenza ^a ; West Nile ^a and other Flavivirus; Pathogenic <i>E. coli</i> ^a and other zoonotic bacteria; ticks	Many species are migratory, others can act as bridge e.g. between contaminated and clean areas
Carnivores	Widespread	Distemper	Endemic with sporadic outbreaks impacting conservation of local populations
Carnivores	Eastern Europe	Rabies ^a	Zoonosis. Largely controlled by fox oral vaccination
Carnivores	Widespread except UK, Ireland, Finland and Malta	<i>Echinococcus multilocularis</i>	Transmissible also to dogs and cats, zoonosis.
Lagomorphs	Southern/East/Central Africa	Myxomatosis and Calicivirus infections	Some have huge impacts on wildlife and cascading ecosystem effects; farmed rabbits are vaccinated but may contribute to infection spread, as do wildlife translocations
Rodents	Widespread	Tularemia	Multiple hosts, including invertebrates, and spill-over to human beings
Wild boar	Sardinia and 13 countries of mainland Europe	African swine fever ^a	Severe impact on pig industry and on wild boar
Wild boar	Not reported in EU in 2018	Classical swine fever ^a	Severe impact on pig industry. Largely controlled by oral vaccination
Wild boar	Widespread in continental Europe	Aujeszky's Disease (pseudorabies) ^a	Almost under control in pigs but endemic in wild boar with occasional spill-over to carnivores
Wild boar	Widespread in continental Europe	Swine brucellosis	Epidemiological links between pig and wild boar
Alpine ibex	Northeastern France—Alps	Brucellosis (<i>B. melitensis</i>) ^a	Locally endemic with spill-over to cattle and sporadic human cases
Multi-species	Widespread	Sarcoptic mange	Variable effects, mainly on local wild ungulate populations
Multi-species	Widespread except Scandinavian countries	Animal tuberculosis ^a	Badger, wild boar, red deer and others

(continued)

Table 2 (continued)

Identified interface	Area/Region	Specific /Major diseases at the interface	Main characteristics and relevance
Multi-species	Widespread, depending on the distribution of the tick species linked to the specific disease, e.g. Atlantic habitats for <i>Ixodes ricinus</i> or Mediterranean ones for <i>Hyalomma</i> species.	Ticks and tick-borne diseases such as Anaplasmosis, Babesiosis, Lyme disease and Crimean-Congo haemorrhagic disease	Many mammals play a role in tick maintenance or tick-borne pathogen epidemiology

^aIndicates for each disease the existence of Governmental Programs

manage to enter high-biosafety pig farms. However, farming systems where one or several domestic species are in contact with wildlife (and farmed game) represent fertile ground for the maintenance of multi-host infections. Such settings include communal pastures, free-range and open-air production systems, and backyard or small-scale farm holdings.

All across the continent the transhumance of livestock (cattle, sheep and goat) from the low lands towards mountains in summer is common practice and this exposes livestock to contact with wild ruminants and increase the risk of transmission of pathogens, such as the case of brucellosis in chamois and Alpine ibex, Schmallenberg virus, vector-borne pathogens and a lot of other transmissible agents that represent a treat also for wildlife conservation such as Infectious keratoconjunctivitis (e.g. Giacometti et al. 2002). In contrast to the past when livestock ranging in the mountains in summer was largely represented by dairy ruminants, in the last decades, there has been a shift towards beef cattle that require less human labour. This however increases the risk of overlapping between wild and domestic ruminants. Social changes and EU agricultural policy will deeply affect this trend so wildlife and mutual transmission of diseases must be considered in every future EU plans.

Means of risk mitigation are available for all situations but will depend on the means of transmission of the target pathogens, on the local livestock and wildlife situation, and on the willingness and capacity of veterinary authorities, farmers and eventually hunters to take action on specific risks. Some settings are particularly challenging, for instance the open-air duck production in southwestern France, where contact with waterfowl and gulls is almost unavoidable and hence influenza virus will often circulate at the interface. A similar risk setting is given by those regions where free- or semi-free range pigs share woodlands or pastures with wild boar. ASF virus and other pathogens will, if entering the system, become very difficult to control due to the limited possible actions on the wild reservoir. Such settings occur on the Mediterranean islands of Corsica, Sardinia and Sicily (with ASF and CSF circulating on Sardinia, Fig. 3e), but also in southwestern Spain (where tuberculosis is a major concern) and in parts of Eastern Europe (for instance Mangalitsa pigs in Romania and Hungary).

Research on Diseases at the Wildlife/Livestock Interface

A few diseases at the interface, such as fox rabies, badger TB or CSF in wild boar, have traditionally received the most attention. In the last few decades, this selected group has grown to include avian diseases such as influenza and West Nile, emerging diseases in wild ruminants such as bluetongue, TB in other wildlife, brucellosis or mange, and several others. The key maintenance host species are well characterised although many aspects of transmission mechanisms and disease dynamics still deserve additional research. Also, in the last decades, European research on wildlife diseases has broadened its spectrum from the initial case reports and prevalence surveys to risk factor analyses using quantitative epidemiology tools and to intervention-oriented research aiming at improving disease surveillance and at assessing disease control options (Gortazar et al. 2015a, b, 2016).

However, long-term studies are still extremely scarce and only a few monitoring schemes do yield accurate time trends considering both host populations and disease prevalence (Vicente et al. 2013). One important gap is the generalised lack of the so-called “denominator data,” i.e. data on the susceptible (wild) host populations. Only for birds (and not for all) are there reasonable data available on numbers or at least relative abundances. For mammals in the best of cases, there are hunting back records, which can indicate large-scale trends but are generally not suitable for comparisons in space or at local scales. Therefore, in the context of the ongoing ASF crisis, the European Food Safety Authority promoted the ENETWILD consortium (www.enetwild.com, see Box 3). This consortium is combining abundance and distribution data with innovative spatial modelling techniques to generate valuable information on wildlife population size and trends, in collaboration with all EU member states.

Once a sound, integrated, disease and population monitoring scheme has been set up, options for intervention are relatively few. Direct intervention options include (1) prevention and biosafety; (2) vector control; (3) host population control; and (4) vaccination. Alternatively, indirect intervention may include zonification or compartmentalisation (Gortazar et al. 2015b). Some diseases, notably rabies and CSF, even imply obligatory wildlife vaccination if EU funding is requested for control programs. In other cases, such as animal tuberculosis, the role of wildlife is increasingly acknowledged, but significant steps are still required to really address TB as a multi-host system (see Box 2). Steps towards a more holistic approach to the control of multi-host diseases are often limited to certain countries.

Box 1 Animal Tuberculosis: A Multi-Host Infection

Animal tuberculosis (zoonotic TB) is caused by *Mycobacterium bovis* and other closely related members of the *M. tuberculosis* complex (MTC). This disease, often named “bovine TB,” is far from being limited to bovines: in Europe, at least seven other domestic and wild animal species can contribute to

(continued)

Box 1 (continued)

MTC maintenance depending on the local epidemiological circumstances: goat, sheep, pig, badger, wild boar and red and fallow deer (Gortazar et al. 2012, 2015a). Moreover, MTC can survive for a certain time in the environment, for instance in water or mud, on feed or even on saltlicks. Therefore, TB control is unlikely to be achieved if interventions only target one or two maintenance hosts (cattle and badger in the British Isles; cattle and goat in Iberia), instead of targeting the whole reservoir community (Santos et al. 2020, (see Fig. 5 top)).

In 2018, 18 EU member states (MS) were officially TB-free (OTF) and the overall EU proportion of cattle herds infected with, or positive for, bovine tuberculosis (herd prevalence), considering all OTF and non-OTF regions, remained low (0.9%). However, the EU herd prevalence was 0.4% in 2005, indicating a slow but steady recent increase. While TB prevalence is declining in the OTF regions, it is increasing in the non-OTF ones, with some regions still recording cattle TB herd prevalence >10%. Moreover, nothing is reported on the time trends of TB prevalence in other domestic or wild maintenance hosts in Europe (EFSA and ECDC 2018).

The way out is not easy and might prove unrealistic in some settings. In most cases, a One Health approach consisting of integrated TB control using all available tools in all relevant domestic and wild hosts will at least reduce the impact of TB (and TB control) on farmers. This process is represented in the Fig. 5 bottom. First, an honest epidemiological diagnosis is required. This implies identifying all hosts that are relevant for MTC maintenance in this setting, as well as their likely interactions. Second, decide whether to intervene or not, but in any case, set up an integrated disease and population monitoring scheme: if you do not have indicators, you will not be able to assess any effects of future intervention. Third, once proper monitoring has been set up, decide on the tool or tools to be employed for intervention. These tools range from biosafety, through population control, to vaccination. Most probably, suitable tools will vary between species, for instance combining test and cull in domestic animals with population control, biosafety or even vaccination in wildlife. In any case, a periodic re-assessment of the strategy is advised.

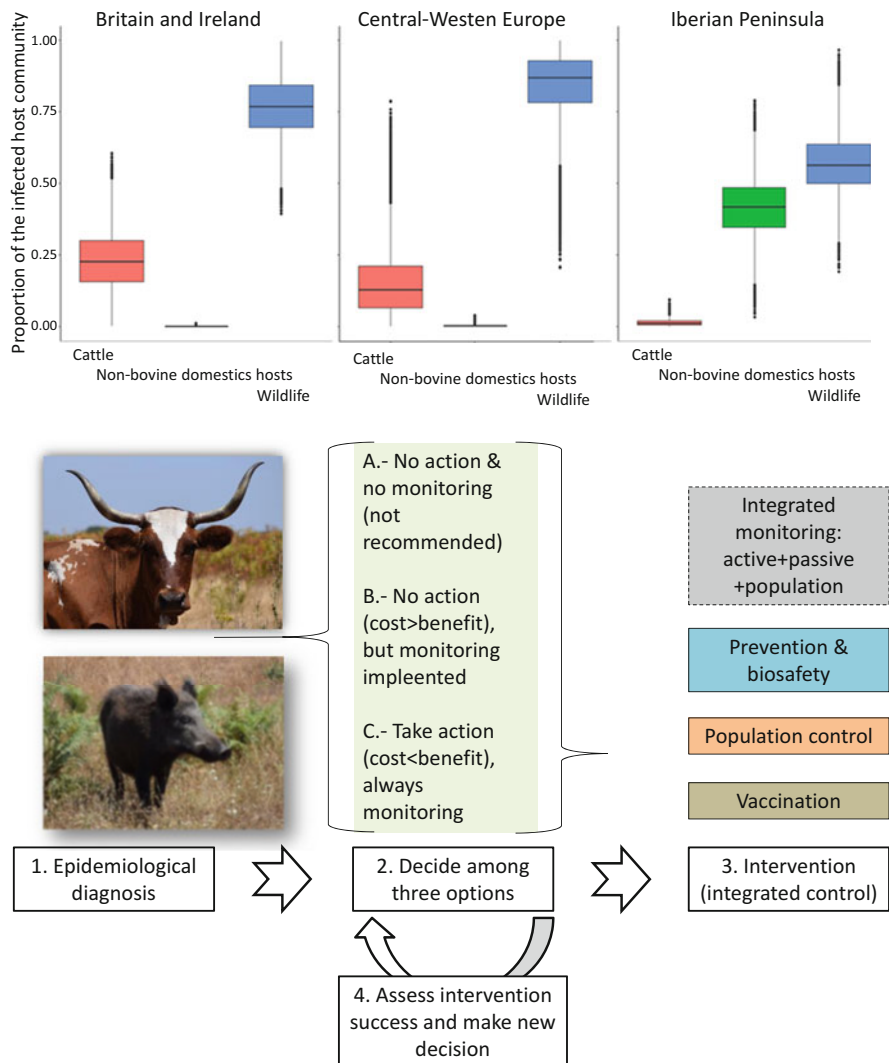


Fig. 5 Upper panel: Boxplots of the proportion of *Mycobacterium tuberculosis* complex infected cattle, non-bovine domestic hosts, and wildlife in the host community by region (Source: Santos et al. 2020), evidencing that cattle are just a small part of the total number of infected hosts. Lower panel: Flowchart representing a proposal for animal tuberculosis management in Europe, with a One Health perspective. The main steps are (1) carry out an epidemiological diagnosis, (2) decide whether to act or not, (3) intervention (ideally, integrating several tools), and (4) assess intervention success to make new management decisions (Source: modified from the Spanish Action Plan on Wildlife TB PATUBES, Ministry of Agriculture, Spain)

Box 2 African Swine Fever Emergence: The Consequence of Overabundance

African swine fever and its current situation in Europe is a relevant One Health case-study. As this chapter is written, ASF not only survives since the 1970s on the Italian Mediterranean island Sardinia, but has emerged since 2007 first in Georgia, expanding through Russia, Ukraine and Belarus to Poland, Lithuania, Latvia and Estonia in 2014, with posterior expansion to Moldova and Romania in 2017, to Hungary and Bulgaria in 2018, with further expansion to other countries in south-eastern Europe. The Czech Republic is again ASF-free after successfully controlling a local ASF outbreak that started in 2017 in wild boar, while a second long-distance jump still affects Belgium (since 2018, although almost under control), very close to France and Luxembourg. Despite the long-standing idea that wild boar do not significantly contribute to ASF maintenance, the current European situation demonstrates the opposite, namely that wild boar are able to maintain ASF circulation in many parts of Europe, even in the absence of domestic pigs and even at relatively low population density (EFSA AHAW Panel 2018).

There are several possibly contributing factors which may explain this, but the main driver is clear: wild boar overabundance. In Spain, a country that managed to get ASF-free in 1995, wild boar numbers have increased ten times in the last 35 years. Similar wild boar population growths have been recorded in all other European countries with data for this period. This huge increase in wild boar numbers is mainly a consequence of habitat change, with an increase in cover (Spain, for instance, increased its forest surface by 33% in the last 15 years) and an even steeper increase in crops that provide food and shelter, such as maize. Along with these favourable land-use changes, hunter numbers are slowly declining in most of Europe (Massei et al. 2015) and this is an enriched solution for the perfect storm.

Intervention is difficult. First, proper (integrated) disease and population monitoring need to be set up, and wild boar are no easy targets. Innovative methods for passive surveillance (such as boxes for easy pre-paid sample submission by hunters) are helping to improve the likelihood of early detection, and all efforts are made to improve population monitoring (www.enetwild.com). Once this is in place, and given the absence of applicable vaccines, the remaining options for intervention are biosafety and population control. Biosafety means avoiding ASF virus entry, good hunting hygiene and farm protection. In already infected areas it also includes carcass removal and destruction. Modelling (e.g. O'Neill et al. 2020) and field evidence suggest that a combination of culling and infected carcass removal is the most effective method to eradicate the virus, and that early implementation of these control measures will reduce infection levels. Regarding wild boar population control, the available options are few and sometimes complex to implement: increase the recreational hunting pressure, use professional shooters to cull (additional)

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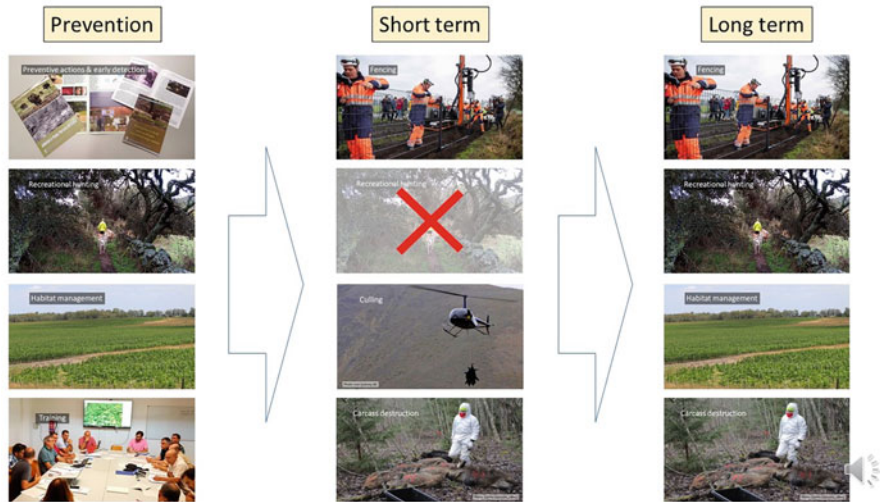


Fig. 6 Options available for African swine fever prevention and control depend on the epidemiological situation (see Fig. 6). In ASF-free regions, prevention should include information, training, and stakeholder engagement to maximise the likelihood of early detection, as well as hunting and habitat management to manage wild boar overabundance. During local outbreaks, short-term intervention options include fencing, culling and carcass destruction. In endemic regions, available tools include fencing, hunting, habitat management and carcass destruction. Culling and fast removal of animal carcasses are critical for the control of the ASF in wild boar. Drivers of virus maintenance will change depending on factors such as temperatures, wild boar density and management, and availability of obligate scavengers contributing to carcass removal (O'Neill et al. 2020)

Box 2 (continued)

wild boar, and act on the habitat carrying capacity for wild boar through feeding bans and crop-protection (i.e. fencing). The latter is possibly the most sustainable and efficient tool, but also the most challenging one to implement. One difficulty is that this needs close collaboration between veterinary authorities, hunters, the environment authorities in charge of regulating hunting activities, and farmers and agriculture authorities. Population control presents additional challenges since hunters are almost by definition amateur, and since hunting and culling faces increasing opposition in Europe.

There are several lessons to be learned from the ASF experience for the next disease emergence in Europe. First, since wildlife are involved in most of the relevant diseases, a better monitoring of wildlife populations, integrated with passive and active wildlife disease surveillance, is an urgent need for every country and at the EU level (see Box 3). Second, the epidemiology of shared multi-host infections is still insufficiently known, and insights from experimental interventions are only exceptionally available. The ASF crisis, but also the endemic animal TB one described in Box 1, provide opportunities for setting up and testing improved monitoring and intervention tools to cope with diseases at the interface (Fig. 6).

Box 3 Why Do We Need Denominator Data for Disease Surveillance? ENETWILD, a Network Providing Reliable Data on Species Distribution and Abundance of Wildlife for Risk Assessment in Europe

Risk assessment for pathogens of interest for humans and livestock requires the availability of presence and abundance data on wildlife which can represent reservoirs for pathogens. Many European countries and organisations collect spatial data on the distribution and abundance of wildlife, but each one has its own specific characteristics with respect to the methodology used, the type of data acquired, the repository implemented and their accessibility. This particularly applies for mammalian species, whereas there exist pan-European ornithological organisations and programs which study the population, distribution and demographics of European birds in order to inform conservation and management efforts, and hopefully, disease prevention and management (e.g. <https://www.ebcc.info/what-we-do/pecbms/>). The European Food Safety Authority (EFSA) funds ENETWILD (www.enetwild.com), a project to collect comparable data at the European level in order to analyse risks of diseases shared between wildlife, livestock and humans, data that are also essential in conservation and wildlife management. This project attempts to improve the European capacities for monitoring wildlife populations, developing standards for data collection, validation and, finally, create and promote a data repository. The objectives of ENETWILD were initially specifically focused on wild boar due to the African swine fever outbreak.

The harmonisation of the European data framework for wildlife (distribution and abundance) is a key milestone since it opens the space to aggregate these data from the whole of Europe. Initially, the project developed standards for presence/abundance data of the required species under the criteria of being effective for filtering data by quality as needed to produce high-quality maps and models, and compatible with existing biodiversity data collection systems in order to guarantee interoperability between them, thus widening the possible use of such data within a global framework of wildlife monitoring (<https://efsa.onlinelibrary.wiley.com/doi/10.2903/sp.efsa.2020.EN-18419>). The standards allow aggregating data on occurrence, abundance and hunting statistics of wildlife in Europe, either as raw data or as results of statistical estimation. These data come from a large community of administrations, researchers, hunters and wildlife managers. The ENETWILD consortium also aims defining the spatial interface between wildlife and livestock in Europe. The first

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Box 3 (continued)

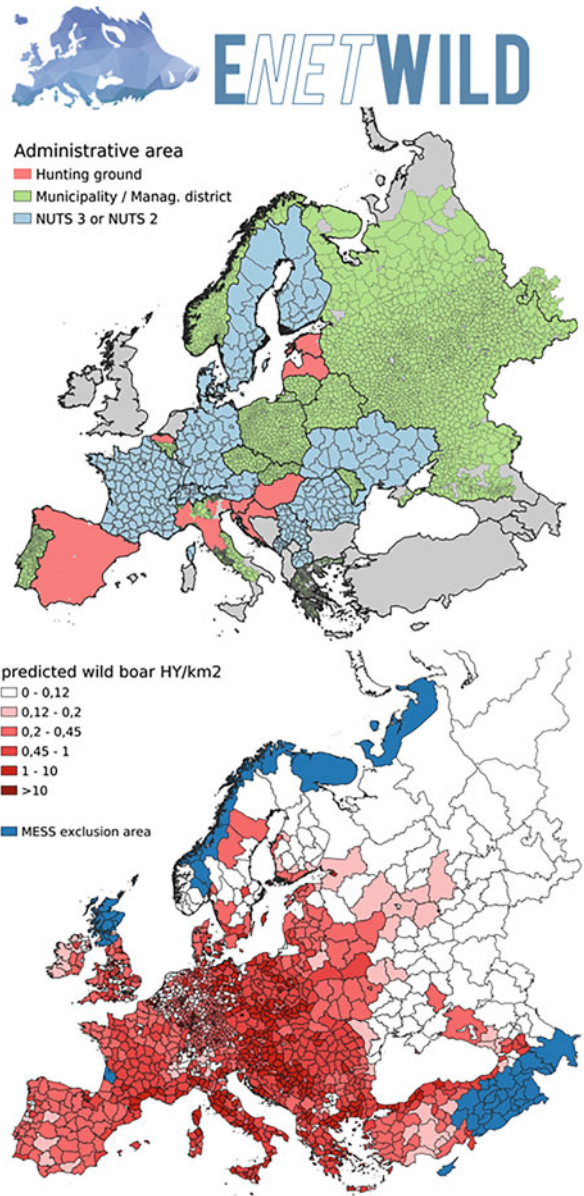
case being addressed is that of wild boar and domestic pigs (Fig. 2, Chapter “Host Community Interfaces: The Wildlife-Livestock”), which is essential to evaluate the risk for ASF spread across wild and domestic populations. A first report describes the different sources of data for domestic pigs in Europe and develops a preliminary risk map of possible spatial interaction between both groups (<https://efsa.onlinelibrary.wiley.com/doi/10.2903/sp.efsa.2020.EN-1834>).

The organisation and collection of wildlife hunting statistics and their analysis are essential not only for hunting management but also for developing wildlife policies. On a large spatial scale, hunting data statistics are available and, potentially, comparable across Europe for use in the predictive spatial modelling of wild boar abundance. But the procedures, methods and type of data collected concerning hunting bags (official statistics) can show a great heterogeneity between countries and regions. At present, each country and organisation collects hunting data using its own different procedure, and acquires different types of data that are later implemented in different repositories with variable accessibility: this hampers the comparison and common use of data across Europe (<https://efsa.onlinelibrary.wiley.com/doi/abs/10.2903/sp.efsa.2018.EN-1523>). The sources of hunting statistics providing quantitative information on wild boar (and by extension, for other big game species) in Europe are lacking or are not harmonised across Europe, as well as incomplete, dispersed and difficult to compare. A feasible effort is needed to achieve harmonisation of data in a short time for the most basic statistics at the hunting ground level, and the coordination of the collection of hunting statistics must be achieved first at the national and then at the European level. For these purposes, the following is recommended: countries should collect data at hunting ground level; efforts should be focused on data-poor countries (e.g. Eastern Europe), and the data should be collected at the finest spatial and temporal resolution, i.e. at hunting event level (Fig. 7).

Conclusions and Perspectives

Europe is probably the place where human activities have had the deepest impact on the environment and, as a consequence of the agricultural and hunting activities, also on wildlife populations. Such changes are still in act, but respect to the past, nowadays the trend is reversing with an increase of rewilding both in terms of wooded or forested areas and wild animal populations distribution and abundance.

Fig. 7 Top: Spatial distribution and resolution of hunting bags data collected for wild boar by ENETWILD (June 2020). Bottom: output of wild boar spatial model for abundance (hunting yield by km², <https://enetwild.com/reports-docs/>)



At the same time global changes, such as global warming and an increase of movement of humans, animals and trade, represent a risk for the emergence/re-emergence of vectors or pathogens. Human behaviour and activities are at the base of such changes, and, due to the deep social and cultural changes that European citizens are facing, they have evidenced the increased importance of the human-livestock-wildlife-diseases interface all across the continent. The increase of wildlife abundance, at least for some species, the changes in livestock breeding and the extension of urban areas represent a culture media that favours disease emergence of re-emergence both in animals and also for many zoonoses. In the last decade, there was an increase of reports on the spread of vectors to new areas, both for a natural expansion in Europe (i.e sandflies have moved thousands of kilometres to the North) or because of accidental introductions (i.e alien mosquitoes species) or migration from other continents (i.e *Hyalomma* ticks from Africa). Such trends pose a serious threat for both the animal and human health and represent a good example of the need of a One Health approach that include wildlife diseases monitoring and diseases mitigation actions in political decisions and plans. After centuries where wildlife, due to the human activities that greatly reduced the habitats available for wild species, was a marginal player for pathogen spread, the changes that occurred in the last decades have reversed this role. Unfortunately, this new scenario is not fully recognised by policymakers and citizens, that still consider wildlife as “sign of nature” without understanding the complex link of the One Health, even if recently there are signs of a change. The expansion in the Carrying Capacity of the environment for certain species, and the subsequent rise in population abundance of those species, has not been matched with an increase in the Cultural Carrying Capacity (Decker et al. 2012) of authorities and citizens. The new green deal that represents Europe’s biggest challenge for the coming years must include monitoring of wildlife abundance as well as monitoring of vectors and of diseases in wildlife, as well as integrate wildlife diseases management in plans and action. Generally speaking, European authorities have had a passive approach towards diseases in wildlife and only the emergence of local or more widespread emergencies have raised the interest of politicians and managers for this topic. Nowadays there are signs of a change that aim to change this attitude favouring a more open and holistic approach where wildlife and wildlife diseases are a key point in animal health, but also, in a wider view, for the One Health policy.

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Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Asia



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Introduction

According to the United Nations, there are approximately 4.5 billion people living in Asia, which makes up 60% of the world's population (United Nations 2019). The two most populous countries of the world, China (1.4 billion) and India (1.3 billion) are located in Asia. The human population in the region is growing more slowly than before but will likely continue to increase for the next 30 years. The growing population leads to rapid urbanization and land transformations with the expansion of industrial activities and agricultural. Changing landscape patterns and whether patterns were caused by human activities has resulted in serious impacts on natural ecosystems, such as ecosystem degradation, habitat, and biodiversity loss. There are ten major factors inducing the biodiversity decline, including farming, hunting, and trade, deforestation, mining, reservoir construction, wetland drainage, fire, pollution, invasive alien species, disease, and climate change (Hughes 2017). The weakened ecosystem is influencing both the health of the planet and the quality of human life (Fund 2017). Under these circumstances, human-wildlife conflicts have intensified in recent years. These conflicts arise due to the demands of wildlife encroaching on those of humans or the other way round. Climate change may increase competition for water and habitats, which can aggravate these conflicts. The main problems caused by human-wildlife conflicts cover the following aspects: (1) Safety and security. For example, large carnivores and large herbivores sometimes attack humans when near waterways, often resulting in injury or death. (2) Food security and livelihoods. For example, wildlife such as deer, elephants (*Elephas maximus*), or wild boar (*Sus scrofa*), destroy crops and carnivore animals prey on livestock, which negatively impacts economies and food security in some developing agricultural countries. (3) Transmission of diseases between livestock and humans. For example, many wild species can transmit diseases to livestock when they share living space and resources such as food or water. Additionally, some zoonotic infectious pathogens can be transmitted from wildlife to humans (Food and Agriculture Organization 2015).

Socioeconomic and Biogeographical Circumstances of the Wildlife-Livestock Interface

Asian countries have their own perspectives and practices on livestock production. The production systems can be categorized as production for personal or domestic consumption, which extends to production for sale locally, and the industrialized or intensive production, a large volume of livestock products supported with advanced technology in production practices, such as poultry and pig production by conglomerate groups.

The tropical climates and environments of Asia are conducive to the growth of some pathogens, and the favoring of productive hybrid animals that have low

resistance to diseases for their high turnout of meat, milk, and eggs, will eventually require producers to put in place adequate biosecurity measures and other strategies (Devendra 2012).

For developing regions like in tropical Asia, agricultural expansion, and intensification of the wildlife interface is associated with external economic and development pressures and may drive spillover or emergence. The problem of poorly regulated production systems and weak public health systems, as is the case in many Asian countries, generates health risks for local, regional, and global populations. Expansion of agricultural areas through deforestation can lead to increased wildlife-livestock and wildlife-human contact and thus increased pathogen transmission amongst all. One good example is a Nipah virus outbreak in Malaysia, where the fruit bats were the natural reservoir infecting domestic pigs, which in turn infected humans coming into contact with the pigs. The close association of pig farms with orchards and the design of pigsties, combined with the destruction of natural habitats for the bats, increased the interface between bats and pigs and thereby contributed to the interspecies transmission of the virus. Another example comes from Vietnam where a farming tradition is that duck keepers move their flocks between rice paddies for feeding after the harvest. Movements of domestic ducks carrying potent H5N1 virus is regarded as contributing to an efficient spread of the HPAI (Highly Pathogenic Avian Influenza, see Box) disease to waterfowl in the country (FAO 2008).

The Prevalent Livestock, Farm Typologies, and Opportunities for Interface

The developing Asian and Pacific region has generated more than half the gains in global livestock production and consumption up to 2012 (Ahuja and Mehta 2012). Asia accounted for about 84% of the world's pigs, 70% of poultry, 49% of cattle, and 44% of sheep and goats. ASEAN (Association of Southeast Asian Nations) countries comprise one of Asia's significant subregions which is home to more than 2.6 billion chickens, 47 million cattle, 71 million pigs, 38 million sheep, and goats to feed over 600 million ASEAN people. Asia is also home to a diversity of small farm systems, including both ruminant and non-ruminants. Relatively large numbers of more than 75% of ruminant (basically buffaloes, *Bubalus bubalis*) and about 70% of non-ruminants are found on small farms (Devendra 2012). Asian agriculture is characterized by mixed farming activities, typified by a variety of mixed or integrated systems in the various agro-ecological zones (AEZs), the diversity of crops and animals, mainly small farms and poor people (Devendra 2007). Mixed farming systems are synonymous with crop-animal systems, are varied and integrated with cropping in various ways. These systems are likely to see important growth and continue to be predominant in Asia (Devendra 2012).

The potential importance and impacts of integrated oil palm-animal (most of the ruminant) systems have recently been reviewed (Devendra 2009) and this strategy is slowly expanding to take advantage of its many economic benefits and impacts. Currently, about 3% of the 4.7 million hectares of land under oil palm cultivation is used for integration, and it is expected to increase with increasing awareness and policy support. The integration model with oil palm offers extension of the principles involved with other tree crops like coconuts in the Philippines, Sri Lanka, and South Asia, rubber in Indonesia, and citrus in Thailand and Vietnam (Devendra 2012).

Dairy farming in Asia can be broadly classified into three major types of production systems as follows: (1) mixed farming, in which milk production only contributes a relatively small proportion of total farm income, milking herd sizes range from fewer than five to about 20 cows; (2) smallholder dairy farms, where milk production has increased over recent years to become a major contributor to farm income, milking herd sizes range from five to 10 cows; and (3) larger specialist dairy farms, which were established primarily to produce raw milk. Dairy facilities on specialist dairy farms have been better planned to satisfy the requirements for a predetermined number of milking cows. In fact, smallholder dairy farms produce over 80% of the developing world's milk, making a significant contribution to the annual world production. In most of Asia, poultry farming has progressed significantly from backyard farming into the sophisticated agro-based industry that has grown significantly in size. As about 60% of the world's population live in Asia and the average consumption of eggs and poultry meat among most of the people in this region is well below that in developed countries. This means that the developed countries will have the fastest growing demand for Asian poultry products in the future (Sugiyama et al. 2003). developed countries are where the demand for poultry products from Asia will increase most in the future.

Smallholder swine farms are commonly associated with rice farming since rice bran is used as a feed supplement and swine farming is a practical additional source of protein and income for the family. The absence of veterinary law and the illegal movement of animals from neighboring countries are the main problems in having more robust swine production. Thus, there is also a need to improve surveillance and immediate reporting of suspected outbreaks of diseases (FAO 2011). Passive surveillance is the main method used in most Asian countries to collect information on livestock diseases. The national surveillance for Foot and Mouth Diseases (FMD) is implemented to establish an OIE FMD free zone with the use of vaccination by the National Nipah Encephalitis Surveillance Programme. Since the majority of farms are small scale in nature, infectious diseases, such as FMD and PRRS, occur due to low biosecurity and low vaccination coverage. There is also lack of veterinary staff in rural areas and the disease network at the grassroots level is largely undeveloped (Dung 2011). The focus is also mainly given on disease control rather than prevention in the majority of the Asian nation's governments.

Wildlife and Protected Areas in Asia

Asia has long been recognized as a major biodiversity hotspot of global importance (Myers 1988), emphasizing the exceptionally high levels of diversity and endemism of the flora and fauna of Indo-Burma, Philippines, Eastern Himalayas, and Wallacea regions (Mittermeier et al. 1998, 2011; Sodhi and Brook 2006; Morand and Lajaunie 2018). All vertebrate groups including mammals, birds, amphibians, and reptiles are diversified (Sodhi et al. 2010). Even large herbivores, despite the misleading perceptions of the general public and many scientists alike, have an exceptionally high ratio of the number of species/unit area, and many protected areas in South Asia support biomass densities comparable to iconic African parks.

However, the exceptional Asian biodiversity is also associated with an exceptionally high level of threat (Sodhi et al. 2004; Schipper et al. 2008; Wilcove et al. 2013; Hughes, 2017). The situation is particularly serious for land mammals with the combined effects of overharvesting and habitat loss (Schipper et al. 2008). In the last 50 years, almost two-thirds of large and medium-size mammals have become threatened with extinction in South Asia, India, and China (Tilman et al. 2017). All Indochinese large ungulates other than wild boar (*Sus scrofa*) and southern red muntjac (*Muntiacus muntjak*) are now globally threatened, while the endemic kouprey (*Bos sauveli*) is now considered most likely extinct (O’Kelly et al. 2012). Once widespread and abundant throughout their range, the distribution of large herds of wild cattle, including Gaur (*Bos gaurus*) and Banteng (*Bos javanicus*), have shrank and they are now found mainly inside a limited number of protected areas (Walston et al. 2016).

Although protected areas (PAs) have been part of Asian landscapes for more than a century and have played an important role in biodiversity conservation (Gadgil et al. 1993; Paine et al. 1997), they are under considerable pressure due to human population and economic growth in the region. The situation is extremely variable among countries, both quantitatively (number and size of PAs, number of newly created PAs) and qualitatively (the type of protection, efficiency, and effectiveness of protection) (Don et al. 2013). According to the United Nations Environment Programme-World Conservation Monitoring Centre, there are more than 10,000 protected areas covering 13.9% of the terrestrial environment in the Asian Region (Juffe-Bignoli et al. 2014). However, the type of protection and the proportion of the national territory that they cover varies greatly: more than 40% for Bhutan and Brunei Darussalam, while 10 countries do not reach 10% (Juffe-Bignoli et al. 2014). In addition, several Asian countries have further impaired their capacity to preserve their biodiversity by downgrading, downsizing, or degazetting some of their protected areas (Mascia and Pailler 2011). As a result, most Asian countries have compromised their capacities to attain the Convention on Biological Diversity Aichi Target 11 for terrestrial protected area coverage (17% of the total national surface under protection by 2020; CBD-AT11), while other countries such as India and Vietnam are far behind.

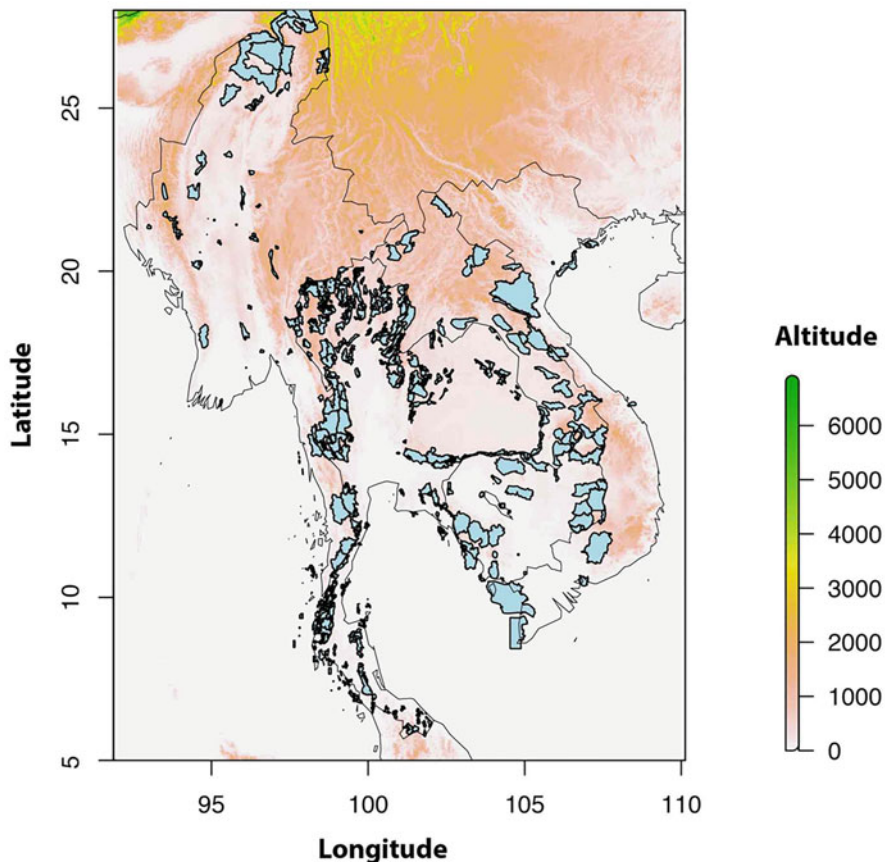


Fig. 1 Map of protected areas (light blue) in the Indochinese region (Data from UICN protected areas categories I-VI; database accessed March 2018)

For example, the five countries of the Indochinese region differ markedly; not only in the type and coverage of areas under protection but also in their distributions and representativeness of their respective national ecosystems (See Fig. 1). The World Database on Protected Areas records more than 200 terrestrial protected areas in Thailand and in Vietnam, whereas Cambodia, Lao People's Democratic Republic (PDR), and Myanmar have less than 60 (UNEP-WCMC 2016). Less than 8% of the national land surface benefits from some kind of protection in Myanmar and Vietnam, whereas the three other countries have already reached the 17% objective set by the CBD-Aichi target 11, even exceeding $\frac{1}{4}$ of the national territory for Cambodia. However, more critical than the surface under official protection is the coverage of the most species-rich areas, which may not be appropriate in Southeast (SE) Asia for most taxa (Hughes 2017), and the effectiveness of management and wildlife protection. Because of direct persecution of wildlife (Sankaran and

Ahrestani 2016), the forests of the region are increasingly being described as empty due to increasing and widespread illegal hunting pressure observed across SE Asia, including within dedicated wildlife reserves (Harrison et al. 2016).

Asia is very diverse, not only in terms of habitats and wildlife communities, but socioeconomical contexts and wildlife management. More developed countries, such as in other parts of the North hemisphere (Europe, North America), have experienced decrease in anthropogenic pressures on wildlife during the last decades (e.g., hunting and habitat alteration), and certain species may benefit, like wild ungulates (Fig. 2).

The Disease at the Interface: One Heath Perspective

With the continuing development of Asian societies and their economies, numerous factors are influencing the wildlife and dynamics of pathogen transmission. For example, (1) land-use, habitat change, (2) domestic animal husbandry, and (3) impact of conservation programs. All these factors can influence disease risks at the wildlife-livestock interface. Many synanthropic species have been shown to carry zoonotic pathogens and in some cases act as reservoir hosts for these pathogens (Hassell et al. 2017). And the impact of major zoonosis on the economy and costs of intervention is important, as evidenced by COVID-19 worldwide. This is the third significant Coronavirus to emerge in humans in 17 years, indicative of the increased risks for pathogens to jump from infected wild animals to humans. It jumped from infected wild animals to humans resulting in millions of infected people worldwide in just a few months (Morens et al. 2020). Human, animals (both domestic and wild), and ecosystems are tightly linked, more than ever in Asia, and this also affects global health. The magnitude of this pandemic, while certainly huge in proportions, remains to be estimated under its multiple angles, i.e., not just purely from the public health perspective, but in terms of its economic and social impact yet to come (Table 1).



Fig. 2 Asia is very diverse, not only in terms of habitats and wildlife communities, but socioeconomical contexts and wildlife management. More developed countries, such as in other parts of the North hemisphere (Europe, North America) have experienced decrease in anthropogenic pressures on wildlife during the last decades (e.g., hunting and habitat alteration), and certain species may benefit, like wild ungulates. As wildlife recovery, human-wildlife conflict increases. **(a, b)** Rural landscapes in Japan integrated in the “recovered” nature. **(b)** The segregation of wildlife and human uses is becoming a problem. Protection in crops against wild ungulates in Hokkaido island (Japan) where its natural predator, the wolf, is extinct. **(c–d)** Yezo sika deer (*Cervus nippon yesoensis*) in proximity to human activities (Hokkaido island, Japan) (images: J. Vicente). **(e–f)** triple human-wildlife-livestock interface examples in Nepal (images: C. Gortázar)

Table 1 Major disease systems at the interface of wildlife and livestock in Asia

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Avian influenza	Wild birds-poultry Wild birds-pigs	Asia	Avian influenza virus occurs mainly in birds and is highly contagious among them. Influenza A virus is a zoonotic infection with a natural reservoir almost entirely in birds. Asian HPAI is especially deadly for poultry. Human are infected with Asian H5NI have been associated with severe disease and death. The economic burden of influenza in low-and middle-income countries encompasses multiple dimensions such as direct costs to the health service and households, indirect costs due to productivity losses as well as broader detriments to the wider economy.	de Francisco et al. (2015), Wietheoelter et al. (2015)
Newcastle disease (ND)	Wild birds-poultry	Asia	Newcastle disease is caused by virulent forms of avian paramyxovirus of serotype 1 (APMV-1) and has global economic importance. Waterfowl, cormorants, and pigeons are natural reservoirs of all APMV-1 pathotypes ND has been a devastating disease of poultry, negatively impacting poultry industries.	Dimitrov et al. (2016)
Poxvirus infection	Wild birds-poultry	Asia	Avipoxviruses are unable to complete their replication cycle in non-avian species. Like other avian viruses, it	Sanchez-Sampedro et al. (2015), Bernard and Anderson (2006)

(continued)

Table 1 (continued)

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Avian chlamydiosis	Wild birds-poultry	Southeast Asia	<p>can be transmitted through vectors mechanically such as through mosquitoes. There is no evidence that this virus can infect humans.</p> <p>A bacterial disease of birds caused by members of the genus <i>Chlamydia</i>. Some individual birds carry <i>C. psittaci</i> asymptomatically, others become mildly to severely ill. Avian chlamydiosis (AC) can be economically devastating to producers and a serious public health problem. Most infections in humans are due to exposure to psittacine birds and pigeons.</p>	Andersen and Vanrompay (2000)
	Wild birds-small ruminants			
Brucellosis	Wild ungulate-ruminants	Japan	Brucellosis is caused by bacteria of the <i>Brucella</i> genus. Human can be infected by contact, ingestion, or inhalation of organisms from infected animals, for example: Cattle, goats, and sheep. Brucellosis is a granulomatous disease that can affect any organ. Infections with <i>Brucella</i> species are rarely fatal in human and animal populations.	Rubach et al. (2013)
Fasciolosis	Wild ungulate-ruminants	Asia	Fasciolosis is a common parasitic disease of sheep and cattle caused by	Cwiklinski et al. (2016)

Cysticercosis	Wild ungulate-pigs Carnivores-cattle	India/China/ Indonesia/Thailand/ Korea/Taiwan/ Nepal	the trematode <i>Fasciola hepatica</i> , which is located in the liver. The major clinical symptoms are persistent diarrhea and chronic weight loss. Cysticercosis is a tissue infection caused by the larval form of the pork tapeworm. Exposure to the parasite and consumption of raw pork are factors contributing to the infection of the disease. Hospital-based data on human cysticercosis in Asian countries reveal that this disease in India was most common. Cysticercosis is a major public health problem in several Asian countries and also result in loss of revenue to pig rearers.	Rajshekhkar et al. (2003)
Foot and mouth disease (FMD)	Wild ungulate-livestock	Asia Temperate Asia/ subtropical Asia,	Foot and mouth disease is caused by infection with foot and mouth disease virus (FMDV), a picornavirus. FMD is a highly contagious disease of cloven-hoofed animals including cattle, pigs, sheep, and many wildlife species (not zoonotic). Outside Africa, FMD is maintained mainly in domestic ruminants, particularly cattle, and wildlife occasionally become infected incidentally by spillover. This disease can reduce animal productivity and the restrictions on international trade in animal products thus can cause enormous economic losses.	Jamal and Belsham (2013),

(continued)

Table 1 (continued)

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Peste des petits ruminants	Wild ruminants-domestic ruminants		<p>Peste des petits ruminants (PPR) is a viral disease, caused by a morbillivirus closely related to rinderpest virus, which affects goats, sheep, and some wild relatives of domesticated small ruminants. In the worst situations, PPR-related morbidity is as high as 100%, with a mortality rate that can reach 90%. In areas where the disease is endemic, the mortality rate may be lower, but the disease has a more insidious impact on flock productivity. Each year, PPR causes economic losses worth an estimated USD 1.2 to 1.7 billion, due to animal deaths, reduced production and the cost of fighting the disease. Approximately a quarter of the financial impact occurs in South Asia. The OIE and the FAO, in their joint Global Strategy for control and eradication of PPR, have set the goal of eradicating this disease by 2030. The Strategy includes several tools and components to be implemented through a approach to decreasing levels of epidemiological risk and increasing levels of prevention and control.</p>	<p>Aziz-ul-Rahman et al.(2018), Parida et al. (2015), https://rr-asia.oie.int/en/projects/peste-des-petits-ruminants-ppr/</p>

Equine piroplasmosis	Equines (Przewalski and domestic horses)	Central Asia	Equine piroplasmosis, which is caused by <i>Babesia caballi</i> and <i>Theileria equi</i> , is considered as an economically significant tick-borne disease in horses. Death is sometimes observed among the affected horses.	Munkhjargal et al. (2013)
Paratuberculosis	Wild ungulate-ruminants	Central Asia/East Asia	Paratuberculosis is a chronic bacterial digestive disease in domestic and wild ruminants, caused by <i>Mycobacterium avium</i> subsp. Lack of adequate vaccine is the reason why the disease is difficult to control on the farm. The disease can cause substantial economic losses to the cattle industry mainly due to increased premature culling, replacement costs, decreased milk yield, reduced feed conversion efficiency, fertility problems, reduced slaughter values, and increased susceptibility to other diseases or conditions.	Garcia and Shalloo (2015)
Animal tuberculosis (<i>Mycobacterium tuberculosis</i> complex)	Wildlife (ungulates, elephants)-livestock	Asia	Animal tuberculosis, caused by <i>Mycobacterium tuberculosis</i> complex (MTC), mainly <i>M. bovis</i> and <i>M. caprae</i> , is a transmissible disease that mainly affects livestock and a wide variety of free-ranging wildlife. Recently, awareness of the importance of MTC in wildlife as a potential reservoir of infection for domestic animals but also as zoonosis, has increased. Its real distribution at the	Jang et al. (2017), Che-Amat and Ong (2018)

(continued)

Table 1 (continued)

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Rabies	Wild ungulate-ruminants	Central Asia Asia	interface still remains unknown in most Asian countries. Eradication programs are not always properly implemented. With very little information on livestock and wildlife tuberculosis and potential hotspot regions, attention should be given by the researchers, policy makers, and various stakeholders to assess the disease threat and the impact on tuberculosis control in livestock.	Hampson et al. (2015) Baby et al. (2015)
	Bats-pigs			
	Carnivores-cattle			
West Nile virus	Wild birds-equines	West Asia/Central Asia	West Nile virus (WNV) was first recognized in 1937 in Africa and then transmit to bordering countries including West Asia. WNV is a mosquito-borne flavivirus whose reservoir includes many species of birds, humans, horses, and other mammals. Currently, there are no vaccines or	Paz and Semenza (2013), Bernkopf et al. (1953)

Echinococcosis	Wild ungulate-ruminants Carnivores-cattle	Central Asia East Asia	<p>medicines to protect humans. Isolation of West Nile virus in Israel in 1953. West Nile virus is now endemic in Africa, Europe, the Middle East, West and Central Asia, Oceania (subtype Kunjin), and North America.</p> <p>Echinococcosis is caused by accidental ingestion of eggs and tissue cyst of several tapeworm species belonging to the genus <i>Echinococcus</i>. Transmission occurs between carnivore definitive hosts and herbivore/omnivore intermediate hosts through predator-prey interactions. It is a relevant zoonosis.</p>	Ito and Budke (2017), Eckert and Deplazes (2004)
Classical swine fever	Wild suid-pigs	North Asia/East Asia	<p>Classical swine fever (CSF), caused by classical swine fever virus (CSFV), is an OIE-listed, highly contagious, often fatal disease of swine worldwide. Currently, the disease is controlled by prophylactic vaccination in Asia. Though CSF is essentially under control, complete eradication of CSF in some countries (e.g., China) remains a challenging task and needs long-term efforts of stakeholders. Classical swine fever virus cannot infect humans. It is unknown its impact on other wild suids than wild boar.</p>	Luo et al. (2014),

(continued)

Table 1 (continued)

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Africa swine fever	Wild suid-pigs	Asia	<p>African swine fever (ASF), caused by a virus, has emerged since 2007, first in Georgia, expanding Europe and Asia. It is a serious threat to a growing threat to the pig industry. Most countries in Asia notified events related to farm outbreaks; meanwhile, only a few wild boar cases were reported. However, wild boar is able to maintain ASF circulation in many parts of Europe, even in the absence of domestic pigs and even at relatively low population density. It is hypothesized that the virus circulates unnoticed in wild boar populations in Asia.</p>	Cabezón et al. (2017), Vergne et al. (2020)
Middle East respiratory syndrome (MERS)	Humans and Dromedary camels, however, bat are potential reservoir/ancestral hosts		<p>MERS-CoV causing Middle East respiratory syndrome (MERS) emerged in Saudi Arabia in 2012 and continues to cause human disease with a case fatality rate of 35%. Dromedary camels are a natural reservoir host for MERS-CoV. In the Arabian peninsula and across Northern Africa, the seroprevalence rate for MERS-CoV in dromedary camels ranges from 70% to nearly 100%. Although camels are thought to be the</p>	Banerjee et al. (2019), Woo et al. (2018)

	<p>primary zoonotic reservoir for human transmission, there is strong evidence that bats are the ancestral reservoir host for MERS-CoV. MERS-CoV is a group C betacoronavirus and is phylogenetically related to BatCoVs identified in various bat species that belong to the Vespertilionidae family. It is not clear when MERS-CoV spread from bats to camels, but widespread exposure to the virus in the Middle East and North and East Africa dates back as early as the 1980s, suggesting that camels have served as a zoonotic reservoir for MERS-CoV for at least 30 years.</p>			
<p>Surra</p>	<p>Rodents-poultry Bats-pigs</p>	<p>East Asia Southeast Asia</p>	<p>Surra, caused by protozoan of the genus <i>Trypanosoma</i>, is a major disease in camels, equines, and dogs, in which it can often be fatal in the absence of treatment and exhibits nonspecific clinical signs which are variable from one host and one place to another. It is mostly mechanically transmitted by tabanids and stomoxes.</p>	<p>Desquesnes et al. (2013)</p>
<p>Q fever</p>	<p>Rodents-poultry-ungulates</p>	<p>East Asia China</p>	<p>Q fever is a worldwide zoonosis. <i>Coxiella burnetii</i> is a strict intracellular bacterium and the etiologic agent of Q fever. The bacterium is highly infectious by the aerosol route. This disease prevalence in goats,</p>	<p>Suputtamongkol et al. (2003)</p>

(continued)

Table 1 (continued)

Specific /Major diseases at the interface Disease	Identified interface	Area/Region	Main characteristics and relevance	References
Japanese encephalitis	Bats-pigs	East Asia/Southeast Asia/South Asia	sheep, and cattle. Humans are infected by inhaling contaminated aerosols from amniotic fluid or placenta or handling contaminated wool. Two forms of the disease are typical: Acute and chronic. Acute Q fever is the primary infection and the major clinical manifestations of acute Q fever are pneumonia and hepatitis.	Heffelfinger et al. (2017)
Leishmaniasis	Rodents-Canidae Bats-pigs	East Asia Southeast Asia South Asia Asia	Japanese encephalitis (JE) virus is the most important vaccine-preventable cause of encephalitis in the Asia-Pacific region. JE is a mosquito-borne disease. Approximately 30%–50% of survivors have long-term neurologic sequelae. Vaccination is the cornerstone of JE control and prevention measures. Leishmaniasis is a tropical disease caused by an intracellular parasite of the genus <i>Leishmania</i> . The vector of transmission is the sand-fly, which deposits one of the 20 disease-causing protozoan species during a blood meal. There are three main forms of leishmaniasis—visceral, cutaneous, and mucocutaneous.	Heffelfinger et al. (2017)

<p>Bovine viral diarrhea</p>	<p>Wild ruminants-domestic ruminants</p>	<p>East Asia</p>	<p>Bovine viral diarrhea virus (BVDv) is associated with bovine respiratory disease complex and other diseases of feedlot cattle worldwide. BVDV is classified into two species, namely BVDV-1 and BVDV-2, within the genus Pestivirus. BVDV continues to be of economic significance to the livestock industry in terms of acute disease and fetal loss.</p>	<p>Larson (2015)</p>
<p>Nipah virus encephalitis</p>	<p>Bats-pigs</p>	<p>South Asia/Southeast Asia</p>	<p>Fruit bats were the natural reservoir hosts of Nipah virus, infecting pigs, which in turn infected humans coming into contact with the pigs. Notably, in pigs, the virus caused encephalitis and respiratory diseases. Infected pigs are asymptomatic and can contribute to the spread of the disease.</p>	<p>Lim (2009)</p>
<p>Hendra</p>	<p>Bats-horses</p>	<p>East Asia/Southeast Asia/South Asia</p>	<p>Hendra virus (HeV) infection is a rare emerging zoonosis that causes severe and often fatal disease in both infected horses and humans. Symptoms of HeV infection in humans range from mild influenza-like illness to fatal respiratory or neurological disease. There is no specific treatment for human cases of Hendra virus.</p>	<p>Kung et al. (2013)</p>

Box 1 The Role of Wildlife as the Source of Influenza A Viruses in Asia and Its Expansion Worldwide

Among the three influenza genera (A, B, and C), only influenza A viruses infect birds. Eastern Asia provides the setting for the mixing of poultry, pig, and human influenza A viruses (diverse subtypes) circulating in the avian, swine, and human host reservoirs. They represent a serious risk of the emergence of new highly pathogenic avian influenza (HPAI) viruses through recombination. Avian Influenza (AI), is highly contagious disease and affects the respiratory, digestive, and nervous systems of domestic and wild bird species. It has become a major veterinary and public health concern (due to its potential to infect humans), occurring worldwide. AI is one of the most worrying and expanding threats in South East and East Asia. Human infections with novel avian influenza virus-like Asian HPAI virus H5N1 are concerning because of this pandemic potential. This virus occurs mainly in birds and is highly contagious among them. The virus was first detected in 1996 in geese in China and was first detected in humans in 1997 during a poultry outbreak in Hong Kong. Since 2003, this avian and other influenza viruses have repeatedly spread from Asia to Europe and Africa, despite the efforts made to eradicate H5N1 in Southeast Asia. By autumn 2006 it caused outbreaks in poultry or wild birds in 53 countries and hundreds of human cases (Kilpatrick et al. 2006, https://www.who.int/influenza/human_animal_interface/en/). Before the spread of Asian H5N1 HPAI, very few HPAI outbreaks had been described in wild birds. The factors involved in the local, national, regional, and global spread of such newly emerged AI are complex. Migratory birds, the transport of poultry and poultry products, and the trade in wild birds all were hypothesized as pathways of introduction. Asian H5N1 continues to circulate and has been responsible for human infections. When HPAI virus H5N1 enters a new host population (e.g., chickens, wildlife), it can jump to further species (including human) and can spread across very large distances to new susceptible populations. As indicative, the bird-poultry interface was the most frequently cited wildlife-livestock interface worldwide, ranking first in Asia, Europe, and North America and second in Oceania, Africa, and South America in a recent review (Wiethoelter et al. 2015). Kilpatrick et al. (2006) reported introductions to countries worldwide and found that, in Asia, 9 out of 21 introductions of HPAI H5N1 were most likely through poultry and 3 out of 21 through migratory birds. However, the transmission at the wildlife-livestock interface is seldom documented and proven. The main challenges for effective management of outbreaks in Asia are the multidisciplinary approach required, the lack of experts, the need to train at all levels, and the diversity of outbreak scenarios. H5N1 HPAI has been perhaps the first time that the One Health concept has been applied for an international threat (Beltrán-Alcrudo et al. 2011) (Fig. 3).

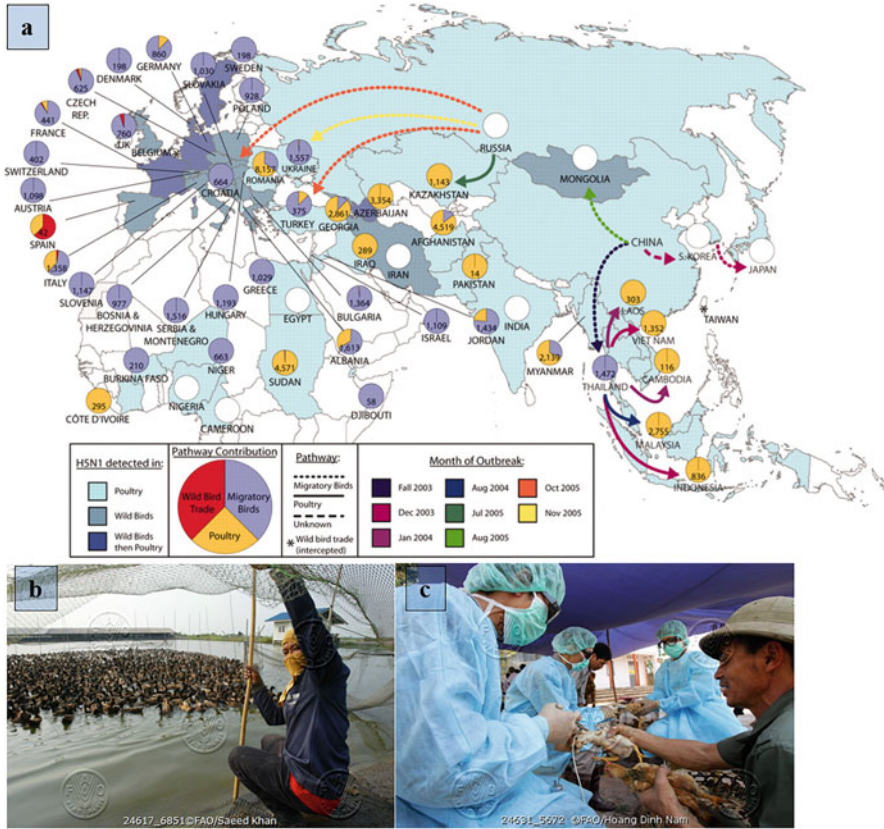


Fig. 3 (a) This figure illustrates the spread of H5N1 in Asia, Europe, and Africa from 2003 to 2005. Pie charts show the total number of infectious bird days (number of infected birds × days shedding virus) and fraction from each pathway for birds moving between previous H5N1 outbreak countries and the focal country. Arrows give the month of the outbreak and hypothesized direction of spread for 2003–2005 introductions. Reproduced from Kilpatrick et al. (2006, PNAS, under creative common license). (b) A local farmer tending to his ducks that are well protected by a net covering to avoid contact from outside birds that may be infected with the avian flu virus in northern Thailand (Credit: ©FAO/Saeed Khan). (c) Veterinarians administering free vaccines to chickens to prevent another outbreak of the H5N1 virus at one of the many vaccination points set up by the Vietnamese Government (FAO Project, Credit: ©FAO/Hoang Dinh Nam)

Box 2 Wildlife Tuberculosis in Southeast Asia

Across the world, several evidences had shown severe problems associated with wildlife reservoirs of animal tuberculosis (Animal tuberculosis, caused by *Mycobacterium tuberculosis* Complex, MTC, mainly *M. bovis*), involving different host species in different geographical conditions. Wildlife tuberculosis is a threat to domestic livestock, other wildlife species, and human, which may cause an impact to the economy, wildlife conservation and serious public health issues. Increasing trend in the detection of wildlife tuberculosis reservoir has hindered the progress of controlling this disease. The current concern is that the presence of infection in certain wild maintenance hosts may hamper disease control in livestock in certain regions of Asia. South East Asia is known for its biodiversity hotspots in the world, with high species richness including abundance potential wildlife tuberculosis reservoirs such as wild boar and multi-species of deer. Furthermore, one-third of the world's human tuberculosis is found in South East Asia. With very little information on livestock and wildlife tuberculosis and potential hotspot region, attention should be given by the researcher, policy makers and various stakeholders to assess the disease threat and the impact on tuberculosis control in livestock in South East Asia. South East Asia countries also face issues and limitation in conducting tuberculosis surveillance and detection. Such limitations may be overcome by collaboration and networking with expertise under One Health alliance by outsourcing the capabilities of funding, human and laboratory resources, and knowledge. Targeted surveillance system should be applied in order to get a better status of unknown livestock and wildlife diseases particularly for bovine tuberculosis. Determination from unknown to known tuberculosis status in wildlife in this region may help to complete the Asian and global maps of bovine TB distribution and will help to understand a potential spread of disease due to further exportation of disease from this region to another region. The figure below illustrates a non-systematic review that attempts to give an overview on MTC causing wildlife tuberculosis in SEA (Che-Amat and Ong 2018), a less known status region with a potential disease occurrence based on their bio diversified wildlife population which could potentially act as a reservoir for domestic livestock at the wildlife interface (Fig. 4).

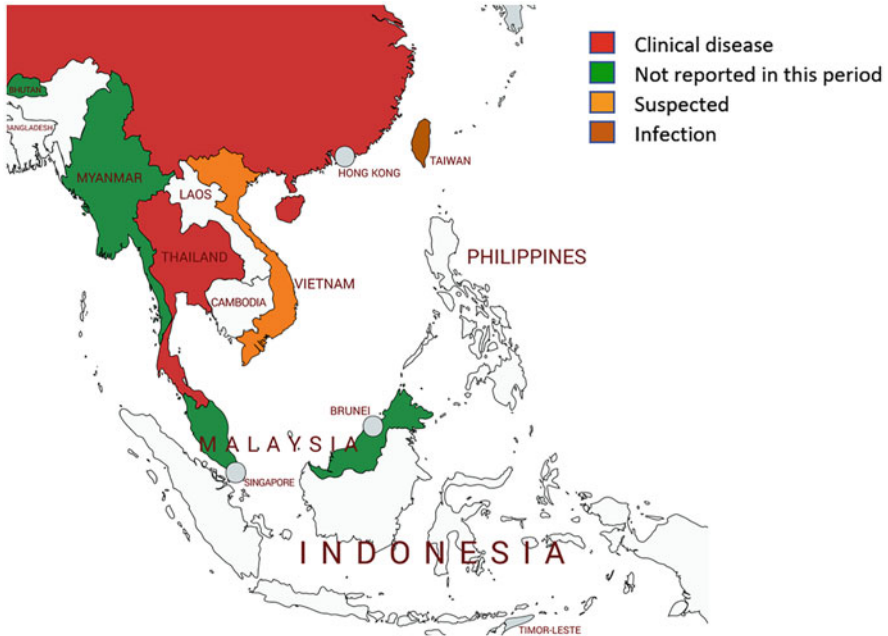


Fig. 4 Reported tuberculosis distribution maps for livestock and wildlife until the end of 2013 (Che-Amat and Ong 2018)

Management Practices at the Interface

As human populations in Asia expand and land-use conversion intensifies, and as large wildlife populations have drastically decreased and are now mostly concentrated within a limited number of protected areas, close contacts with humans and livestock in the future is inevitable. In fact, nowhere is this problem likely to be more acute than in Asia (Sankaran and Ahrestani 2016). Primary drivers of disease-causing emerging infectious agents of vertebrate wildlife include exposure to domestic sources of pathogens and exposure to wild sources via human interventions (Tompkins et al. 2015). Major cases of Emerging Infectious Diseases (EID) in Asia have been associated with mixing at high densities of wild and domestic animals, which may happen within or near protected areas where the remaining populations of large endangered wild mammals persist, or in areas where mobile and still abundant wildlife (e.g., rodents, bats, wild boar) get into contact with livestock where congregation occurs.

As illustrated for Indochinese countries, livestock production units are widely distributed throughout the region (Fig. 5). On average, livestock densities are similar among the five countries at the national level, with the notable exception of Lao PDR, which has 25% lower livestock density (see Fig. 6). Overlapping maps of livestock densities and protected areas reveals markedly different patterns for

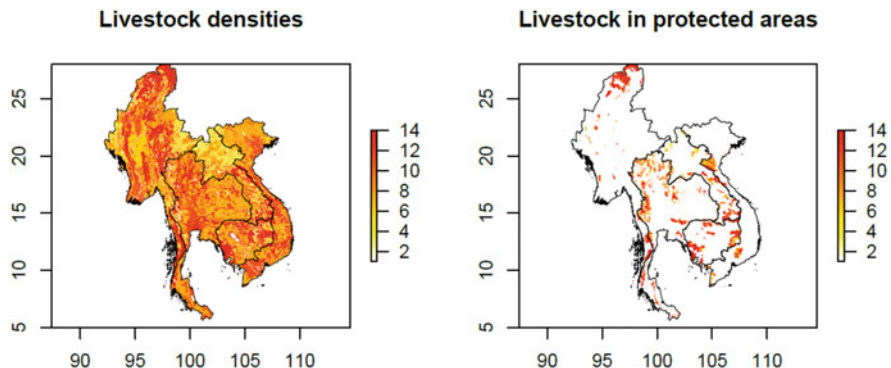


Fig. 5 Map of livestock densities in interface areas and protected areas of Indochinese countries (Cambodia, Lao PDR, Thailand, Vietnam). Data are compiled from <http://www.fao.org/dad-is/data/fr/>

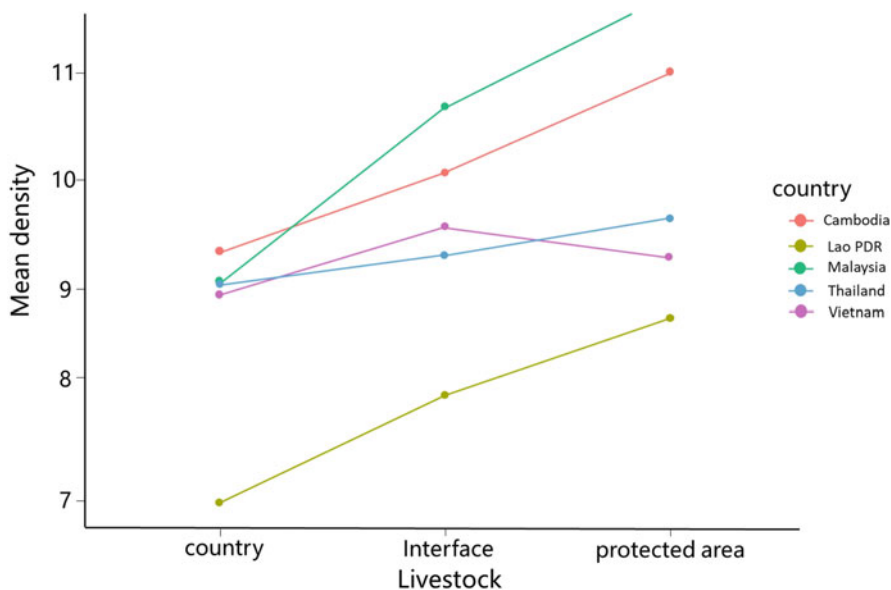


Fig. 6 Livestock densities in protected areas and peripheral areas of Indochinese countries (Cambodia, Lao PDR, Thailand, Vietnam). Data are compiled from <http://www.fao.org/dad-is/data/fr/>

interface areas among the five countries. Two countries, Thailand and Vietnam have similar livestock densities inside protected areas compared to interface areas (1 km each side of PA boundary), whereas Cambodia, Lao PDR, and Myanmar have significantly higher livestock densities inside and outside protected areas (Fig. 6).

This could illustrate the growing pressure for agricultural land in these countries, and suggests that livestock grazing in protected areas is poorly regulated (Chaiyarat and Srikosamatarata 2009). Cambodia and Myanmar, which have a limited number of protected areas, also apparently have the highest livestock densities inside these protected areas, whereas the relatively low population density in Lao PDR (less than 30 people/km², compared to 150 people/km² on average in SE Asia; (Anonymous 2017a, b)) may have buffered the need for additional livestock pastures. One example of management at the wildlife-livestock interface is the case of AI. Closed systems for duck farming are promoted (FAO, http://www.fao.org/newsroom/en/focus/2006/1000348/article_1000353en.html) to control highly pathogenic avian influenza in Asia. Ducks roam freely in the rice paddies could be contributing to the spread, unwittingly, of the Avian Influenza virus. National authorities have helped farmers change over to this new method of raising ducks in order to protect humans and the poultry sector, in particular smallholder producers, against HPAI, in Asia and beyond, through the effective control and prevention of the disease and the restoration towards a sustainable, viable poultry production sector.

Although most large mammals of conservation importance in Asia are now confined within protected areas, wildlife-livestock interactions are not restricted to protected areas and their vicinities. First, there are few notable exceptions of large wild mammalian species that not only persist but even locally thrive outside of protected areas in Asia, including wild boar and primates (e.g., *Macaca* spp. (Fuentes 2011)). Second, as emphasized by Capelle and Morand (2017), two groups of micro-mammals which are very diverse and ubiquitous or very mobile, bats and rodents, are likely to play a major role as reservoirs of emerging infectious diseases in Asia (Capelle and Morand 2017). Third, the loss of biodiversity, which has been occurring over the past decades in Asia with unprecedented speed and magnitude, is a major driver of the emergence of infectious diseases (Morand et al. 2014).

For decades, communities have been viewed as a threat to forest biodiversity and commercial production and, as a result, only a very small percentage of the public forest land in Asia has been brought under co-management. Yet, participation in forest governance institutions by local stakeholders has been shown to be strongly associated with joint positive outcomes for biodiversity conservation and forest users in South Asia and Africa (Persha et al. 2010). Bringing communities formally into the management of protected areas and their peripheries is a dramatic, albeit absolutely essential, the shift of direction to improve the monitoring and management of wildlife-livestock interfaces in the Asian sub-continent. Equally, because hunting is the major cause of the decline of large mammals and birds (Harrison et al. 2016) it is of paramount importance that the rules and regulations adopted to preserve them are enforced and sanctions applied to all offenders. The paradox is that the economic pressure for agricultural land that has largely been responsible for the decline of biodiversity in Asia over the last decades may provide new opportunities for innovative wildlife-livestock co-management outside protected in the future. Indeed, because of reduced economic profitability and predictability, some regions of SE Asia (e.g., Thailand) are currently experiencing a decrease in the number of farmers,

as the younger generations prefer alternative professional activities perceived as less insecure and generating more income than crop production. This has direct consequences on land-use in rural areas (e.g., Thailand) with an increasing surface of ex-farmlands going fallow. This could provide opportunities to demonstrate that nature and agriculture can work together (Gordon et al. 2016), as these areas may be used to test mixed livestock-wildlife controlled grazing experiments which have proved ecologically and economically promising in other parts of the world (du Toit 2011; Fynn et al. 2016).

Final Remarks

Although both wildlife and livestock reservoirs can be considered as important sources of emerging infectious diseases in Asia, it is the anthropogenic influence on ecological systems that causes serious consequences that operate at the interface among wildlife-livestock-humans, and contribute to significant economic losses and ecologic problems (Belden and Harris 2007). The importance of wildlife in the dynamic of emerging infectious diseases, particularly zoonosis, is becoming a big challenge for the countries in the Asian region. Probably, many pathogens and hosts have not been listed here because there is not data/research about them. Without this information, a further understanding and management of the system, under a One Health perspective is not possible. One Health in Asia is promoted by prominent organizations including the World Health Organization, Food and Agriculture Organization, World Organization for Animal Health, Hubnet in Asia, and The International Federation for Animal Health, Global Alliance for Rabies Control. Though wildlife species have occasionally been demonstrated to play a role of reservoir host for shared diseases in Asia, their role is still unclear in most cases. There is a lack of adequate scientific information in such a diverse continent, and epidemiological studies addressing the distribution of pathogens and assessing the roles of wild hosts, livestock, and human practices for shared diseases at the interface are urgent.

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Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Africa



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Introduction

The African continent has been for centuries perceived as the lost Eden for wildlife populations. Some areas are indeed, home to the largest concentrations of large mammals in the world and harbor an incredibly high level of biodiversity. At the same time, this abundant and rich diversity of mammal hosts comes together with a large diversity of pathogens, many of which are the cause of the most threatening infectious human and animal diseases in the world today. Warthogs (*Phacochoerus africanus*) and soft ticks in East and Southern Africa represent the wild reservoirs of the African Swine Fever (ASF) virus, a virus threatening the world pig industry (Jori and Bastos 2009; Dixon et al. 2020). Similarly, buffalo (*Syncerus caffer*) populations in sub-Saharan Africa, are the main wild reservoir of Foot and Mouth Disease (FMD), considered as one of the major threats for the livestock industry in developed countries (Thomson et al. 2003; Knight-Jones and Rushton 2013). From the public health perspective, there is equally evidence that nonhuman primates from Central and West Africa forests were at the origin of the Human Immunodeficiency Virus (HIV), the largest human pandemic in the last century. Therefore, for the common public, Africa could be also easily be perceived as sources of pathogens of global importance.

In addition, Africa is intensively exposed to many and very serious development and environmental challenges that are progressively transforming natural environments and increasingly encroaching on wildlife populations. This is leading many wildlife populations towards a higher rate of interactions with anthropic compartments (humans and their domestic animals), rising the risk of emergence of new diseases and re-emergence of old diseases on new territories.

The development and globalization of Africa also involve new forms of wildlife exploitation, which are intensifying and expanding across the continent. Traditional subsistence hunting and bushmeat consumption are rapidly evolving towards organized commercial trade (Fig. 1b) to supply increasing consumption demands towards large cities in the continent and beyond (Van Vliet et al. 2016). Moreover, new forms of consumptive and non-consumptive wildlife exploitation activities are developing and generating new patterns of interaction between wildlife humans and their livestock.

This chapter reviews the changes and transformations of Africa, the conjunction of drivers that affect a diversity of interactions between wildlife, domestic animals, and humans, the main characteristics of those interactions, and the problems and consequences related to them.



Fig. 1 Wildlife utilization activities have developed in Africa in recent years. Different forms of wildlife exploitation such as cane rat farming in West Africa (left) and the bushmeat trade (right) have been expanding during recent decades in different parts of Africa and generating new forms of the interface between wild animals and the human environment (Photos: Ferran Jori)

History of the Wildlife-Livestock Interface in Africa

Major infectious animal diseases circulating at the wildlife-livestock interface have been historically interlinked and influencing each other in Africa. Rinderpest, one of the most destructive viral diseases circulating among ruminants, is a good example: Initially introduced from Asia in the late nineteenth century, it decimated millions of wild and domestic herbivores with very serious ecological, epidemiological, and social implications. The removal of approximately 90% of susceptible wild and domestic ruminants induced a dramatic shortage of animal protein availability resulting in the mass starvation of human populations in sub-Saharan Africa (Sunseri 2018). At the beginning of the twentieth century, the ruminant population was so small that pathogen transmission was limited and the burden of diseases circulating between domestic and wild ungulates such as FMD or animal trypanosomiasis (AAT) were reduced to historical low levels. From an ecological perspective, the lack of grazing pressure allowed the expansion of thick savannah vegetation, favoring abundant breeding grounds for tsetse fly populations and an increase in the prevalence of human and animal trypanosomiasis. As a result, human populations abandoned tsetse-infested areas in search of more comfortable living territories. These regions became exclusive wildlife habitats with negligible human presence, turning into African game reserves and national parks during colonial times.

Towards the middle of the twentieth century, the development of a vaccine against rinderpest allowed repeated mass vaccinations campaigns against this virus and resulted in an extraordinary recovery of wild and domestic ungulate populations, which expanded into new territories: a new and abundant wildlife-livestock interface was then restored. This situation favored the re-emergence of bovine diseases such as FMD and AAT across large parts of the continent in the second half of the twentieth century (Brito et al. 2016; Van den Bossche et al. 2010).

Ecological, Socioeconomical, and Geographical Drivers Affecting the Wildlife-Livestock Interface

Climate Change

The African continent is highly exposed to climate change and its mean annual temperature will increase more than +2 °C in the course of the present century (Pereira 2018). The greatest negative impacts on livestock are expected in grazing systems in arid and semi-arid areas. Exacerbated drought conditions will reduce forage and range productivity and may contribute to overgrazing and land degradation. This phenomenon can enhance competition for grazing lands, and water sources (Fig. 2), increasing the frequency of interactions between wild and domestic animals around those common and increasingly scarce resources such as vegetation



Fig. 2 Water points in arid environments congregate large numbers of species including different species of animals and humans. This congregation will increase with climate change (Photo: B. Faye)

cover, water surfaces, or pasture. The alteration of these climate-dependent resources may also force animals to adjust their migratory movements towards new ecosystems where they may encounter or introduce new pathogens (Altizer et al. 2011).

In addition, climate change is able to modify the distribution of many diseases and pathogens affecting wildlife and livestock, particularly vector-borne diseases. Warmer temperatures have an impact on the range patterns of vectors and their pathogens to new temperate or higher latitudes, exposing naïve host populations to new diseases (Kaeslin et al. 2012; Van den Bossche et al. 2010).

Climate change is reducing the distribution of tsetse fly habitat, allowing the expansion of cattle production in areas where it was previously limited by AAT, with several ecological, socioeconomic, and epidemiological implications (Anderson et al. 2011). One of them is for an instance an increase of conflicts between wildlife and livestock, which threaten the survival of top African predators such as lions or wild dogs (Carter et al. 2018; Easter et al. 2018).

Finally, climate change can have an impact on the immune status of animals due to heat or nutritional stress, increasing their susceptibility to parasites and pathogens, facilitating co-infection with multiple organisms, and the occurrence of clinical disease in normally resistant host species. This phenomenon has been recently observed in Serengeti lions (*Panthera leo nubica*) infected with canine distemper virus and with high levels of infection with *Babesia leo*, a usually non-pathogenic

tick-borne parasite. This co-infection was suspected to be responsible for abnormal mortality events in lions in 1994 and 2001 (Dybas 2009).

Population Growth and Movements

Africa has one of the youngest human populations on Earth and its demographic growth in the next decades is likely to rise exponentially. Now home to 1.2 billion, the African population is expected to double to 2.5 billion by 2050, exceeding a growth of 42 million people per year. Conversely, the perspectives of protein production are inversely proportional, exposing many regions to an extremely serious challenge of the local sustainable food supply. Many of those areas include large surfaces of dry land and forested areas, where a combination of growing populations and land degradation are increasing the vulnerability of people to both economic and environmental changes (Van Vliet et al. 2016). While the rate of replacement of forested areas by pastoral systems is expected to decline between 2020 and 2050, the expansion of humid cropland systems at the expense of forest is expected to continue for decades ahead.

Another important impact of demographic growth is the increased frequency and number of migratory movements, which influence the exchanges of agricultural products. Those transactions can facilitate the long-distance spread of some pathogens, once localized in some areas of wildlife-livestock interface to distant territories. In this manner, strains of FMD originating from wildlife interface areas in Southern Africa have managed to cross country boundaries thousands of kilometers away, generating outbreaks in Northern African countries (Jori et al. 2016). At a larger trans-continental scale, African swine fever strains originating in warthog burrows have been introduced in Eastern Europe, generating huge economic losses to the pig industry (Quembo et al. 2017).

Rural Exodus

By 2050, more than two-thirds of the world's population will live in towns. Urbanization will primarily be the result of the expansion of the main megalopolis such as Lagos, Kinshasa, Cairo, or Luanda. One of the major challenges in this context, is how to feed those people sustainably, since the future will bring risks of non-renewable natural resource shortages. In forested Africa, cultural habits of wildlife consumption linked with demographic growth have driven the development of a very important bushmeat trade. This places at risk of extinction many vulnerable wildlife species and reduces at the same time the food supply of people dependent on these resources in rural forested source areas in the longer term (Van Vliet et al. 2016).

Deforestation

Across Africa, oil, gas, and mining projects are driving investments in new and improved infrastructure. Within these developments, forests are vulnerable to loss or severe degradation through conversion to agriculture or colonization by settlers seeking employment and other economic opportunities (Edwards et al. 2014). This trend is the cause of the disappearance of close to 90% of the West African forest during the last century. Given the extent and rate of forest fragmentation due to roadside farming and logging, up to 30% of Central African forests are expected to disappear by 2030. This process facilitates the overlapping of anthropic activities with natural habitats (Chukwuka et al. 2018) and the contact of humans and domestic animals with wildlife reservoirs, generating a higher rate of exposure of previously naïve host populations to new zoonotic pathogens (Wolfe et al. 2005). In addition, habitat destruction is conducting many endangered species to a serious situation of vulnerability because they are increasingly confronted with challenges of overexploitation and contacts with infectious pathogens from human or domestic animals, which can equally threaten their survival.

Characteristics Affecting the Wildlife Interface in Different African Regions

African Rainforests (Congo Basin, Remaining Forests in West Africa or East Africa)

African equatorial rainforests encompass a very high level of animal and plant biodiversity. The Congo Basin contains 20% of the world's tropical forests and supports the highest biodiversity of the continent. African tropical rainforests are separated into the Congo Basin in Central Africa, the Guinean Forests of West Africa, and some relics of forest on the East African Coastal area, which support rich wildlife populations, including numerous endemic species of high conservation priority (Mayaux et al. 2013). Nevertheless, forest habitats in East, Central, and West Africa are seriously encroached by highly dense human populations and their livestock and are exposed to tremendous pressure by commercial logging, slash-and-burn plantation agriculture, weak governance, industrial-scale mining or logging, and unsustainable bushmeat hunting (Nogherotto et al. 2013). In addition, many of these areas are often threatened by civil unrest and political conflicts, which add a further strain when refugees turn to the forests for shelter and firewood.

African Rangelands

African savannahs are distributed across the West African Sahel, Eastern, and Southern Africa. Most of sub-Saharan agriculture takes place in savannah areas, which support most of the cropland and pasture areas. Importantly, savannah landscapes are also home to the largest wild mammal populations on Earth. For this reason, large surfaces of these landscapes are devoted to transboundary conservation such as the Mara-Serengeti Ecosystem, the Kavango-Zambezi Transfrontier Conservation Area, or the W complex in West Africa. Although these processes are positive for wildlife conservation, they enhance the presence of common grounds where wildlife and livestock interact, generating new challenges for the control of shared infectious diseases (Thomson et al. 2013).

However, future changes in the climate could have an impact on these landscapes by increasing the number of droughts or increasing rainfall. Furthermore, another major threat for savannah habitats is the shift of agricultural practices towards intensification and conversion of very large areas of grassland into cropland. Unfortunately, all these biotic and abiotic changes are pushing rates of extinction of many large emblematic mammals of Africa to unprecedented and dramatic levels (Archer et al. 2018).

Transition Areas

Transition areas constitute a mosaic of habitats and climates extremely rich in biodiversity. A diversity of ecosystems changing from forested to open shrub savannah areas exists in coastal areas of Central Africa, West Africa, and East Africa. Highly diverse habitats are also found on the slopes of many high peaks such as Kilimanjaro, Mount Cameroon, or the boundaries of the Ethiopian plateau. These areas are particularly prone to interactions with wildlife because they host important human population densities with their domestic animals. Therefore, these transition areas are considered as hot spots for emerging zoonotic infectious diseases at the human-animal-ecosystems interface that have the potential to spread across borders such as Yellow Fever, Ebola Virus disease, Marburg Viral fever, Crimean Congo hemorrhagic fever, Hepatitis E virus, or Rift valley fever (Olivero et al. 2017).

African Deserts

Those include the Saharan region in North Africa and the Kalahari and Namib deserts in Southern Africa. Due to the lack of water, these habitats host a limited number of large mammal species, compared to other regions.

Interphase Between Phylogenetically Close Species

Phylogenetically close species such as wild and domestic ruminants or birds often share the same ecological spaces, similar resources, and a wider range of pathogens. This is for instance the case between wild and domestic bovids or between avian species.

The Ruminant Interface

Livestock production is a deeply rooted traditional activity and represents the cultural, socioeconomic, and nutritional basis of many agro-pastoral societies in Africa. The continent hosts almost 20% of the world cattle population (326 million heads), which has increased by 100 million heads since the beginning of the twenty-first century (Figs. 3 and 4). In the Sahelian regions of West, East, and northern Africa, small ruminants kept by rural agro-pastoral communities in mixed crop-livestock settlement areas, represent more than 60% of the continental mammal production (Fig. 3) and are a major source of income generation, despite the challenges posed by infectious diseases, land pressure and climate change (Otte et al. 2019).

In many countries with deeply rooted pastoral culture, there is a traditional opposition between livestock production areas and territories protected for wildlife use (national parks and game reserves). Despite the substantial contribution of wildlife-based tourism (Fig. 5) to many African economies, demographic growth and climate change increase the dependence of livestock herders to areas rich in pasture and water and the competition with wildlife for natural resources (Gordon 2018). This competition is particularly acute at the boundaries of protected areas in savannah ecosystems, where agro-pastoral societies often share grazing spaces and water sources with wildlife populations (Miguel et al. 2017).

In this context, a diversity of wild and domestic large and small ruminants interact, sharing a diversity of diseases (Table 1). The wild domestic bovid interface in Africa is well described in the literature due to its role in the maintenance of many economically important infectious diseases such as FMD (Box 1), while information on diseases circulating between other wild and domestic ruminants species is scarcer (Mahapatra et al. 2015; Wambua et al. 2016).

Short Cycle Species (Pigs and Poultry)

Pigs and poultry are a crucial food source for rural populations in Africa due to their fast growth, quick turnover, and prolificacy. They both play very important roles in Africa by improving food security, reducing poverty, and providing employment.

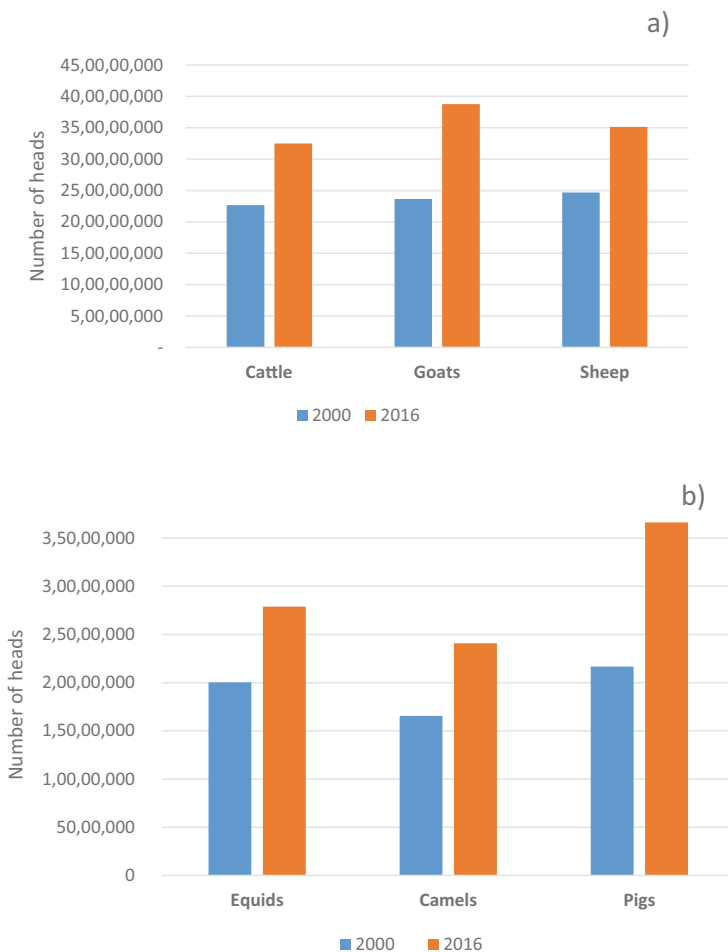


Fig. 3 Trend of the total numbers of live domestic mammals in the African continent since the beginning of the twenty-first century until 2016: (a) Ruminant species and (b) Non-ruminant species. (Source: FAOSTAT)

The Avian Interface

Chickens are the most numerous of all domestic animals raised in Africa. The vast majority of rural households keep chickens or other poultry species as a way to provide income, cheap proteins, or gifts for friends and families (Guèye 2000). Additionally, some countries such as South Africa, Egypt, Nigeria, or Ghana have developed modern poultry value chains for meat and eggs production.

Poultry production systems are classified into four categories (or sectors) based on the level of integration of operations, the level of biosecurity, and the type of marketing system. The category corresponding to village or backyard production

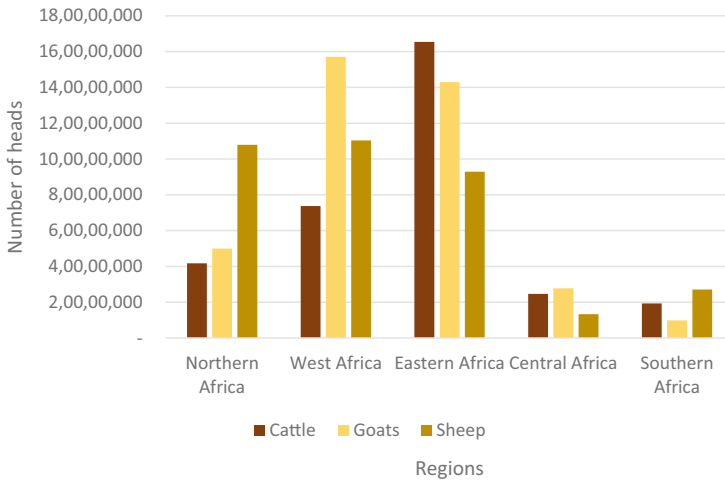


Fig. 4 Distribution of domestic ruminants per region in the African continent in 2016. Source: FAOSTAT (<http://www.fao.org/faostat>)

systems, with minimal biosecurity, is largely predominant in sub-Saharan Africa where it represents between 70 and 99% of the national poultry flock in most countries. This lack of biosecurity is characterized by free-roaming of poultry flocks and possible contacts with other animals including wild birds, which may have large consequences in terms of flock vulnerability to infectious diseases such as avian influenza (Box 1) or Newcastle disease (Molia et al. 2015). Transmission of other avian diseases is poorly covered by the research.

The Pig Interface

Although in lower figures than other domestic animals, pig numbers are growing steadily and have more than doubled in the last three decades, to supply meat to expanding urban markets. Current pig figures are estimated at 36.6 million heads (Fig. 3) mostly concentrated in Nigeria, South Africa, Mozambique, and Uganda. Despite being negligible in Northern Africa due to religious considerations, some West African predominantly Muslim countries (Senegal, Mali, or Burkina Faso) host large numbers of pigs kept by animist or Christian populations. The sector is characterized by (1) a high proportion of traditional, small scale, subsistence farmers mainly localized in rural areas, (2) a large-scale intensive pig farming mostly located in peri-urban areas to access the market of major cities, and (3) a whole range of production systems between those two extremes (Penrith et al. 2013). Interactions with wild suids can occur under traditional free-ranging domestic systems. Some studies suggest that direct contact between domestic pigs and warthogs is rare. However, serious shared diseases (ASF or AAT) are mostly transmitted by vectors such as argasid ticks or tsetse flies (Kukielka et al. 2016). Conversely, direct

Fig. 5 Wildlife tourism generates new opportunities for close encounters between African mammals such as banded mongooses (left), nonhuman primates (center) or antelopes (right), and human populations, and allowing for potential pathogen transmission on both directions. (Photos: Ferran Jori)



interactions between domestic pigs and bushpigs are suspected in different African areas. However, the nature of those interactions and the importance of other potential shared pathogens remain unknown (Jori et al. 2017).

Table 1 Summary of identified interfaces between phylogenetically close wild and domestic species

Identified interface	Area/Region	Specific/Major diseases at the interface	References
Wild-domestic carnivores	East Africa Zambia, Ethiopia	Distemper	Berentsen et al. (2013), Gordon et al. (2015)
	Tanzania	Rabies	Lembo et al. (2008), Sillero-Zubiri et al. (2016)
	East Africa	Babesiosis	Dybas (2009)
	Zambia	Canine parvovirus	Berentsen et al. (2013)
	East Africa Botswana	Feline immunodeficiency virus	Roelke et al. (2009)
Wild-domestic Bovids	Botswana	Brucellosis	Alexander et al. (2012)
	South Africa Zimbabwe Zambia Tanzania	Bovine tuberculosis	Hlokwe et al. (2016)
	Southern Africa	Foot and mouth disease	Brito et al. (2016), Jori et al. (2009)
	Southern Africa Eastern Africa	Tick-borne diseases	Van der Bosche et al. (2010) Espinaze et al. (2018)
	Southern and Eastern Africa	Malignant catarrhal fever	Swai et al. (2013), Wambua et al. (2016)
	Eastern Africa Southern Africa	Bovine Trypanosomiasis	Anderson et al. (2011) Auty et al. (2012)
	Southern Africa	African horse sickness	Gordon et al. (2013)
Wild and domestic equids			
Wild domestic pigs	Mozambique	African swine fever virus	Quembo et al. (2016)
		Trypanosoma spp	Anderson et al. (2011), Jori et al. (2017)
		<i>Trichinella</i> spp.	Jori et al. (2017)
Wild domestic birds	South Africa	Avian influenza	Abolnik et al. (2016)
	Mali	Newcastle disease	Molia et al. (2015)
Small ruminant interface	Kenya	RVF	Lembo et al. (2013)
	Zimbabwe	Anthrax	Mwakapeje et al. (2018)

The Carnivore Interface

A wide diversity of small and large wild carnivore species share savannah and forest ecosystems in Africa. With the encroachment of wildlife habitats, new ecologic landscapes dominated by human activities with an increased presence of domestic dogs and cats facilitate interactions between wild and domestic carnivores and the circulation of a diversity of pathogens (Table 1). Studies on pathogens among domestic dogs at the carnivore interface are more common than for cats. Some

retrospective studies in the selected shared ecosystem, suggest that the dynamics of those pathogens at the interface are variable, depending on the geographical location, the available wild and domestic carnivore population density and distribution (Gordon et al. 2015; Lembo et al. 2008). Theoretically, implementation of control measures such as vaccination or deworming can reduce the circulation of pathogens in domestic carnivores at the interface. However, in practice, dogs and cats in rural African communities rarely receive veterinary attention from their owners.

The Equine Interface

There are almost 28 million domestic equids in Africa, mostly located in East and West Africa. African horse sickness is transmitted by arthropods and does not require direct contact between wild and domestic species. Information on other shared diseases is limited (Horak et al. 2017). Direct interactions between domestic equids (donkeys, horses, and mules) and zebras (*Equus* spp.) are described and biologically possible, although in natural conditions, they are limited. The expansion of game farms in Southern Africa can increase the availability of virus from natural sources. However, vaccination can prevent infection in domestic equids (Gordon et al. 2013). Although occurring outside the African continent, movements of wild equines from Africa to zoological collections in, have triggered the emergence of African horse sickness outbreaks among equine populations of Europe (Sánchez-Matamoros et al. 2016) and more recently in Thailand.

Interface Between Phylogenetically Distant Species

Interactions between species that are not genetically close can also occur when a generalist pathogen circulates in a multi-host ecosystem or in the case of man-driven ecosystem or habitat transformations.

The Multi-Species Interface

In multi-host ecosystems hosting a large diversity of mammals, generalist pathogens find numerous opportunities to cross-species barriers. In Southern or Eastern African mixed grazing systems, domestic and wild mammals are highly connected, facilitating cross-infestation of a diversity of species with common pathogens (Abu Samra et al. 2013; Espinaze et al. 2018). *Mycobacterium bovis* (Hlokwe et al. 2016) in the Kruger National Park affects an increasing range of wild species over the years (Hlokwe et al. 2014) and to a lesser extent, FMD (Box 3) can affect a diversity of ungulates in multi-host African savannah ecosystems (Casey et al. 2014). In Kenya,

serological surveillance among wildlife populations after Rift Valley Fever outbreaks provides evidence of exposure of a large community of wild and domestic mammal hosts to the virus (Britch et al. 2013). Environmental contamination of soil or water with some infectious pathogens such as *Bacillus anthracis* can generate outbreaks affecting a diversity of wild and domestic mammals and humans in a diversity of habitats including forest and savannahs (Mwakapeje et al. 2018; Hoffmann et al. 2017).

New Interfaces in Africa

Current patterns of change in the African continent enhance the occurrence of contacts between species of different genera. Living in different ecological niches, phylogenetically distant species have fewer common pathogens because they seldom encounter each other in natural environments. However, man-driven ecological transformations and social changes are facilitating new forms of interaction between wildlife and anthropogenic environments.

The Human-Wildlife Interface

The wildlife-human disease transmission is particularly relevant in sub-Saharan Africa considering the important poverty levels, the abundance of wildlife populations, and diversity of opportunities of interaction between humans and animals with or without the participation of domestic animals (Tables 1, 2 and 3). Pathogen transmission can occur through bushmeat hunting (Fig. 6) (Filippone et al. 2015), game butchering and cooking (Rimoin et al. 2017), collection of carcasses (Monroe et al. 2015), holding wild pets, the practice of certain traditional rituals or medical practices and exposure to bites from hunted species or their arthropod vectors. These opportunities are more common in forested areas where there is less availability of domestic animal protein and the exploitation of wildlife for food is more widespread.

Monitoring zoonotic spillover events dynamics in remote regions can be extremely laborious and challenging. In the case of Ebola, for instance, the natural life cycle of the virus, the role of reservoir species (wild or domestic), and the

Table 2 Cases of multi-species transmission at the wildlife-livestock interface

Rabies	Lembo et al. (2008)
Distemper	Berentsen et al. (2013)
Bovine tuberculosis	Hlokwe et al. (2014, 2016)
Foot and mouth disease	Casey et al. (2014)
<i>Cryptosporidium</i> spp	Abu Samra et al. (2013)
Peste des Petits ruminants	Lembo et al. (2013)
Rift Valley fever	Evans et al. (2008)

Table 3 Cases of pathogen transmission into wildlife populations from humans and livestock in Africa

Wildlife species	Area	Specific pathogen	References
Mongoose	Botswana	<i>Mycobacterium tuberculosis</i> <i>M. mungo</i>	Flint et al. (2016)
Multi-hosts	South Africa	<i>Mycobacterium bovis</i>	Hlokwe et al. (2016)
Mountain Gorilla	Rwanda	Metapneumovirus	Palacios et al. (2011)
African Buffalo	Zimbabwe	FMD virus	Casey et al. (2014), Brito et al. (2016)
Nonhuman primates	South Africa	Cytomegalovirus, hepatitis A virus <i>Cryptosporidium</i> spp. <i>Giardia</i> spp	Drewe et al. (2012), Odeniran et al. (2018)

interspecies transmission dynamics remain largely unknown. Direct contact of human index cases with some wild animal sources was clearly reported in at least eight Ebola outbreaks, providing some strong indication of zoonotic transmission from wild animal species (Leroy et al. 2005). Similarly, the role of domestic livestock in Ebola virus epidemiology remains unknown. Pigs (*Sus suis*) are the only known domestic animals to be naturally susceptible to Ebola-like viruses, with the ability to transmit them to other pigs as well as to nonhuman primates (Atherstone et al. 2017).

The Camel Interface

Except for national parks situated in arid lands where camel herds (*Camelus dromedarius*) are common, (e.g., Awash National Park in Ethiopia), interactions between camels and wild species are scarce, the density of antelopes in the desert being low, and wild camels' populations (only in Central Asia) almost extinct. However, some global changes affect traditional camel production:

1. Climate change is leading to the expansion of the camel farming systems to southern parts of Sahelian countries (Central African Republic, Uganda, Tanzania, Cameroon, or Senegal) and longer transhumance migration routes.
2. Traditional camel farming systems become more sedentary to be closer to town markets (for camel milk and meat), increasing the interface with peri-urban wild species such as bats or rodents.
3. Increasing regional demand in camel meat generates trade movements of live camels from the Sahel to North Africa and from the Horn of Africa to the Arabian Peninsula (Faye et al. 2012).



Fig. 6 Wildlife interactions in rural areas of Africa are common through hunting or by keeping wildlife as pets: (a) Hunters transporting a bush pig (*Potamochoerus larvatus*) in Madagascar (Sophie Molia); (b) Village boy playing with a hunted bat in Guinee Conakry (Helene de Nys); (c) Cormoran kept as a pet bird in Mali (Sophie Molia)

These changes facilitate new forms of interactions between camels and other domestic or wild species and have the potential to impact on public health and the dissemination of transboundary diseases. For instance, the cohabitation between camels and small ruminants facilitated the emergence of PPR outbreaks in camels in Ethiopia or of the Rift Valley Fever outbreak in Mauritania (Roger et al. 2000). Similarly, it could have contributed to the emergence and spread of MERS-COV in the Middle East (Box 2).

New Interfaces through Different Wildlife Utilization

Any new form of wildlife utilization, consumptive or not, can generate new situations of interaction between wildlife and other hosts. Growing industries based on wildlife such as tourism or game production have increased in the last decades and represent new opportunities for the circulation of pathogens between wildlife and human or domestic animal hosts.

Wildlife Tourism

Every year millions of persons travel to some of the approximately 400 national parks and reserves in Africa to experience a diversity of activities that allow some degree of contact with wildlife species. Tourism contributes more than 8% to the GDP in Namibia, Zimbabwe, and Tanzania, 4–8% to Ethiopia, Kenya, Uganda, Rwanda, and Botswana (UNCTAD 2017). This industry generates new and unprecedented pathways of disease transmission between humans and wildlife (Odeniran et al. 2018). Indeed, repeated exposure of animals to human presence can alter their behavior, cognitive reactions, and immune responses increasing the probability of cross-species transmission between humans and wildlife. There is, for instance, evidence that elephant-back safari camps facilitate the risk of infection of elephants with human strains of *Mycobacterium tuberculosis* and *M. bovis*. Similarly, herds of banded mongooses (*Mungos mungo*) habituated to tourist camps in Southern Africa have become infected with tuberculous mycobacteria from human or domestic animal origin (Flint et al. 2016; Rosen et al. 2018). In addition, safari camps generate closer contacts between humans and habituated nonhuman primates such as baboons (*Papio* spp.) and vervet monkeys (*Chlorocebus pygerythrus*), facilitating the transmission of infectious and parasitic diseases between the two groups (Drewe et al. 2012; Odeniran et al. 2018) which have the capacity to challenge human health and biodiversity conservation.

Wildlife Production. A New Growing Interface

Global changes have enhanced the shortage of animal protein and the need to explore the development of new protein sources. Wildlife production creates new opportunities for interaction between wild species, domestic animals, and humans. In West Africa, the domestication of the greater cane rat (*Thryonomys swiderianus*), an extremely popular large edible rodent (Jori et al. 1995) has allowed the development of several thousands of small-scale farmers. This activity generates a potential new interface between domestic and wild rodents in close contact with humans that have received little scientific attention to date (Fig. 1a).

In Southern Africa, a flourishing wildlife industry based on mixed-ranching of several species of antelopes in private properties has been expanding in the last decade. Since the year 2000, more than 14,000 game ranches are reported, covering an area >200,000 km² and harboring between 16 and 20 million wild mammals (Child et al. 2012; Lindsey et al. 2013).

As an example, the extensive nature of ostrich (*Struthio camelus*) production systems in South Africa bears the continual risk of point introductions of avian influenza virus (AIV) from wild birds (Abolnik et al. 2016).

Despite their diversity, different wildlife production initiatives face similar problems. The development of the sector is often faster than the conception of guidelines and legal requirements to regulate its value chain. This situation affects the implementation of surveillance programs and monitoring of animal movements in game farms, which can have a huge impact on the risk of disease emergence and spread among a naïve population. The intensification in the production and the frequent mixing of individuals from different origins for trade or translocation exposes exploited wildlife species to stress and immunosuppression. These factors, together with the lack of availability of performant and validated diagnostic tests limit the capacity to routinely monitor disease in wildlife species (Hlokwe et al. 2016), facilitate the emergence of unsuspected infections such as avian Influenza in ostrich farms (Abolnik et al. 2016), or the emergence of rabies outbreaks in captive kudu (*Tragelaphus strepsiceros*) populations in Namibia (Mansfield et al. 2006; Scott et al. 2013). Poor education of animal handlers on management and handling of the game, lack of quarantine facilities, drug misuse, and poor record keeping can equally have a significant effect on the prevalence of wildlife pathogens in captive wildlife populations.

Problems and Impacts Related to Wildlife-Livestock Coexistence

Human Wildlife Conflicts

Human wildlife conflicts (HWC) are defined as any interaction between humans and wildlife resulting in negative socioeconomic impacts in human communities, the conservation of wildlife populations, or their environment (Madden 2004). HWC usually implies several negative outcomes such as the loss of human and animal lives, crop damage, habitat destruction, predation on livestock, and serious reduction of wildlife populations at the edge of protected areas in Africa or their habitats (Penteriani et al. 2016; Williams et al. 2017). The fact that rural communities living in this context are seldom compensated for socioeconomic losses incurred by wildlife contribute to exacerbate negative perceptions of wildlife among human communities and the perpetuation of HWC. Diseases circulating at the wildlife-livestock interface and affecting livestock such as FMD, act as an additional trigger of HWC.

With human population growth in Africa and the need for land facilitating encroachment into natural areas, we can anticipate an increase in HWC (including disease emergence) in wildlife and livestock populations.

Implications of HWC for Conservation

HWC contribute to generate a negative perception among rural communities cohabitating with wildlife at the edge of protected areas and can jeopardize conservation efforts (Kahler and Gore 2015; Matseketsa et al. 2019). Large African predators such as lions, leopards (*Panthera pardus*) or African wild dogs (*Lycaon pictus*), or cheetahs (*Acinonyx jubatus*) often pay a very serious price to HWC since livestock owners often eliminate raiders. One of the most commonly used practices to achieve this purpose is poisoning, which has a dramatic environmental impact because it can also affect other species. This widespread use of poison represents for instance one of the main causes of drastic vulture declines in Africa together with the use of environmentally toxic veterinary drugs such as diclofenac. Subsequently, this decline in scavenger numbers can have serious impacts on the removal of carcasses from diseased animals and the deterioration of environmental health.

Disease Transmission and Its Implications

Disease transmission is considered as another form of HWC. In many instances, outbreaks of diseases of wildlife origin among livestock populations from rural communities living at the edge of protected areas can jeopardize the peaceful

cohabitation between wildlife and livestock interests in Southern or East Africa (Swai et al. 2013; Thomson et al. 2013; Wambua et al. 2016). Scientific research has abundantly covered some diseases at this interface in Africa in the last few years (avian influenza, rabies or FMD, or BTB). However, the list of diseases has increased in the last decades (Tables 1, 2, and 3) as wild and anthropic ecosystems become more intermingled. The majority of them are poorly investigated despite their suspected impact on domestic animals, public health, and the conservation of wild species.

Implications of Disease Transmission for Human, Domestic Animal, and Wildlife Health

Except for some specific animal diseases, the impact of diseases circulating at the interface with livestock is seldom quantified and, in many cases, completely unknown. In any case, it clearly goes beyond morbidity and mortality in livestock and has numerous socioeconomic implications such as the cost of diagnosis, control, and treatment, loss of man-power, negative social and psychological status, and indirect effects to commercial markets (Knight-Jones and Rushton 2013). The impact is even higher if we take into consideration the public health perspective of zoonotic diseases (Welburn et al. 2015). In the case of Africa, the widespread circulation of HIV increases the vulnerability of human populations to many wildlife-borne zoonotic infections.

As seen earlier with several examples, increasing proximity between domestic and wild hosts also puts wildlife populations at risk of disease outbreaks. Over a quarter of domestic mammal pathogens are infectious to wildlife species and their spillover to natural ecosystems can have variable levels of impact on wildlife populations (Cleaveland et al. 2001). There is evidence of transmission of bovine tuberculosis, brucellosis, or FMD from livestock to wildlife populations in Southern and East African ecosystems. The introduction of bovine tuberculosis in African rangelands has generated a chronic devastating impact in a diversity of wild species sharing the same environment (Hlokwe et al. 2016). Great apes such as the endangered mountain gorilla or some chimpanzee populations are highly susceptible to respiratory pathogens carried by humans such as human metapneumoviruses, human respiratory syncytial viruses, and *Streptococcus pneumoniae*, being able to cause high morbidity and mortality rates in great ape populations (Calvignac-Spencer et al. 2012; Köndgen et al. 2017; Palacios et al. 2011).

Management Practices to Reduce the Risk of Disease Transmission at the Interface

Adequate management practices to prevent disease spread at the wildlife-domestic animal-human interface are crucial.

Fencing and Zoning

One proposed solution to protect both people and wildlife from the negative outcomes of HWC is the physical separation of both populations through the erection of fences. However, there are numerous social, economic, and conservation drawbacks to fencing large areas. In dryland ecosystems, fences prevent the mobility of animal populations and can have very serious ecological impacts on migratory species such as zebra and wildebeest (Durant et al. 2015). Historically, fences started to be erected in South Africa in the 1950s in order to separate livestock from wildlife, once it became scientifically evident that the African buffalo represented a wild reservoir of Foot and Mouth Disease (Jori et al. 2009; Thomson et al. 2003).

During the 1980s, South Africa started establishing disease-free areas based on the guidelines of the World Animal Health Organization (OIE), in order to be able to export livestock and beef commodities from areas where FMD had been eradicated (Thomson et al. 2013). These FMD-free zones were achieved through the use of fences to separate livestock from infected wildlife, repeated annual vaccination of livestock herds, and strict control in animal movements. This approach, known as commodity-based trade, successfully increased beef exports from South Africa and was subsequently adopted by other exporting countries in the region such as Namibia, Botswana, or Zimbabwe. However, fences are more than just physical barriers. Despite having a significant ecological impact on the migrant population of wild herbivores, they also influence economic growth and development enhancing social and economic discrimination between disease-free exporting areas and infected areas where rural communities are unable to export and sell their livestock at competitive prices (Naziri et al. 2015).

Control in Targeted Hosts

In general, the control of pathogens is rarely implemented in free-ranging wildlife populations, with the exception of valuable animals in game ranches or the case of extremely endangered wildlife populations such as the Ethiopian wolves (Sillero-Zubiri et al. 2016). In other circumstances, wildlife-borne infectious and parasitic diseases are controlled through vaccination or control measures implemented in human or livestock populations. Treatment of livestock with acaricides is

recommended to prevent tick-borne diseases at the edge of protected areas (Espinaze et al. 2018). Dog vaccination is the strategy of choice to prevent rabies cases in domestic carnivores and humans (Lembo et al. 2008) and the vaccination of ruminant populations is common to prevent the spread of outbreaks of Rinderpest, Rift Valley Fever or FMD in East or Southern Africa (Jori et al. 2009; Roeder et al. 2013).

Surveillance at the Interface

In Africa, active surveillance of wildlife populations takes place in exceptional situations because it often requires expensive equipment and specialized expertise, which is only available in a few selected countries in Southern and East Africa where the wildlife sector contributes substantially to national economies (Fig. 7). In the majority of African countries, funds to monitor disease in wildlife are very limited and passive surveillance approaches are the method of choice. They often involve the participation of local communities or staff working in wildlife departments or protected areas. A common approach is the collection and analysis of wildlife carcasses found in natural habitats (Lembo et al. 2008). The availability of mobile phone technologies in recent years helps to overcome the constraints of poor physical infrastructure by real-time transmission of field observations such as unexpected mortalities or reports of carcass findings (Karimuribo et al. 2017).

In countries where wildlife management and capture expertise is lacking, cooperation with hunters for the collection of animal samples in bushmeat networks (Fig. 1) can be a cheaper way to collect wildlife specimens (Ravaomanana et al. 2011). However, one should be cautious in avoiding incentives for hunting, which would be legally and ethically questionable. The collection and conservation of samples in remote areas is nowadays easier with filter papers (Picard-Meyer et al. 2007; Smit et al. 2014). However, this approach is only suitable for the detection of certain pathogens and the availability of validated tests for disease detection in wildlife samples remains a major constraint for wildlife surveillance (Hlokwe et al. 2014; Jori et al. 2014).

In order to prevent the introduction of pathogens into new territories, a comprehensive risk analysis approach should be implemented before any translocation or relocation of animals for wildlife management or game farming purposes (Hartley and Sainsbury 2017).

In case of new emerging outbreaks, genomic technologies based on new generation sequencing can rapidly identify new viruses and pathogens in the most remote areas on the planet and facilitate the identification of reservoir species and the pathogen dynamics among different host populations (Gardy and Loman 2017).



Fig. 7 Wildlife management skills lack in the majority of African countries. High wildlife management and capture skills are very efficient to monitor the health of wildlife populations. However, they are only available in a minority of countries in East and West Africa, where the wildlife industry contributes substantially to the national economies. The large majority of African countries lack this kind of expertise, which is out of their financial reach. Innovative and cheaper ways to obtain wildlife health information are needed (Photos: Ferran Jori)

Raising Awareness among Exposed Stakeholders

Awareness among stakeholders about risk practices and their mitigation is a useful approach to prevent the transmission of wildlife pathogens to livestock. The risk of African swine fever in Southern Africa is highly associated with free-ranging pigs interacting with the soft tick in warthog habitats. To prevent infection of domestic pigs by infected tick bites, important efforts are deployed to raise awareness about the importance of increasing biosecurity in pig farms (Penrith et al. 2013). This practice has the advantage to reduce the transmission of other zoonotic diseases such as trichinellosis or hydatidosis.

In another context, awareness about the importance of global health and the potential health risks related to different types of interaction with wildlife within protected areas, tourist camps, exposed communities and different sectors of the wildlife industry is instrumental to facilitate proper surveillance, reporting, and implementation of preventive measures among the exposed human population (Jori et al. 2014).

Future Directions for Improving Health Management at the Wildlife-Livestock-Human Interface

Community Based Natural Resource Management (CBNRM) projects in Africa promote the integration of conservation of natural resources with rural development by empowering communities in their right to use and manage their natural resources and wildlife populations. The benefits from wildlife-based activities (tourism or sport hunting) are reinvested in community development activities. This approach, which promotes the concept that rural communities will protect wildlife if they can benefit from it, has met some success in Southern African countries like Namibia and Zimbabwe (Lindsey et al. 2009, 2013).

The concept of commodity-based trade is based on the principle that beef commodities that follow certain manufacturing procedures such as deboning, removing the lymph nodes, maturing, or heating meat beef products reduce to negligible the probability of spreading FMD through beef products trade (Thomson et al. 2013). Wildlife conservation organizations have promoted the implementation of this approach in the Southern Africa Development Community (SADC) region as a way to facilitate the trade of beef products originating from rural communities living at the edge of protected areas, and therefore potentially infected with FMD virus through their contacts with wildlife-infected species. Indeed, the development of such trade has the potential to improve benefits derived from rural livestock production, attenuating the conflict derived from cohabitation between wildlife and livestock (Thomson et al. 2013). However, in practice, the socioeconomic and technical feasibility of this approach requires demonstrative data through several pilot

projects, and this is a long-term on-going process that will only yield results in a few years.

Conclusion

Africa is the last place on Earth with a significant presence and variety of large mammals and has extraordinary levels of biodiversity. Nevertheless, the continent is transforming quickly, and these changes generate a huge biodiversity loss and threaten nature's contribution to human livelihoods. The drivers of change in the African continent are all on the rise and we can anticipate an exponential growth of interactions between wildlife, livestock, and people, with serious implications in the level of conflict and in disease emerging events. In this confrontation, wildlife is likely to pay a heavy tribute in terms of species conservation, if no action is taken to highlight the potential value of wildlife and ecosystem services to improve human livelihoods and empower local rural economies. New formulas and approaches to promote cohabitation and resilience between natural ecosystems and farming systems, need to be tested and successes disseminated at national, regional, and continental levels to promote new ways of acting and thinking. In that sense, initiatives that have met some levels of success in increasing benefits from wildlife for local rural communities should be monitored, assessed, and disseminated (Lindsey et al. 2009; Thomson et al. 2013).

From the disease perspective, zoonotic pathogens from wildlife origin are more likely to emerge from forested areas while transboundary animal disease events are more likely to come from interactions between livestock, humans, and wildlife in savannah areas. However, the risk of unexpected events resulting from new wildlife use activities should not be underestimated. Mitigating the risk of emergence and increasing protection against pathogens requires research for understanding disease transmission dynamics. The use of high technologies such as new generation genetics, geomatics, and new diagnostic techniques can provide some specific epidemiological answers. However, sophisticated expensive technologies that most countries will not be able to apply are not necessarily sustainable solutions at the large scale. Surveillance and prevention methods need to be technically simple, have a limited cost, and be accompanied by awareness and capacity building campaigns. They also need to be adapted to the new types of wildlife interface developing in Africa.

The concept of the interface in all its dimensions is complex and susceptible to change together with the evolution of African landscapes. In that sense, capacity building in wildlife health and management, sustainable use of wildlife, and new paradigms of system thinking applied to health management such as the concept of One Health or Ecohealth are instrumental to expose young generations to new ideas, change perceptions, and design and experiment new practical solutions. There is a growing need for investigating new methods to facilitate the integration of different

disciplines in order to improve the understanding of complex socio-ecosystems which require multiple and diverse disciplines and solutions.

Box 1 Avian Influenza in Africa

Avian influenza has had a large negative socioeconomic impact in Africa. The arrival of highly pathogenic avian influenza (HPAI) virus type H5N1 in 2006 and its subsequent spread to 17 countries has caused the loss of hundreds of millions of poultry, either by death or culling, and has killed 122 humans mainly in Egypt (Ekong et al. 2018). Outbreaks of HPAI virus H5N2 in 2004, 2006, and 2011 in South Africa have also been very detrimental with up to 10% of the country's domestic ostrich population being lost (van Helden et al. 2016).

The interface between domestic and wild birds has played a key role in the propagation of avian influenza. AI viruses find periodically their way in Africa via wild birds migrating from Eurasian regions. They then circulate among populations of wild birds and are transmitted to domestic fowl by direct contact or through the contamination of surface water, river muds, and wetland banks (Gaidet and Caron 2016). A wild bird origin of HPAI strains causing outbreaks in domestic birds has been demonstrated in Nigeria and South Africa by molecular phylogenotyping (Abolnik et al. 2016). Similarly in Egypt, a migratory common teal (*Anas crecca*) sampled in the Nile delta was found infected with a H5N1 virus, closely related to the parent of the group of viruses responsible for subsequent outbreaks in poultry and humans (Saad et al. 2007).

Further spread within or among countries is then largely due to trade, both legal and illegal, of poultry and poultry products as well as to the limited biosecurity of the traditional poultry breeding systems in Africa (Van den Berg 2009). In Africa, the biosecurity of small-scale poultry is unlikely to improve in the short term because its popularity is based on its very limited inputs in terms of food and facilities. To prevent cases of HPAI in humans, it is necessary to rapidly control outbreaks in poultry and to raise awareness among stakeholders (poultry farmers, collectors, market sellers, and consumers) about risk mitigation measures. These include sourcing poultry from outbreak-free areas, avoiding close cohabitation of humans and poultry, and wearing personal protective equipment (gloves, masks) when handling domestic fowl and poultry products (Van Kerkhove et al. 2011).

Box 2 Mers-CoV Emergence Could Be the Result of an Unexpected Wildlife-Livestock Interface

The MERS-coronavirus was described for the first time in a man in Saudi Arabia in June 2012 and subsequently in many other countries, mostly in the Middle East (Gossner et al. 2016). By the end of 2017, 2102 human cases of MERS-CoV including 733 fatalities were confirmed. Camels and bats were suspected as the main reservoirs of this new coronavirus. The bats are at the origin of many diseases and different investigations showed that 5.3–24.9% of the bats were positive to MERS-CoV. However, the bats existing in Saudi Arabia belong to other species than those tested, and finally, it was concluded that MERS-CoV was not transmitted through bats (Memish et al. 2013). Camels were found serologically positive to MERS-CoV in almost 100% of samples from the Middle East, confirming the wide circulation of the virus among the camel population, but without clear clinical expression of the disease. It was concluded that camels could act as a reservoir of the virus, especially in North Africa and the Middle East where camel farming is culturally important. The incidence of MERS-CoV in humans was 15 times higher in camel shepherds and 23 times higher in camel slaughterhouse workers than in the general population (Al-Osail and Al-Wazzah 2017). The MERS-Cov isolated in camel was identical to the human CoV while MERS-CoV does not infect other domestic species, including Bactrian camel and small camelids (Miguel et al. 2016). However, despite the high seroprevalence observed in camel populations from North Africa (up to 100%) for more than 30 years, no camel-human transmission case has been demonstrated to date. This data suggests that the transmission of the virus from camel to human is unclear and the role of other small mammals (rodents) deserves further investigation.

Box 3 The Different Sides of FMD at the Wildlife-Livestock Interphase in Africa

Foot and Mouth Disease (FMD) affects over 70 species of domestic and wild cloven-hoofed animals and is caused by an RNA virus from the family *Picornaviridae* that exists as seven serotypes (O, A, C, Asia 1, SAT1, SAT2, and SAT3). FMD is one of the most feared transboundary animal diseases, it is highly contagious and can survive sub-clinically for several years in persistently infected animals called “carriers.” In Southern African beef exporting countries, FMD is mitigated in livestock populations and the African buffalo is considered the major ancestral maintenance host of SAT serotypes. Other wild ungulates only act as spillover hosts rather than

(continued)

Box 3 (continued)

maintenance populations and occasionally, high-density impala populations are involved as intermediate hosts between buffalo and cattle (Vosloo et al. 2009). Experimental evidence of FMD transmission from buffalo to cattle is lacking, however, it has been repeatedly demonstrated by field data and molecular phylogenetics (Bastos et al. 2003; Vosloo et al. 2006). East Africa, encompasses the highest numbers of wild ruminant and livestock populations in the continent, harboring a large continuum pool of wild and domestic susceptible hosts, rich in potential interactions between buffalo, other wildlife, and livestock species (Casey et al. 2014). In West and Central Africa, the wildlife-livestock interface has received very little attention to date. Recent investigations show that some African buffalo populations are infected with SAT1, SAT2, A, and O (Di Nardo et al. 2015). Their capacity to act as a reservoir of FMD for cattle requires further investigation, although it is probably circumscribed, to those few regions where viable buffalo populations are maintained.

Overall, the prospects of immunological control of the disease in sub-Saharan Africa are extremely challenging. Current vaccines for SAT viruses produce short-term immunity (often less than 6 months), are not cross-protective and thermosensitive. In Southern Africa, traditional methods of control such as veterinary fences are confronted by the development of Transfrontier Conservation Areas, which facilitate animal movements and wildlife-livestock interactions (Jori and Etter 2016). In East Africa, the broad spectrum of wild and domestic hosts and large and scale of animal movements creates an ideal scene for the emergence of a diversity of strains (Casey et al. 2014). In this context, non-geographic approaches of FMD control such as commodity-based trade, have the potential to provide access to beef African producers and allow a more balanced cohabitation between conservation and livestock development interests (Thomson et al. 2013).

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Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Oceania



Simon Humphrys and Michel De Garine-Wichatitsky

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Introduction

Oceania's thousands of islands result in a plethora of microhabitats, but can be broadly categorized into four geographical groups comprised of distinct island clusters from a geographical, cultural, and climatic perspective (Fig. 1). Melanesia, Micronesia, Polynesia, and Australasia consist of low-islands built from corals, high islands positioned along the ring of fire created through volcanic activity, and continental islands consisting of Australia, New Zealand, and West Papua/Papua

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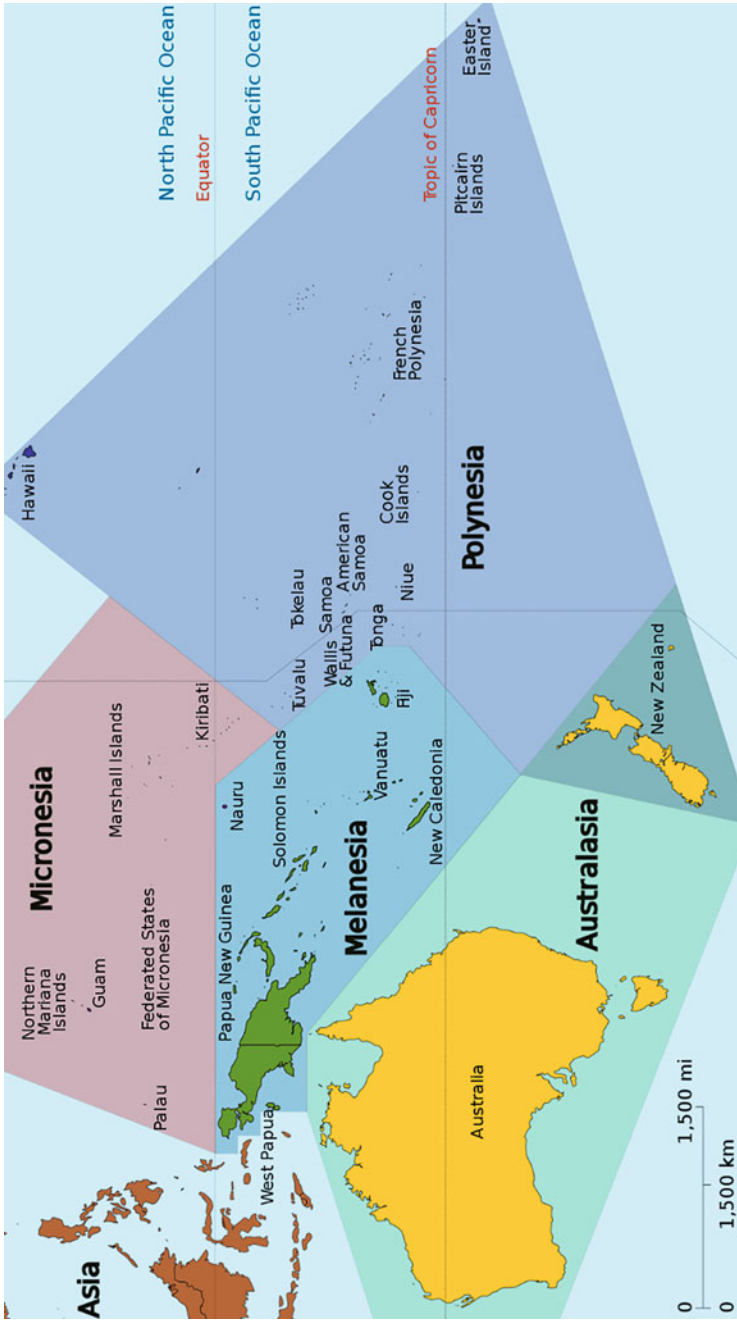


Fig. 1 Geographical grouping of regions comprising Oceania (Wikipedia)

New Guinea. While the central and western Pacific low and high islands have relatively uniform flora, fauna, and climates (sub-tropical and tropical), the continental islands exhibit far greater diversity of ecosystems, including arid deserts, Mediterranean habitats, temperate and tropical rain forests, alpine environments, mountainous plateaus, fiord lands, and sub-tropical savannas.

Oceania is also home to two of the 17 “megadiverse” countries on earth (Australia and Papua New Guinea; Shi et al. 2005), which refers to the world’s top biodiversity-rich countries measured by the total number of species and [endemism](#) at the [species](#), genus, and family levels (McNeely et al. 1990). While being a megadiverse country does not involve a fauna criterion, a unique feature of the three continental islands’ (i.e., Australia, New Zealand, and Papua New Guinea) native fauna is the relative scarcity of placental mammals. Oceania is a continent of marsupials ([macropods](#), [possums](#), and [dasyuromorphs](#)), birds, reptiles, and insects that occupied many of the [ecological niches](#) placental mammals dominated elsewhere in the world. In Australia alone, 87% of mammals, 93% of reptiles, 94% of frogs, and 45% of birds are endemic and exist nowhere else on earth (Chapman 2009).

Humans have inhabited Australia, Papua New Guinea, and a number of the Melanesian Islands for tens of thousands of years, while a majority of the Micronesian and Polynesian Islands have been inhabited for 700–3500 years (Anderson 2009; Jupiter et al. 2014). European colonization of the continent has been relatively recent at less than 250 years (Flexner 2014). Micronesians, Melanesians, and Polynesians traditionally husbanded pigs and poultry prior to European arrival. The first European domesticated livestock (cattle, horses, sheep, goats, pigs, poultry) were introduced into Oceania within the last 300 years (Kiple 2007). Also, with English colonization came game species (deer, rabbits, hare) to Australia and New Zealand. From the small, self-sustaining family farms of a century ago to the present, the scale and efficiency of agricultural animal production principally across larger islands with the greater arable land area such as Australia, New Zealand and to a lesser extent Papua New Guinea and Fiji, has increased significantly with advances in mechanization, intensification, and improved animal genetics. These changes resulted in greater agricultural production scales where climate and land availability allowed natural capital to be modified to support livestock grazing or fodder production. The scale of this transformation also necessitated greater transportation of livestock through supply chains as they evolved to be more efficient and enterprises specialized to focus on specific segments of livestock production like breeding (studs), growing out (grazing/feedlots), transacting (sale yards), and processing (abattoirs). Transport of livestock across significant distances and presence on multiple properties demonstrated in Fig. 2 before being processed at an abattoir or live export facility exponentially increases the biosecurity risks of disease transmission from wildlife-livestock as well as livestock-livestock interfaces that need to be managed to maintain a robust animal health system.

Across the region, agriculture is pivotal to economic stability and contributes up to 30% of the national gross domestic product in some Pacific Island states (Stewart 2006), and livestock production is a significant agricultural sector in a majority of Oceania’s economies. While not generally realized as large producers, a number of

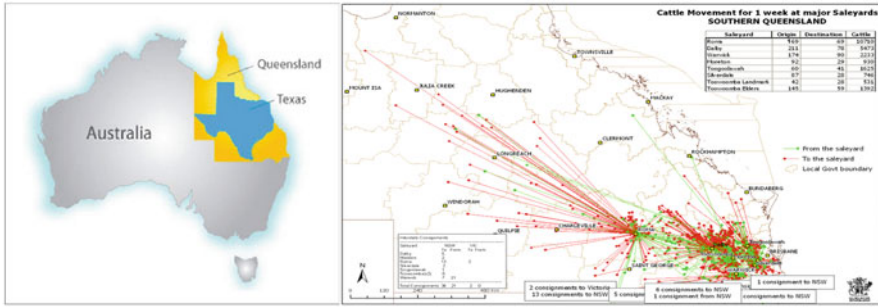


Fig. 2 An illustration of the extensive movement of 23,640 cattle through 8 sale yards in 1 week within southern Queensland, Australia's second-largest state by land area

Pacific Islands and territory countries (PICTs) have the highest pig and poultry densities in the world. Ten of the 22 PICTs rank in the top-25 countries globally for pigs/hectare of agricultural land area and 13 of the 22 PICTs rank in the top half of countries globally for poultry density (Brioudes 2016). For continental islands, the livestock sector also provides significant export revenues (Alexandratos and Bruinsma 2012). Almost at odds with the importance of agriculture, Oceania is a highly urbanized continent (Fig. 3), with a majority of the human population living in or near urban centers. The extremes in the region are Australia, which is quite developed, and Papua New Guinea, which retains a relatively low human density due in part to the majority of the population continuing to lead an agrarian tribal existence (Bourke and Harwood 2009; United Nations 2019). Australia's urbanization, coupled with its vast land area, results in expansive tracks of land where wildlife and livestock can intermingle in the absence of human intervention. A similar dynamic, although not to the same geographical extent, occurs in New Zealand, Papua New Guinea, and other islands across the region that can sustain extensive livestock production.

The scaling and stratification of livestock production systems that have occurred in Australia and New Zealand has not been possible for other countries within Oceania due to climate and land availability/type. These limitations, along with cultural imperatives, have resulted in the importation of processed livestock products for most of Oceania's countries being driven by human demand, much of which comes from Australia and New Zealand. Exportation of livestock and livestock products besides Australia and New Zealand is modest. The dynamic of inter-Oceania trade involving Australian and New Zealand livestock products being exchanged within regional island nations and highly regulated importation of livestock and livestock products from the rest of the world that is very limited in scale is one of this region's biosecurity advantages, irrespective of the wildlife-livestock nexus present across Oceania's livestock production systems.

The arrival of Europeans and the livestock/game species they brought with them to many PICTs also impacted native wildlife. Old World diseases (e.g., bovine tuberculosis, foot and mouth disease, rabies), land clearing for grazing,

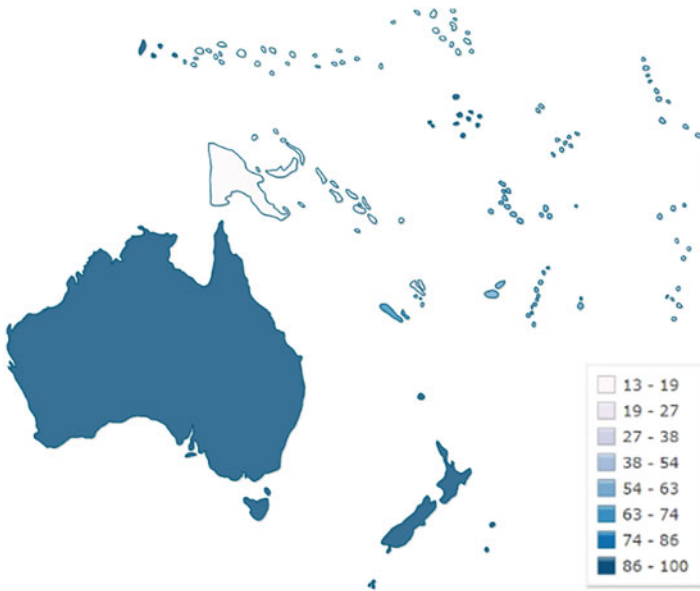


Fig. 3 The map below shows how urban population (% of total) varies by country in Oceania. The darker the shade, the higher the urbanization. The country with the highest value in the region is Nauru, with a value of 100%. The country with the lowest value in the region is Papua New Guinea, with a value of 13%. Source: The United Nations Population Division’s World Urbanization Prospects



Fig. 4 Pictured are European rabbits in high densities decimating pasture ecosystems in Australia and New Zealand

overexploitation, and introduced species rapidly transformed landscapes (Jupiter et al. 2014; Kepple et al. 2014). This led to precipitous declines in native vegetation communities as well as pasture systems designed to support domestic livestock production. A good example of an introduced herbivore that can have devastating impacts on native plant populations is the European rabbit (*Oryctolagus cuniculus*; Fig. 4). Response to the agricultural and environmental threat posed by rabbits was the advent of government-led wildlife management, including research into disease as a biocontrol (e.g., myxomatosis and rabbit hemorrhagic disease). This effort took



Fig. 5 Pictured left panel are wild pigs near cattle in Australia and the right panel shows direct contact between brush-tailed possums and cattle in New Zealand

advantage of a disease-wildlife interface that fortunately (as researched) was specific to European lagomorphs and left Oceanic wildlife unaffected (Cook and Fenner 2002; Edwards et al. 2002).

While rabbit biocontrol has proven effective over the last 50 years, management at other wildlife-livestock interfaces has been less successful. Across Oceania, wild pigs (*Sus scrofa*; Fig. 5) and domesticated, free-ranging swine are noted vectors for the transmission of leptospirosis and brucellosis (Ridoutt et al. 2014; Guernier et al. 2018). In New Zealand, introduced brushtail possums (*Trichosurus vulpecula*) from Australia act as a secondary host that transmit bovine tuberculosis to cattle (O'Neil and Pharo 1995), akin to European badgers (*Meles meles*) transmitting the same pathogen (*Mycobacterium bovis*) to cattle in the United Kingdom (Hone and Donnelly 2008; Fig. 5). Both of these wildlife-livestock interfaces are nearly impossible to prevent in the extensive grazing systems that dominate livestock production in the continental islands or indeed in the more subsistence, free-range husbanding of livestock in the low and high islands of Oceania. This has resulted in entrenched endemic disease reservoirs on islands within Oceania for bovine tuberculosis and other bacterial diseases, including leptospirosis and brucellosis variants (Crump et al. 2001; Victoriano et al. 2009). Additionally, Hendra and Nipah viruses have become emergent in Oceania, which sporadically spill-over from native fruit bats (*Pteropus* spp.) into domestic horses and pigs and then into humans (Mackenzie 2005; Field et al. 2011; Fig. 6).

There is a continuum of biosecurity throughout Oceania, from little in free-ranging livestock, too highly organized, intensive raising of poultry, pigs, and cattle. The level of biosecurity in place depends on geographic location, species, and type of agricultural enterprise. In virtually all these scenarios there is opportunity for direct and indirect transmission of diseases between livestock and wildlife as they directly or indirectly share resources. While available evidence suggests that most, if not all, of Oceania's islands remain free of many of the most impactful diseases of livestock elsewhere in the world (e.g., foot and mouth disease, pestivirus, classical swine fever, highly pathogenic avian influenza; Brioude 2016), maintaining disease-free status will require an enormity of investment to prevent pathogen



Fig. 6 A horse being tested for Hendra virus in Australia (left panel). Fruit bats are the primary host of Hendra virus (right panel)

entry, contain and eradicate diseases if pathogen entry occurs, and surveillance and monitoring to prove disease freedom or detect disease presence.

Socioeconomic and Biogeographical Drivers of the Wildlife-Livestock Interface

The first livestock introduced across the majority of Oceania's islands included pigs and poultry (chickens and occasionally ducks), which provided a valuable food source. Excess animals were usually traded with neighbors and occasionally seafaring visitors. Pigs and poultry were primarily free-ranging, and many went feral, leading to large and expanding populations across Melanesia and Polynesia (e.g., Hawaiian Islands). Like pigs, poultry traveled from southeast Asia with their human counterparts, based on genetic evidence (Storey et al. 2012). Poultry's main purpose was egg production, a protein source that could be kept for extended periods and did not require refrigeration. At this time, poultry meat was only occasionally eaten. Similarly, the original primary purpose of cattle was not as a source of meat either; cattle were primarily valued as beasts of burden that facilitated the cultivation of crops and as a source of leather.

Approximately 250 years ago, Europeans created a new livestock-wildlife interface across Oceania's largest land masses that has had a far more profound influence on their natural capital and civilizations. As Oceania's largest islands were settled by Europeans, socioeconomic aspirations and cultural considerations that were multi-generation old traditions in Europe drove a desire to replicate livestock husbandry practices in Australia and New Zealand. For example, Australia's livestock industry began in 1788 with the arrival of the first fleet of English settlers. The initial count of 7 horses, 7 cattle, 29 sheep, 74 pigs, 5 rabbits, 18 turkeys, 29 geese, 35 ducks, and 209 chickens (Australian Bureau of Statistics 2001) grew exponentially to the degree that Australia began exporting livestock. From that nucleus of livestock in the late eighteenth century, Australia became arguably the largest exporter of sheep and goat meat to global markets, and currently exports more than 70% of its beef production

annually (Meat and Livestock Australia 2019; Eather 2020). The only contender to the mantle of greatest sheep meat exporter emanates from the mid-1800s when New Zealand became a pasture-fed livestock powerhouse of production, even exceeding Australia's sheep population in the 1980s. The ever-increasing land clearing and transformation of native vegetation to grazing land to support livestock and agricultural production has transformed Australian and New Zealand landscapes and not always for the better (Knight 2009; Bradshaw 2012; Kepple et al. 2014). Different breeds of cattle, pigs, sheep, goat, horses, deer, and poultry were imported with the intent of creating a domestic supply that ultimately supported substantive domestic and export markets. Mixing of livestock, as well as cultural preferences, led to strategic breeding and genetic gains that have improved livestock phenotypic traits for a range of climates, soils, and flora and fauna to which they were not originally acclimated. Numerous introductions of non-native game species also occurred and altered ecosystem dynamics across the region. Multiple cervid species, the European rabbit, hare, and red fox (*Vulpes vulpes*) were imported to Australia and several of these also soon arrived in New Zealand (Krull et al. 2014). Shipping and human movement also facilitated commensal rodent-island hopping, which has been catastrophic for some bird species across Oceania's islands (Matisoo-Smith and Robins 2008; Towns 2009). Livestock competing for resources, and game species that became invasive in Australia and New Zealand, has impacted the bulk of the continent's landmass and consequently its native wildlife. This was exacerbated by human activity like hunting where the perceived impacts of some species were considered to put sheep husbandry at risk (e.g., the extinction of the Tasmanian tiger (*Thylacinus cynocephalus*; Paddle 2000), while clearing of native vegetation for livestock grazing caused the decimation of numerous other species (Reside et al. 2017).

With European settlers and livestock came diseases that Oceanic humans and native wildlife were ill-prepared for. For native islanders across Oceania, the impacts of diseases such as smallpox were sometimes large. Other introduced diseases that impacted humans during this time period and remain even now include chickenpox, cholera, diphtheria, influenza, measles, scarlet fever, typhoid, typhus, tuberculosis, and pertussis (whooping cough). To a lesser extent, imported livestock diseases impact Oceania's native wildlife. Old World diseases that were introduced to wildlife during this period included leptospirosis, brucellosis, and bovine tuberculosis. Additionally, foot and mouth disease was introduced to Australia during the early 1800s and was eradicated in 1872 (Productivity Commission 2002). The primary diseases found throughout Oceania and the interfaces they occur at can be found in Table 1.

As European populations colonized the larger islands and island chains, livestock trading increased, but innovations in mass land transport of refrigerated goods were not developed yet. Thus, overlanding or droving was common, where livestock grazed hundreds of kilometers to trading posts and urban centers. Gradually, small-scale subsistence farming began to give way to livestock production as a business, primarily in Australia and New Zealand, and to a lesser degree in New Guinea and

Table 1 Major disease systems at the interface of wildlife (W) and livestock (L) in Australia (AUS) and New Zealand (NZ)

Pathogen system	Primary species		Contact	Transmission direction	Distribution	References
	Domestic	Wildlife				
Avian influenza	Poultry	Waterfowl	Direct, indirect	L ← W	AUS, NZ	Bulach et al. (2010), Grillo et al. (2015)
Newcastle disease (non-virulent)	Poultry	Migratory birds, native birds	Direct, indirect	L ↔ W	AUS	Hoque et al. (2012)
Blue tongue	Ruminants	Deer, water buffalo	Direct, indirect	L ↔ W	AUS	Firth et al. (2017)
Leptospirosis	All	All	Direct, indirect	L ↔ W	AUS, NZ	Guernier et al. (2018)
Paratuberculosis	Cattle, goats, sheep	Wild ruminants	Direct, indirect	L ← W	AUS, NZ	Abbott (2002), Nugent et al. (2011)
<i>Neospora</i>	Cattle	Wild canids (dog/red fox)	Vector borne	L ↔ W	AUS	King et al. (2011)
Bovine tuberculosis	Cattle	Australian brushtail possum (wild pig, deer, ferrets, deer)	Direct	L ← W	NZ	Nugent et al. (2018)
Swine brucellosis	Swine, dogs	Wild pigs	Direct, indirect	L ↔ W	AUS	Mason and Fleming 1999
Lyssavirus	All	Wild bats	Indirect	L ← W	AUS, NZ	Merritt et al. (2018)
Anthrax	All	All	Direct	L ↔ W	AUS	Barro et al. (2016)

(continued)

Table 1 (continued)

Pathogen system	Primary species		Contact	Transmission direction	Distribution	References
	Domestic	Wildlife				
Arboviral pathogens: Murray Valley encephalitis, Kunjin, Ross River fever	Vertebrate hosts and the arthropod vectors (e.g., herons and egrets for Murray Valley encephalitis)	All (e.g., marsupials macropods for Ross River fever)	Vector borne	Mackenzie et al. (2017)	AUS	Mackenzie et al. (2017)
Hendra virus	Horses	Flying foxes	Indirect	L←W	AUS	Middleton (2014)

Polynesia. Mechanization advancements fueled this increasing trend, with railroad systems and steam-powered river transports in place by the mid-1800s (DITRDC 2020; Beeson 2020). Technology advanced and the first refrigerated frozen meat was exported from Port Adelaide in South Australia to the United Kingdom in 1895 (Maurovic 2007). Cattle, sheep, and their products could be raised across vast tracks of land, shipped via rail or river systems to human population centers for processing, and then exported globally. These advances led to increased movement of livestock and increased contact among livestock and native animals.

By this time the majority of Australian and New Zealand livestock production had transitioned from open range to behind fences, and though water and feed resources were managed, they were still available to native species as well. Wire-based fencing provided an inexpensive way to enclose large pastures and water sources like artesian bores or windmills that tapped underground water sources and allowed pastoralists to graze cattle and sheep in areas that would otherwise be unproductive for livestock. This led to shared resources that were more concentrated, which resulted in the potential for enhanced wildlife-livestock contact. However, the same production pressures are not evident for the rest of Oceania. This dichotomy is especially evident today where poultry is highly valued for meat in addition to their value from egg production. Poultry across the larger population centers is Oceania's preferred source of protein (Whitnall and Pitts 2019). Oceania's largest land masses and the livestock agriculture they support have changed dramatically in the last 250 years. The region has expended much effort into preventing disease incursions, containing and even eradicating intractable highly contagious animal and human diseases (Sabirovic and O'Neil 1999). Management of diseases considered endemic is undertaken across the largest countries in an effort to maintain their impacts below economic thresholds and to prevent their spread within and among Oceania's islands.

The Prevalent Livestock, Farm Typologies, and Opportunities for Interface

PICTs of Oceania have some of the highest densities of pigs and poultry per arable landmass on earth (Brioudes 2016). Conversely, Australia and New Zealand have large populations of cattle, Asian buffalo, sheep, horses, donkeys, and goats, with the majority of them being free-range or existing within extensive grazing production systems. As a result, these countries have some of the lowest commercial cattle and sheep stocking rates on earth. While a majority of livestock production is extensive, greater intensification is a growing trend and the larger Oceanic islands support intensive and free-range poultry and pig production systems. Cattle and sheep are by far the primary livestock species by population across Oceania by virtue of two countries, Australia and New Zealand.

Australia is one of the largest beef, sheep, and goat meat exporters in the world and is an industry valued at \$13.5 billion (Meat and Livestock Australia 2019; Black et al. 2008). Australia is also a large live animal exporter, exporting 1.1 million cattle, and 1.1 million sheep (Meat and Livestock Australia 2019). New Zealand is the top global exporter of milk and butter (FAO 2019). The demand for protein will continue to grow significantly as the world's populations continue to grow. The movement of livestock (dead or alive) may offer rapid spatial and temporal animal disease transmission routes and complicate the management of infectious diseases. Understanding these livestock aggregations and movements, including buying and selling patterns, and rapid identification and tracing of animals from infected premises have been done in Australia to help prevent and manage infectious disease outbreaks in livestock (DAWE 2019).

The Wildlife

Oceania, with its continental islands and more secluded high and low tropical islands, hosts some of the most unique flora and fauna assemblages found anywhere in the world. Plate tectonics and changing sea levels have resulted in ecosystems that have been isolated from the rest of the world for millions of years. It is this remarkable diversity and endemism that has resulted in the region being recognized for encompassing 6 of the world's 39 hotspots of diversity (Mittermeier et al. 2004). Australia is well known for its iconic kangaroos and koalas, as well as hosting the only mammals in the world that lay eggs (e.g., the platypus and four species of echidna). Birds are also relatively common in Oceania, with 110 endemic species occurring there, including many flightless species (e.g., kiwi, emus, cassowaries). The immensely rich coastal communities and oceans surrounding these large and small islands also host many marine species found only in the region.

Most recreational hunting in Australia is of feral or introduced species. Many of these species were introduced by Europeans to create a hunting experience similar to Anglo-Saxon traditions (Sharp and Wollscheid 2009). Hunting primarily occurs on private lands. Highly invasive species, such as rabbits, wild pigs, goats, and certain species of deer, are declared pests by most states and territories and highly encouraged to be hunted. Australia also allows for the commercial harvest of kangaroos and sets annual quotas (Pople 2004). Elsewhere in Oceania, hunting ranges from highly sophisticated operations where hunters pay considerable amounts of money for property access and guiding services (Davys et al. 1999) to local or subsistence hunting which not only provides food and supplies, but also serves religious and cultural functions (Oliver 1989). Waterfowl hunting is also a popular recreational activity in Australia and New Zealand and on other islands in the South Pacific, collection of seabird eggs is important to local indigenous communities (Bauer and Giles 2002).

Although there has been an increasing global trend in research on diseases at the wildlife-livestock interface, publications focusing on the region of Oceania are

lacking (Wiethoelter et al. 2015). In New Zealand, tuberculosis (TB) transmission between brushtail possums and livestock, and to a lesser degree wild and farmed deer, has been occurring for decades and is well studied (Morris and Pfeiffer 1995; Warburton and Livingstone 2015; Nugent et al. 2018). As with other countries where TB independently cycles in wildlife reservoirs (i.e., Great Britain, Spain, South Africa, and North America), eliminating TB at the livestock-wildlife interface has been a challenge (Palmer et al. 2012; Gortazar and Cowan 2013). This is partly because humans have over time introduced 31 species of mammals to New Zealand (King 1990), including feral livestock, which now occur naturally in the wild, of which 14 have been documented with TB (Coleman and Cooke 2001).

Also occurring in the region are two emerging bat-borne viruses that occasional spill-over into horses and pigs, Hendra and Nipah viruses, respectively (Mackenzie 2005). Fruit bats are the natural reservoir hosts for both viruses and in Australia, it is suspected that transmission of the Hendra virus is from ingestion of contaminated bat urine or feces on horse feed or water (Prowse et al. 2009). Although Nipah virus outbreaks have only been recognized in Malaysia, India, and Bangladesh, Oceania is nearby with fruit bats as a transmission source having broad spatial overlap throughout the region (Mackenzie and Field 2004; Plowright et al. 2019).

Australia, New Zealand, and other South Pacific islands lie at the southern end of the East-Australasian flyway. For example, 99 bird species are known to move between Australia and Asia and 63 of these undertake frequent migrations (Tracey et al. 2004). It is these wild birds, particularly waterfowl, which use this flyway and have been known to carry and spread high and low pathogenic forms of avian influenza (Viyahkrishna et al. 2013; Endo and Nishiura 2018; Sullivan et al. 2018). Periodically, spill-over events occur, and the virus is transmitted to domestic poultry, swine, or humans. Reducing the spread of avian influenza in migratory birds is unlikely, but increased disease surveillance and heightened biosecurity at the wild bird-poultry interface can lower the risk of disease outbreaks (Glass et al. 2019). Table 1 summarizes the major disease systems at the interface of wildlife and livestock in Australia and New Zealand.

Box 1 Wildlife-Livestock Interfaces in New Caledonia: Artiodactyl Introductions, Invasions and Sympatric Parasite Speciation

The archipelago of New Caledonia is a French Overseas Territory that lies at the southern extremity of Melanesia. The main island of Grand Terre is an ancient land, once part of the great ancient continent of Gondwanaland, from which it became separated 65–80 million years ago (Mittermeier et al. 1996). The flora and fauna are characteristic of an isolated ancient land, with an exceptional diversity and endemism within several plant and invertebrate

(continued)

Box 1 (continued)

groups. With the exception of bats, all terrestrial mammals have been introduced (Pascal et al. 2008). Significant wildlife-livestock interfaces, therefore, only involve species that have been introduced onto the archipelago, either deliberately, such as livestock and game, or not.

Two species of wild ungulates, wild pigs (*Sus scrofa*) and rusa deer (*Rusa timorensis*), are now widespread on the main island of Grande Terre, responsible for extensive negative impacts on native invertebrates, plants, and habitats (de Garine-Wichatitsky et al. 2004). Wild pigs, which are believed to have been first introduced in New Caledonia by the navigator James Cook during the end of the eighteenth century, have extensive impacts on the native flora and fauna, and on crop production (Pascal et al. 2006). However, wild pigs have not been demonstrated to play a role in the maintenance or spread of any diseases of zoonotic or veterinary importance, such as bovine tuberculosis, as in Australia and New Zealand (bovine tuberculosis is currently absent from New Caledonia). Similarly, rusa deer have invaded all natural and human-transformed habitats of Grande Terre, where they have very significant negative impacts on the native vegetation (de Garine-Wichatitsky et al. 2003, 2005), and frequently compete for pastures with free grazing cattle and small ruminants (Fig. 7). The small number of individual deer introduced in 1870 (Barrau and Devambe 1957), as confirmed by genetic analysis (de Garine-Wichatitsky et al. 2009), do not appear to have introduced new pathogens from their native range. Despite repeated screening of wild and farmed populations, rusa deer in New Caledonia appear to harbor few parasites and pathogens, and no significant livestock diseases have been detected in them.

However, the southern cattle tick (*Rhipicephalus microplus*, formerly *Boophilus microplus*) offers a remarkable example of the far-reaching consequences of wildlife-livestock-parasite interactions. The tick was accidentally introduced to New Caledonia during the mid-twentieth century with the importation of animals from Australia (Chevillon et al. 2013), and quickly invaded the cattle farms of the entire island of Grande Terre, favored by suitable local climatic conditions and the high susceptibility of *B. taurus* cattle breeds that had been imported by Europeans (Barré 2003). Intensive tick control programs have been implemented using acaricides since the tick was introduced onto the island, and resistance to all acaricides used have appeared (Ducornez et al. 2005; Chevillon et al. 2013). Rusa deer were initially considered a poor host for southern cattle tick, because ticks attached to deer are usually unable to engorge fully (Barré et al. 2002). However, significant tick infestation levels on rusa deer have been recorded and a large-scale tick genetic survey has been conducted (Koffi et al. 2006; De Meeûs et al. 2010). The analysis revealed a substantial and highly significant genetic differentiation between sympatric deer ticks and cattle ticks sampled from the same locations (De Meeûs et al. 2010). The southern cattle tick has actually diverged

(continued)

Box 1 (continued)

into two differentiated genetic pools: one on cattle, its original host on which intense acaricide tick control was applied for decades; and one on rusa deer, a new host that is widespread, locally abundant, and not subject to acaricide treatments. Remarkably, this sympatric isolation has occurred over a relative short period of time as a consequence of differential selection pressure, illustrating the complex ecological and evolutionary processes that may occur at wildlife-livestock interfaces.

The Disease at the Interface: One Health Perspective

Wildlife-livestock associated diseases that affect humans and domestic animals present extreme challenges for governmental agencies, natural professionals, and livestock producers. Differing attitudes and perceptions of the problem often reveal controversial opinions on how best to formulate solutions for the management and control of these diseases. A One Health approach to the problem acknowledges that animal and human diseases are intricately related and tools to reduce disease transmission at the animal-human interface must be multi-disciplinary; address the well-being of wildlife, livestock, and humans; incorporate socio-political and



Fig. 7 Introduced cattle and rusa deer frequently interact within pastures in New Caledonia. Photo: Nicolas Barré

economic factors, and account for environmental changes (Keune et al. 2017). For example, some wildlife-livestock diseases put entire industries at risk, such as trade restrictions when TB is found in cattle (Cousins and Roberts 2001; Waters et al. 2012; More et al. 2015). Fortunately, Australia was able to successfully eradicate TB from livestock and wildlife through a whole herd test and slaughter program, abattoir monitoring, extensive tuberculin testing, strict livestock identification via tagging, cost-sharing by government and industry, and removal of feral wildlife known to be reservoirs of TB (Cousins and Roberts 2001; More et al. 2015).

The avian influenza virus is another example of a disease(s) found globally in wild waterfowl, but once transmitted with domestic poultry flocks can cause severe mortality, oftentimes results in culling or depopulating entire premises, trade restrictions, and be a cause for concern for human health (Swayne et al. 2017). Wild bird surveillance has revealed some seasonal trends to increased public health and poultry risk of avian influenza transmission and disease outbreaks (OIE 2018). Climate change and how this might affect movements of migrating waterfowl using the Asian-Australasian flyway is another cause for concern as this may expand the range of current influenza viruses into novel areas (Vijaykrishna et al. 2013). Wild and domestic pigs are also susceptible to various avian and mammalian strains of influenza viruses, some more harmful than others, where genetic reassortment may occur and result in new, highly transmissible strains of the virus (Hall et al. 2008; Wang and Palese 2009).

Recently, a large pig die-off, which was confirmed to be the result of African swine fever, occurred in the Southern Highlands Province of Papua New Guinea (FAO 2020) and has spread to neighboring provinces. African swine fever is a devastating disease affecting both domestic and wild pigs of all ages. Reducing the spread of the disease in Oceania is crucial as pigs not only serve as an important commodity, they are also a vital cultural resource. People that live in the region have been instructed to not move pigs (wild or domestic) or pig meat out of the infected districts and provinces.

The health of humans, wildlife, livestock, and the environment is interconnected and strategies to reduce illness and death in people and animals must be global in approach. Zoonotic diseases from wildlife and associated pathogens spill-over and account for more than half of known human infectious diseases (American Public Health Association 2018). Some wildlife diseases have multiple reservoirs, whether wild or domestic, and pathogen transmission can be bidirectional (Coleman and Cooke 2001; Bengis et al. 2002; Hlokwe et al. 2014). Human population growth and expansion into wildlife habitat is one contributing factor to these disease spill-over events. Climate change and changes in land use is another factor tied to pathogen spread. Increasing globalization or movements of humans, livestock, and sometimes illegal transport of wildlife also leads to the spread of harmful pathogens. We must also acknowledge that infectious diseases should be investigated at local and regional scales as indigenous communities on small, remote islands of Oceania may be more vulnerable to disease outbreaks because existing animal and human populations are immunologically naïve and may be highly susceptible to infectious agents (Horwood et al. 2019).

Box 2 Host Status is not a Species Fixed Characteristic: Tuberculosis and *Sus scrofa* in Oceania (by Joaquín Vicente & Christian Gortázar)

While maintenance hosts can maintain infection in an area in the absence of cross-transmission from other species of domestic or wild animals, spill-over hosts need a continuing acquisition of infection from other species. The transmission of tuberculosis (TB) caused by the *Mycobacterium tuberculosis* complex (MTC) is dependent on a number of factors. The MTC has an extensive host range and the same host species have been introduced in new areas where the disease is present, providing an example to evaluate if host status is a species fixed characteristic. In Oceania and a number of other countries, TB has become established in one or more wildlife hosts capable of independently maintaining the disease. Evidences supporting that wild boar (*Sus scrofa*) in its natural range, Western Europe, is a TB reservoir host include (Naranjo et al. 2008): (1) presence of common MTC genotypes in wild boar, domestic and wild animals and humans, (2) high prevalence of MTC among wild boar in estates fenced for decades in the complete absence of contact with domestic livestock and other wild ungulates, (3) TB lesions are frequently seen in thoracic lymph nodes and lungs, suggesting that respiratory infection and excretion may occur, and (4) extensive tuberculous lesions in more than one anatomical region occur in a high proportion of juvenile wild boar that probably represents the main source of mycobacterial excretion.

Wild pig densities in Oceania may be 10 times lower than wild boar densities in Spain, on average (Acevedo et al. 2006; Hone 1990, see table below). Previous studies found that most wild suids had lesions exclusively in mandibular lymph nodes (e.g., 62% in Australian wild pigs; Corner et al. 1981). In Australia, the low prevalence of generalized TB disease in wild pigs, the absence of pulmonary lesions, the lack of other obvious routes of excretion from infected pigs, and the lack of contact between wild pigs and other species, particularly water buffalo and cattle, lead to the conclusion that wild pigs were spill-over and not a source of TB infection (Corner et al. 1981). TB was essentially eradicated from the bovid population and subsequently almost disappeared from the wild pig population (Corner 2006). To date, only Australia has eradicated TB from a wildlife potential maintenance host (not demonstrated this role) (Fig. 8, Table 2).

In New Zealand, introduced brushtail possums (*Trichosurus vulpecula*) are the most important wild animal maintenance host for TB (Nugent et al. 2015). In contrast, wild deer (predominantly red deer (*Cervus elaphus*)) and wild pigs are considered to be spill-over hosts for MTC, in spite that TB prevalence in New Zealand wild pigs can reach 100%. Elimination of TB from possums (and livestock) resulted in the eventual disappearance of TB from wild pigs and wild deer. The high rate at which pigs acquire MTC infection from dead possums makes them useful as sentinels for detecting TB in wildlife.

(continued)

Box 2 (continued)

Infections in lymph nodes of the head and alimentary tract predominate, indicating that TB is mostly acquired through scavenging TB carrion, particularly possums, infection is usually well contained, and transmission between seems to be rare. The spill-over host status of wild pigs in New Zealand is likely to be the result of comparatively low intra-specific contact rates, which in turn result from the unrestricted year-round New Zealand hunting system reducing average densities to low levels and keeping the pigs widely dispersed. Wild pigs (and wild deer) play a secondary role in the complex epidemiology of TB in New Zealand and their active management is not required for local TB eradication. The national goal is eradicating TB from livestock and wildlife reservoirs by 2055. Unless the disease is often self-sustaining in a variety of wildlife hosts, authorities are well on the way to achieving this outcome based on abundant and rigorous scientific orientated management.

The case of wild pig populations on the Hawaiian island of Molokai is particularly interesting (Essey et al. 1981). After an infected cattle herd was removed from the area, the prevalence of TB in wild pigs declined markedly from 20% to 3.2% (Essey et al. 1983). Initially, it was suggested that the disease was maintained on the island through spill-over from cattle; however, *M. bovis* was detected in wild pigs after the removal of cattle, indicating that the bacteria could persist without cattle.

Management Practices at the Interface

The interface between native wildlife, domestic livestock, and livestock that have gone feral is vastly important from a disease ecology perspective. Infectious diseases can be transmitted from wildlife to livestock and vice versa and information for managing these transmission events is lacking (Rhyan and Spraker 2010). The goal for any management action is to reduce the potential for contact (direct and indirect) and therefore pathogen transmission. Disease outbreaks can threaten the health and well-being of wildlife, livestock, and human populations and can have serious social and economic consequences. Disease detection and surveillance, vaccination, therapy, quarantine, test and slaughter, and depopulation are just a few management practices used to reduce pathogen transmission (Rhyan and Spraker 2010). Infectious contacts between livestock and wildlife will continue to increase as humans encroach into wildlife habitat, remove or alter existing habitat, climate change removes or creates new habitat, and producers intensify livestock production to keep up with human population growth (Gortazar et al. 2007; Black et al. 2008; Decker et al. 2010). Moreover, the recent emergence of novel coronaviruses and the devastating threats they pose to global public health should highly necessitate future



Fig. 8 Wild pig-livestock interfaces in Oceania. (a–b) Wild pigs grazing in proximity to horses in Hawaii (images: USDA). (c–f) Wild pig-cattle interface in Australian savanna (images c–f: Brendan Cowled and Steve Lapidge). (c) and (d) illustrate wild pigs roaming and grazing near rangeland cattle, (e) shows potential indirect interaction at water sites, and (d) represents a wild pig scavenging on a cattle carcass. For comparison, see Figs. 2 and 3 of Chapter “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Europe” for wild boar in Europe

research into emerging wildlife and zoonotic diseases (Ahmad et al. *In Press*; Bonilla-Aldana et al. 2020).

Controlling diseases at the wildlife-livestock interface is tremendously complex, with state and federal agencies, wildlife managers, and livestock producers having to address environmental, biological, and social issues. Oceania, with some of its outlying regions or islands, has the luxury of not having to deal with some global diseases transmitted at this interface due to its remoteness or isolation. New Zealand represents a unique regional marsupial-cattle interface where brushtail possums are

Table 2 Comparative data on wild pig and wild boar ecology and TB epidemiology

	Australia	New Zealand	Molokai (Hawaii)	South and central Spain	References
Animals/km ²	<11	1 pig/km ² (entire area occupied)	>8km ²	Up to 90 pig/km ²	Corner et al. (1981), Acevedo et al. (2007), Mayer and Brisbin (2008)
TB prevalence	0–40%	Up to 100%	0,2	18–100%	Corner et al. (1981), Wakelin and Churchman (1991), Knowles (1994), Lugton (1997), Vicente et al. (2006, 2007)
Prevalence trend	Decreasing	Decreasing	¿?	Increasing	Vicente et al. (2013), Corner (2006), Essey et al. (1983)
Lung lesions	Not found	0–63%	77% (7/9 culture + individuals)	38–52%	Corner et al. (1981), Gortazar et al. (2003), Martín-Hernando et al. (2007)
Percent generalized	25%	0–63%	Unreported	58%	Lugton (1997), Nugent et al. (2002)
TB host status	Spill-over	Spill-over	Reservoir	Reservoir	Corner (2006), Vicente et al. (2006, 2007)
Other relevant hosts	Buffalo	Possum, red deer, ferret, cattle	Cattle	Red deer, fallow deer, livestock	McInerney et al. (1995), Essey et al. (1981), Gortazar et al. (2011), Nugent et al. (2001)

the maintenance reservoir host for *M. bovis*. The preferred method to stop or reduce transmission of bTB to cattle herds is lethal control or culling of possums (Caley et al. 1999; Nugent et al. 2011; Green and Rohan 2012). Australia eliminated bTB from domestic cattle in 2006, representing a major Commonwealth, State, and Territory governmental success story and providing considerable benefits to the cattle industry. To help achieve this goal, national eradication programs were implemented, which included: improved livestock identification, a cattle test and slaughter program, improved diagnostic tests, national herd traceback programs, severe restrictions on cattle movement, and being fortunate that there was no feral wildlife that were reservoirs of *M. bovis* (Cousins and Roberts 2001; Turner 2011; Gormley and Corner 2018). Feral water buffalo (*Bubalus bulalis*) were the exception, but they were eradicated in areas where there was evidence of bTB in the wild population (Radunz 2006). The eradication campaign also included financial assistance and subsidies to help offset the costs of mustering and holding cattle to be tested, low-interest loans for temporary cattle yards, constructing water facilities, fencing, and restocking freight fees (Radunz 2006).

Transmission of pathogenic avian influenza occasionally occurs in poultry in Australia. Control currently includes culling poultry, whether commercial facilities

or “backyard” operations and improved biosecurity where measures are lacking (Tracey et al. 2004). Improved biosecurity measures at poultry facilities include restrictions on water access and treatment, secure feed storage areas, and improved cleaning of sheds (East 2007; DAWE 2009; Glass et al. 2019).

Hendra virus is believed to be transmitted from fruit bat to horse, horse to dog, and horse to human (Queensland Government 2018). Monitoring the distribution and abundance of fruit bats, the primary host of the Hendra virus, in Australia is essential to predicting disease risk to livestock and humans. Spill-over risk may be lowered via roost dispersal or modification activities, but best management techniques need to be developed (Edson et al. 2015). A registered vaccine to help prevent Hendra virus disease in horses is available and is the most effective way to manage the disease. Other methods believed to reduce virus transmission at the wildlife-livestock interface include: removing horse feed and water from under trees and possible place under shelters, removing horses from paddocks that are routinely visited by fruit bats (e.g., bats visiting flowering/fruited trees), fencing off areas in paddocks that contain flowering/fruited trees, removing horses from paddocks during peak fruit bat activity periods (i.e., dusk through the night).

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Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in North America



Kurt C. Vercauteren and Ryan S. Miller

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Introduction

North America is graced with a vast diversity of animal and plant life, from the icy tundra of Greenland, northern Canada, and the United States (US) state of Alaska south to the deserts and plains of the US and into northern Mexico. This large continent boasts several distinct ecoregions, each with characteristics that have determined the native flora and fauna as well as the human-driven activities that occur within them. More than 200,000 species inhabit the US alone and the country

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Fig. 1 An illustration of the extensive movement of cattle within the United States. Panels a and b represent annual cattle shipments into and out of the state of Nebraska (adapted from Lindström et al. 2013). Panel c illustrates shipments of cattle imported into the United States from Mexico (adapted from Gorsich et al. 2018). In panel c, yellow indicates counties receiving imported cattle directly from Mexico. Blue shading represents counties that received shipments of cattle from counties that imported cattle from Mexico

is host to a broader spectrum of ecosystems than any other nation (Stein et al. 2000). Much of the biodiversity of the continent exists in large expanses of deciduous forests, temperate grasslands, and Mediterranean habitats. The majority of the human population and associated human impacts also occur in these ecoregions of North America. Home to a growing population of over 500 million people, the demands and impacts on the continent's natural resources is ever increasing. To the point that, in just the 500 years since Europeans initiated the settling of North America, most of the natural vegetation of these ecoregions has been modified or lost due to human influences. De-forestation and reforestation, row-crop agriculture, livestock production and practices, the sprawl of human infrastructure development and transportation systems, climate change, and introduction of destructive invasive species of plants and animals are all having immense impacts on the continent of North America.

The first domestic livestock was introduced to the continent by Europeans approximately 500 years ago. From the small, self-sustaining family farms of a century ago to the present, the scale and efficiency of agricultural animal production across North America has increased immensely and is continuously evolving. These changes include much more transportation of livestock within and among North American countries as animals proceed through stages from birth to slaughter. For example, market demand within the North American countries and globally have led to the US being the largest producer of beef and the third-largest producer of pork. Annually 1.8 million cattle and 11.2 million pigs originate in Mexico and Canada before being transported to and throughout the US for finishing (USDA ERS 2018). Imported cattle and pigs combined with US domestic production results in the shipment of 21.8 million cattle and 26.9 million pigs annually within the US (Shields and Mathews 2003) (Fig. 1). Though in many ways biosecurity is high and livestock is well cared for, the sheer volume of livestock being produced and shipped to and fro increases the potential for diseases to be spread, not only within the continent's livestock populations, but to and from endemic species of wildlife.

The arrival of Europeans and their associated livestock to North America also had impacts and implications for native wildlife. Old World diseases, a ravenous need for



Fig. 2 Here pictured with a dairy cow, white-tailed deer are a primary species of wildlife at the interface with livestock in North America

space and resources, and market hunting quickly led to precipitous declines of many species of wildlife. The advent of government led wildlife management and a conservation ethic over the last 100 years has resulted in the rebounding of many species of wildlife. To the point that some species that play a primary role in disease transmission at the wildlife-livestock interface, like white-tailed deer (*Odocoileus virginianus*) (Fig. 2), are enjoying higher populations than ever and increasing their geographic ranges.

There is a continuum of biosecurity throughout the country, from none to extensive, depending on the geographic location, species and growth stage of livestock and type of operation. With the exception of limited reindeer herding in the northern climes of the continent and seasonal grazing of hoof stock on public or communal lands, livestock are no longer free range. Although in many of the more arid regions of North America the size of fenced in properties and pastures can be immense. These scenarios present the opportunity for direct and indirect transmission of diseases between livestock and wildlife. At the other end of the spectrum, large-scale commercial pork and poultry production is conducted totally indoors. And, there are a plethora of other husbandry practices, including small subsistence or hobby farms, feedlots, captive exotic and cervid facilities, open-air poultry operations and pasture-raised swine.

Socioeconomic and Biogeographical Circumstances of the Wildlife-Livestock Interface

The 500-year history of the wildlife-livestock interface in North America is brief in comparison with the Old World, where much of the domestication and development of today's primary species of livestock originated. As North America was settled and livestock introduced, socio-economical and biogeographical considerations drove livestock husbandry practices. As these considerations have changed and evolved, so have the nature of wildlife-livestock interactions. The numbers of livestock steadily increased and their presence steadily expanded as settlers of European descent increased in their numbers and expanded their presence across the North American continent. Different breeds of cattle, pigs, sheep, and poultry were imported with the intent of placing them in regions of North America that they were best suited. Factors considered included regional climate characteristics, available feed, and the needs of the settlers. All this mixing of livestock, as well as human nationalities, led to strategic (and happenstance) breeding in attempts to improve the livestock's ability to thrive in the New World. At the same time developments in technology and consumer demand dictated how and where each type of livestock was raised and used. Concurrently, these same demands impacted the continent's landscape and native wildlife. For example, heretofore unharvested forest resources were logged to provide lumber for rapidly growing and expanding populations of immigrants and their associated infrastructure. At the same time, market hunting and trapping of wildlife to provide food and fur led to the extinction of some species (e.g., passenger pigeon) and decimation of others (e.g., bison [*Bison bison*], white-tailed deer, wild turkey [*Meleagris gallopava*], beaver [*Castor canadensis*]) (e.g., Allen 1954).

The first livestock introduced included pigs, cattle, poultry, sheep, and goats (e.g., Cochrane 1993; Gras 1925). In general, settlers kept and maintained the livestock they needed to support themselves with any excess being sold or traded with neighbors and city dwellers. A household often kept several pigs as a primary food source. Pigs, often allowed to be free ranging, escaped, and have led to large and expanding populations of wild pigs today. Many of the first fences were not employed to keep pigs in, but to keep them from damaging crops. Domestic poultry, primarily chickens but including ducks and geese, was also introduced to North America at this time. Their main purpose was egg production, a protein source that could be kept for extended periods and did not require refrigeration. At this time, the meat of poultry was only occasionally eaten. Similarly, the original primary purpose of cattle was not as a source of meat either, cattle were primarily valued as beasts of burden and a source of leather.

With the settlers and livestock, of course, came diseases (e.g., Crosby 1972). For Native American humans, the consequences were often immense, with smallpox epidemics decimating their populations across much of the continent. Other diseases impacting humans and introduced during this time period include bubonic plague, chickenpox, cholera, diphtheria, influenza, measles, scarlet fever, typhoid, typhus, tuberculosis, and pertussis (whooping cough). At the same time, some of these

diseases, and others harbored by imported livestock, began to also impact North America's native wildlife. Additional Old World diseases that were introduced to wildlife during this period included brucellosis, bovine babesiosis, and bovine tuberculosis.

As human populations grew and expanded inland and across North America, fewer people raised livestock, and the ones who did increased the volume they produced to be sold. More so in the US and Canada than in Mexico, small-scale subsistence farming began to give way to livestock production as a business. Technological and transportation advancements fueled this process, with the railroad system that was in place by the mid to late 1800s being a primary driver. Cattle, poultry, and pigs could be raised in large numbers where geographically appropriate and shipped via rail to human population centers for fattening and slaughter. Then, with the advent of refrigerated rail cars, slaughterhouses could be located in proximity to large centers of livestock production, and the practice of establishing feedlots containing high densities of animals emerged. These factors, primarily increased movement of livestock and increased concentrations of livestock and waste, led to the emergence of disease outbreaks and fueled spread and prevalence.

Across central, western, and southwestern regions of the USA and northern Mexico, this was an iconically romantic time in North America's history (e.g., Turner 1920). Large-scale, open-range cattle production was the primary agricultural endeavor at this time in these vast grassland regions. Each year cowboys, known as vaqueros in Mexico, on horseback ushered cattle from outlying areas to centers of human populations and railheads. The cattle and horses, of course, carried with them Old World diseases that native wildlife like bison, elk (*Cervus elaphus*), and deer were susceptible to.

Sheep were also introduced to these regions during this same era, to grasslands as well as more mountainous areas. Prior to 1800, most sheep production in North America consisted of turning flocks loose on islands along the east coast and visiting them each spring for shearing and harvesting. Never as numerous as cattle, sheep production in the North American west peaked in the 1940s. Sheep brought with them acute fibrinopurulent bronchopneumonia, to which the native species of wild ovids are highly vulnerable (e.g., Foreyt and Jessup 1982). Pneumonia from domestic sheep remains a considerable risk to wild sheep and has negatively impacted their populations, so efforts are made to prevent overlap and interaction.

To a large degree, open-range, nomadic livestock production was phased out during the early 1900s due to the invention barbed wire and American-style windmill water pumps. Barbed wire provided a cheap way to fence in large pastures and windmills allowed producers to pasture cattle in areas far from above-ground sources of water. This led to more sedentary strategies for raising livestock and to new potentials for wildlife-livestock contacts, like concentrating wildlife and livestock at the small water tanks associated with windmills.

Primarily in the eastern third of the continent, poultry began to be valued for meat, in addition to their value from egg production, concurrent with the human slave trade throughout the 1700s and well into the 1800s. Slaves often maintained small flocks of chickens, the meat from which they valued for its versatility. Cooking it in hot oil

led to the popular contemporary recipe for preparing chicken known as “Kentucky fried.” Chicken became increasingly popular during World War II when much of the US’ beef and pork was being sent overseas to feed soldiers. Subsequently, demand kept on increasing, like from Jewish immigrants looking for kosher protein options. This led to the development of the broiler chicken industry, which brought about challenges with density-dependent diseases and impacts on wildlife.

The landscape and livestock agriculture in North America has changed dramatically in the last 100 years and while much effort has been expended upon disease control most of the diseases initially introduced are now considered endemic and additional diseases seem to be emerging at an increasing rate. Today’s multi-billion dollar livestock industry meets demands worldwide and pressure for higher volumes has made small-scale farming exceedingly difficult for small producers to sustain. In the late 1800s, about half of the continent’s population was employed by animal or plant agriculture, and now less than 1.4% of US workers are employed directly on-farm with 11% of total US employment related to agriculture (US Department of Commerce 2017). The majority of livestock now live in confined stockyards or indoor facilities and are largely comprised of only a few breeds. The use of work animals has been essentially totally replaced by machinery and breeds which are not suited for the mass production desired by industry have gone extinct or are kept only by hobbyists in small numbers. National and worldwide demand for pork, beef, and chicken are increasing with the increasing global population of humans. A small sector of the industry, however, has been reclaimed by high quality, heritage-breed-based, locally grown livestock. Products labeled as organic, free range, or grass fed have recently gained popularity in the US and Canada as being healthier, leaner, and better-tasting protein. Their higher purchase prices, though, cannot compete with industrialized and mass-produced meat.

The Prevalent Livestock, Farm Typologies, and Opportunities for Interface

As described above, in the US and Canada more so than in Mexico, livestock husbandry in North America has become quite industrialized, which serves to mitigate against wildlife-livestock contact in many ways. The majority of pigs, chickens, and turkeys spend their entire lives indoors, often being shipped to different facilities specializing in different purposes (i.e., breeding, grow out, processing) during this time. Large-scale dairy producers manage their cattle in much the same way. Despite this industrialization, farms in North America are diverse and range from very small subsistence production to large enterprises. Small family farms account for 90% of farms, operating on 46% of farmland but accounting for just 22% of production. The majority of farm production (68%) occurs on 9% of midsize or large-scale family farms that operate on 51% of farmland (Hoppe and MacDonald 2016).



Fig. 3 Blackbirds feeding with dairy cattle in southwestern United States. Photos: USDA/APHIS/Wildlife Services



Fig. 4 Raccoon (*Procyon lotor*) and white-tailed deer visiting resources meant cattle

The diversity of farm typologies results in differences in disease risks and the potential for contact with wildlife (Fig. 3). Small farms are frequently subsistence farms in which most of the production is maintained on site and increasingly the producer is employed outside of the farm. Off-farm employment for small farms has increased to 45% in the US. Small farms are however an important component of North American agriculture, providing greater than 50% of poultry production (mostly under contracts with large companies) (Hoppe and MacDonald 2016). Small farms tend to have fewer resources available and are less likely to adopt biosecurity practices when compared to larger farms (Hoe and Ruegg 2006) (Fig. 4). In addition, when small farms do have disease issues the proportion of infected animals is higher (within-herd prevalence) when compared with larger farms, presumably due to reduced biosecurity practices (Hill et al. 2009). The presence of small farms has also been associated with increased disease prevalence in wildlife. Pedersen et al. (2018) found that the presence of small domestic swine operations increased the prevalence of a common domestic swine disease, porcine reproductive and respiratory syndrome virus, in sympatric wild pigs by 11%.

While biosecurity practices on large farms tend to be greater, the scale of production can attract wildlife and thus increase the potential for contact and disease transmission. Large feedlots and dairy production in North America can attract peridomestic wildlife such as raccoons which forage on livestock feed (Atwood et al.

2008). In addition, avian species frequently feed directly from feed troughs and on spilled animal feed. Farm-to-farm movement of wild birds has been proposed as a mechanism of mechanical transport of malignant catarrhal fever virus in farmed bison (Li et al. 2008), bovine tuberculosis in dairy cattle along the US-Mexico border (Pillai et al. 2000), and also Salmonella in cattle feedlots (Carlson et al. 2011).

A relatively recent trend that is increasing the diversity of farm typologies in North America is consumer demand for cage-free or organic meat and egg products. This has resulted in an increase in the number of farms producing pasture-raised pigs and cage-free poultry. Although often leading to higher quality and healthier products, this type of farming increases exposure to wildlife and increases the risk of disease transmission to or from wildlife. Relative to more mainstream production methods, fewer strategies for biosecurity control and mitigation of disease transmission have been developed or are implemented. Methods to reduce risks are necessary, though, as pigs have an increased risk of *Trichinella* infection when raised on pasture or provided outdoor access (Gamble et al. 1999) and wild pigs have been observed to have higher prevalence of swine influenza virus (~90%) and porcine circovirus (~71%) in areas with high densities of transitional domestic pigs (Corn et al. 2009). In the case of poultry, the presence of peri-domestic mammals on the farm increased the odds of a farm being infected with avian influenza virus by 90% (McQuiston et al. 2005) and small enterprise poultry farms in proximity to waterfowl are 2.5 times more likely to be exposed to avian influenza virus (Madsen et al. 2013).

The use of antibiotics is a common management practice employed to contend with exposure to pathogens resulting from animal husbandry practices that allow contact with wildlife or industrialized production which stresses the immune systems of livestock. Antibiotic use has become common across all stages of production in North American livestock to prevent and control common production diseases and to enhance animal growth (Landers et al. 2012). Use of antibiotics in livestock has a long history in North America and first began in the 1930s shortly after the discovery of penicillin and sulfonamides (Aarestrup 2006). One of the first uses was to combat infections of *Mycobacterium bovis* infection in both humans and cattle (Olmstead and Rhode 2004). However, the growth promotion benefits for food animal production were recognized almost immediately and antibiotic use has become common across all sectors of animal production in North America. For example, 16% of all lactating dairy cows in the US receive regular antibiotic therapy (McEwen and Fedorka-Cray 2002). Antibiotic use is greatest in the later stages of animal production (e.g., feedlots, swine grow-out facilities). Approximately 88% of growing swine in the US receive antibiotics to prevent disease and increase growth. And a large percentage (42%) of beef calves entering feedlots receive antibiotics (USDA APHIS 2008). Unfortunately, there is increasing evidence that the use of antibiotics in food animal production has increased antibiotic resistance in both wildlife and domestic animals (Aarestrup 2006).

The Wildlife

North America is home to a large diversity of native wildlife, including several species of mammals and birds that interface with livestock and have become infected with diseases of livestock. Modern wildlife conservation and management in the US and Canada differ from other countries, adhering to a structure that has come to be known as the North American Model of Wildlife Conservation. The principles of the model are that (1) wildlife and fish are for the non-commercial use of citizens, and (2) are to be managed and made available at optimum population levels in perpetuity (Organ et al. 2012). It is comprised of seven tenets:

1. Wildlife as public trust resources.
2. Elimination of markets for game animals.
3. Allocation of wildlife by law.
4. Wildlife should only be killed for a legitimate purpose.
5. Wildlife is considered an international resource.
6. Science is the proper tool for the discharge of wildlife policy.
7. Democracy of hunting.

For a thorough description of the Model, see Organ et al. (2012). The North American Model of Wildlife Conservation is clearly focused on game species, maintaining the culture of easily available recreational hunting to citizens, and using hunters as a primary means of managing wildlife populations. Some species of wildlife that have benefitted the most from the Model and are the most beloved and popular amongst hunters are also major players in pathogen transmission from and to livestock (e.g., white-tailed deer, elk, bison, bighorn sheep [*Ovis canadensis*]). Thus, it is easy to see how conflict can arise between the interests of hunting and agricultural publics. Hunters and wildlife management agencies may be motivated to stimulate wildlife populations to be maintained at high densities, while those with agricultural interests would prefer lower densities of wildlife to reduce pathogen transmission risks to livestock and consumption of crops and stored feed.

Relative to susceptibility to livestock diseases, wild ungulates are among the most vulnerable and the continent is home to several species of wild ungulates. One of the most ubiquitous is the white-tailed deer, which is the most abundant and widespread of all the New World species of deer (Heffelfinger 2011). Subspecies of white-tailed deer are distributed from the boreal forests of Canada, south throughout the US and Mexico with the exception of some mountainous and dry regions and along the West coast. White-tailed deer are a good example for demonstrating how wildlife management strategies and populations in North America have changed and evolved. Following a period of overexploitation, populations of white-tailed deer have rebounded to levels even higher than prior to the settlement of North America by European immigrants (VerCauteren 2003; VerCauteren et al. 2011). To the point that white-tailed deer are considered overabundant in many areas and causing considerable damage to agricultural crops, feed meant for livestock, natural ecosystems, vehicles, and urban gardens, and landscaping (e.g., McShea et al. 1997). The

range of white-tailed deer overlaps substantially with that of livestock, most especially beef and dairy cattle, sheep, goats, swine, and poultry.

In the Greater Yellowstone Area of the US, it is elk and bison that overlap with beef cattle. Though populations of these wild ungulates are centered in an expansive national park, they migrate off seasonally and interact directly and indirectly with cattle. The disease of concern, in this case, is brucellosis. Similarly, several species of wild sheep reside across diverse habitats in western US, Canada, and northern Mexico. The comingling of wild sheep with domestic sheep has resulted in the transmission of pathogens that cause pneumonia from domestic sheep to wild sheep. Pneumonia-induced mortality in wild sheep populations has created a conservation issue for wild sheep (Cassirer and Sinclair 2007).

Invasive wild pigs are another widespread ungulate in North America that interface routinely with domestic livestock. Their densities and distribution have increased immensely in recent decades and only white-tailed deer range more widely across the continent. With this proliferation of wild pigs, they have become a major reservoir and vector of livestock diseases (Miller et al. 2017). Being invasive, or non-native, and often times having a detrimental impact on native species of wildlife, wild pigs are not covered by the North American Model of Wildlife Conservation (Bodenchuk and Vercauteren 2016). In the US there is currently a large-scale, government-sanctioned effort to eliminate wild pigs where possible, reduce the amount of damage they cause, and mitigate human and domestic animal health concerns (see <https://www.aphis.usda.gov/aphis/resources/pests-diseases/feral-swine/feral-swine-program>).

North America also has a large economically and recreationally important population of migratory waterfowl. An estimated 53.8 million waterfowl migrate from breeding grounds in Canada and the northern US to wintering grounds in the southern US and Mexico (U.S. Fish and Wildlife Service 2017). This large and mobile population also harbors several diseases of concern for poultry. Most notably, avian influenza (AIV), which has a well-documented wild waterfowl reservoir, continues to plague the domestic poultry industry in Canada and the US with outbreak-associated losses ranging from USD\$5 million to USD\$3 billion (Capua and Alexander 2010; Saif and Barnes 2008; Greene 2015). Estimated impacts to the US in the event of an epizootic AIV pandemic are at least USD\$71 billion (Meltzer et al. 1999; Arnold et al. 2006). Aquatic birds play an important role in the introduction of new AIV into North America and the spread of both newly introduced and endemic AIV within North America. An estimated 2.91 million aquatic birds move annually between Eurasia and North America with an estimated AIV prevalence as high as 32.2% (Hill et al. 2012). Identifying the mechanisms that drive transmission of AIV to poultry from infected waterfowl have been elusive but have been proposed to include direct contact with infected waterfowl, indirect contact via contaminated poultry feed, peri-domestic mammals, and human movement of the virus from waterfowl habitats to poultry farms (Miller et al. 2015).

The Disease at the Interface: One Health Perspective

The management of diseases affecting livestock, wildlife, and humans as a single, linked system in North America presents several obstacles. Conflicting agency and institutional missions, program goals, and cultural differences that limit the potential for developing comprehensive mitigation programs for pathogen transmission have hampered efforts in this area across and within countries (Miller et al. 2013). Nevertheless, research and policy at the wildlife-livestock-human interface have received increased attention in recent years with the advent of additional tools to identify and mitigate risk (Miller et al. 2017; Manlove et al. 2016). This is driven, though not exclusively, by a rapid increase in the number of zoonotic disease events associated with wildlife in the latter part of the twentieth century (e.g., Woolhouse et al. 2001; Ostfeld and Holt 2004; Decker et al. 2010). The emergence and re-emergence of diseases like CWD, bovine spongiform encephalopathy, West Nile virus, variants of highly pathogenic AIV, plague, and rabies in recent years highlights the need for collaboration and communication among multiple allied disciplines working locally, nationally, and internationally to maintain the health of humans, domestic animals, wildlife, and the environment (e.g., VerCauteren et al. 2012).

In North America at least 53 OIE listed pathogens are present and at least 79% have a potential wildlife component associated with the transmission, maintenance, or life cycle of the pathogen (Miller et al. 2013). The majority of these pathogens (71–87%) involve direct or indirect transmission between wildlife and domestic animals and cattle and poultry are the most common domestic animals involved (Miller et al. 2013; Miller et al. 2017). At least 75% of OIE listed cattle diseases, 87% of swine diseases, and 91% of poultry diseases present in North America have a wildlife component. However, cattle, swine, and poultry are not exclusively impacted with 38% of the OIE listed diseases present in North America affecting multiple species of livestock, all of these have a wildlife component, and 81% are zoonotic.

In the US, 21 pathogens are currently actively managed with 11 of these having a Federal eradication or control program (Table 1) (Miller et al. 2013). Thirteen (62%) of these actively managed diseases have a wildlife component and at least six (bovine tuberculosis, paratuberculosis, brucellosis, avian influenza, rabies, and cattle fever tick [vector control]) have a wildlife reservoir that is a recognized impediment to eradication due to continued spill-over to domestic populations. Of these diseases, bacterial pathogens, such as bovine tuberculosis and brucellosis, have established foci of infection in at least four wildlife populations in North America as a result of spill-over from livestock to wildlife (Olsen 2010; Miller and Sweeney 2013) (Fig. 5). In contrast, pneumonia-induced mortality in wild sheep populations is largely due to the transmission of *Mycoplasma ovipneumoniae*, *Pasteurella multocida*, and other respiratory pathogens from domestic sheep to wild sheep (Besser et al. 2012). There is little evidence, though, of transmission back to domestic sheep from wild sheep (Wehausen et al. 2011).

Table 1 Major disease systems at the interface of wildlife and livestock in North America (adapted from Miller et al. 2013)

Pathogen system	Primary species		Region	Contact	Transmission direction	Government program
	Domestic	Wildlife				
Avian influenza	Poultry	Waterfowl	CA, US	Direct, indirect	D←W ^a	Control
Bovine babesiosis	Cattle	White-tailed deer, nilgai	MX, US	Vector borne	D↔W	Eradication
Bovine brucellosis	Cattle	Elk, bison	US	Direct, indirect	D←W	Eradication
Bovine tuberculosis	Cattle, captive cervids	White-tailed deer, elk, bison	CA, MX, US	Direct, indirect	D↔W	Eradication
Chronic wasting disease	Captive cervids	White-tailed deer, mule deer, elk,	CA, US	Direct, indirect	D↔W	Certification program
Paratuberculosis	Cattle, goats, sheep	Wild ruminants	CA, MX, US	Direct, indirect	D←W	Control
Pneumonia	Sheep	Bighorn sheep	CA, MX, US	Direct	D→W	None
Pseudorabies	Swine	Wild pigs	US	Direct, indirect	D↔W	Eradication
Rabies	Many	Raccoons, skunks, fox	CA, MX, US	Direct	D←W	Eradication
Swine brucellosis	Swine, cattle	Wild pigs	US	Direct, indirect	D↔W	Eradication
Vesicular stomatitis	Cattle, equine	Wild ruminants	MX, US	Vector borne	D↔W	Control

^aD Domestic livestock, W Wildlife

Risk factors most frequently reported as important to the establishment of livestock diseases in wildlife populations in North America include the commingling of infected domestic animals with susceptible wildlife, supplemental feeding of wildlife in proximity to domestic animals, inadequate surveillance of at risk wildlife, and unrecognized emergence of alternate wildlife species as successful maintenance hosts (Miller et al. 2013; Conner et al. 2008). Commingling of livestock, particularly cattle and sheep, with wildlife has been associated with the introduction of several pathogens into wildlife populations (e.g., Cross et al. 2007; Maichak et al. 2009) (Fig. 6). As discussed in more depth earlier in the chapter, examples include *Brucella abortus* in elk and bison, *Mycobacterium bovis* in white-tailed deer, elk, and bison, multiple respiratory pathogens in bighorn sheep (Olsen 2010; Wolfe et al. 2010; Cassirer et al. 2017), and multiple pathogens in invasive wild pigs (Miller et al. 2017). Commingling of cattle

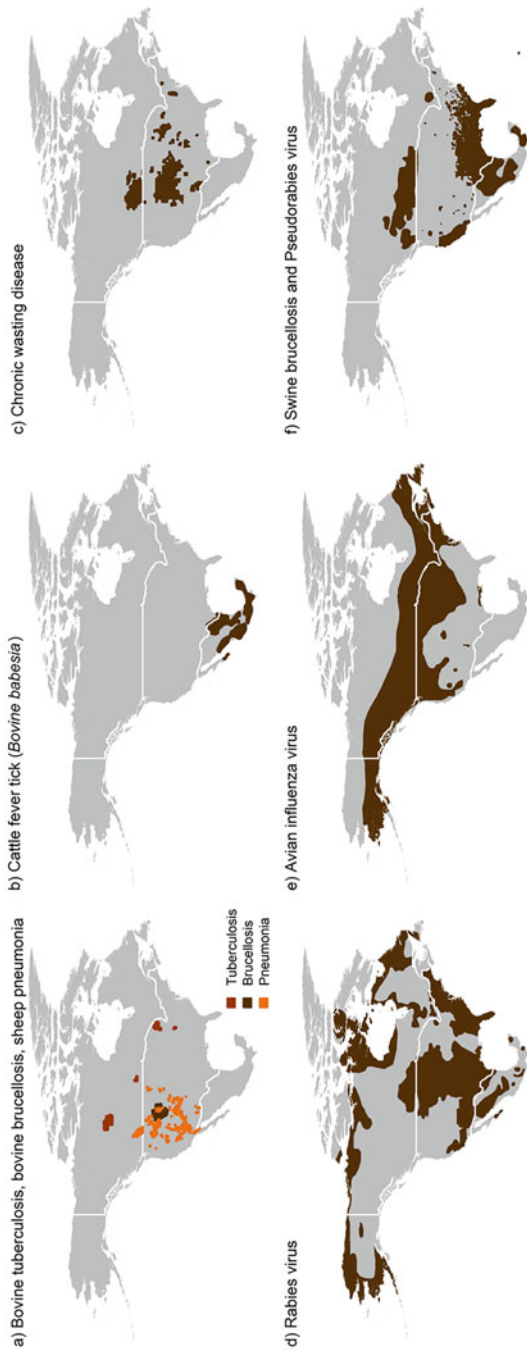


Fig. 5 Distribution of nine important wildlife-livestock disease interfaces in North America



Fig. 6 Example of livestock and wildlife use of a protein feeder in south Texas. Source: Anonymous private ranch in south Texas

and sheep with wild pigs and cervid species is common throughout North America where domestic and wild ruminants share pasture resources. Research indicates that supplemental feeding and baiting have been major factors in the propagation and persistence of several bacterial pathogens in white-tailed deer and elk populations (O'Brien et al. 2006). This is often complicated by infections in free-ranging wildlife that can be silent, existing for years or even decades before being detected in hunter-killed animals, or emerging or re-emerging in local populations of captive wildlife. Traditionally, it was assumed that many of these livestock pathogens would not persist in populations of free-ranging wildlife unless they had contact with infected domestic animals (Essey et al. 1983). The emergence of wildlife as suitable hosts for a diversity of livestock pathogens as well as vectors such as cattle fever ticks (Wang et al. 2016) has challenged this historic paradigm.

The integrated surveillance and control strategies to address rabies in North America make it one of the best examples of addressing a disease at the continental scale from a One Health perspective. Rabies is one of the oldest documented diseases in the world. It first surfaced during the early colonization of North America, and in 1768 an epizootic occurred when rabies spilled over from foxes and dogs to swine and other animals (Steele and Fernandez 1991). As the continent was settled and human populations spread, rabies followed suit, likely vectored by

domestic animals and spilling-over into native wildlife. Currently, in North America, a few primary species of mesocarnivores and bats serve as a reservoir to rabies and perpetually infect livestock, pets, and humans. Though dog rabies is largely controlled in the US and Canada through compulsory vaccination of pets, and both countries maintain large-scale efforts to vaccinate free-ranging wildlife, rabies still persists. Though the numbers of mortalities are not high, each year livestock, often the young, interact with infected wildlife and contract rabies. The livestock often succumbs after displaying symptoms that, for the most part, are recognized by the owners. The owners, and all others who had been in contact with the infected animal, then, must undergo post-exposure prophylaxis.

A trilateral North American Rabies Management Plan guides surveillance, control, and research across the three countries and including sovereign nations of Native American lands. Each country, then, has their own National Plan for Wildlife Rabies Management, detailing their strategy for addressing this disease. The need for these large-scale coordination efforts was recognized due to the plethora of anthropogenic factors (i.e., increasing human population, intensive agricultural practices, wild and domestic animal translocation) and natural factors (e.g., wildlife population biology, interactions among susceptible and rabies host species, animal movements, changing habitats, environmental degradation, climate change) that continually threaten the re-emergence of rabies as a major zoonosis (VerCauteren et al. 2012). The high level of emphasis on rabies surveillance and control in wildlife in addition to continued domestic animal vaccination and human post-exposure prophylaxis are, in combination, the key to the ultimate goal of eradicating terrestrial rabies in North America.

Management Practices at the Interface

Pathogen transmission at the wildlife-livestock interface has necessitated the development of control programs to mitigate transmission risk and manage disease. Control is often focused on domestic animals even when wildlife are infected. In fact, some of the earliest control programs in North America (e.g., bovine babesiosis and bovine tuberculosis) were focused solely on managing pathogens in domestic animals with the presumption that the diseases would not persist in wildlife populations. The primary tools for most eradication efforts historically and to date in North America rely upon test and remove strategies and for some diseases cleaning and disinfection of animal husbandry facilities. These are often implemented as part of the animal production system, monitoring for the disease at slaughter and then using trace-back investigations to identify farms of origin. Affected and exposed livestock on these farms are then commonly culled. Though this has been successful for many pathogens, once disease spills-over from livestock to wildlife and becomes established it often persists and greatly complicates control efforts. This has necessitated additional on-farm management strategies to reduce contact between livestock and wildlife. The implementation of these efforts has

taken many forms, in North America one of the most common has been the establishment of accreditation programs. These programs typically use a combination of routine animal testing and evaluation of disease mitigation strategies. Producers that meet accreditation standards often gain greater access to markets. Other approaches have used risk assessments to identify zones with higher risk for transmission between livestock and wildlife. Restrictions on livestock movement and increased testing are then implemented to reduce the risk of infected domestic animals being shipped outside the control zone. Zoning approaches sometimes referred to as regionalization, are often implemented to maintain international trading market access for producers outside of the zone. These have largely been implemented in the US and Canada when deer and elk have been chronically infected with bovine tuberculosis and brucellosis or as part of vector control programs such as those used for cattle fever tick control.

Specific strategies implemented by livestock producers to mitigate direct interaction of wildlife and livestock or indirect interaction via livestock feed fit into two general categories, physical and psychological. Physical control methods often include some form of fencing. To lessen the potential of wild ungulates gaining access to livestock pastures, a wide variety of fencing options exist (VerCauteren et al. 2006). Options range in efficacy and expense, from permanent and very effective to temporary with decreasing efficacy over time. Choosing the best fence for a particular situation depends on multiple variables, to include, pathogen transmission risk, degree of protection desired, degree of permanence required, and cost. In the US and Canada, government agencies often assist producers with purchasing and erecting fences and gates to reduce pathogen transmission. Psychological frightening devices and strategies elicit fear in wildlife, with the intent of keeping them from interacting with livestock or livestock feed. Predator effigies, predator odors, repellents, propane cannons, cracker shells, and mylar tape are all examples of strategies attempted, with varying results and duration of effectiveness, to discourage wildlife. A perpetual problem with frightening devices, that limits their value relative to mitigating against persistent pathogen transmission threats, is that wildlife can become habituated and ignore them. Livestock protection breeds of dogs can also fit into this category and they can be successfully used to lessen disease transmission risk by lessening the potential for wild ungulates to come in direct contact with livestock, contaminate feed and water meant for livestock, and even enter pastures (VerCauteren et al. 2008).

While often controversial, another strategy practiced in the US and Canada to mitigate against disease in livestock is to reduce the density of wild ungulates in proximity to livestock. When infected wildlife are thought to be localized, density reduction is often attempted by encouraging, through liberal bag limits and seasons, recreational hunters to harvest wild ungulates in areas where they represent a risk to livestock. Additionally, agency sharpshooters may be employed to suppress ungulate populations in a timely and efficient manner. Local area density reductions have had relatively limited success in eradicating pathogens from wildlife and to date have only been successful in eradicating foot and mouth disease from deer (Spear 1982) and bovine tuberculosis from white-tailed deer (Carstensen and DonCarlos 2011)

and invasive wild pigs (Smith 1968). In these few successful instances of eradication, culling by agency sharpshooters was used nearly exclusively.

Research of Disease at the Wildlife-Livestock Interface

Much research has been conducted throughout North America to increase knowledge and aid management relative to the diseases shared by wildlife and livestock, the ecology of their hosts, their impacts, and strategies to mitigate or eradicate them. These efforts have intensified in recent years, primarily due to (1) a response to the introduction, or threat of introduction, of a plethora of foreign animal diseases, and (2) a response to the emergence of new (e.g., CWD, Lyme disease) or re-emergence of endemic (e.g., plague, rabies) diseases. Most research to date can be generally categorized as focusing on specific pathogens, host populations (wild or domestic), elements of the environment that influence transmission, or, less commonly but more importantly, a combination thereof (Delahay et al. 2009). Though often host and disease-dependent, primary knowledge gaps to be addressed relate to disease ecology, development of cost-effective monitoring tools, and the development of practical and effective means of curtailing contact and pathogen transmission at the wildlife-livestock interface.

Proactive research is required to prepare for the inevitable disease introductions that North America is ever more at risk from due to increasing global trade and the movement of people and products that facilitate the ferrying of diseases around the world. The primary foreign animal diseases being addressed currently include foot and mouth disease, African swine fever, classical swine fever, and avian influenza. A common focus of these studies is to predict and assess what areas are at greatest risk for the introduction and what role native or introduced wildlife could play in the establishment and spread of foreign animal diseases (e.g., Pepin and VerCauteren 2016; Drolet et al. 2013; Brown and Bevins 2018). They range from tabletop and modeling exercises to experimental infection studies of likely wildlife host species to empirical studies measuring epidemiologically important risk factors such as host contact rates.

For diseases that are endemic in North America, the amount of research effort put into addressing them varies greatly and relates directly to the disease's current or potential impacts on human health, economic impacts to agriculture, and environmental impacts. The development of practical mitigation strategies that can be implemented by producers are a common research focus. The effort is steadfastly being expended to improve husbandry practices and exclusion strategies that reduce the potential for contact and transmission (e.g., Walter et al. 2012). Research to develop and effectively deliver vaccines to wildlife is a priority or potentiality for some diseases, like rabies (e.g., Berentsen et al. 2018) and brucella (Davis and Elzer 2002). Species-specific delivery of oral pharmaceutical baits containing vaccines, contraceptives, and toxicants is important to prevent non-target animals from being dosed and minimize the wasting of bait (e.g., Smyser et al. 2015; Lavelle et al. 2018).

Whenever a new disease is introduced or begins to emerge, it stimulates a flurry of research. Chronic wasting disease, a prion disease of cervids, for example, was first documented in a research facility in Colorado, USA, and in the subsequent 50 years has spread to 26 US states and 3 Canadian provinces. And, in the last 40 years there have been well over 300 scientific papers written on CWD. The disease is impacting populations of wild cervids and the continent's captive cervid industry. Though related to scrapie and bovine spongiform encephalopathy, outside of experimental infection studies (e.g., Hamir et al. 2005; Moore et al. 2017), CWD has not been demonstrated to naturally impact primary species of domestic livestock in North America.

The development of reliable diagnostic capabilities for North American wildlife is also of importance. Diagnostic tests are typically developed for domestic animals, however, their performance in wildlife is often unknown. The empirical investigation of wildlife-livestock contact and routes of pathogen transmission (direct or indirect) is also critical. Not only is this useful for developing better mitigations but it is also important for estimating important pathogen transmission measures such as the basic reproductive number (i.e., R_0) which measures how fast an infectious disease can move through a population. Epidemiologic measures such as this can be used to predict if a pathogen can successfully establish in a wildlife population, how quickly it might spread, and what proportion of an affected population must be treated to manage the disease.

Though there is currently no comprehensive, integrated, and all-inclusive approach to disease surveillance across North America, the need to develop such a system that includes livestock, wildlife, and human components has been suggested (Mörner et al. 2002; Miller et al. 2013). Across much of the continent, though, programs are in place to conduct surveillance for a wide variety of diseases in wildlife and domestic animals. These programs often span many federal agencies, state and provincial governments. These programs have detected the presence of new diseases (H5 clade 2.3.4.4 subtypes H5N2, H5N8, and H5N1) and documented the spread of existing diseases (e.g., CWD) into new populations. Surveillance systems are valuable for monitoring changes in the prevalence of endemic diseases and for triggering the implementation of proactive risk mitigations. The US, for example, has a surveillance program in place for detecting classical swine fever in domestic swine that includes strategies for rapid detection, documenting freedom, and monitoring risk of introduction relative to the international presence (APHIS Veterinary Services 2007). Additionally, targeted surveillance is conducted in wild pigs for classical swine fever and other diseases of domestic concern and in waterfowl for AIV.

Among the obstacles to comprehensive surveillance at the livestock-wildlife interface is inconsistent or lack of funding for surveillance activities (Leighton et al. 1997; Stitt et al. 2007) and often a narrow focus on only a few diseases (Miller et al. 2017). For example, a recent assessment of disease surveillance in North American for swine diseases in wild pigs found that only 49% of OIE listed domestic swine diseases had any published surveillance findings (positive or negative). Funding for surveillance is often in response to emergency directives (e.g.,

highly pathogenic AIV H5N1 and H5N8) and once the threat is perceived to no longer exist the system is discontinued. Predictably, this generates problems for developing national, much less continental, infrastructure that can be maintained over the long-term and used to generate baseline surveillance information across many host-pathogen systems. Limited surveillance data makes it challenging to model or otherwise understand the spatial and temporal risks associated with pathogens at the interface of wildlife and livestock. Research to optimize surveillance by improving cost-effectiveness and efficiencies is greatly needed. This includes not only improving diagnostic test capabilities for North American wildlife, but also developing methods that allow for cheaper and more practical surveillance like paper-based analytical devices (e.g., Srisa-Art et al. 2018), volatile organic compound detection (e.g., Stahl et al. 2015), and environmental DNA (e.g., Bohmann et al. 2014).

Conclusion and Perspectives

Nearly 80% of the pathogens present in the US have a potential wildlife component. To successfully manage and control these pathogens at the wildlife-livestock interface will require the development of cross-discipline collaborations and establishing common goals among agencies and organizations that in some cases have rarely worked together or have been at odds. The control of one health diseases will benefit significantly from increased communication and collaborations that combine program objectives and activities across agency and country jurisdictions. While challenging from political and cultural perspectives, the outcomes could be beneficial and would enhance the ability to quickly identify and respond to new and emerging disease issues. Despite these challenges, there remain opportunities to develop new collaborations and leverage new technologies to mitigate disease risks at the wildlife-livestock interface. We believe the principles of adaptive management offer the greatest opportunities to formulate a framework from which collaborations can be developed and progress made.

Concepts for integrated adaptive management of diseases at the livestock-wildlife interface have been proposed by multiple authors (Thirgood 2009; Wasserberg et al. 2009; Miller et al. 2013). Furthermore, many countries have developed surveillance systems for disease events in wildlife (Mörner et al. 2002). Many of these systems implement integrated adaptive disease management using risk assessments and disease monitoring systems for wildlife (Sainsbury et al. 2001; Lysons et al. 2007; Hartley and Gill 2010). Despite efforts to establish prevalence estimates for a diversity of pathogens in wildlife in North America, there are gaps for pathogens of interest for wildlife, livestock, and human health. For more than 50% of OIE listed pathogens present in North America, there have been no studies assessing their prevalence in wildlife. This lack of knowledge severely limits the ability to make sound management decisions.

Adaptive disease management principles can help integrate and prioritize surveillance activities along with the development and deployment of effective, practical, and economical mitigation measures designed to lower pathogen transmission risk (Franklin and VerCauteren 2016). Furthermore, control tools such as intensive agency culling or recreational hunting of host wildlife species with the intent of reducing disease transmission could be attempted in an adaptive management framework. This allows for the incorporation of uncertainty such as the limited understanding of the effect population reduction might have on wildlife populations and disease dynamics. Strategies such as selective culling of high-risk individuals or groups could even be tested as part of the management process to improve the development of practical and effective culling programs. Integrating these practices with non-lethal mitigation strategies like fencing could greatly reduce contact and transmission risk.

Estimates of economic impacts to livestock, recreational hunting interests, and to governmental agencies resulting from pathogen transmission at the livestock-wildlife interface are elusive. Though some assessments exist for diseases such as bovine tuberculosis (Horan and Wolf 2005; O'Brien et al. 2011), more research evaluating the economics of diseases at the interface is needed. The same is true relative to human dimensions and the need to educate the gamut of publics in democratic societies to help ultimately lead to sound, long-term disease management choices.

Though control and management of endemic and foreign animal diseases in North America are daunting, the future is bright. The existing baseline and framework of global knowledge increased cooperation and collaboration amongst countries, and the recognition of the importance of addressing disease issues proactively and head on all bode well for protecting our natural and agricultural resources.

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Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Central and South America



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Introduction

The Region of Central and South America, which extends from northern Guatemala to Tierra del Fuego, is full of sharp contrasts in many of its descriptive parameters (e.g., economic, social, geographic, agriculture and livestock production, wildlife, etc.). While it is in fact one of the Regions with the largest biodiversity, it also encloses the largest livestock producing and exporting countries. Against this complex regional backdrop, many opportunities for interaction arise at the wildlife-livestock interface, for which it is necessary to assess their reciprocal impact. On one hand, to explore whether livestock diseases are posing a threat for wildlife conservation; but at the same time, determining how the interaction with wildlife reflects on livestock diseases.

This scenario at the wildlife-livestock interface enables the occurrence of important infectious diseases, including rabies, avian influenza, leishmaniasis, brucellosis, bovine tuberculosis, and a group of arboviruses (Cunningham et al. 2017). These diseases imply different impacts (on the economy, on public health, on conservation); have different epidemiology, with uneven prevalence distribution across the Region and several ways of transmission (with or without the role of vectors); and present different threats and opportunities. Thus, a detailed focus on the regional outlook of these diseases would allow getting a comprehensive view of potential situations that can be encountered within the topic.

Beyond the issue of disease sharing at the wildlife-livestock interface, it is important to identify those strategies for surveillance and control that are contributing to resolve the spillovers; particularly comparing what is being done with what should be done. Likewise, in this heterogeneous context, there is an opportunity to describe the main knowledge gaps about those interactions not well understood yet and to add to the wishlist those potential key topics that need more and better research. Additionally, since the increase in deforestation has been one of the major problems due to the development of the livestock sector in the Region, it is necessary to recognize the direct impact on wildlife and on the occurrence of vector-borne diseases.

Socioeconomical and Biogeographical Circumstances

The Region represents a complex socioeconomic area where the wide income inequality is still a major problem (Tsounta and Osueke 2014; World Bank 2014). In the past, its natural resources, such as precious metals, sugar, rubber, coffee, and cacao, made it a strategic Region; and likewise, it was also favored by the recent pattern of global recovery (Sinnott et al. 2010). In fact, the national policies implemented across the countries have contributed to support the domestic demands in the regional larger economies, as well as external demand from fast-growing emerging markets, boosting export (Sinnott et al. 2010).

A large part of the Region is often affected by natural hazards such as earthquakes, volcanic eruptions, tsunamis, or hurricanes, together with the alternation of serious floods and droughts linked to El Niño-Southern Oscillation (Tollefson 2014). These natural disasters disturb the basic welfare state (e.g., food security, access to drinking water, housing, etc.) and have an impact on the occurrence of infectious diseases in human being, livestock, and wildlife (Watson et al. 2007; Cohen and Thompson 2012; Kouadio et al. 2012). Central and South America includes a variety of geographical features such as the Amazonian rainforest, the biome of Pampas, the tropical wetlands of the Pantanal, the Andean mountain range, tropical forest, large rivers, and a combination of natural and human-made grasslands and shrublands across the whole Region.

The livestock regional map has drastically changed over the last five centuries, along with the pastures-deforestation landscape. Among the Pre-Columbian civilizations, the only domesticated species were the dog, turkey, guinea pig, and Andean camelids (Martínez et al. 2012). Livestock species (including cattle, horses, donkeys, pigs, sheep and goats) were brought since the late fifteenth century, in the first trips to the Americas from Europe during the colonization. The cattle expanded throughout the Americas, adapting to a wide range of environmental conditions and giving origin to what is currently known as Creole cattle (Martínez et al. 2012; Anderson et al. 2015). After nearly 300 years of expansion, together with the development of more intensive production systems, several other European breeds were brought (Martínez et al. 2012). Likewise, at end of the nineteenth century, *Bos indicus* cattle breeds were also introduced and quickly disseminated throughout the Americas, especially in tropical regions (Martínez et al. 2012).

Among the major livestock diseases occurrence in the Region, Foot-and-Mouth Disease (FMD) would be on the top. It was introduced at the end of the nineteenth century in South America, and it has never been detected in Central America (Naranjo and Cosivi 2013). FMD is still one of the major livestock diseases worldwide as a result of the highly infectious nature of the virus and the significant direct impact of the virus on animal production and trade (Garland and de Clercq 2011; Clavijo et al. 2017)—and hence on food security. This disease, now almost eradicated, has contributed to the framing of the veterinary services of the Region on strategies such as surveillance, control programs, prevention, and emergency preparedness (Clavijo et al. 2015). In South America, the total annual costs of the countries involved in FMD control, surveillance, and prevention are estimated to be over one thousand million USD per year (Centro Panamericano de Fiebre Aftosa – OPS/OMS 2017).

The livestock expansion did not take place without an impact on the wildlife landscape. It is estimated that between 1990 and 2010, deforestation reached 88 million hectares in Central and South America, where large-scale forest conversion for livestock-based and commercial agriculture is a primary cause of deforestation (Lambin et al. 2003; FAO 2017a). Hence, the areas for livestock grazing have expanded in the past and will continue to increase, although at a moderate pace, in this Region (Alkemade et al. 2013). The largest deforestation front took place in the Brazilian Amazon, which extended more recently outside Brazil, east of the Andes,

and even to Venezuela (Lambin et al. 2003). Likewise, the Chaco (that includes areas of Argentina, Bolivia, Brazil, and Paraguay) and parts of Atlantic forest in South America have been identified as areas of forest loss. Central America has significant deforestation areas in the Yucatan and at the Nicaraguan border with Honduras and Costa Rica (Lambin et al. 2003).

The Prevalent Livestock, Farm Typologies in Every Region, and Opportunities for Interface

Its geography, and its associated climatic conditions, draws an eclectic map of livestock production, with a broad variety of species and ways of production, which ranges from farming of llamas in the Andes to the vast territories of cattle grazing in grasslands, together with key areas for pig and poultry intensive production. In fact, the Region has the elements to be a major livestock producer, to meet local food needs, and contributing to world food security (FAO 2017b).

The Region combines subsistence livestock production and smallholders with a strong intensive animal farming industry, which positions some countries of the Region among the largest cattle, pig, and poultry producers in the world. In fact, the livestock sector has boomed in recent decades, particularly in the Southern Cone, due to the growth in world food demand (FAO 2017b). Four countries of the Region (Brazil, Uruguay, Paraguay, and Argentina) appear among the top ten exporters of beef and veal in the world (USDA 2018). Likewise, Brazil together with Chile are among the top ten pork exporters in the world, and Brazil and Argentina among the top ten broiler meat exporters (USDA 2018).

The forecast indicates that the Region will maintain a position among the leaders in meat production. Brazil's growth will benefit from an abundant supply of natural resources, and will also count on noteworthy potential contributions to additional meat production from Argentina (OECD/FAO 2017). These two countries from the Region, together with China, India, Mexico, and Pakistan, will account for 75% of the additional beef produced by 2026 (OECD/FAO 2017).

These promising regional scenarios on livestock production are hampered by concerns on: the limited availability of quality animal feed and by an inefficient use of available resources; the risk of introduction of transboundary animal diseases and costs related to livestock disease prevention, surveillance, and control; and damages associated with the conversion of land use and threats due to the negative impact of climate change on the livestock sector (Sinnott et al. 2010; PANAFTOSA 2015; FAO 2017b).

Livestock expansion into the Americas has also interacted with the wildlife populations. Thus, the *Desmodus rotundus* (common vampire bat) has a preference for the blood of large mammals, such as horses, cattle, and pigs, and since the introduction of these livestock species into the New World (Turner 1975), the *D. rotundus* populations adapted to use this source of feeding which allowed a

population burst. It has been demonstrated that high livestock densities are an important factor to understand the pattern of bat expansion (Reis et al. 2007). Likewise, deforestation has been one of the straightforward and determinant causes for climate and environmental changes, favoring the expansion of leishmaniasis to areas with no previous transmission (Cardenas et al. 2006, 2008; Gottwalt 2013). Indeed, several studies have demonstrated the effect of the actions generated by agriculture and livestock in the occurrence of vector-borne diseases, such as leishmaniasis (Mayen 2003; Molyneux 2003; FAO 2012; Gottwalt 2013).

The Wildlife

The wildlife outlook is also heterogeneous, considering that six of the nine countries with the greatest diversity of terrestrial fauna on the planet are within the Central and South American regions (Butler 2016, Figs. 1 and 2). A large part of this diversity is composed of species of three orders (i.e., Chiroptera, rodents, and primates), recognized as hosts or reservoirs for major animal diseases and zoonoses (Jones et al. 2008; Olival et al. 2017). In addition, the Region has an eclectic variety of species of ungulates (South American camelids, cervids, tapirids, tayasuids), carnivores (canids, didelphids, felids, procyonids, mephitids, mustelids), and the greatest diversity of birds on the planet. In short, this scenario represents a wide range of potential hosts for relevant infectious diseases at the livestock/wildlife interface. All this enables an epidemiological scenario for the occurrence of important infectious diseases, having the wildlife as a modulator, such as rabies, avian influenza, West Nile virus (WNV), brucellosis, or tuberculosis.

While a number of studies to investigate the exposure (or infection) of livestock pathogens to wildlife species have been carried out (De Sousa et al. 2017; Maciel et al. 2017), only a few have shown disease or pathological implications (Deem et al. 2002; Filoni et al. 2009; Morales et al. 2017). There is a series of parameters (e.g., clinical signs assessment, anatomo-pathology/histopathology, or laboratory diagnostic such as molecular characterization of the agent) allowing the evaluation of the consequences in the conservation of a species that could be used to help understand the direct impact of livestock diseases on wildlife health (Hidalgo-Martínez et al. 2008; Preece et al. 2017; Grogan et al. 2018). Evidence of this impact has been identified in other regions of the world. For Central and South America, however, the episodes of mortality in wildlife are associated with other factors than the transmission of the pathogen at the interface of the wildlife-livestock. Indeed, there is no evidence in this Region, either through molecular epidemiology or pathological studies, to confirm any substantial impact of livestock on wildlife health.

In the Region, rabies, leishmaniasis, Venezuelan equine encephalomyelitis (VEE), leptospirosis, and avian influenza appear among the diseases with implications on wildlife-livestock interface that are most often addressed in scientific publications (Wiethoelter et al. 2015) (Table 1). In the rabies aerial cycle, in which



Fig. 1 (a–b) Camera trappings of cattle and ocelot (*Leopardus pardalis*) in the same spot in Ecuador. Tropical forests are increasingly destroyed to clear land that is ultimately used for agriculture, the largest driver of tropical deforestation globally. (c) There are vast forested areas at risk of conversion for pastureland expansion in South America. The picture shows a cleared area where black vultures (*Coragyps atratus*) wait for cows to defecate and/or give birth. (d) The capybara (*Hydrochoerus hydrochaeris*) is the largest living rodent in the world (wild or raised under free-ranging or semifree-ranging conditions), and increasingly present in urban areas, living near bodies of water. The capybara is one of the wildlife species in the Region susceptible to FMDV (image: “Wild Llanos—Agro Tours” Colombian Llanos, Yopal, Casanare). (e) Vicuña (*Vicugna vicugna*) in Chimborazo (Ecuador). The vicuña is one of the two wild South American camelids which live in the high alpine areas of the Andes, the other being the guanaco (*Lama guanicoe*). Vicuñas are the wild ancestors of domesticated alpacas. Sheep (f) occupy the same habitat (except extremely high altitudes) as camelids including vicuña and guanaco, see also next figure) (image: C. Gortazar)



Fig. 2 (a) The greater rhea (*Rhea americana*) is a South American ratite endemic to Argentina, Bolivia, Brazil, Paraguay, and Uruguay. This bird has been greatly affected by habitat alteration (farming) and hunting. The image shows a close interaction with cattle (image: M. M. Guerisoli-Grupo de Ecología Comportamental de Mamíferos). (b) These images illustrate the human face of the triple human-wildlife-livestock interface; a peccary piglet is fed by local villagers in proximity of domestic pets and poultry in Peru (images: C. Gortazar). (c–e) Livestock, such as horses, and guanacos, and huemul (*Hippocamelus bisulcus*) share habitat in the Magallanes Region (Torres del Paine National Park, Chile) (images: Ezequiel Hidalgo). The guanaco is the wild ancestor of the lama and inhabits the Andean and Patagonian steppes from sea level to high altitudes. It is considered a key engineer species for the Patagonian steppe. According to historical data, guanaco populations in pre-Columbian times reached 30–40 million specimens from the north of Peru to the

Table 1 Summary of the main features of the identified interfaces, including types of interface and relevant diseases

Main species involved in the interface	Major diseases at the interface/pathogen/transmission	Main characteristics and relevance	Area of distribution
Multispecies	Rabies Lyssavirus genus Transmission is through saliva from infected animals entering the body through wounds or by direct contact with mucosal surfaces. Typically, by bites from carnivores (e.g., dog) and hematophagous bat	<ul style="list-style-type: none"> • Major zoonosis • Wildlife (bats) are the reservoirs of the diseases • Livestock are victims of bat attacks and get the disease • Important economic losses including cost of vaccination • Interventions have an impact on populations of bats 	Widespread across the region
	Foot-and-mouth disease Foot-and-mouth disease virus, Picornaviridae family Transmitted by close contact with infected animals, airborne spread, fomites, and mechanical	<ul style="list-style-type: none"> • Non-zoonosis with impact on food security • The regional wildlife can have the infection but do not play a major role in the epidemiology of the disease, distinctive from other regions 	South America
	Brucellosis Bacteria of the genus <i>Brucella</i> (essentially <i>B. abortus</i> , <i>B. melitensis</i> , <i>B. suis</i> and <i>B. ovis</i>) Transmitted mainly by contact with infected birthing tissues and fluids (e.g., placenta, aborted fetuses, fetal fluids, vaginal discharges)	<ul style="list-style-type: none"> • Neglected zoonosis • Control/eradication plans in place for livestock • Important economic losses including cost of interventions • Within the region, the role of the wildlife-livestock interaction in the epidemiology of the disease is still unclear 	Endemic in most of the Region

(continued)

Fig. 2 (continued) extreme south of Chile, at present (IUCN) the total world population would not exceed 600,000 individuals. (f) Pudu (*Puda puda*), a species considered as high probability of population decline, and cattle sharing habitat Nahuelbuta National Park of the Bio Bio Region in Chile (images: Dario Moreira Arce). (g) Wild-domestic carnivore interaction by a dog approaching an American sea lion (*Otaria flavescens*) carcass in the Chilean coast (image: C. Gortazar)

Table 1 (continued)

Main species involved in the interface	Major diseases at the interface/pathogen/transmission	Main characteristics and relevance	Area of distribution
	Leishmaniasis Protozoa of the genus <i>Leishmania</i> Transmitted to vertebrate animals and man by infected females from the Psychodidae family, <i>Lutzomyia</i> genera	<ul style="list-style-type: none"> • Increase in the occurrence associated with deforestation (livestock production expansion) • Wild vectors have been adapted to domestic environments and to a greater contact with man • Neglected zoonosis 	The whole Region except by Chile and Uruguay. Greatest occurrence in the subtropical range
Avian	Avian influenza Avian influenza virus, Orthomyxoviridae family Transmitted by close contact (typically through aerosol) with infected animals, or with surfaces contaminated, also possible airborne	<ul style="list-style-type: none"> • Potential zoonosis (and pandemic) • Highly pathogenic form is absent/sporadic in the Region, low pathogenetic form is widespread in wildlife • Key role of wildlife (birds) in the transmission and dispersion of the disease 	Widespread across the Region
Bovine	Tuberculosis <i>Mycobacterium bovis</i> Transmitted mainly by close contact with infected animals (airborne) or by ingestion of contaminated material (foodborne)	<ul style="list-style-type: none"> • Neglected zoonosis • Control/eradication plans in place for livestock • Important economic losses including cost of interventions • Within the region, the role of the wildlife-livestock interaction in the epidemiology of the disease is still unclear 	Endemic in most of the Region
Equine	Venezuelan Equine Encephalitis (VEE), Eastern Equine Encephalitis (EEE), West Equine Encephalitis (WEE), and West Nile Encephalitis (WNE) Arboviruses of the genus Alphavirus (VEE, EEE, WEE) and Flavivirus (WNE) Transmitted by arthropods (mainly <i>Culiseta</i> sp. and <i>Culex</i> sp.).	<ul style="list-style-type: none"> • Zoonoses • Control plans in place for livestock • A better surveillance is necessary to understand the occurrence of the infection both on wildlife and livestock • Potential relevance of peri-domestic species 	Present in grand part of the Region

bats are the reservoir of the virus, the presence of rabies-infected bats in urban and rural areas represents risks to livestock and public health, due to feeding from large herbivores and to synanthropic habit (Kotait et al. 2009). Although other species of hematophagous bats are present in the Region, i.e., *Diaemus youngi*, *Diphylla ecaudata* (Reis et al. 2007), the *D. rotundus* (common vampire bat) is the main responsible for the incursions of rabies (associated with attacks) from the aerial cycle into the rural cycle, that is characterized by the transmission of rabies to livestock (and human) populations (Reis et al. 2007; Kotait et al. 2009; Albas et al. 2011). *D. rotundus* has a wide distribution, being the most common and abundant species of vampire bat, found from the north of Mexico to the north of Argentina. It feeds from mammal's blood, both wild and domestic, including man and occasionally on birds (Reis et al. 2007). In its natural habitat, its roosts are caves, stone burrows, hollow trees, fallen trees, and even termite nests (Gomes and Uieda 2004). Deforestation and occupation of wilderness by livestock and other man-made activities (Kunz and Fenton 2003), forced them to adapt to the new conditions in urban areas (Reis et al. 2002). Besides *D. rotundus*, other bats have shown to play a role in the disease maintenance, contributing in that way to the aerial cycle (Calisher et al. 2006), but without participating in the transmission of rabies to livestock.

Venezuelan equine encephalitis (VEE), eastern equine encephalitis (EEE), west equine encephalitis (WEE), and West Nile encephalitis (WNE) are emerging arboviruses that can affect humans, equines, other mammalian species, and birds. These pathogens represent another example where livestock affecting diseases are influenced by wildlife. As in other diseases transmitted by arthropods, they have cycles involving wild vertebrates (reservoirs/amplifiers), mosquitos (vectors) equines, and humans (final hosts) (Mesa et al. 2005). These are characterized by different epidemiological attributes; all of them, however, are involved in a complex interaction between equine livestock and a wide range of wildlife reservoirs that include both mammals and birds, with the additional potential impact on public health. The cycle for leptospirosis also involved wildlife, and the most frequent reservoirs in the Region are members of the order Carnivora (e.g., *N. vison*, *C. thous*, and *N. nasua*), that may get exposed to these bacteria by consuming infected prey, such as rodents (Vieira et al. 2017). Avian influenza is another key disease having wildlife reservoirs. Among the reported events of avian influenza in the Region, most of them has been associated with migratory birds, particularly of the orders Anseriformes and Charadriiformes (Hurtado et al. 2016; Afanador-Villamizar et al. 2017), which play a major role in the disease spread and its transmission to domestic poultry.

Leishmaniasis, conversely, is an example that contributes to illustrate the complex interface between wildlife and livestock that has an impact on human health. The parasite does not have direct implications for livestock; however, the deforestation, which in turn, is partially associated with livestock expansion has contributed to change the dynamics of leishmaniasis and favored human contact with

Leishmania wild vectors. Its complex and dynamic transmission cycle is characterized by a variety of vectors, reservoirs, and *Leishmania*. Twenty-two *Leishmania* species—15 in the Americas—have been identified as being pathogenic to humans (Alvar et al. 2012; Desjeux 2004; World Health Organization 2010). In Central and South America members of the family Canidae, of the order Rodentia and of the infraclass Marsupialia have been identified as the main reservoirs (Roque and Jansen 2014). The maintenance of the *Leishmania* in nature depends on the transmission cycle, which can be zoonotic (as in this Region) or anthroponotic. Likewise, the different species of phlebotomine, involved in the transmission, present a unique and complex biology that affects the distribution, cycle, and control of the disease (Gramiccia and Gradoni 2005; WHO 2010).

The Disease at the Interface: One Health Perspective

The concept of One Health comes to recognize the inextricable relation between its three main components: animal, human, and environment health (Gibbs 2005; Zinsstag et al. 2011). There are indeed interesting contributions brought with the application of this concept, and it also helps to think broadly about problems and solutions beyond the boundaries of just one component. Thus, it is used in this chapter to explore different scenarios of health interaction between wildlife (a term that, here, intentionally merges together wild animals and their habitats) and livestock; which additionally, when relevant, is tangentially presented with the human interplay.

Within the One Health triad, the human component cannot be ignored, even when it is not the priority of this chapter, since humans interfere, module, and somehow control the wildlife-livestock interface. The human population in the Region is mainly distributed in urban areas. Since it is the world's most urbanized Region (UN-HABITAT 2012; Atlantic Council 2014), the rural population needs to be protected and more valued—as it holds a socioeconomic and environmental relevance. Among developing regions, Latin America has possibly the longest experience in the application of the territorial development approach. National programs for rural territorial development, aimed at alleviating poverty, improving education levels, and reducing regional disparities, are underway in Argentina, Brazil, Colombia, Costa Rica, Honduras, Mexico, and Nicaragua (FAO 2017a). Besides, rural incomes respond to agricultural development, even though many rural households do not necessarily rely on agriculture as their direct or main income source (de Ferranti et al. 2005). Thus, policy reforms that began in the 1980s led to an overall growth and trade which contributed to increase the rural income, the reduction of poverty, and improvements in welfare indicators (de Ferranti et al. 2005; FAO 2017a).

Apart from some of the abovementioned diseases (rabies, avian influenza, leishmaniasis, and arboviruses), other three major diseases with an important economic impact on livestock production are also explored here: FMD, brucellosis, and bovine tuberculosis. Hence, these diseases are used as a model to present the main features of One Health interaction together with the problems and opportunities. FMD is presented in this chapter not because wild animal species are relevant to FMD control in the Region (as it happens in other regions such as Africa), but because of the opposite—it represents an exception. Brucellosis and bovine tuberculosis (both zoonoses) are briefly presented as a complex interaction between livestock species and wildlife, which is not yet understood and hence presents opportunities to throw some light on the aspects of the epidemiology.

Box 1 Rabies

The rabies terrestrial cycle in the Region, mostly transmitted by dogs—with an apparent insignificant role of native terrestrial wild mammals—is under efficient control measures in most of the countries. The aerial cycle, however, remains a serious issue (Albas et al. 2011). It is estimated that *D. rotundus* rabies seroprevalence is more than 40% (da Costa and Fernandes 2016), particularly associated with variant 3 in this species (Schneider et al. 2009). So far, Rabies is the disease transmitted from wildlife to livestock that has the major impact in the Region. Today, in geographic areas with no control measures this disease might cause the death of around 100–500,000 cattle per year, and forecasts for the coming decades report that conditions in the Region may become increasingly favorable to predation of herds by *D. rotundus* (Swanepoel 1994; Lee et al. 2012). In Brazil, during the years 2002 to 2015, more than 665 million bovines were vaccinated against rabies throughout the national territory, which reveals an annual mean vaccination of 51 million animals (MAPA 2015). In addition to vaccination costs, Belotto et al. (2005) estimated that losses to livestock production in Latin America amounted to US\$50 million per year. Although predation of humans is not the first choice for hematophagous bats, when there is a reduction or absence of local herds, leading to a decrease in the feeding sources, the attack on humans might increase, as it has been reported particularly in the Amazon (Schneider et al. 2009). Furthermore, herbivores that were bitten and infected by vampire bats, sometimes, accidentally transmit rabies to people; therefore, beyond economic losses, herbivorous rabies also represents an impact on public health (Kotait et al. 2009).

Surveillance of rabies in wild animals involves veterinarians, forest rangers, local people, and animal rights groups, as it is important to monitor the behavior of wild animals, especially in endemic areas for rabies. Rabies must be a notifiable disease (both in humans and animals) in all countries (WHO 2013; OIE 2018), which requires the active involvement of the local

(continued)

Box 1 (continued)

health services and private veterinarians and owners of domestic herbivores—that should inform the official veterinary services. Also, suspected bites with consequent nervous symptoms in people or animals, and the presence of bat roost should be reported. The official veterinary service, in turn, must attend to the notifications by collecting samples and investigating epizootics. Upon deciding on the implantation of any strategy, it is necessary to distinguish rabies reservoirs from animals that are just susceptible to rabies infection, so that their epidemiological importance can be established, and suitable surveillance and control measures can be implemented. *D. rotundus* is thus the target of surveillance and control strategies in the countries. Latin America has an extensive network of more than 100 laboratories to diagnose cases of rabies in humans and animals, as well as the typification of the viral variant (REDIPRA 2003). Annually, the official veterinary services notify in Latin America, more than 1500 herbivore rabies outbreaks with laboratory confirmation (SIRVERA 2018). However, it is believed that official notifications represent only 10% of total outbreaks (Kotait 1998). Among the factors for the underreporting are the difficulty to collect and send samples to the official laboratory services in a country, an insufficient number of professionals to implement surveillance, unspecific clinical signs that can be mistaken with other diseases, difficulty to reach some territories, and local population ignorance about rabies (Mayen 2003; Belotto et al. 2005; Mallewa et al. 2007).

Box 2 Avian Influenza

Avian influenza is classified in two forms according to its pathogenicity level, i.e., high and low (OIE 2017). While highly pathogenic avian influenza (HPAI) is a key disease at the wildlife-livestock interface in other regions, that is not the case for Central and South America, where this form has only been reported in Chile (Mathieu et al. 2015). In poultry, low pathogenic avian influenza (LPAI) has been only reported in Belize and Chile (WAHIS-OIE 2018) for the H5 and H7 OIE notifiable subtypes (OIE 2017); however, other low pathogen strains might be present in the poultry population of the Region (Bravo-Vasquez et al. 2016; Jiménez-Bluhm et al. 2016). The scenario for LPAI is different in wildlife, with several reports informing of the presence of this form in Argentina, Bolivia, Brazil, Chile, Colombia, and Peru (Spackman et al. 2006; Pereda et al. 2008; Ghersi et al. 2009; Karlsson et al. 2013; De Araujo et al. 2014; Mathieu et al. 2015). In general, the number of isolates has been small in the Region, in correlation with the small sampling size of the surveys. This said, it is necessary to consider that some evidence suggests that

(continued)

Box 2 (continued)

the prevalence of avian influenza might be actually lower in this Region than in other parts of the world (Hurtado et al. 2016). Avian influenza is only briefly presented in this chapter due to its low frequency of occurrence in poultry across Central and South America, and to the limited knowledge on its presence in wild birds.

Box 3 Equine Encephalitis and West Nile Encephalitis

Among the group of diseases caused by arboviruses presented here, three of them (i.e., EEE, WEE, and VEE) only occur in the American continent; whereas WNE is also found in Asia, Africa, and Europe. They are associated with specific environmental characteristics together with economic, political, and social factors (Mesa et al. 2005). VEE is of great importance because of its severity, high morbidity, and lethality in equines, and also due to its periodical presentations in epizootics and epidemics in a great part of the American continent (Acha and Szyfres 2003). One of the major outbreaks of VEE in Central and South America occurred in 1969, involving 31,000 humans and the death of approximately 20,000 horses only in Ecuador, resulting in losses of around US\$1,200,000 (Acha and Szyfres 2003). The high morbidity and mortality in equine livestock, as occurred in 1969, affects the rural economy of the Region, since these animals are used in agricultural tasks and individual transport. In addition, VEE impacts on public health, due to the incapacitation of workers, treatment costs, and hospitalization of individuals, cause a decrease in community well-being and might contribute to a collapse in health services (Acha and Szyfres 2003; Alder et al. 2005; Mesa et al. 2005).

The EEE virus has been isolated in most of the countries of the American continent, including Brazil, Argentina, Colombia, Peru, Panama, Haiti, Guatemala, Mexico, USA, and Canada (OIRSA and PAHO 2014). The EEE virus variant found in North America is more pathogenic to horses and humans than the variant present in South and Central America (Smith et al. 2009). In recent years, the EEE and VEE have been showing unusual behavior in the Region and outbreaks of both diseases were reported in humans and horses in Panama in 2010. These occurrences in humans may be the result of increased human contact with enzootic transmission cycles, genetic changes in EEE viral strains that resulted in increased human virulence, or an alteration of host range (Carrera et al. 2013). The Table 1 provides a summary of the major diseases at the wildlife-livestock interface presented in this chapter.)

Like EEE and VEE, WEE virus circulates in regions of North, Central, and South America. Thus, WEE has been identified from Argentina to western

(continued)

Box 3 (continued)

Canada, usually presenting sporadic cases in horses in a widespread manner (OIRSA and PAHO 2014). It is worth mentioning that in the enzootic cycle of equine encephalitis, the transmission involves rodents (VEE) and wild birds (EEE and WEE) to a variety of mosquitoes. Equines and humans may accidentally engage in this cycle when they enter the enzootic ecosystem and get affected when susceptible (e.g., born after an epizootic, unvaccinated, or that came from free areas) (Mesa et al. 2005).

The occurrence of VEE, EEE, and WEE epidemics poses a serious risk to Central and South American countries since most countries have favorable conditions for the development and distribution of these arboviruses (Acha and Szyfres 2003). Between 2000 and 2015, several outbreaks of equine encephalitis were reported in different countries of Latin America (Table 2). The main factors associated with the emergence of epidemics in the region are: the presence of reservoirs and vectors, the population of susceptible equines, migrations, human displacement and their congregation in areas surrounded by amplifying animals, expansion of agricultural frontiers, climatic changes, water accumulation, and the poor hygienic conditions (PAHO 2011).

The WNE is relatively new in the Americas—first reported in 1999 (USA) (Lanciotti et al. 1999)—but has managed to spread rapidly, particularly in North America, by finding ecological conditions and habitats that favor the migration of many species of birds—virus amplifiers in this region. The most pressing concern regarding the reports of WNE in the Region is the absence of robust data on the disease burden in people, horses, or birds (Komar and Clark 2006). Serological evidence indicates that the virus has spread southwards in different countries of Central and South America (Table 2). In Argentina, the viral particles identified as WNV have already been isolated in horses with neurological symptomatology (Morales et al. 2006; Chancey et al. 2015). Although the disease has not yet posed a serious threat to the Region, the high equine population density and ecological conditions favorable to the proliferation of arthropods are factors that may result in WNV epidemics in this region (Ward 2005; Komar and Clark 2006). The role of migratory birds in the spread of WNV is still unknown, but the rapid diffusion of the agent in the USA and later in Central and South America points to a probable participation of these birds (LaDEAU et al. 2007). In this respect, the zoological parks can be used as sentinels for WNV in natural or urban environments (Ludwig et al. 2002; Pultorak et al. 2011).

Table 2 Evidence of VEE, EEE, WEE, and WNV infection in Central and South American countries

Disease	Country	Species	References
VEE	Argentina	Humans	Pisano et al. (2013)
	Colombia	Humans and equines	OIRSA and PAHO (2014)
	Panama	Humans and equines	Carrera et al. (2013)
	Peru	Humans	Aguilar et al. (2004), Vilcarromero et al. (2010)
	Venezuela	Equines	Valero et al. (2004)
	Belize	Equines	Nachon Cicciarella and Bosisio (2005)
	Brazil	Humans and equines	Cunha et al. (2009), Melo et al. (2012), Romano-lieber and Goldbaum (2000)
EEE	Colombia	Equines	OIRSA and PAHO (2014)
	Panama	Humans and equines	Carrera et al. (2013)
	Venezuela	Equines	OIRSA and PAHO (2014)
	Brazil	Humans and equines	Campos et al. (2013), de Novaes Oliveira et al. (2014), Romano-lieber and Goldbaum (2000), Silva et al. (2011)
WEE	Brazil	Equines	Heinemann et al. (2006)
WNV	Guatemala	Wild and domestic birds, equine	Morales et al. (2006), OIRSA and PAHO (2014)
	Jamaica	Native birds	Dupuis et al. (2003)
	Colombia	Equines	Komar and Clark (2006)
	Venezuela	Native birds	Bosch et al. (2007)
	Argentina	Equines	Diaz et al. (2008), Morales et al. (2006)
	Brazil	Equines and native birds	Silva (2010)
	Costa Rica	Mexican crocodiles (<i>Crocodylus moreletii</i>) Hoffman's two-toed sloths (<i>Choloepus hoffmanni</i>)	Medlin et al. (2016)

Box 4 Leishmaniasis

In the past, in Central and South America, leishmaniasis had two well-established transmission patterns: visceral leishmaniasis was considered a primarily rural disease, and cutaneous leishmaniasis had a predominantly sylvatic pattern. Since the 1980s, other transmission patterns became epidemiologically important, determining different scenarios (Maia-Elkhoury et al. 2008; Salomón et al. 2015). These scenarios were established when cutaneous

(continued)

Box 4 (continued)

and visceral leishmaniasis began to occur in peri-urban/urban areas, since new risk factors and changes in the biology of the wild vector favored their adaptation to domestic environments and to a greater contact with man (Desjeux 2004; Rangel and Vilela 2008; Salomón et al. 2006, 2008, 2015). This process was consolidated with the increase of cases, a 30% increase in total cases of cutaneous leishmaniasis during the period of 2001–2010, and widening the geographic of the disease, reaching large cities and other countries of the region (Maia-Elkhoury et al. 2008, 2016; Salomón et al. 2015; PAHO 2016).

Risk factors such as deforestation, modification of the land usage, climate change, and migration have contributed to this growth due to greater humans–vectors–reservoirs contact (Maia-Elkhoury et al. 2016). Different reports from Argentina, Bolivia, Brazil, Colombia, Mexico, Costa Rica, and Peru have shown a relationship between the occurrence of cutaneous leishmaniasis and environmental alterations due to climate change, deforestation, and economic activities, including agriculture (Davies et al. 2000; Cardenas et al. 2006, 2008; Chaves and Pascual 2006; Valderrama-Ardila et al. 2010; Gottwalt 2013).

Box 5 Foot-and-Mouth Disease

Central America is free from the disease—in fact, it is considered historically free—while in the South American countries the disease is heading to its eradication (Clavijo et al. 2017). In this subregion, FMD virus infection has been caused by viral types O, A, and C, which reached a wide distribution during the first half of the twentieth century. While it was recognized that bovines are responsible for the presentation of the main patterns of the diseases, it was suspected that wild animals could have also played a role in the persistence of the virus in the field during the interepidemic periods (Rosenberg and Gomes 1977). An FMD outbreak in Colombia in 1976, where type A virus was isolated from a capybara (*Hydrochoerus hydrochoeris*) presenting clinical lesions and living with pigs and cattle (Brasileira and Agropecuária) brought the attention to this species due to its abundance in endemic areas and its high degree of ecological competition with the bovine species (Rosenberg and Gomes 1977). The susceptibility of the species to FMDV infection has been confirmed both by intramuscular route and by direct contact. It has been also proved that capybaras inoculated with the virus could transmit the infection to cattle and pigs by direct contact, which was evidenced by both the appearance of clinical signs together with virus

(continued)

Box 5 (continued)

isolation and antibody production. But even though it has been postulated that this rodent could contribute to the spread of the infection due to their migratory habits, it would not act as natural reservoirs (Gomes and Rosenberg 1984).

There is little information on the epidemiology of FMD in South American camelids from field research. In only one report, mild clinical signs were observed in alpacas (*Vicugna pacos*) in connection with an outbreak occurring in cattle (Wernery and Kaaden 2004). Experimental studies in llamas (*Lama glama*) and alpacas indicate that they can be infected by direct contact, but in general, they are not susceptible animals and do not represent a risk to transmit the infection. Likewise, their carrier status has not been verified in South American camelids (Wernery and Kaaden 2004). Serological studies have been carried out on Mexican deer (*Blastocerus dichotomus*), free-ranging vicunas (*Vicugna vicugna*) in Argentina and Bolivia (Marcoppido et al. 2010; Beltrán-Saavedra et al. 2011), gray brocket deer (*Mazama gouazoubira*) in Bolivia (Deem et al. 2004), in pampas deer (*Ozotoceros bezoarticus sceler*) in Argentina (Uhart et al. 2003), and guanacos (*Lama guanicoe*) in Argentina (Karesh et al. 1998) with no evidence of FMDV infection.

Beyond the valuable experimental work that has been done to evidence FMD infection in wild species, the literature does not clearly distinguish between evidence of infection and the ability to maintain infection at the population level, i.e., it might persist and be transmitted to other species (Weaver et al. 2013). Despite many speculations about the possible role of wild animals as reservoirs of FMD in South America, to date, there is no robust evidence to support such a hypothesis. Moreover, the fact that no outbreaks have been linked to transmission of the infection by wild animals also stands against that theory. In addition, in South America, systematic vaccination of the bovine species, leaving goats, sheep, and pigs as sentinels, has succeeded in eradicating the disease in most of the subcontinent (Sutmoller et al. 2003; Clavijo et al. 2017). This situation contributes to confirm that in those regions where the reservoir of FMD virus has been domestic animals, the disease eradication from them has usually led also to the disappearance of the infection of wild animals (Thomson et al. 2003).

Box 6 Brucellosis and Bovine tuberculosis

Brucellosis and bovine tuberculosis are present in the livestock population of most of the countries in South and Central America (WAHIS-OIE 2018); and the implementation of successful control/eradication strategies for these diseases are of the utmost importance to this Region, following the examples from others such as North America and Europe. The presence of these two infectious diseases is closely linked to underprivileged socioeconomic factors, being among the diseases with the greatest impact in low-income populations (Perry et al. 2002), and both are regarded as neglected human diseases according to the World Health Organization. Besides the impact on public health, they cause major economic losses in the livestock sector. It was estimated that yearly losses related to bovine brucellosis in Central America could reach up to US\$25 million; while in South America, only in Brazil, the losses could be in the range of US\$250 million (Moreno 2002; Santos et al. 2013). Although there is a lack of published data about specific losses due to bovine tuberculosis in this Region, the reported global annual losses of US 3 billion can help provide an idea of the current economic importance of this disease in the Region (Garnier et al. 2003).

In other regions, wild mammal species are known to act as reservoirs of *Brucella* and *M. bovis*, playing an important role in their dissemination and maintenance (Muñoz et al. 2010; Palmer 2013; Van Campen and Rhyan 2010). In Central and South America, although some studies reported several terrestrial wild mammal species naturally exposed or infected by *Brucella* spp. and *M. bovis* (Tables 3 and 4), there is a lack of information regarding their epidemiological role. Thus, considering that *Brucella* spp. and *M. bovis* are found in livestock and wild animals in Central and South America and that the expansion of cattle ranching over wildlife natural habitats increases the chances of contact and mutual disease transmission (Bengis et al. 2002), there is a crucial need to understand the wildlife-livestock interface for these diseases in this Region. On one hand, there is a need to clarify the impact of these diseases on native wildlife species. While on the other hand, the fact that wild species are known as reservoirs of these etiological agents in other regions reflects the need to clarify the epidemiological link between wildlife and livestock in this Region, particularly to determine if wild animals constitute reservoirs able to maintain and transmit *Brucella* spp. and *M. bovis* back to adjacent domestic animal populations (Van Campen and Rhyan 2010).

Table 3 Terrestrial wild mammal species with evidence of past/present naturally infection by *Brucella* spp. in Central and South America

Mammal species	Country	<i>Brucella</i> species	Diagnostic test	Number of seropositive animals/ number of animals tested	References
Common opossum (<i>Didelphis marsupialis</i>)	Argentina	<i>B. abortus</i> and <i>B. suis</i> (biovar 1)	Isolation		Lucero et al. (2008)
Culpeo fox (<i>Pseudolapex culpaeus</i>)	Argentina	<i>Brucella</i> sp.	ELISA	8/28 (28%)	Martino et al. (2004)
Ferret (<i>Mustela putorius</i>)	Argentina	<i>B. abortus</i>	Isolation		Lucero et al. (2008)
Large hairy armadillo (<i>Chaetophractus villosus</i>)	Argentina	<i>B. suis</i> (biovar1)	BPAT, SAT, 2ME, CFT, isolation	24/150 (16%)	Kin et al. (2014)
Pampas gray fox (<i>Pseudolapex gymnocercus antiquus</i>)	Argentina	<i>B. abortus</i>	PAT, STAT, CFT, FPA, 2 ME isolation	104/410 (25.4%) 6/41 (14.6%)	Fuchs et al. (2009), Lucero et al. (2008), Szyfres and González Tomé (1966)
Patagonian gray fox (<i>Pseudolapex griseus</i>)	Argentina	<i>B. abortus</i>	PAT, STAT	69/318 (21.7%)	Szyfres and González Tomé (1966)
South American gray fox (<i>Pseudolapex griseus</i>)	Argentina	<i>Brucella</i> sp.	ELISA	7/56 (12.5%)	Martino et al. (2004)
Crab-eating fox (<i>Cerdocyonthous</i>)	Brazil	<i>Brucella</i> sp.	RBT and FPA	5/38 (13.1%)	Dorneles et al. (2014)
Crab-eating raccoon (<i>Procyon cancrivorus</i>)	Brazil	<i>B. abortus</i>	RBT and CFT	4/8 (50%)	Oliveira-Filho et al. (2012)
White-eared opossum (<i>D. albiventris</i>)	Brazil	<i>Brucella</i> sp.	RBT	3/50 (6%)	Antunes et al. (2010)

(continued)

Table 3 (continued)

Mammal species	Country	<i>Brucella</i> species	Diagnostic test	Number of seropositive animals/ number of animals tested	References
Giant anteater (<i>Myrmecophaga tridactyla</i>)	Brazil	<i>B. abortus</i>	BPAT	1/21 (4.8%)	Miranda et al. (2015)
Greater grison (<i>Galictis vittata</i>)	Brazil	<i>B. abortus</i>	RBT and CFT	2/2 (100%)	Oliveira-Filho et al. (2012)
Hoary fox (<i>Pseudalopex vetulus</i>)	Brazil	<i>B. abortus</i>	BPAT, 2 ME RBT RBT, CFT	4/60 (6.7%) 1/2 (50%) 1/3 (33.3%)	Antunes et al. (2010), de Azevedo et al. (2010), Oliveira-Filho et al. (2012)
Pampas deer (<i>Ozotoceros bezoarticus</i>)	Brazil	<i>Brucella</i> sp.	Blood PCR	9/44 (20.4%)	Elisei et al. (2010)
South American coati (<i>Nasua nasua</i>)	Brazil	<i>Brucella</i> sp.	RBT and FPA	3/34 (8.8%)	Dorneles et al. (2014)
Lesser anteater (<i>Tamandua tetradactyla</i>)	Brazil	<i>Brucella</i> sp.	RBT	1/1 (100%)	Antunes et al. (2010)
Lion (<i>Panthera leo</i>)	Brazil	<i>Brucella</i> sp.	RBT	1/2 (50%)	Antunes et al. (2010)
Lowland paca (<i>Cuniculus paca</i>)	Brazil	<i>Brucella</i> sp.	RBT	2/8 (25%)	Antunes et al. (2010)
Maned wolf (<i>Chrysocyon brachyurus</i>)	Brazil	<i>Brucella</i> sp.	RBT	1/6 (16.7%)	Antunes et al. (2010)
Tayra (<i>Eira Barbara</i>)	Brazil	<i>B. abortus</i>	RBT and CFT	1/5 (20%)	Oliveira-Filho et al. (2012)
Capybara (<i>Hydrochaeris hydrochaeris</i>)	Venezuela	<i>B. abortus</i> and <i>B. suis</i> (biovars 2 and 3)	CT, STAT, 2ME, Riv isolation	117/201 (58.2%)	Lord and Ricardo (1983), Lucero et al. (2008)

(continued)

Table 3 (continued)

Mammal species	Country	<i>Brucella</i> species	Diagnostic test	Number of seropositive animals/ number of animals tested	References
Collared peccary (<i>Tayassu tajacu</i>)	Venezuela	<i>B. suis</i> (biovar1)	STAT, 2ME, CFT, CT, Riv and isolation	69/139 (49.6%)	Lord and Lord (1991)

PAT Buffered plate antigen test, *CT* Card test, *CFT* Complement fixation test, *ELISA* Enzyme-linked immunosorbent assay, *FPA* Fluorescence polarization assay, *PAT* Plate agglutination test, *PCR* Polymerase chain reaction, *RBT* Rose Bengal test, *Riv* Rivanol test, *SAT* Serum agglutination test, *STAT* Standard tube agglutination test, *2ME* 2-mercaptoethanol

Table 4 Terrestrial wild mammal species with evidence of naturally infection by *Mycobacterium bovis* in Central and South America

Mammal species	Country	References
Brown rat (<i>Rattus norvegicus</i>)	Argentina	Abdala et al. (2015)
Pampas fox (<i>Pseudolapex gymnocercus</i>)	Argentina	Abdala et al. (2015)
White-eared-opossum (<i>Didelphis albiventris</i>)	Argentina	Abdala et al. (2015)
Coatis (<i>Nasua nasua</i>)	Brazil	Murakami et al. (2012)
Pampas deer (<i>Ozotocerus bezoarticus</i>)	Brazil	Alves and Albertti (2014)
Mandrill (<i>Mandrillus sphinx</i>)	Uruguay	OIE WAHIS (2012)
Wild boar (<i>Sus scrofa</i>)	Uruguay	Lombardi et al. (2015)

Management Practices at the Interface

Depending on the scenario, different approaches are used in the management and control of the diseases at the interface. Some of the strategies are focused on the management of the wildlife population, as it is done for rabies in the bat roosts; for which it is recommended to have a georeferenced registry. Among the interventions implemented in the roosts, the application of anticoagulant paste to decrease the population of *D. rotundus* is a widely used option provided for in the national strategies (Reis et al. 2007; MAPA 2009; Lee et al. 2012). Captured bats are coated with the paste, that when are released and get back to the roosts, will be transferred to others during the social grooming (when bats engage in cleaning one another). There are researches, however, arguing that these strategies aiming at decreasing bats population are not effective (Streicker et al. 2012), besides being regarded as a

poorly humane practice. There exists a potential for ingestion of anticoagulant poisons by other bat species or through contamination of shared roosts, included endangered ones, although *D. rotundus* occupy specific sites within roosts and this may reduce impacts on other bat species (Wohlgenant 1994). As an alternative, other strategies to reduce the damage caused by rabies in livestock are suggested, such as the use of an oral vaccine, which is applied on captured bats and released to other roosts cohabitants in a similar manner that the anticoagulant paste (Lee et al. 2012). This alternative, however, still requires further investigations due to its unknown effectiveness as a control measure in the Region.

Other strategies for control should be based on areas at risk. Thus, in the control of rabies in herbivores, once the risk areas are defined, it is necessary to optimize the use of resources and reduce costs to ensure complete vaccination coverage. Another fundamental action for a control program is the educational campaigns to establish activities of health education to the population, using materials with images, such as posters and educational books for children, bringing information about the specific area in native languages that allow efficient sensitization of the population at risk (da Costa and Fernandes 2016). In addition, it is important to take on board a multidisciplinary strategy, involving all relevant stakeholders, in the prevention and control of disease at the interface. In fact, official programs start to recognize that an engagement with animal rights organizations by bringing them to the discussion table at the planning stages against rabies can deliver niche-specific approaches to local problems (Del Rio Vilas et al. 2017). The prevention and control of bat-transmitted rabies should involve health and agriculture with environment, education, housing, and infrastructure sectors from each country (Schneider et al. 2009).

Another essential component in the management of the diseases at the interface involves strengthening laboratory capacity for diagnosis to support the epidemiological surveillance. This is particularly important for arboviruses, and countries should prioritize the implementation of new diagnostic techniques for EEE, VEE, WEE, and WNO, ensure a continuous supply of essential inputs for the diagnosis, and provide the necessary laboratory equipment to ensure that both diagnosis and communication of results are timely (ICA-INS-MAVDT 2004; OIRSA and PAHO 2014). The measures for the prevention and control of these arboviruses should include training plans for health professionals, health promotion and education programs, quality control of vaccines, followup and evaluation of vaccination activities, timely attention to outbreaks, movement control of susceptible domestic animals, research, vector control, and community participation (Mesa et al. 2005).

Systems for enhancing surveillance such as target or risk-based strategies should be utilized to increase the sensitivity and timely detection of disease at the wildlife-livestock interface. These enhanced strategies should indeed be applied to diseases such as avian influenza, for which the regional epidemiological surveillance targeting wildlife is weak; and it would require extensive and constant efforts focused on local and migratory wild birds (Hurtado et al. 2016; Afanador-Villamizar et al. 2017). Furthermore, surveillance strategies for avian influenza need to be adapted to target the wildlife-poultry interface, focused on subpopulations at greater

risk, such as backyard poultry units or farms with poor biosecurity near wetlands with the presence of aquatic wild birds and/or on the route of migratory birds. For the arboviruses, it is important, as well, to conduct risk characterization and monitoring (through entomological studies, detection of wild bird mortality, detection of viral circulation in wild reservoirs and sentinels, ecological and environmental characterization). These elements provide information to alert agriculture and health authorities in order to timely establish methods to prevent and control equine encephalitis in the region (OIRSA and PAHO 2014).

Research of Diseases at the Wildlife-Livestock Interface

For a region that comprises a high percentage of the wildlife diversity of the Earth, it actually produces substantially less scientific knowledge on wildlife diseases than others, and therefore only a little—occasionally nothing—is known of endemic wild animal species (Wiethoelter et al. 2015). The lack of systematic research on baseline wildlife diseases in this Region hampers the comparisons with other regions of the world like North America, Europe, or Africa. As presented here, there are some descriptive data of diseases of importance in the livestock-wildlife interface, with some public health implications.

The greatest need comes from the lack of systematic studies that allow responding to basic occurrence, prevalence studies, identification of hosts and determination of their role, disease dynamics and spread, short-term and long-term studies, address of entire host communities, disease monitoring in natural populations, need for new and validated diagnostic techniques.

Likewise, knowledge on socioeconomic aspects contributes to inform the decision-making process about control strategies. Some data are already available for rabies in herbivores; indeed it has become apparent that, since the initiation of bat control methods and vaccines for cattle in the Region, the number of reported cattle deaths due to rabies declined from 500,000 in 1968 (Arellano-Sota and Arellano-Sota 1988) to 9904 in 1983 and 1580 in 2006 (Lee et al. 2012). However, there is still a need to add more knowledge about the socioeconomic factors of rabies aerial cycle occurrence, maintenance, and evolution; in order to establish more effective measures for its control in the endemic regions (Kotait et al. 2009). For other important livestock diseases, such as brucellosis and bovine tuberculosis, it is still essential to elucidate the epidemiological role of wildlife to define efficient control strategies or even to move into their eradication.

Apart from those diseases mentioned here, there are still other livestock diseases to be added to the “wish list” for more structured research on the interface livestock-wildlife: e.g., bluetongue, classical swine fever, Tick-borne diseases (such as bovine anaplasmosis and babesiosis), Aujeszky’s disease, Q fever, *Pasteurella* spp., Newcastle disease, or disease such as canine distemper virus, feline leukemia virus, feline parvovirus, toxoplasmosis. Besides, more studies will be needed to confirm these implications for species with a high probability of population decline and extinction

by infectious diseases at the interface as a cause such as Darwin's fox (*Pseudolapex fulvipes*), huemul (*Hippocamelus bisulcus*), maned wolf (*Chrysocyon brachyurus*), chacoan peccary (*Catagonus wagneri*), pudu (*Pudu puda*), and marsh deer (*Blastocercus dichotomus*).

Other regional outstanding topics comprise the possible role of wild exotic species introduced in the dynamics of pathogens (e.g., red deer, wild boar, fallow deer), and the impact of wild species released from rescue centers (or those seizures of wildlife trafficked illegally or in private hands) in the spreading of pathogens or in the environmental contamination with antibiotics. Finally, another line of applied research should be focused on evaluating the detection of zoonotic infectious agents in bushmeat.

Conclusion and Perspectives

Unfortunately, there is a relevant knowledge gap on the importance of infectious diseases at the wildlife-livestock interface for Central/South American countries, where on balance there are more questions than answers. This increasing recognition of the importance of wildlife in the dynamic of emerging infectious diseases is becoming a big challenge for the countries in the Central and South American regions. There is a lack of adequate scientific information that responds to the regional scenario (Wiethoelter et al. 2015; Olival et al. 2017), which urges the need for more epidemiological studies in wildlife (e.g., reservoirs, occurrence, risk factors) to clarify its role in the transmission dynamics of diseases of economic importance. Probably, many pathogens and hosts have not been listed here because there is not data/research about them. Without this information, a further understanding and management of the system under a One Health perspective is not possible.

A hard topic addressed in this chapter is the impact of deforestation on the wildlife-livestock interface, since it creates favorable conditions for some vectors and allows the displacement and adaptation of others to new environments (Molyneux 2003; FAO 2012; Gottwalt 2013). This land transformation problem and its consequences need to be monitored, and structural national and Regional solutions, based on regulatory policies, should be implemented. In addition, over the last few years, there has been a global awareness of the need to discuss and define strategies to minimize the impacts of social, environmental, and economic changes on the health of the population. Nevertheless, this scenario is still limited by the uncertainties and scarcity of sustainable projects, as well as specific tools to support decision-makers in defining effective interventions to reduce health risks and control vector-borne diseases.

Undoubtedly, bat-transmitted rabies will remain for a while on the table as a top health problem at the wildlife-livestock interface. Certainly, the eradication of the disease is not an achievable target due to its epidemiology; however, it urges consensus among the different stakeholders on the control strategies to be

implemented. Another relevant disease at the interface to be monitored in the near future is avian influenza. HPAI is present worldwide and has been reported several times recently in North America, so the Region needs to remain vigilant as the disease could be spread southward via continental bird migrations. Likewise, it is important to monitor the occurrence and distribution of LPAI, in both poultry and wildlife populations, as the virus can be transboundary spread through wild birds and has the capacity to evolve to highly pathogenic forms (Suarez et al. 2004; Spackman et al. 2006; Hurtado et al. 2016).

It is highly recommended to implement comprehensive programs involving integrated surveillance and other strategies for enhancing surveillance, that could contribute to detect the presence of different pathogens either of the livestock population or among wildlife. The revision of the surveillance strategies needs to be accompanied by the strengthening of the laboratory diagnosis capacities, particularly on arboviruses. Likewise, biosecurity policies in farming need to be revised and strengthened. Both, official services and the private sector must take a more proactive role to keep away, insofar as possible, some of the diseases mentioned in this chapter (e.g., avian influenza, bovine TB, and brucellosis).

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Part III
Characterization of the Wildlife-Livestock
Interface

Collecting Data to Assess the Interactions Between Livestock and Wildlife



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Introduction

The study of interactions among species or conspecifics has aroused interest in epidemiology as an approach by which to detect effective contacts involving pathogen transmission within communities of hosts. In the last few decades, anthropogenic expansion has led to an increase in the risk of transmission of pathogens both within the wildlife reservoir and between wildlife and livestock, thus originating conservation and socioeconomic conflicts (e.g. Gortázar et al. 2007, 2010). In this changing world, the wildlife-livestock interface defines where the interaction between free-ranging wildlife and livestock (under specific livestock husbandry practices) takes place. In this context, the development of methodologies used to characterise the risk of pathogen transmission at this interface has become crucial.

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By epidemiological interaction, we mean an event during which different species/individuals/populations/environment come directly/indirectly into contact with one another with the potential to transmit pathogens. One single interaction is a contact (one-time or continuous) that can be identified in the predefined spatio-temporal context, which may be direct (i.e. close or even physical contact) or indirect (i.e. mediated by the environment through the asynchronous use of resources or mediated by vectors). The interaction among the elements in a given system may normally involve several means of interaction at once. The simultaneous use of water points may, for example, concomitantly operates with vector-borne and environmental indirect transmission. Intensity may also vary among interactions since, for example, it is not the same for one cow to interact with a single buffalo at a distance of 5 m as it is for five buffalos to interact with one cow at a distance of 1 m. The specific definition of interaction and the selected properties under study are, therefore, different in each work and are malleable to specific scenarios and objectives. The approaches that are able to quantify real interactions (i.e. one individual close to another, or close to a commonly used resource) are always more precise than those that employ proxies (i.e. the presence of tracks of different species at a particular resource). The concept of interaction is relevant per se but is more informative if the risk of disease transmission can be associated with it on the basis of empirical knowledge. For example, relevant parameters are the survival period for specific pathogens in specific environments, the mode(s) of transmission of the pathogen, the probability of specific types of interactions involving an infected host (or vector) leading to transmission, or the rates of infection of hosts, vectors, level of infectivity, and the presence/abundance of propagules in the environment.

The study of epidemiological interactions has been a relevant topic in applied sciences for many years (e.g. Noonan et al. 1975). However, interactions are multiple and complex, and many of the approaches employed to monitor animal interactions with a potential risk of pathogen transmission have, therefore, been developed and adapted from other fields, mainly in the last two decades. In order to describe the research trends, and particularly the relevance of the different methods applied to the study of interactions at the wildlife-livestock interface, on 7 December 2018 we performed a bibliometric analysis. This was done by entering the search code “(interaction OR contact) AND (wildlife OR livestock) AND interface” in the web database Scopus (<https://www.scopus.com/search/form.uri?display=basic>). The results were filtered to the fields of “Agricultural and biological sciences”, “Veterinary”, and “Environmental sciences”. After the search had taken place, we selected only those references that addressed the study of epidemiological interactions among species or individuals at the wildlife-livestock interface ($n = 43$). We then extracted the methodologies employed, the species studied, and the countries in which the studies were carried out from the papers selected.

The result of this analysis (Fig. 1) showed that the methodology most frequently used to study the interactions between species at the wildlife-livestock interface is epidemiological sampling, which includes the study of the community of shared pathogens, molecular epidemiology, and the analysis of risk factors associated with infections (see the following section for more details). Questionnaires have also been



Fig. 1 Word cloud of the main methodologies (in red), taxa (in black) and regions (in blue) for which studies on interactions have been performed. See text for further details

widely used for this purpose, followed by camera traps and global positioning system (GPS) technology. The regions in which most studies regarding interactions have been developed are African countries, North America and, to a lesser extent, Europe. Finally, the analyses showed that the taxa that have most attracted researchers' attention in this respect are cattle and wild ungulate species.

This simple bibliometric study allows us to provisionally conclude that most of the methods employed to study the interactions at the wildlife-livestock interface are adapted to range, pasture, and farmlands occupied by domestic livestock and wild ungulates. A detailed analysis of the different approaches that can be used to assess interactions is provided as follows.

Methodologies Used to Collect Data on Interactions at the Wildlife-Livestock Interface

We have classified the multiple methods used to collect data on interactions at the wildlife-livestock interface according to their capability to quantify or simply detect potential interactions (non-quantitative approaches) among species or individuals. The objective of quantifying direct and indirect interactions is to obtain the number of interactions per unit of time. As the precision of methods is normally not perfect, any attempt to quantify the total number of interactions is, in practice, an index or a proxy. Non-quantitative approaches provide a potential for interactions (i.e. the existence of favourable circumstances or evidence that can lead to interactions). Figure 2 illustrates that quantitative methods include focal studies for the direct observations of interactions, along with the use of camera traps and proximity loggers. Non-quantitative methods include animal detection through the use of linear transects and epidemiological sampling (the study of the community of pathogens,

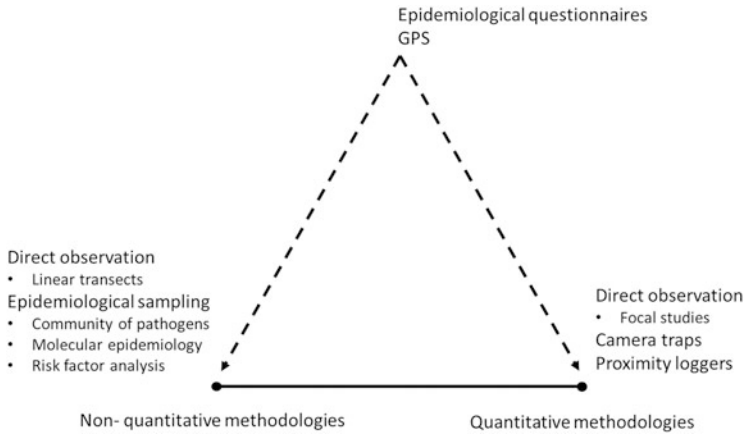


Fig. 2 Classification of methodologies used to assess the interaction between wildlife and livestock according to their capacity to quantify or detect potential for interactions

molecular epidemiology, and the analysis of risk factors). The approaches that employ technology based on the use of GPS to track individuals (and also the classical VHF telemetry) and epidemiological questionnaires can be considered as quantitative or non-quantitative, depending on the study design.

Direct Observation

Figure 3 illustrates different methodologies and procedures to define interactions. The first approach used to infer direct and indirect interactions at the wildlife-livestock interface was the direct observation of animals, by either observing the intra- and interspecific interactions (focal studies) (e.g. Richomme et al. 2006) or locating animals along transects and subsequently inferring interactions through the analysis of their occupancy patterns (e.g. Focardi et al. 2006). Both approaches have their specific *pros* and *cons*; however, one common constraint is the temporal nature of sampling. Daily and seasonal variations in species' behaviour and/or detectability require that sampling be synchronised during periods of higher detectability (e.g. Léna 2002). The study of indirect interactions among species with non-overlapping activity rhythms implies that the sampling effort should be extended to include the target species' peak of detectability. Species detectability is limited by numerous external factors, such as habitat and season (e.g. the peak of detectability of mountain ungulates in summer pastures). The behaviour of populations and individuals is determined by factors such as the health status of animals or the breeding period (e.g. Kéry and Schmidt 2008; Lachish and Murray 2018). Finally, the detection and identification of individuals is normally imperfect,

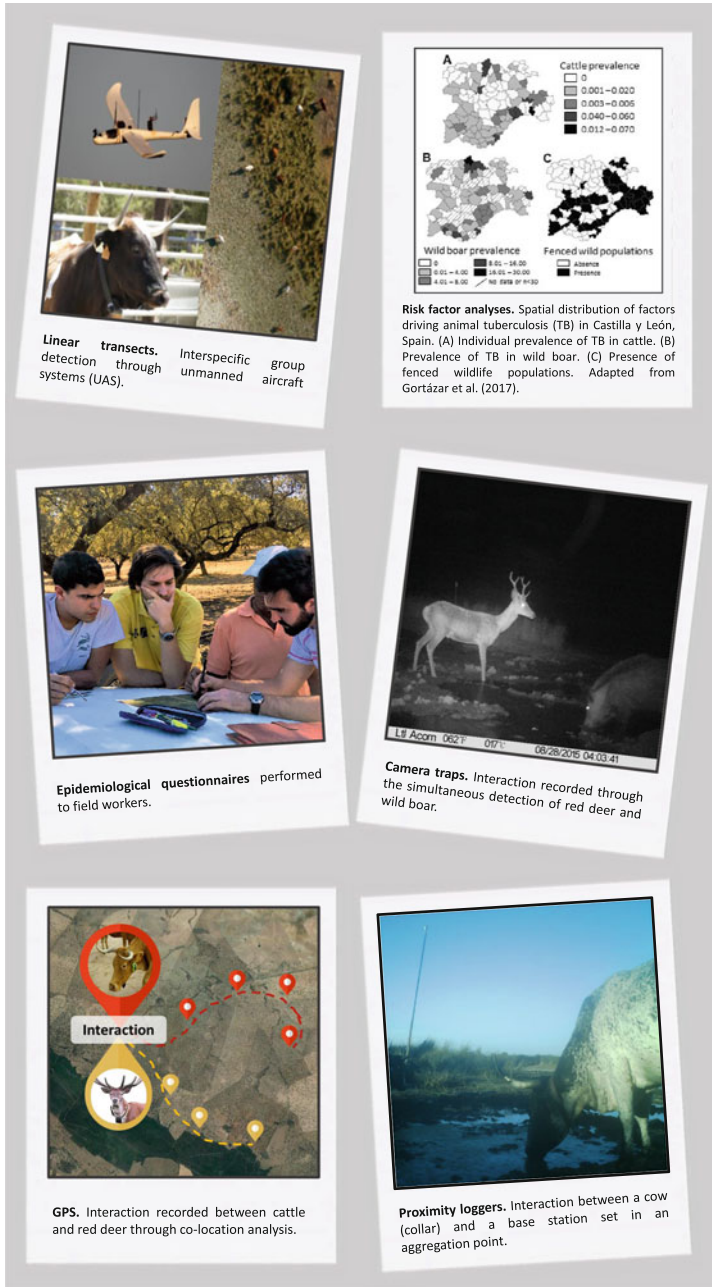


Fig. 3 Illustration of different methodologies and procedures to define interactions

even when marked if marks are temporal or are not identifiable at resights (e.g. resights by camera traps, and/or at large distances from observers).

Focal Studies

The direct observation of interactions has been employed not only to quantify interactions between individuals (Day et al. 2000; Richomme et al. 2006) but also to validate the information collected by other approaches, e.g. proximity loggers (Walrath et al. 2011; Drewe et al. 2012) (Table 1). Focal studies based on direct observation is a method that is applicable only in the case of highly detectable species that inhabit open lands (van der Jeugd and Prins 2000) during appropriate seasons (e.g. alpine areas, migratory species), animals captured and held in captivity (Walrath et al. 2011), or species with activity patterns concentrated towards attraction points during certain periods of the season and/or day (Grenier et al. 1999; Totton et al. 2002). All these aspects, which are specific to the species and study site, must be accounted for when designing a study. This method is often not feasible owing to the difficulty involved in visually following animals for a sufficient amount of time and without impacting their behaviours. Behavioural observations are also expensive in terms of people/time, and even then, not all animals are observed simultaneously.

The definition of interaction in focal studies, along with that of the sampling design, depends on the specific aims of each study and the peculiarities of the system being studied (Fig. 2). Several studies have identified recognisable individuals and quantified the number of interactions among them by marking them through the use of ear tags or coloured collars (Totton et al. 2002). However, most studies rely on unmarked animals, signifying that only descriptions of interaction rates can be

Table 1 Examples of focal studies registering direct interactions between wildlife and livestock. Target species, spatial window between interacting individuals and aim of the study are shown

Species	Spatial window	Aim of the study	Reference
White-tailed deer (<i>Odocoileus virginianus</i>)	Five body lengths	Study of aggressive interactions between conspecifics around feeding points	Grenier et al. (1999)
White-tailed deer	1 m	Validation of proximity logger performance	Walrath et al. (2011)
Cattle	One cattle head's width between cows (1.7 m approx.)	Validation of proximity logger performance	Drewe et al. (2012)
Racoon (<i>Procyon lotor</i>)	Bites between individuals	Transmission of rabies between conspecifics and between raccoons and other mammals	Totton et al. (2002)
Wild and domestic ungulates	20 m	Transmission of <i>Mannheimia haemolytica</i> (agent of pasteurellosis) between domestic and wild ungulates	Richomme et al. (2006)

produced (e.g. Richomme et al. 2006). Observations are carried out from natural or built strategic points from which observers monitor the largest possible area, with the goal of minimal disturbance to the animals' normal behaviour. Most of these studies have quantified direct interactions, defined as the simultaneous presence of individuals within a given area of a few metres. Indirect interactions can also be quantified as the presence of an individual of a certain species in an area in which another has grazed within the temporary survival period of the pathogen being studied. For instance, Richomme et al. (2006) studied interspecific interactions between livestock (sheep and cattle) and wild ungulates (*Rupicapra rupicapra* and *Capra ibex*) in alpine pastures as a risk of the direct transmission of pasteurellosis and the indirect transmission of brucellosis. Regardless of the type of interaction, focal studies make it possible to record the date, time, species involved, group size, and the beginning and end of each interaction (e.g. White and Harris 1994; Richomme et al. 2006; Drewe et al. 2012).

Although focal surveys are useful as a first approximation by which to infer interaction rates, there are multiples sources of bias. The study of interactions in nocturnal species has been carried out within enclosures with sufficient light to allow the observation of individuals, but this could be questionable since artificial light can alter individuals' behaviour (but see Day et al. 2000). As such, the direct observation of animals is usually limited to species with diurnal behaviours, but recent advances in thermal imaging could facilitate monitoring nocturnal species (Lavers et al. 2005). What is more, the representativeness obtained with focal surveys may be limited, since they usually include a reduced number of study points (e.g. 10 observation units in Richomme et al. 2006) or relatively small study areas. This entails an extensive sampling effort in order to extend the study area, which supposes a real constraint of the method when the aim of the study is to gather representative information for large territories.

Linear Transects

Data concerning an individuals' location on a transect can be obtained using various field procedures. The most common are the traditional linear transects, which are carried out both by walking or by using a vehicle (Eberhardt 1968; Anderson et al. 1979) and, more recently, by using new technologies such as unmanned aircraft systems (UAS) (e.g. González et al. 2016).

Data obtained from linear transects can be used to study the abundance/density, distribution, and/or individuals' aggregation patterns within the population, which are useful when attempting to infer potential interaction rates. For instance, potential interaction rates can be inferred through the study of similarities in habitat use in sympatric species, the overlapping of abundance/density distribution patterns, and the potential for intra- and interspecific aggregation (e.g. Focardi et al. 2006; Barasona et al. 2014a; Laguna et al. 2018), which can subsequently be used to create transmission networks (Vanderwaal et al. 2014). The interactions described by this kind of data are, therefore, mostly based on only the potential for interaction,

and it is not possible to quantify the number of (intra- or interspecific) interactions (but see Laguna et al. 2018). However, it is possible to calculate a relative degree of association (e.g. the percentage of observations of two species/individuals within a given distance relative to the total number of times those species/individuals have been observed together or apart, Vanderwaal et al. 2014). Moreover, linear transects usually produce a static picture of how the animals are distributed, and this could, therefore, imply a temporal bias that should be handled by carrying out multiple replicates at various times and under diverse conditions in order to attain a more complete description of the potential for interactions.

Linear transects are focused on obtaining information regarding time, habitat structure, species, number and group structure (number of individuals per sex and age class, if possible), individual recognition (for marked or identifiable individuals), and the geographical coordinates for each sighting. The geographic component of the observation is the most important when carrying out studies on species interactions by studying similarities in individuals' spatial patterns. Coordinates are not always directly measured in the field and can be calculated from the precise location of the observer on the transect and the distance and angle (measured using digital telemeters) between the animal and the observer (Focardi et al. 2006; Acevedo et al. 2008). Fortunately, technology is advancing and there are now telemeters that are capable of simultaneously providing the distance, the angle, and the precise coordinates of the detected animals (Lämås 2010).

The ability to perform autonomous flights and the incorporation of georeferencing sensors have made the UAS a powerful tool for wildlife monitoring and for studying biological processes over large areas (Barasona et al. 2014a; González et al. 2016). The incorporation of on-board high-resolution cameras has made it possible to obtain high-quality georeferenced images of animals with minimal disturbance (Vermeulen et al. 2013; Mulero-Pázmány et al. 2014; Christie et al. 2016). Initially, UAS provided an acceptable alternative to on-the-ground surveys, however, were limited to linear transects in open areas with easily recognisable species. More recently, the incorporation of multispectral sensors and thermal imagery has significantly improved the detection of cryptic species and those with nocturnal activity or inhabiting forested areas (González et al. 2016). UAS are, therefore, a feasible tool for spatial ecology in general (e.g. Anderson and Gaston 2013), with a strong potential for the study of wildlife and livestock (e.g. Fornace et al. 2014).

Epidemiological Sampling

The need for understanding of transmission routes of pathogens, the actors involved, and causative variables of transmission has led to the development of epidemiological studies on various spatio-temporal scales. On a broader scale, the study of the community of pathogens among potential hosts can provide information concerning the actors involved in transmission pathways (Abu Samra et al. 2013). Spatial

epidemiological studies have inferred interactions from correlations of health and population status between wild and domestic species (Humblet et al. 2010; Martínez-López et al. 2014). Finally, on the finest scale, interactions can be studied through the molecular characterisation of pathogens shared by multiple individuals (Aranaz et al. 2004).

Community of Pathogens

Multiple pathogens can be shared between livestock and wildlife (Cleaveland et al. 2001; Gortázar et al. 2007). In recent years, there has been a growing concern about these shared infections, mostly because they are oftentimes zoonotic and cause significant economic losses (e.g. Ruiz-Fons 2017).

The appearance of certain pathogens in individuals within a community of host species suggests the existence of direct or indirect interactions between infected and susceptible species. It is, therefore, possible to describe the occurrence of interactions between species that share the same pathogen or community of pathogens. There are many studies on interspecific interactions based on this approach. For instance, Abu Samra et al. (2013) found one African buffalo (*Syncerus caffer*) infected with *Cryptosporidium bovis*, a parasite that typically infects cattle, thus suggesting that the buffalo and cattle were interacting. A similar study was the discovery of the *Eucoleus contortus* nematode in little bustard (*Tetrax tetrax*) when the same parasite was found concurrently in red-legged partridges (*Alectoris rufa*) from a neighbouring hunting estate on which the release of farm partridges had been practiced (Villanúa et al. 2007). This suggested that the released farm-reared partridges were the source of the infection for the wild populations (Villanúa et al. 2008). Overall, these descriptive studies provide relevant information that can be used to propose a hypothesis regarding potential epidemiological interacting species that can subsequently be reaffirmed through the use of experimental research (Abu Samra et al. 2013). Most of the interactions between wildlife and livestock described in historical literature were obtained from this type of evidence.

Molecular Epidemiology

As a further step in the study of the pathogen community, molecular epidemiology is a research field that includes information obtained from molecular, cellular, and other biological measures in order to identify the determinants of diseases and their role during transmission (Schulte and Perera 1998; Boffetta 2000). Molecular epidemiology elucidates the route of transmission of a particular pathogen between different individuals/species, and this approach has allowed the identification of hybridisation patterns in pathogens such as the bacteria of the *Mycobacterium tuberculosis* complex (Kamerbeek et al. 1997).

Genotyping, the characterisation of the genome of a particular species or strain through the analysis of the DNA sequences, allows the inference of interspecific

interactions by demonstrating that hosts sharing the same geographic area are infected with the same pathogenic strain. Aranaz et al. (2004) described an epidemiological connection between a community of wild ungulates and sympatric domestic animals by identifying the same shared strains of *Mycobacterium bovis*. A similar pattern was observed in Portugal between wild ungulates and livestock herds (Cunha et al. 2012), and in other areas with a relevant community of *M. bovis* hosts (e.g. Gortázar et al. 2011). Although genotyping can reveal an epidemiological connection between different species, it does not identify the origin of the infection, and therefore, the directionality of the transmission (Aranaz et al. 2004). However, this approach can be useful as regards creating transmission networks and identify species of concern for management action (Vanderwaal et al. 2014). Recent advances in genotyping have demonstrated the value and possibilities of employing molecular epidemiology to assess interactions and pathogen transmission (e.g. Crispell et al. 2017). In summary, genomic studies should be conducted in parallel with detailed interaction studies in order to define which interactions are meaningful for transmission.

Risk Factor Analyses

The study of pathogen transmission between wildlife and livestock has, along with disease dynamics, been based on risk factor analyses, that is, on identifying those factors associated with the transmission of diseases at the interface, including the presence, population size, density, aggregation, and health status of potential wild host species. The relationships between these demographic parameters and the prevalence rates in livestock and wildlife have frequently been used to infer interactions between wild and domestic animals. For instance, the incidence of animal tuberculosis (TB) in cattle in Spain has been related to the presence of wild hosts (Rodríguez-Prieto et al. 2012) and, subsequently, to the abundance of wild populations, namely wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) (García-Saenz et al. 2014; Martínez-López et al. 2014). In a more recent study regarding the same epidemiological scenario, the prevalence of TB in cattle was correlated with the prevalence of this disease in wild boar (LaHue et al. 2016), even in those areas in which wildlife was present at low densities (Gortázar et al. 2017). Even without quantitative interaction data or shared habitat use patterns, the correlation of TB rates between domestic and wild hosts on a spatial scale provides indirect evidence of interactions at the wildlife-livestock interface.

Similar to that which was described in the section concerning linear transects, the geographical component of the data is crucial for risk factor analyses. Spatial data make it possible to overlay different data sources, namely livestock data (the farm, county, or other administrative unit referred to), environmental data (usually available in regular grid cells), and wildlife information (related to natural or administrative territorial units), among others. Spatial epidemiology tools increase the possibilities of analyses and the reliability of the results that can be obtained (Pfeiffer et al. 2008).

Epidemiological Questionnaires

Questionnaires and interviews have been employed to obtain qualitative and quantitative information in both ecological and epidemiological studies (e.g. Brannen 2017; White et al. 2005; Brook et al. 2013). These surveys are especially useful for studies in which data is needed for an extensive geographical area (White et al. 2005) or when a preliminary description and delimitation of the interface is required. The information regarding direct and indirect interactions that is gathered in questionnaires is qualitative or semi-quantitative, since it will be limited to interviewees' opinions regarding the frequency with which different types of interactions have been observed (without systematic sampling). A direct interaction is usually defined as the interviewee's simultaneous detection of a domestic and a wild species in the same space and at the same time (Abu Samra et al. 2013; Kukielka et al. 2016), or as an event in which the responder detects physical contact between animals (Dejene et al. 2016). Indirect interactions are defined either as the detection of wildlife and livestock in the same area but not simultaneously, or as the use of a shared resource within a significant timeframe (Kukielka et al. 2016). Other relevant information can be included in the questionnaires, such as the proximity of detected interactions to farm facilities, resources contacted, the species involved and their behaviour during the interaction, season, etc. (Brahmbhatt et al. 2012; Abu Samra et al. 2013; Kukielka et al. 2016; Jori et al. 2017). Even when relevant information can be obtained from questionnaires, a face-to-face interview is sometimes useful to record more precise information about the interaction events (Brannen 2017). Farmers are a valuable resource for information regarding wildlife visitation and interactions with livestock as they are typically present on the farm routinely, at various times of the day, and frequently over long periods of time—even generations, potentially providing otherwise unidentified trends and historical data. Questionnaires, therefore, also allow other aspects of the interaction, such as different stakeholders' perceptions of the problems and solutions, to be studied in greater depth (Brook and McLachlan 2006).

The use of questionnaires also allows quantitative information that is useful for risk factor analyses to be obtained, such as the number of risk points (attraction points for both livestock and wildlife, e.g. water holes in a dry environment), wildlife and livestock management practices, the health status of neighbouring estates and the number of animals hunted, or information relative to historic disease outbreaks. All this information can be collected through thoughtful design of questionnaires, usually on broad spatial scales (Griffin et al. 1993; Cowie et al. 2014; Kukielka et al. 2016).

Overall, questionnaires and interviews have been widely used in Africa to study disease transmission involving cattle. For instance, Brahmbhatt et al. (2012) obtained information from farmers and field rangers that was used to study the wild species most frequently involved in interactions with cattle in relation to the transmission of foot-and-mouth disease. Questionnaires have also been employed in Canada and other parts of the world to study the transmission of pathogens at the

wildlife-livestock interface, both as part of surveys implemented during specific research (e.g. Pruvot et al. 2014; Kukielka et al. 2016) and surveys carried out routinely after the appearance of an outbreak (e.g. Marangon et al. 1998; Guta et al. 2014).

Closed-format questionnaires are less uncertain than open-ended ones. However, open-format questionnaires capture the interviewees' opinions in greater detail (White et al. 2005). The format in which questionnaires are presented varies from a physical sheet format to a mail application, depending on the specifications or special requirements of the different studies. Despite their utility, questionnaires and interviews designed to collect data on interactions benefit from a complementary study using other tools (e.g. GPS, camera traps, proximity loggers) (Griffin et al. 1993; Kukielka et al. 2016). The use of questionnaires in epidemiology has a certain bias inherent to the method that must be realised. First, studies that use questionnaires and interviews as a sampling method need to specify the process in order to provide context and verify the credibility of the data, along with the representativeness of the population being sampled (White et al. 2005). Additionally, the different perceptions collected in questionnaires can lead to a misinterpretation of reality if the opinions collected under or overestimate reality (Jori et al. 2011). Finally, there is a risk of bias if different interviewers conduct the interviews, thus emphasising the importance of standardising procedures (Cowie et al. 2014).

Several recommendations should be taken into account in order to design good questionnaire-based studies (White et al. 2005): the population interviewed must have been randomly selected, a previous test of the survey is recommended so as to detect confusing questions and to minimise the number of non-respondents prior to the distribution of the final survey, and finally, statistically robust results require a sufficient sample of the target population. Bearing these issues in mind, questionnaires and interviews can be used beneficially as a preliminary step when attempting to attain information about the wildlife-livestock interface, which is very valuable as regards formulating hypotheses and designing further field studies.

Camera Traps

Camera traps (CTs) are devices that automatically record images, videos, and/or sound after being triggered remotely by movement or an animal or at predetermined intervals. The capability of CTs to monitor ecological processes in a non-invasive manner has increased the value and use of this technology in wildlife research (Swann et al. 2011), particularly since the appearance of digital cameras (Rovero et al. 2013). As they are inconspicuous in form and function, CTs are widely used to detect elusive species (Sanderson and Trolle 2005) or to study parameters such as the population abundance/density and behaviour of individually recognisable and non-recognisable species (e.g. Rowcliffe et al. 2008; O'Brien 2011). Most CTs are equipped with a passive infrared (IR) sensor that detects the motion of an object that differs in temperature from the background (Rovero et al. 2013). The addition of

video and sound capabilities has allowed the characterisation of the behaviours of the animals recorded (Bridges and Noss 2011), which in the case of interactions, allows us to understand the specific behaviour of animals during the transmission process (Lavelle et al. 2014). When used in their video-mode, CTs can serve as an alternative to video surveillance equipment, which can also be triggered remotely and can include IR sensors (Tolhurst et al. 2009). Moreover, the time-lapse mode in CTs is a useful tool with which to sample both aggregation points (as it allows battery saving) and the temporal activity patterns of target species (Tack et al. 2016). Most importantly, the time-lapse mode enables the collection of comparable data for reliable and robust analyses. For example, CTs, installed similarly at 30 aggregation points, previously programmed to record an image every half hour around the clock will provide a directly comparable index of visitation to those aggregation points. All of these features make CTs non-invasive devices with a high potential to collect data on animal behaviour such as visitation rates, presence/absence, and resource partitioning.

Features that need to be considered during the selection of the appropriate device are the detection zone (i.e. the area in which a CT can detect an individual, which is defined by the radius and detection angle), the trigger speed (i.e. the time that elapses between when an individual is detected by the sensors and the device records a photo/video), the type of flash required for night periods (white or traditional/black infrared) and the sensitivity of the passive sensor (low-medium-high), which will depend on the size of the target species and the aims of the study. Finally, the power supply for CTs can be provided by alternating current or by direct current (batteries alone or batteries supplemented by solar energy), which will have a trade-off with the devices' configuration as regards the number of photos or videos recorded and the recovery time between consecutive events (Swann et al. 2011; Rovero et al. 2013). Further, without supplemental charging with solar panels, the duration of function of the CT is limited by the finite life of the batteries, which could be a concern for long-term studies in remote study locations.

The placement of CTs is also a crucial factor to take into account, depending on the aim of the study. The problem of representativeness and spatial resolution can be minimised by carefully selecting the setting points. With regard to the detection of interactions using this methodology, CTs have traditionally been placed at aggregation points or on tracks frequented by the target species (Kukielka et al. 2013; Sparkes et al. 2016). However, the use of control points or the setting of the devices along an environmental gradient is recommended in order to reduce the spatial bias of these estimates (Triguero-Ocaña et al. 2020).

Although CTs have proven to be a remarkably useful technology for monitoring ecological processes, very few studies have employed them to monitor intra- and interspecific interactions (e.g. Kukielka et al. 2013; Sparkes et al. 2016). The definition of interaction has depended on the purpose of the study and on the characteristics of the target species, including both hosts and pathogens. Both direct and indirect interactions can be recorded using CTs (e.g. Kukielka et al. 2013). As the detection zone is limited in these devices, indirect interactions will depend on the temporality between consecutive events recorded by CTs. Two or more animals are,

therefore, considered to interact directly if they appear in the same photograph. However, an indirect interaction is considered as consecutive visits to a given CT by different individuals within a predefined critical time window. Kukielka et al. (2013) and Sparkes et al. (2016) defined interactions according to a critical time window depending on the characteristics of transmission and the survival of the target pathogen, along with the behaviour of the species monitored. Camera traps have also been included as an additional device together with proximity loggers and GPS, in order to validate the performance of these two last technologies when recording interactions between animals (Lavelle et al. 2014). The results suggested that, when compared with these other technologies, CTs are the only means to adequately describe circumstances in which interactions occur (e.g. scenario or animals' behaviour), which is crucial if effective biosecurity measures are to be applied. Unfortunately, the power requirements of cameras are relatively high, limiting their effective deployment in this type of studies to the life span of their batteries, since battery replacement requires the recapture of animals. Production-model video camera collars are now available and have been incorporated into wildlife research (i.e. Thompson et al. 2012).

Despite their usefulness, CTs are not a perfect method by which to collect data on interactions, since they can fail to detect animals, thus leading to false negatives in the detection of interactions (MacKenzie et al. 2004). The major constraint in their utility is their limited spatial resolution, since CTs have traditionally monitored only the small area in front of the devices (Sparkes et al. 2016). However, the development of new camera traps with a 360° detection angle has improved their field of view, although their detection range is still lower (11–30 m; Meek et al. 2012) than that provided by other monitoring systems, such as proximity technology (up to 400 m; Tambling and Belton 2009). Recent technological advances in CTs have increased their feasibility and precision. Most of these advances are related to the reduction in the time required to process the information obtained from them, which is perceived as one of their current drawbacks when used in large-scale monitoring programmes (e.g. Ivan and Newkirk 2016). Ivan and Newkirk (2016) developed freely available database software that facilitates image organisation, data collection, and analyses enabling multiple observers to process massive numbers of CT images simultaneously. Others developed a computer model incorporating machine learning to classify wildlife species from images, greatly improving the efficiency in processing information from CTs (Tabak et al. 2018). We, therefore, expect that, as is already occurring in other research areas in ecology, CTs will become the key devices as regards monitoring interactions at the wildlife-livestock interface in the relatively near future.

Global Positioning System (GPS)

The GPS has, since the end of the twentieth century, been one of the technologies most widely used to study interactions among wildlife and livestock, and has

replaced classical VHF telemetry owing to its capacity to locate animals with a high spatial and temporal resolution (Di Orio et al. 2003; Schaubert et al. 2007). The GPS determines the position of individuals by means of satellite trilateration using the network of 24 satellites available in orbit. These satellites send radio signals with which the receiver of the signal is able to determine the location of the satellite and the distance between the receiver and the satellite (Bajaj et al. 2002). The simultaneous localisation of individuals allows the rate of direct interaction between the target species to be estimated. A low positioning error is, therefore, necessary in order to describe close interactions with a greater potential for pathogen transmission. Indirect interactions can be inferred from GPS data by evaluating the temporal gap between visits by different individuals to the same location (Schauber et al. 2007; Cowie et al. 2016; Triguero-Ocaña et al. 2019a). Data derived from GPS can also be used in studies concerning habitat selection (Van Moorter et al. 2016). Finally, key resources (preferred by multiple individuals) that suppose an increased probability of intra- or interspecific interactions can be identified by means of GPS (Proffitt et al. 2011; Nunn et al. 2014).

Authors have defined direct and indirect interactions within the limits of the devices employed, the transmission or survival conditions of the pathogen of interest, or the characteristics of the ecological process studied. GPS data is used to study interactions by following the approaches shown below:

- Home-range overlap, using different indices. The simplest ones are the proportion of the individuals' home range overlap and the home-range overlap probability, but more complex ones can also be used, such as the utilisation distribution overlap index (UDOI), the volume of intersection index, or Bhattacharyya's affinity index (Fieberg and Kochanny 2005; Robert et al. 2012).
- Habitat-mediated interaction, which consists of assessing how animals use their environment, and how this affects interspecific interactions. It is possible to transfer the expected fine-scale interaction to large areas by using habitat selection modelling (Barasona et al. 2014b).
- Co-location rates, for which spatial or spatio-temporal windows are predefined and used to detect those locations of different individuals that become interactions, normally indirect (Miguel et al. 2013; Triguero-Ocaña et al. 2019a).

Direct interactions have principally been defined as those that occur between individuals located simultaneously within the established spatial window. This spatial window is calculated by means of the Euclidean distance between locations, and spatial separations of between 10 and 350 m have been considered in order to study social affiliations between White-tailed deer (Schauber et al. 2007, 2015) and the community structure of wild boar (Podgórski et al. 2014), respectively. However, direct interactions with the potential for pathogen transmission were defined within a smaller (<20 m) spatial window (Cooper et al. 2010). Indirect interactions have principally been studied owing to the probability that disease transmission by environmental contamination is related to the frequency with which an individual occupies a place previously occupied by an infected individual (Schauber et al. 2007). The studies concerning transmission modelling describe the temporal gaps

between different individuals' visits to the same location in a range of between 4 h and 30 days (Schauber et al. 2007; Williams et al. 2014). However, when considering the survival characteristics of pathogens and the average climate of the area studied, Cooper et al. (2010) and Miguel et al. (2013) respectively employed a time lap of 360 minutes and 15 days in order to consider indirect interactions with the risk of transmitting foot-and-mouth disease. Finally, potential interactions can also be inferred by studying the target species' resource selection functions. For instance, Proffitt et al. (2011) and Barasona et al. (2014b) identified and characterised areas with an increased potential for interaction between livestock and wildlife.

One problem regarding the use of GPS technology is the occurrence of unsuccessful fix acquisition. Fix rates have been observed to range between 68 and 100% (D'Eon et al. 2002; Frair et al. 2004; Barasona et al. 2014b). The use of three-dimensional fixes (≥ 4 satellites) rather than two-dimensional fixes (three satellites) achieves more accurate locations (Rempel and Rodgers 1997; Jiang et al. 2008), but the availability of satellites may reduce the fix acquisition rate (D'Eon et al. 2002; Cain III et al. 2005). Furthermore, dense canopy cover can also reduce fix rates (Jiang et al. 2008). The fix rate is also related to the fixation interval, when higher rates are obtained at lower intervals, since intervals of less than one hour may use the information obtained from the last position of the satellites that concern the previous event (Cain III et al. 2005). However, there is a trade-off between a high frequency of fix acquisition and the lifespan of batteries, which will be dictated by the weight that an individual can carry. The temporality of fixes in relation to animals' activity patterns should also be considered when programming fix acquisition. For instance, fix rate success will suffer when animals are bedded under thick canopy cover and the orientations of antennas are insufficient (Dussault et al. 1999; D'Eon et al. 2002; Graves and Waller 2006; Sager-Fradkin et al. 2007; Frair et al. 2010).

In spite of the above-mentioned problems, the major constraint of the GPS is the effect of external factors (e.g. vegetation, atmospheric particles, or buildings) on the reception of the radio signals (Bajaj et al. 2002). The range of positioning error ranges between < 1 m (for military navigation) and even 300 m (for civil navigation), and this error varies with the habitat conditions (Hurn 1989; Lewis et al. 2007). Excessive overhead cover and the limited availability of satellites can greatly increase the positioning error (Moen et al. 1996; Rempel and Rodgers 1997). Causes of GPS errors are covered in detail by Frair et al. (2010).

Despite the aforementioned limitations, GPS is still a fundamental tool with which to monitor wildlife movements owing to its ability to record animal locations with high precision, during the whole day, in different habitats, under different weather conditions, and at increasingly lower prices (Cagnacci et al. 2010). This technology is being incorporated into epidemiology in general, and into studies at the wildlife-livestock interface in particular, owing to its ability to produce relevant information on species' spatial ecology (e.g. Podgórski et al. 2014). With vast quantities of movement data being collected, efforts to share and make GPS data from tagged animals accessible within the scientific community are ongoing (e.g. EUROMAMMALS, <http://euromammals.org>). These online platforms will improve the scientific quality and representativeness of studies based on GPS data.

Proximity Loggers

Proximity loggers (PLs) are based on a relatively new technology that enables the collection of data when devices are at a predetermined distance from each other. Proximity loggers incorporate transceivers that communicate by means of the emission of a unique ID through the use of UHF waves while simultaneously listening for other nearby IDs. First experiences using proximity technology employed devices as transmitters—devices emitting unique VHF pulses—or as receivers (Ji et al. 1999, 2005). PLs are now commonly used on animals as transceivers (receiving and emitting a signal) and packaged as collars, or as base stations that can be used to study the importance of focal sites of increased visitation in the landscape. In this context, interactions recorded by PLs are defined as two animals, or an animal and a base station that are sufficiently close to be identified by the other's loggers.

Two configurations of PLs are available:

- Continued transceivers (ConT), which are devices that emit UHF signals at a predefined frequency and simultaneously receive the other's ID code. ConT were originally developed by Sirtrack Ltd (Havelock, New Zealand) and used in field studies such as those of Ji et al. (2005) and Prange et al. (2006).
- Alternated transceivers (AIT), which are devices that alternate the emission of signal pulses and listen for other signals during a predetermined period. Such AIT devices are not synchronised, which guarantees that at least one device of a dyad will be able to receive the other one (for further information see Picco et al. 2015).

For each interaction, PLs record the ID of the interacting devices, the date, the time, and depending on the manufacturer, the distance or the received signal strength indicator (RSSI—as a measure of device-to-device distance). Depending on the model of the PLs, the duration of the contact can be obtained directly with ConT (Prange et al. 2006), or it can be estimated during the post-processing of data from AIT by identifying continuous records throughout the predefined listening period. The resolution of the data depends on the users' requirements and can be adjusted within the programmable parameters of the PLs: frequency of pulse emission, width of the listening band (for AIT), or separation time between consecutive interactions to be considered as different interactions (for ConT). However, the configuration of PLs needs to be carefully designed, since it has a trade-off with the battery lifespan. Similar to GPS, the battery size of PLs is limited by the size of the device and by the weight-carrying capability of the species being studied (Mennill et al. 2012). Promising advances in wireless batteries charged through inductively powered systems at, for example, feeding points for dairy cows (Minnaert et al. 2017), would eliminate the constraints of battery size. Furthermore, there is the potential to adapt this technology to smaller species for which energy transmitters could be set in commonly used feeding or water resources, or nests.

The use of PLs to record inter- and intraspecific interactions is expanding, especially since the miniaturisation of devices has made it possible to use them on

smaller taxa, such as bats or passerine birds (Mennill et al. 2012; Ripperger et al. 2016). The first study of free-ranging animals recorded interactions between possums at very short distances (40 cm) (Ji et al. 2005), but, as time has passed, PLs have been employed to detect more complex ecological processes, such as the association between lions (*Panthera leo*) at a kill site (Tambling and Belton 2009), the transmission of pathogens in a multi-host scenario (Böhm et al. 2009; Lavelle et al. 2016), or the social links between individuals (Rutz et al. 2012). The use of PLs to collect information has depended mainly on the possibility of including additional sensors according to the weight of the devices and the size of the target species. According to this, three possibilities have been employed: the recapture of marked individuals (Prange et al. 2011), the passive transmission of information to base stations (Meise et al. 2013; Levin et al. 2015), and the use of GSM/GPRS technology (Tambling and Belton 2009).

PLs have triggered a revolution in telemetry studies owing to their capacity to record close interactions and their duration with a small location error. From an epidemiological point of view, this technology is becoming essential owing to its capacity to record interactions with the real potential for pathogen transmission (effective contacts) through direct and indirect pathways. When base stations at focal sites are incorporated into a particular study, the ability to record indirect interactions with pathogen transmission potential occurring at those focal sites makes a significant addition to the value of the study. However, this addition further complicates the analysis, especially when considering pathogens that have seasonally variable survival. For example, Lavelle et al. (2016) monitored focal sites visited by both wildlife and livestock that had the possibility of transmitting *M. bovis*. This pathogen has increased environmental persistence in cooler cloudy conditions, such as those experienced during the winter months in Michigan, USA. In order to account for the increased temporal window for the indirect transmission of disease during the winter months, a 30-day window was used to define an indirect interaction between visiting animals. Conversely, during warmer sunny months when survival is reduced, a 7-day window was used to define an indirect interaction between animals visiting a focal site.

One of the main constraints of PLs is the lack of geospatial information concerning the interactions recorded, signifying that extra GPS devices are necessary to obtain spatial information. Information obtained from PLs requires thoughtful analysis owing to the effects that both external factors and the intrinsic and inevitable differences between devices have on data acquisition. The performance of PLs depends on factors such as antenna orientation, the properties of surrounding objects, the height and size of collared animals, and the presence of vegetation (Prange et al. 2006). The capabilities of attenuation or the absorption of UHF waves that these factors have made it necessary to conduct preliminary testing to convert RSSI values into distances between devices (Rutz et al. 2015). For instance, RSSI values may vary in a range of 2–3 m depending on antenna orientation (Meise et al. 2013), and vegetation may cause a reduction in RSSI values of 20% (Ceriotti et al. 2010). It is also necessary to check the correct performance of PLs, such as assessing the reciprocity between devices recording information, the comparison between PLs

and direct observations, or quantifying the reception success rate. The reciprocity in the number of contacts registered between dyads is usually low (40% approx.; Drewe et al. 2012; Triguero-Ocaña et al. 2019b). However, better results have been registered as regards reciprocity when recording the duration of contacts between dyads (80% approx.; Drewe et al. 2012; Boyland et al. 2013), suggesting that the duration of the contact is a better parameter to use for calibration purposes. In a study performed by Walrath et al. (2011), the efficacy of PLs recording contacts was significantly higher (64%) and detected longer contacts (112.908 s) than those registered by an observer (34%; 76.445 s, respectively). The reception success rate would appear to be a new option by which to estimate the capability of PLs to record contacts through the detection of false negatives; recent studies estimate the reception success of devices to be about 80% (Ossi et al. 2016; Triguero-Ocaña et al. 2019b), signifying that the interactions recorded by PL devices are simply a proportion of the actual interactions occurring in the wild and should, therefore, be handled and interpreted accordingly.

Despite having some disadvantages, PLs are the technology of preference when recording direct interactions with epidemiological implications, mainly those that require very close contacts. However, PLs are not the best option as regards recording indirect interactions involving extended spatio-temporal windows (see Triguero-Ocaña et al. 2019a). As technology advances, the possibility of including additional sensors (e.g. temperature loggers, accelerometers, GPS/GSM, VHF waves) will improve the quality of the information at increasingly lower costs (Tambling and Belton 2009; Drewe et al. 2012; Mennill et al. 2012) and, therefore, their feasibility for use in epidemiological research.

Final Remarks

The growing need to understand the process regarding interactions between different individuals and the transmission of pathogens during these interactions has led to the development of multiple methodologies capable of providing data about these processes (Table 2). The different methodologies available have made it possible to answer questions regarding diverse aspects of the epidemiological scenario, the actors involved and their role, the temporality, the spatial pattern, or the effect of several external factors. Although each methodology provides different information necessary to understand the complexity of the underlying process, all of them have their own limitations. Which one(s) to choose depends on: (1) the objectives of the study (pathogen life cycle and survival period, routes of infection, host community, behaviour of target species, relevance of environment); (2) the budget (data collection is costly and time intensive); (3) the access to individuals; (4) the downloading of data, processing and analysis capacity (large datasets can create computational challenges); (5) the level of detail (intra-group, intra-species); (6) the relevance of individuals (super-shedders, super-susceptible); (7) the kind of analyses required, and (8) the possible benefit of combining methods. After we define the study

Table 2 General information on interspecific interactions recorded by the different methodologies, detailing their specific advantages and disadvantages

Method	Quantitative/ non- quantitative ^a	Direct/ indirect/ potential ^b	Invasive/non- invasive ^c	Sampling effort	Spatial scale	Economic costs	Pros ^d	Cons ^d
Direct observation—Focal studies	Q	D/I	I/NI (invasive when marked or sampled individuals are required)	Extensive	Local	Low	First inference of interaction rates	Limited to observable animals Limited to diurnal hours Limited information
Direct observation—Linear transects	NQ	P	NI	Intermediate	Intermediate	Low	Georeferenced information Additional information useful to infer demographic parameters	Temporal limitation Limited observability
Epidemiological sampling—Community of pathogens	NQ	P	I/NI (depending on the samples required)	Intermediate	Intermediate	Intermediate	Acquisition of preliminary information	Few details of interactions and transmission process
Epidemiological sampling—Molecular epidemiology	NQ	P	I	Intermediate	Intermediate	High	Explains route of transmission of pathogens Fast and easily reproducible	Does not identify the origin of infection, or directionality of transmission
Epidemiological sampling—Risk factor analysis	NQ	P	NI	Intermediate	Large	Low	General description of the epidemiological scenario	Few details of interactions and transmission processes

Epidemiological questionnaires	Q/NQ (quantitative information susceptible to responder's opinion)	D//P	NI	High	Large	Intermediate	Preliminary approach Additional information useful for "risk factor analysis"	Dependent on context and representativeness of the population Perception can lead to misinterpretations Necessary standardised procedures
Camera traps	Q	D/I	NI	High	Intermediate	High	Allows us to understand behaviours during the interaction process	Information spatially constrained to monitored points
GPS	Q/NQ	D//P	I	High	Local	High	High spatio-temporal resolution of co-locations of different individuals	Effect of external factors on the fix success rate and on the location precision Limitation of batteries' lifespan
Proximity loggers	Q	D	I	High	Local	High	Capability to record close interactions Capability to record duration of interactions	Do not provide geospatial information Effect of external factors (antenna orientation, vegetation, etc.) and intrinsic differences between devices on data acquisition Differences in the reciprocity recording

(continued)

Table 2 (continued)

Method	Quantitative/ non- quantitative ^a	Direct/ indirect/ potential ^b	Invasive/non- invasive ^c	Sampling effort	Spatial scale	Economic costs	Pros ^d	Cons ^d interactions Limitation of batte- ries' lifespan

^aAbbreviations: Quantitative methodologies (Q), methodologies that are able to quantify the number of interactions between individuals; Non-quantitative methodologies (NQ), methodologies that are not able to quantify the number of interactions

^bAbbreviations: Direct interactions (D), simultaneous presence of two individuals within a given spatial window; Indirect interaction (I), presence of two individuals at a certain point within a specific temporal window; Potential for interaction (P), specific circumstances (shared resources, shared pathogens, etc.) that imply the existence of interactions between different individuals

^cAbbreviation: Invasive methodologies (I), those methodologies that require the physical manipulation of individuals; Non-invasive methodologies (NI), those methodologies that do not require the physical manipulation of individuals

^dAdvantages (Pros) and disadvantages (Cons) of the different methodologies regarding their capability to record interactions

methods, we must be aware that the correlation between interaction and transmission is not straightforward. The subsequent modelling of collected data is addressed in the following chapter.

In general, there are methodologies that are able to quantify interactions between individuals, in addition to others that are able to detect interaction rates, but that cannot provide precise information regarding the frequency of interaction. Regardless of whether or not it quantifies, a methodology can record direct and/or indirect interactions, or the potential for interaction. As technology has advanced, new devices capable of quantifying more precise interactions (direct interactions with the potential for pathogen transmission) have been developed. However, this type of approach does not allow the recording of descriptive information related to the process of pathogen transmission. Although each methodology has its specific advantages and disadvantages (see Table 2), in general, all those that do not involve the marking of individuals have the common limitation of the spatio-temporal resolution to register interactions and the lack of detailed information regarding the individuals involved in such interactions. Furthermore, the major limitation of those methodologies that imply the marking of individuals (GPS, proximity loggers) is related to the representativeness of the individuals within the study population, which can lead to misinterpretations of the real frequency of interaction. In order to check the representativeness of the sampled population, sensitivity analyses of the selected individuals can be performed. Moreover, Latham et al. (2015) suggested a strategy by which to minimise this problem that consists of the implementation of an experimental design in which two devices are used together so that the information collected by a certain methodology could be validated using the results obtained by the other (e.g. GPS – VHF). Apart from representativeness, determining whether or not to include all device-outfitted study animals is essential if meaningful conclusions are to be obtained. For example, including data from PL-outfitted animals that have left the study area and are no longer available to interact with others will impact on results, suggesting lower rates of interaction than those that may be occurring (Lavelle et al. 2016).

Finally, there is a need to implement several technologies to be able to discover the real situation of the interaction between wild and domestic animals. The different methodologies can benefit from each other in terms of their ability to quantify interactions (directly or indirectly), or of their ability to describe the factors associated with these interactions. Moreover, not all the methodologies require the same effort or provide information at the same level of detail and are, therefore, sometimes used sequentially, starting with those that are more descriptive and ending with the most precise approach. This complementarity and sequencing in the use of different approximations is shown below using the case study of animal tuberculosis in the Iberian Peninsula (Box 1).

Box 1. Animal Tuberculosis in the Iberian Peninsula: The Complementarity of Different Approaches

Animal tuberculosis (TB) is an infectious disease that affects multiple hosts (including humans, livestock, and wildlife) and is distributed around the world (O'Reilly and Daborn 1995). In Spain, the incidence of TB in cattle (especially in the south and the centre of the country) has appeared to increase recently, but was, in reality, probably owing to the increase in diagnostic sensitivity (MAPAMA 2018). Wildlife reservoirs may also be playing a more significant role in maintaining and transmitting the disease to cattle (Gortázar et al. 2012; Guta et al. 2014). In this particular case study, one of the first steps that was carried out in order to understand the transmission of the pathogen between wild and domestic animals was that of interviewing farmers (Cowie et al. 2014). The information collected was focused on the presence and management of wildlife on the farm, the main activity of neighbouring farms, the number and availability of permanent water points, the type of enclosure, and the relative abundance of wild animals. The information obtained suggested the relevance of water points and the presence of wildlife as key factors in the incidence of TB in extensive cattle.

Spatial or spatio-temporal epidemiological models can also infer potential interaction rates. In this respect, Martínez-López et al. (2014) observed a high spatial association between the abundance of wild ungulates and the incidence of TB in cattle at a regional level. A later work identified the relevance of the prevalence of TB in wild animals, in addition to abundance, explaining the presence and incidence of TB in cattle (LaHue et al. 2016). This was the first work to link the prevalence of the pathogen between livestock and wildlife in this particular scenario.

At a finer spatial resolution, UAS were used to determine the spatial pattern of ungulates' abundance in the Doñana National Park (Barasona et al. 2014a). The analyses showed similar patterns for all the domestic and wild species and the relevant role of water points as regards explaining them. A higher probability of TB infection was determined in those territories in which cattle and red and fallow deer (*Dama dama*) were more abundant, and the interaction between domestic and wild hosts was, therefore, again linked to TB positivity, in this case on a fine spatial scale. The information obtained from UAS was also used to describe an aggregation index of individuals (and not just their abundance) as a new measure of potential interaction (Laguna et al. 2018). Regardless of the abundance of the different species, the aggregation of animals determined by the index was significantly associated with the prevalence of TB. That is, in addition to the presence and abundance of wildlife, the aggregation of animals is a relevant risk factor that explains TB transmission in the Iberian Peninsula.

(continued)

Box 1 (continued)

The common constraint of the aforementioned studies was the scarcity of raw field data on the interaction frequency between livestock and wildlife. Most of these studies were based mainly on the spatial association between wild and domestic animals on large spatial scales, although they did not quantify the number of interactions. In order to solve this lack of information, various quantitative methodologies were also applied in subsequent studies. Therefore, 16 risk points (ponds, artificial troughs, supplementary feeding points, and pastures) on a farm with extensive cattle and pig farming, and with a low density of deer and wild boar, were monitored during a year through the use of CTs (Kukielka et al. 2013). The results made it possible to verify the relevance of the indirect interactions when compared to the direct ones (9000 vs. 10, respectively). The work in question was, therefore, able to quantify interactions, those interactions were then characterised according to the risk points at which they occurred, and their directionality was studied, showing a higher probability of transmission from wildlife to cattle.

The second type of methodologies that were used to quantify interactions was those based on telemetry. In contrast to CTs, telemetry allows the frequency of interactions to be quantified with greater precision through the continuous monitoring of individuals. Triguero-Ocaña et al. (2019a) quantified interspecific interactions between cattle and wild boar in the Doñana National Park. The results showed that cattle and wild boar interacted an average of 1.4 times per day, especially in autumn and during crepuscular hours. Furthermore, PLs record interactions with greater spatial resolution and, therefore, allow the detection of direct interactions. The cattle, pigs, red deer, and wild boar on an extensive farm in central Spain were collared with proximity loggers in order to understand the network of domestic–wild animal interactions (Cowie et al. 2016). The study confirmed that interspecific direct interactions were not frequent, although intraspecific ones were, and that most of the interactions occurred close to water points. These results confirmed the results obtained with CTs and provided more precise information on the temporality and the spatial pattern of the interactions.

Finally, molecular epidemiology was able to provide new and detailed information on the circulation of pathogens in the host community. Spoligotypes from both cattle and goats that were circulating in wildlife were determined, and these spoligotypes were even found in some people living around this epidemiological system (Gortázar et al. 2005). In the case of the Doñana National Park, the diversity of spoligotypes in wild animals was observed to be increasing, although the opposite case was detected in cattle (Gortázar et al. 2011). These results suggested the existence of multiple sources of infection in cattle, in addition to the existence of a complex multi-host and multi-pathogen epidemiology, which makes it difficult to

(continued)

Box 1 (continued)

control the disease in livestock despite the efforts made by the official agencies.

Overall, the combined use of several methodologies made it possible to attain in-depth knowledge regarding how the pathogen is transmitted in this multi-host scenario. This information is now being used to implement biosecurity measures with the objective of reducing the risk of transmission between wildlife and livestock and is obtaining promising results (e.g. Barasona et al. 2013). Biosecurity plans are currently being generalised in the Iberian Peninsula, focused on both cattle and free-ranging pig farms, and will probably make a contribution to reducing the circulation of pathogens in this complex epidemiological scenario.

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Characterisation of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field



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Introduction

Wildlife-livestock interfaces are defined as the physical space in which wild and domestic species, as well as humans, overlap in range and potentially interact (see chapter “Host Community Interfaces: The Wildlife-Livestock”). They belong to an interaction between and merging of natural ecosystems and anthropogenic or socio-systems (areas largely impacted by the human footprint such as agricultural or urban landscapes) within socio-ecosystems as defined by Ostrom (2009). Wildlife-livestock interfaces will be dependent on the organisms under study: in the same socio-ecosystem, the European badger (*Meles meles*)/cattle interface will be different from the badger/human interface. Wildlife-livestock interfaces can occur in every environment, even in the centre of megacities where wild species of plants and animals live amongst human infrastructures. In this chapter, the wildlife-livestock interface term is equally used for the term wildlife-livestock-human interface because the focus is on the interaction between “natural” and “human” subsystems. Therefore, examples will equally be drawn from the livestock and human fields. Finally, the wildlife-livestock interface issue is principally and primarily addressed under the prism of disease ecology as our primary field of interest (see chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”).

The progressive domestication of wild species by *Homo sapiens* during the agricultural revolution from between 13,000 and 10,000 years ago (except for the domestic dog which was anterior) triggered increased contacts between wild species, newly domesticated wild animals and humans. At the time, this agricultural revolution had profound consequences on human societies (Diamond 2002) including the emergence and expansion of wildlife-livestock interfaces. They were created by the multiple and increasing use of natural resources by humans and their domesticated species (e.g. pasture, watering points). As a consequence, this domestication process initiated the first extensive bridging of pathogen burden between wildlife, domestic species, and humans, each adding their own pathogen diversity to the mixing pot (Morand et al. 2014). During the last millennium, wildlife-livestock interfaces have evolved in terms of spatial extent and complexity, shifting from a few centres of domestication lost in an ocean of pristine natural habitat to a world dominated by man and its domestic species pressurising the remaining patches of natural habitats.

In recent times, the pace of human expansion across Earth and the combined impacts of global and local changes have increased. Most ecosystems have been impacted by the human footprint and exposed to some form of wildlife-livestock interactions. Technological and economic progress, including the evolution in livestock production systems, have constantly created a diversity of new interactions between humans, livestock and wildlife. At the landscape scale, the progressive intensification of agriculture and the concomitant ecological fragmentation of natural habitats have had important consequences on the pattern of contacts between wild and domestic species. For example, a link between deforestation and Ebola outbreaks has been observed in West and Central Africa (Rulli et al. 2017). Agricultural

intensification and ecological fragmentation also have a negative effect on biodiversity, modifying the diversity of interactions between organisms (e.g. Lyme disease) (Wood and Lafferty 2013). These changes have been implicated as drivers of some recent emerging disease events that had important impacts on human livelihoods and health (Jones et al. 2008; Allen et al. 2017). At finer scales, novel and intensifying agricultural practices can cause new host interactions at the interface and trigger pathogen spill-over. Wildlife-livestock interfaces are therefore diverse, bringing together species that have not interacted before or increasing the frequency or intensity of otherwise rare events. They are the cradle of an unprecedented mixing between organisms, creating novel communities and interactions.

Wildlife-livestock interfaces are also dynamic by nature. The expansion of humans is still recent in evolutionary terms and largely on-going in many ecosystems. Also, human practices and interactions of species at wildlife-livestock interfaces are also very dynamic. One can expect organisms to be continually adapting to these new contexts, which means that some ecological and evolutionary processes could be specific to wildlife-livestock interfaces. Due to the low pace of evolution in macro-organisms, the ecological (e.g. behavioural) adaptation to wildlife-livestock interfaces should be dominant. At the microbial level, micro-organisms are exposed to a faster genetic evolution—including exchanges of genetic material—and the hypothesis of the evolutionary adaptation that could arise from the particularities of the wildlife-livestock interfaces is widely considered. In this sense, specific antimicrobial resistance evolution should be given special attention (Allen et al. 2010). The diversity of contexts in environments and organisms and the spatial and temporal dynamics between organisms feed the complexity of wildlife-livestock interfaces and are crucial for the characterisation of these interfaces.

The wildlife-livestock interfaces defined above impact multiple sectors and levels. For example, some wildlife-livestock interfaces are located at boundaries between land uses with different management objectives. The main objective of protected areas is conserving biodiversity and its ecological functions while rural land is devoted to agricultural activities for the production of food for humans and economic benefits. Wildlife-livestock interactions can impact each land use option and compromise their conservation and development objectives. Human-wildlife conflicts, for example, can negatively impact the livelihoods of farmers living at the periphery of protected areas, through crop raiding by elephants or predation of livestock by wild carnivores (Lamarque et al. 2009; Kuiper et al. 2015). The illegal use of natural resources (e.g. poaching of bushmeat) can affect the conservation of some wild species and associated ecological processes (Lindsey et al. 2015), such as plant successions and soil fertility in grazing ecosystems. Additionally, local people living in interaction with wildlife have different positive and negative representations and perceptions of wild animals, associated with their cultural and individual experience (Guerbois et al. 2012). The issue of pathogen transmission and consequences on wildlife, livestock, and human health at the wildlife-livestock interface is therefore one amongst many sectors impacted by wildlife-livestock interactions (Kock 2005).

The need to characterise these interfaces and develop methodologies adapted to their studies is therefore increasing and multi-sectorial but, until recently, attracted little attention. Wildlife ecology aims at understanding the behaviour and interactions among wild species in their natural habitat. One expects wildlife behaviour and modes of interactions with their environment and other species to change once wild-species interact with domestic species or enter agricultural fields for example. However, this field has not developed the framework to study wildlife ecology at the interface. Wildlife ecology “at the interface” is largely unknown and too few studies take this aspect into consideration (e.g. Naidoo et al. 2012; Murwira et al. 2013; de Garine-Wichatitsky et al. 2013a; Hibert et al. 2010; Proffitt et al. 2010). On the other hand, studies on domestic species mostly consider strictly economic productivity. At wildlife-livestock interfaces, an ecological perspective is necessary to take into account the fact that domestic populations belong to communities including both wild and domestic populations interacting through contacts, competition and facilitation processes for limited resources such as water and pasture (see chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). This is very relevant for extensive production systems and also relevant for more intensive production systems (ex; Nipah virus transmission between bats and pig production systems in South East Asia). Most veterinary and animal science curricula omit those aspects today. The complexity of wildlife-livestock interfaces is therefore largely uncharacterised because of the lack of multi- or interdisciplinary approaches and specifically adapted methodologies and tools.

In recent years, the study of wildlife-livestock interfaces has attracted a growing range of expertise due to their implications in multiple areas of interest. The study of wildlife-livestock interfaces has also benefitted from scientific and technological advances as described in chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife” which, when applied to the specific context of these interfaces, allows for a better understanding of the social and ecological processes at stake. In this chapter, we will characterise the wildlife-livestock interfaces and their properties according to different contexts. Then the different approaches and methods of characterisation of the wildlife-livestock interfaces will be exposed and compared. Case studies will provide examples of how the different types of data and methodologies can be used together to improve the understanding of wildlife-livestock interfaces. Finally, the last section will try to make the case for a “science of the interface” that needs to be embedded in systemic, holistic and participatory approaches such as One Health (e.g. Ecohealth) which considers wild and domestic animal health and human health (Charron 2012).

Characteristics of Wildlife-Livestock Interfaces

Seen and Unseen Wildlife-Livestock Interfaces

Wildlife-livestock interfaces are physical spaces where the home ranges of species overlap, and where they can potentially interact. At the landscape level, some evidence of wildlife-livestock interfaces can be “seen” using aerial or using remote sensing tools. They can be easily defined for example when a land-use boundary such as a fence constrains large species movements and space use (e.g. Fig. 1a, Kock et al. 2014; Ferguson and Hanks 2010). In such scenarios, a gradient of primary

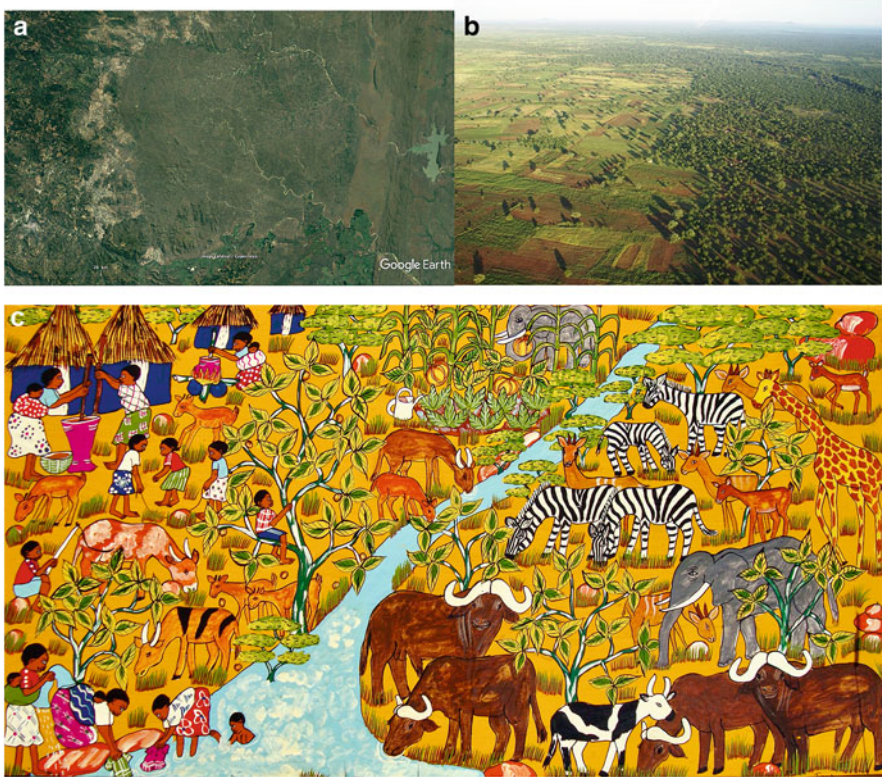


Fig. 1 (a) Satellite view of the southern part of Kruger National Park and periphery, South Africa. The more homogenous and light green right and upper part represents the park and the dense human population at the periphery (left-hand side) and commercial agricultural land (bottom part) delineate a visible hard edge wildlife-livestock interface (Google Earth); (b) aerial view (@ A. Caron) of the unfenced boundary between Gonarezhou National Park and its periphery, Zimbabwe. The interface is also visible but “softer” due to the gradient between agricultural fields and woodland savannah; (c) a wildlife-livestock interface painted by Irène Karuya who lives in Harare, Zimbabwe and perceived clearly the interface, its actors, and interactions (natural resource use, elephant raiding crops, buffalo/cattle contacts)

resource use by consumers (e.g. wild and domestic ungulates) across the land-use boundary may render the interface visible. Even when no physical boundary separates the land uses, differential use of the vegetation resources can create a visible limit between land uses, such as the use of trees by humans for fuel or by elephants for food or overgrazing by livestock or wildlife (Fig. 1b).

In other contexts, interfaces can be much more difficult to define. In urban contexts where the distribution of wildlife populations is heterogeneous and not well known, defining a wildlife-livestock interface cannot be done a priori (Hassell et al. 2016). For example, the human–rock pigeon (*Columbia livia*) interface in cities is important for the transmission risk of zoonotic pathogens (Haag-Wackernagel and Moch 2004). Defining this interface is challenging because of the wide-scale habitat use by people and pigeons, and the diversity of potential interactions in the urban landscape. As another example, intensive commercial livestock production usually aims at zero interface in order to prevent interactions such as pathogen or genetic spill-over from wild to domestic species. The level of interface will however be dependent on biosecurity measures and their compliance. In poultry production buildings, open gates or leftover food directly outside the building or inside during quarantine between two batches of chicks can create resource attractors promoting contacts between wild and domestic birds (Caron et al. 2014). Finally, each stakeholder living or not at a wildlife-livestock interface will have their own representation of wildlife-livestock interfaces (Fig. 1c), and these representations will impact the way they think and behave about the wildlife-livestock interfaces.

Environmental features often do not accurately define wildlife-livestock interfaces. Physical boundaries may not constitute a 100% barrier to animal movements (e.g. van Schalkwyk et al. 2016) and a resource gradient cannot define with precision the range of the wildlife-livestock interface, i.e. where species interact. Hence, even when wildlife-livestock interfaces can be “seen” a priori, defining them rigorously is difficult. Having an *a priori* conceptual model of the wildlife-livestock interface under study based on environmental features (e.g. river, fence) is a requirement, but it should be confirmed or challenged by information on species interaction.

Conceptual Model for Wildlife-Livestock Interfaces

Wildlife-livestock interfaces have multiple dimensions of very different natures and mean different things for different people (Kock 2005). Epidemiologists will define the interface according to the opportunities they provide for pathogen transmission between wildlife and livestock (e.g. Bengis et al. 2002); rangeland managers will consider how it influences competition between wild and domestic herbivores (e.g. du Toit et al. 2017); while anthropologists may consider the non-material cultural and symbolic values of wild animals (e.g. de Garine 2007); and law scholars may focus on boundary delineation and access rights (Andersson and Cumming 2013). These different representations of the wildlife-livestock interfaces will be based on different conceptual frameworks of wildlife-livestock interfaces.

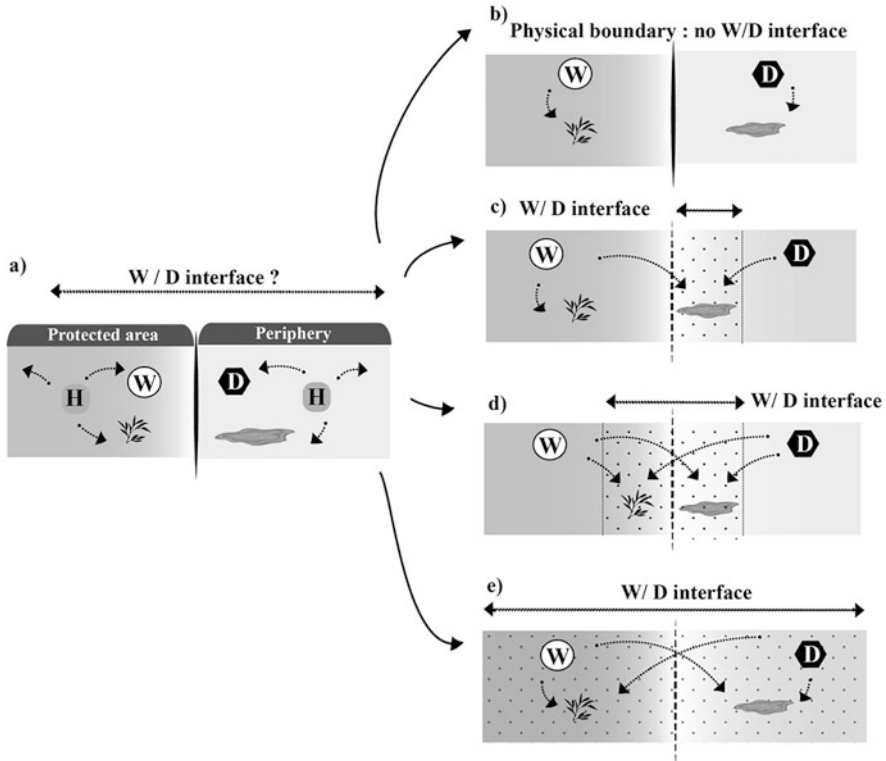


Fig. 2 (a) Theoretical conceptual model of a wildlife-livestock interface including wild (“W”) and domestic (“D”) species, human actors (“H”) as well as key landscape features including land use boundaries (dark line separating an hypothetical protected area and its periphery) and key resources (pasture and surface water for example, represented with icons) that will help define hypotheses about the wildlife-livestock interface (horizontal bidirectional arrow on top); the human component is only represented in panel (a) but it is assumed that the human driver is one of the most important to define wildlife-livestock interfaces impacting on livestock production practices, wildlife management and resource distribution; (b) Hard edge interface: a fence or non-crossable river limits the movements of wild and domestic species: the interface is the hard edge; this type of interface is theoretical for many national park boundaries as animal movement-proof edges are rare; (c) asymmetric semi-hard interface: only the wild species can cross the edge to use natural resources R1; the interface is limited to a small area in the domestic species home range; e.g. in European settings, European badger can cross into farm areas when cattle do not cross farm boundaries; (d) symmetric soft interface: both species can cross the edge and exploit resources across the edge; this type of interface exists for many unfenced protected areas; (e) diffuse interface: there is no edge and the home range of wild and domestic species overlap extensively; this is the case for example for highly mobile animals such as birds, bats, or rodents in rural and urban settings

Representations of wildlife-livestock interfaces will always require a priori definition of the study site, comprising a set of items presented in Fig. 2a: (1) wild and domestic species of interest; there could be several wild and/or domestic species under study and even whole communities; (2) key environmental features such as the presence of

a “visible” land-use boundary that could influence the type and extent of the interface (e.g. river, fence, etc.); the presence of key resources that could influence the behaviour of wild species and livestock practices (e.g. pasture, water point, prey); (3) key local actors involved in activities at and/or in the management of the interface area; and (4) this a priori knowledge will help framing a conceptual model for the wildlife-livestock interface.

This conceptual model usually fits within a finite number of broad categories of wildlife-livestock interfaces. First, the interface can be delineated by a “hard edge” (Fig. 2b). This edge can be man-made: a fence built to prevent wildlife to exit a protected area or to prevent buffalo/cattle interaction to control foot-and-mouth disease for example; or it may be a natural boundary, for instance when a river or a cliff constitutes a natural border between two land uses. In this scenario, the edge prevents the movements of wild and domestic animals from one side of the edge to the other and any direct contact between them. Hard edges do not need to be physical features. Wild animals can perceive a road as a hard edge, and cattle may be prevented to enter a protected area because their owner fears a fine if detected by park rangers. Then, some edges can be soft for some species and remain a barrier for others (Fig. 2c). In semi-extensive production systems, cattle usually remain in pastures that wildlife such as elk (*Cervus canadensis*) can access (Proffitt et al. 2011). This means that the edge may be asymmetrical in terms of who crosses it and that key resources will only be accessible to a subset of the wild and domestic community. Finally, soft edges can still be defined by a land-use boundary (Fig. 2d) where animals from both sides percolate across to access resources on the other side. Most protected areas in Africa are not fenced, allowing wildlife to freely cross park borders and enter adjacent areas of communal land or hunting concession. Inversely, cattle owners may herd their cattle into protected areas, not respecting land use regulations and wanting to access grazing resources within parks. In this scenario, wild and domestic population densities are inversely distributed across soft edges. Finally, the wildlife-livestock interface can be diffuse in space (Fig. 2e) with no hard or soft edge. This scenario encompasses wild birds, rodents and bats, for example, which have the capacity to use very large habitats or regions. Mixed systems defined as open range where wildlife and livestock coexist (and where they are usually used by humans) fall in this case as well (Fynn et al. 2017; Fritz et al. 1996).

The proposed conceptual model may be used as a basis to understand the details of the wildlife-livestock interface under study. Conservation managers can then try to characterise and understand the behaviour of wildlife inside and/or outside the protected area and identify potential hotspots of conflicts or areas for wildlife corridors across a rural landscape (Doherty and Driscoll 2018). Disease ecologists will try to understand when and where target wild and domestic species can be in contact and when this contact could lead to pathogen transmission (Miguel et al. 2013). Anthropologists can work on the representation and perceptions of wild and domestic species in people’s cultural framework and access people’s own representation of the interface. Studies on wild animal behaviour and livestock practices to delineate in more detail the overlap between species will be implemented at the individual, population, or community level depending on the objective. Individual

approaches will be used for individual-based variables such as determining potential infectious contacts (e.g. McDonald et al. 2018) or exploring the behaviour at the interface of specific individuals (e.g. adult elephant bulls for crop raiding or for hunting purposes). Overlap between populations of species will be interesting to assess shared habitat and resources and as an indicator of area of contact as well (Miguel et al. 2017). Finally applying the tools of community ecology to populations of wild and domestic animals has been seldom implemented but can be a useful tool to monitor wildlife-livestock interfaces (e.g. for competition between wild and domestic ungulates (Hibert et al. 2010)).

Host Contacts for Disease Ecology at Wildlife-Livestock Interfaces

Delineating interfaces is a multifaceted process-oriented exercise. A large number of studies undertaken at the interface focus on issues related to disease ecology because of the risks for wildlife and public health and for the sustainability of production systems. The central issue for disease ecology at wildlife-livestock interfaces is the inter-species transmission of pathogens from wild to domestic hosts or vice versa (Chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). Focusing on interspecific contacts is a useful way to define them from an epidemiological perspective. In this sense, the “contact” term is frequently defined as any effective interaction that could potentially allow for the transmission of an infectious agent between a pair of individuals, groups of individuals or within a spatial area. Indeed, interspecific transmission of pathogens and parasites require inter-host contacts to occur and different types of contacts exist. They may occur through direct physical contacts, i.e. at the same place at the same time. They may also occur through indirect transmission via shared resources such as air/aerosols, contamination of water or forage resources, i.e. at the same place, but not at the same time. Finally, vectors can complete the pathogen transmission, i.e. not exactly at the same place and not at the same time. Then, characterising interspecific contact patterns, defined according to the survival capacities of the pathogens and parasites in the environment (a few minutes to decades, e.g. anthrax) and the shared resources with which they are associated, provides a framework to define wildlife-livestock interfaces in the context of disease ecology.

Along a well-maintained wildlife-proof fence erected around a protected area (Fig. 2a, b), the width of the actual wildlife-livestock interface area could range from 0 m (diseases transmitted by direct contact) to several hundred metres wide, depending on the dispersion capacity of the pathogens or their vectors (typically a few metres for ticks or several hundred metres for biting insects). “Hard” edges are often discontinuous, providing opportunities for movements and contacts (“localised”, Fig. 2c) (Ferguson and Hanks 2010; Chigwenhese et al. 2016). On

the other hand, many protected areas are not fenced and the wildlife of interest may reside inside a protected area just seasonally. In this case, the interface may be defined more adequately according to the distribution in space and time of the resources they associate with (Fig. 2c, d) (Murwira et al. 2013). Permanent waterholes or key forage resources shared between wild and domestic herbivores, including artificial supplementary feeding, will define “focal intense interface” during the dry season for example, with numerous localised opportunities for interspecific contacts and pathogen transmission. When the shared resources are more homogeneously distributed in time (e.g. permanent river) or among habitats (e.g. homogenous grassland or forests), the interface will be more “diffuse and low intensity” (Fig. 2e). The definition of the wildlife-livestock interface as presented in Fig. 2 provides the basis to define potential infectious contacts between hosts, as a subset of the contacts between hosts based on the life-history traits of the targeted pathogen or group of pathogens (sharing, for example, a mode of transmission) (Caron et al. 2012).

The frequency and intensity of inter-species contacts will vary in space and time as well as amongst individuals (Miguel et al. 2013). In chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife”, technological and methodological advances were presented (e.g. telemetry, GPS, mark-recapture techniques) that have drastically changed the capacity to follow individual movements across landscapes and model habitat use and contact patterns by populations and communities. Despite these advances, within multi-species communities, the contact rate is a challenging variable to estimate. Using social network approaches (Wey et al. 2008), the idea is to directly relate pathogen transmission events in a transmission network, as contacts in a contact network. In this sense, the transmission network at wildlife-livestock interfaces is naturally a subset of the contact network, owing that not all contacts lead to pathogen transmission (Craft and Caillaud 2011). Classical epidemiology of infectious disease approaches (chapter “Quantifying Transmission Between Wild and Livestock Populations”) assumes that contacts among individuals within a given community are random and mixing is homogeneous. However, the contact structure at wildlife-livestock interfaces tends to have a high degree of heterogeneity and its potential associations may have a substantial impact on the duration, size and dynamics of transmission events (Fleming-Davies et al. 2015). Therefore, contact heterogeneity is independently defined from pathogen transmission function, such that a frequency-dependent system could be heterogeneous in local contact structures, but would appear homogeneous at a global level (White et al. 2017). For example, wide assumptions on random and homogeneous density-dependent transmission were considered in the case of the Eurasian badger, which is a wildlife reservoir for bovine tuberculosis (TB), a shared disease with cattle in the UK. Culling of the badger population was implemented for decades to mitigate TB in both badger and cattle populations. However, several studies have demonstrated mixed outcomes relative to this control measure (Vicente et al. 2007; Bielby et al. 2014). These studies show that culling reduced TB in the immediate area where it was performed, but changed badgers’ behaviour in a wider area in ways

that increased the TB transmission risk among badgers and exacerbated cattle TB incidence rather than reducing it.

The intensity and frequency of contacts at the wildlife-livestock interface are also key parameters that depend on human factors and animal behaviour, which can drive social interactions, resource selection competition, movements, migration, dispersal, social systems and territoriality (Wey et al. 2008). These parameters are an unavoidable consequence of sociality and interspecific interactions owing to the spatio-temporal concentration of potential hosts in the same environments. In free-ranging species, social transmission of pathogens is a cost of living in groups; if pathogen transmission occur between individuals of different species, the intensity and frequency of contacts will vary as a function of species-specific sociality (Kappeler et al. 2015). As mentioned previously, its intensity and frequency must be considered as dynamic throughout the studied interface, species and time. For instance, in a network approach to study interactions between different wild and domestic ungulates species, some zebras (*Equus burchelli*) were identified as “super-movers” or “super-spreaders” and had the highest potential to transmit *Escherichia coli* strains. These individuals may act as bridges between regions and populations of the network that would otherwise be poorly connected, and their high mobility and large home range brought them into contact with other less wide-ranging species (VanderWaal et al. 2014).

Approaches to Characterise the Wildlife-Livestock Interface

To characterise wildlife-livestock interfaces as a space where wild and domestic species interact, the interaction needs to be defined (e.g. home range overlap, contact, competition, predation) and understood in a space–time matrix. In chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife”, the technologies and approaches to collect the data necessary to characterise wildlife-livestock interfaces have been presented.

Behavioural Ecology

Quantifying variables to characterise interactions or contacts among individuals in multi-host and multi-pathogen systems is central to several fields of ecology and epidemiology. Being able to follow simultaneously individuals from different species at the interface is the most straightforward way to characterise where and when they are in contact. Early approaches to measure animal contact rates were performed by direct observation of individuals (Richomme et al. 2006) but recent advances (chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife”) allow us to record animal locations at very high frequency and precision without researchers being present and potentially impacting study animals.

In this sense, spatial information can be used to build individual home ranges. For social animals such as most ungulate species, including all domestic species, the home range of one or a few individuals can be used to infer the group home range (e.g. Cornelis et al. 2011). Then, overlap between individual or group home range from different species can be calculated to characterise the shared space use by both species in the socio-ecosystem (Zengeya et al. 2015; Barasona et al. 2014). Often the spatial behaviour of domestic ungulates is limited in space (e.g. farm, fenced field, herd boy driving the herd) and there is no need to collect spatial information on them as their movements can easily be predicted (e.g. Proffitt et al. 2011). High-resolution satellites, such as Pleiade (CNES Centre National d'Etudes Spatiales, Toulouse, France) or Quickbird (Vandenberg Air Force Base, California, USA), send pictures with a resolution ranging from 0.5 to 4 m in less than 24 h. Proprieties (reflectance, texture properties) of satellite pictures and indexes can be measured at small resolution as the NDVI for the vegetation (Normalised Difference Vegetation Index), the NDWI for water (Normalised Difference Water Index) and brightness of soil for man-made structure versus bare soil. Classification can be made and the landscape categorised in terms of resource availability and habitat use. The area of overlap, i.e. the wildlife-livestock interface, can be then studied with these layers of information and compared with areas without overlap to explore the drivers of interactions. Alternatively, the interaction between inter-species overlap and landscape features can be used to model the niche of wild hosts, of the interaction and/or the pathogen (which needs one or more hosts, sometimes a vector to be present and specific biotic and abiotic conditions) (e.g. Ochieng et al. (2016)). The ecological niche of the wild hosts can be mapped in other or larger areas and provide an estimation of the risk of interspecific interactions in a broader context.

Spatial overlap does not necessarily mean that contact occurs, as previously discussed. For disease ecology studies requiring often more detailed between-hosts contact information depending on the modes of transmission of the pathogen, the frequency of locations acquired by GPS collars will need to be translated into potential infectious contacts. If the pathogen is directly transmitted, the estimation of contacts will be difficult. During a buffalo/cattle interface study in Zimbabwe, location data was acquired once every hour for both species. After 1 year of data collection, no direct contact was observed between cattle and buffalo (Miguel et al. 2013). In this study, the closest distance between a head of cattle and a female buffalo was 86 m with a GPS location recorded every hour. This does not mean that no direct contact occurred as they could have occurred between two locations over a period of 1 h. For indirectly transmitted pathogen (e.g. through the environment), the survival of the pathogen in the environment can be used to define a contact. Bovine TB is known to be able to survive for 5–40 days in the environment (Tanner and Michel 1999). An infected animal using a location at T_0 may infect this location for the remaining time window of pathogen survival. If a naïve individual moves into the location within this time window, it is at risk of being infected. The contact properties will therefore be crucial and collars programmes will need to be adapted to the study objective.

Local Knowledge and Practices

From a social science perspective, the wildlife-livestock interface should be defined in order to encompass the non-material dimensions of human–nature interactions, in addition to the physical, biological and epidemiological dimensions envisaged so far in this chapter. Anthropological studies have long been carried out with traditional pastoral populations, especially in Africa, improving our understanding of the relationships between farmers and their livestock and documenting traditional remedies (Bâ 1996). Local stakeholders such as farmers or livestock production technicians will have their own representation of the local wildlife-livestock interface. This representation will inform their choice of livestock practices and the risks they will take to optimise these practices. Where shall I send my cattle to graze and to drink? Shall I send them into the park to access good grazing during the dry season with the risks of being caught by rangers and paying a fine; and including the risk of predation on my cattle by lions? (Perrotton et al. 2017). The wildlife-livestock interface will therefore be influenced by these perceptions and decisions.

Although livestock production has historically been in conflict with wildlife preservation because of disease transmission (Bourn and Blench 1999), few social science surveys have investigated local perceptions and knowledge of local farmers regarding the disease that are shared by wildlife and livestock, even in areas where these interactions still occur. Studies carried out with populations living at the periphery of or within protected areas in southern or East Africa found very contrasting results. For instance, de Garine-Wichatitsky et al. (2013b) in Zimbabwe concluded that local farmers usually have an accurate perception of the epidemiology of diseases affecting their livestock, and their perception of the potential role played by wildlife species is usually in agreement with the current state of veterinary knowledge. In contrast, Munyeme et al. (2010) in Zambia concluded that a very low proportion of farmers had an idea on how bovine TB was spread between wildlife and livestock. In fact, even if we limit the scope to the epidemiological interactions between wild and domestic animal hosts, defining the wildlife-livestock interface with a local perspective is a major challenge. Disease may be defined very differently by local people according to their cultural background, due to non-material causes that are independent from microbes transmission which may be difficult or even impossible to explain in rational western ways (Schillhorn van Veen 1997). A “healthy” animal may be defined very differently whether it is a domestic animal or a wild animal (and among wild animals depending on the symbolic attributes of a specific species), in contrast with the growing scientific evidence that wildlife and livestock (and humans) do share and exchange a large number of pathogens that cause diseases (de Garine-Wichatitsky et al. 2014).

More recently, ethnoveterinary studies have regained the attention of scholars and practitioners involved in veterinary and livestock development in low- and middle-income countries, especially through the development of participatory epidemiology, which builds on local veterinary knowledge and perceptions of animal diseases (Catley et al. 2012; Goutard et al. 2015). These participatory studies involving local

populations strengthen their participation in livestock disease control programmes using conventional veterinary medicine (Catley and Leyland 2001), and they may provide alternative livestock disease control based on indigenous knowledge where and when conventional veterinary medicine is not accessible or not affordable (Schillhorn van Veen 1997).

Molecular Approaches and Genetics

The recent developments of phylogeography and population genetics gave useful insights concerning the migration patterns, the evolution and the phylogenetic relatedness of populations, as well as relationships among wildlife and domesticated species. Of course, gene transfer seldom occurs between species, except if the wild and domestic species are genetically close as in the case of domestic pig and wild boar (Goedbloed et al. 2013). The phylogeographic field is focused at a large spatio-temporal scale, developing information about the relationship at the species/subspecies level of past historic events occurring during the quaternary geological period (Awise and Hamrick 1996). In contrast, population genetics allows the investigation of recent evolutionary processes operating at smaller spatio-temporal scales (e.g. population level, or at the wildlife-livestock interface (Simonsen et al. 1998). It generally requires the use of highly sensitive markers such as microsatellites (i.e. short tandem repeats on the nuclear DNA) (Paetkau et al. 1995). Their hyper-variability makes it possible to investigate processes at temporal scales ranging from a few thousand years to a few decades ago.

More recently, improvements in molecular and statistical techniques opened the path for the investigation of individual relationships at an even finer scale. These new markers are characterised by a variation in DNA sequence occurring at the scale of a single nucleotide in the genome, called “Single Nucleotide Polymorphisms” (SNPs). These markers offer better accuracy in population screening, with their widespread abundance in coding and non-coding regions, simple mutation models and low mutation rates (Santure et al. 2010). Such markers allow for improving the understanding of inter- and intra-herd dynamics. The parameters inferred include statistical estimations of population differentiations, effective population sizes, migration rates, hybridisation processes among closely related species and population bottlenecks. They also allow estimating gene flow among different populations and therefore the mobility of animals and contacts among different herds of wild and/or domestic animals (Smitz et al. 2014). Such information is of prime importance in order to estimate potential contacts among wild and livestock populations.

The same methods can be also used on micro-organisms including pathogen species in order to better understand the evolutionary history or the mobility of their hosts. Indeed, micro-organisms are often characterised by higher evolutionary rates as compared to their hosts, giving the opportunity to use them as “evolutionary magnifying glasses” to better understand the history of their hosts (Nieberding et al. 2004). Micro-organisms also exchange genetic material in different ways such as

horizontal gene transfer that can be increasingly tracked with new molecular techniques. Moreover, the revolution of Next-Generation Sequencing methods allows analysing complete bacterial/viral communities or bacteriomes/viromes on host species (André et al. 2017). Hence, the fact that different species can exchange other (i.e. non-host) genetic material can be used to track indirectly the contact patterns between species. When micro-organisms are pathogenic to the host, the isolation of different strains of the same microorganism in host populations from different species and the characterisation of the genetic variation between the strains isolated can provide information about their presence; and sometimes can provide information about the direction of an infectious transmission between populations or species. If there has been transmission of a pathogen, then host-to-host contact defined according to the mode(s) of transmission of the pathogen has occurred. The comparison of bacteriomes/viromes among different populations, herds, or wildlife and livestock groups gives therefore the opportunity to precisely analyse their relationships and the transfers of bacteria/virus among them. Since highly pathogenic avian influenza HPAI H5N1 emerged in South-East Asia, multiple strains of viruses have been compared and their phylogeography is used to infer the spread of the virus across species, regions and continents, as well as to question the origin of the virus (Kilpatrick et al. 2006). Interestingly in the case of HPAI H5N1, it was shown that the ancestral low pathogenic strain of the virus originated in wild birds and was transmitted to domestic birds; the subsequent rapid evolution of the virus in the optimal conditions of South-East Asia poultry production systems was responsible for its evolution into a highly pathogenic strain (Munster et al. 2010; Beato and Capua 2011). Today, multi-host emerging infectious disease spread is often characterised by molecular approaches before the mode of transmission between hosts is understood. The case of the Nipah virus at the bat/human interface is a good example (Luby et al. 2006).

The use of non-pathogenic material to infer host-to-host contact and inter-host pathogen transmission pathway is still in its infancy but has attracted recent attention. Here as before, the fact that a genetically quasi-similar microorganism is detected in two host populations can indicate that a contact between these hosts has occurred. The bacterium *Escherichia coli* is a good indicator of transmission pathways within multi-host systems because *E. coli* is ubiquitous, shares the same niche as enteric pathogens and is transferred by the same route, and is one of the best-studied and best-known bacteria. *E. coli* population structure within a host population and between host populations has been used to infer social proxies of contact or proxies of infectious contacts (VanderWaal et al. 2013, 2014; Rwego et al. 2008; Goldberg et al. 2008). This approach is attractive for studies at the wildlife-livestock interface because it can be implemented under certain conditions in a non-invasive way, reducing drastically the costs and logistics of wildlife studies. It could in theory be extended to the comparison of bacterial communities between hosts to assess the extent of their interactions. Finally, antibiotic resistance (ABR) diffusion at wildlife-livestock interfaces belongs also to the process of exchange of genetic material between hosts with or without an environmental stage and requires contacts between hosts. The consequences of ABR diffusion in natural ecosystems are largely

unknown, but the evolution and selection of resistant genes in the wild could compromise the use of antibiotics (Wadman 2001), which represent the main tool to fight infectious diseases in domestic animals and humans (Allen et al. 2010). ABR in bacterial populations can be used as a special case of genetic diversity that can be used to track transmission. The emergence of ABR is mainly anthropogenic, resulting from a high and inappropriate use of antibiotics in humans and domestic animals (Skurnik et al. 2006). The diffusion of ABR in socio-ecosystems represents a special case of wildlife-livestock interface involving a strong anthropological driver (Martinez et al. 2009; Allen et al. 2010; Levy and Marshall 2004). Here the particularity is that the direction of the spread is known, originating in humans and livestock and spreading towards wildlife (Mercat et al. 2015). The risk of spill-back of ABR from wildlife towards livestock and/or humans is completely unknown and unexplored.

Of note, new approaches attempt to infer host-to-host contacts based on vector blood meals containing one or more host DNA materials, using the vectors as “flying syringes” (Bitome-Essonno et al. 2017). Developed in the field of disease ecology, these studies combine different levels of genetic characterisation within blood meals: at the level of host DNA, to infer vector-borne contacts between hosts; at the level of the pathogen of interest, to infer pathogen circulation within host communities; at the level of host-specific pathogen, to infer vector-borne contacts between hosts, a level that seems more efficient than the host DNA level (Makanga et al. 2017). These techniques could increase the capacity to implement non-invasive protocols (for the hosts) at the wildlife-livestock interface.

Wildlife-Livestock Contacts and Disease Ecology: Case Studies

Here we present three case studies mainly drawn from studies investigating the behaviour of wild and domestic hosts to infer contacts. They illustrate some key properties and drivers of wildlife-livestock interfaces. Unfortunately, to our knowledge and to date, no case of genetic studies implemented to infer contacts between wild and domestic host species have yet been published.

Fine-Scale Spatial Interaction Between Wild Boar and Cattle

Fine-scale spatio-temporal interactions between wild and domestic hosts and the role of resource selection may improve the knowledge in cross-species disease transmission. Assessing how animals use their environment and how this affects interspecific interactions is an important factor in determining the local risk for disease transmission and maintenance. In this study, data from concurrently monitored GPS-collared

domestic cattle and wild boar were used to assess spatio-temporal interactions and associated implications for *Mycobacterium bovis* transmission in a complex ecological and epidemiological system, Doñana National Park (DNP, South Spain). To assess annual and seasonal fine-scale interactions and differences in the use of available resources between cattle and wild boar, latent selection difference functions (LSD; (Barasona et al. 2014; Latham et al. 2011)) were estimated. Cattle resource selection or avoidance was assessed relative to wild boar space use, and variables that indicate the habitats most preferred by cattle relative to wild boar, and those most avoided by cattle relative to wild boar were predicted. The results from LSD analyses can then be used to make inferences about the differences or similarities in fine-scale habitat use and spatial overlap among species. The main assumption of LSD is that all resources should be equally available to both species within the study area. Overall, fine-scale spatial overlap of cattle and wild boar was seasonally high in some habitats at DNP. Similar use of water resources by both species resulted in high potential interspecific interaction around these landscape features, especially during the dry season. This high spatial overlap at such small spatial extents (e.g. waterholes are only 15 m in diameter) could influence interspecific transmission rates of bovine TB in this Mediterranean system. Therefore, limited differences in resource selection during summer and autumn, when food and water availability were limiting, resulted in negligible spatial segregation and thus probably high encounter rates. The spatial gradient in potential overlap between the two species across DNP corresponded well with the spatial variation in the observed incidence of bovine TB in cattle and prevalence of bovine TB in wild boar. This case study contributes to an applied understanding of multi-host disease ecology and will help to better target actions to reduce potential interactions in order to prevent disease transmission and design effective control strategies at the wildlife-livestock interface (Barasona et al. 2013, 2014).

Individual Versus Population Heterogeneity in Wildlife-Livestock Interface Studies

The level of heterogeneity of the host species/populations observed does matter to define the wildlife-livestock interface (McDonald et al. 2018). A medium-term telemetry study on African buffalo in southern Africa (spanning 6 years), in between the Northern tip of Kruger National Park in South Africa, the southern part of Gonarezhou National Park and the adjacent communal land, both in Zimbabwe, is a good example (Caron et al. 2016; de Garine-Wichatitsky et al. 2010). Adult female buffalo were first targeted in this study as representative of buffalo herd movement ($n = 47$). The objective was to identify the overlap between cattle herds and buffalo groups at open wildlife-livestock interfaces in between Kruger and Gonarezhou National Parks and the Sengwe communal land separating the parks. The home

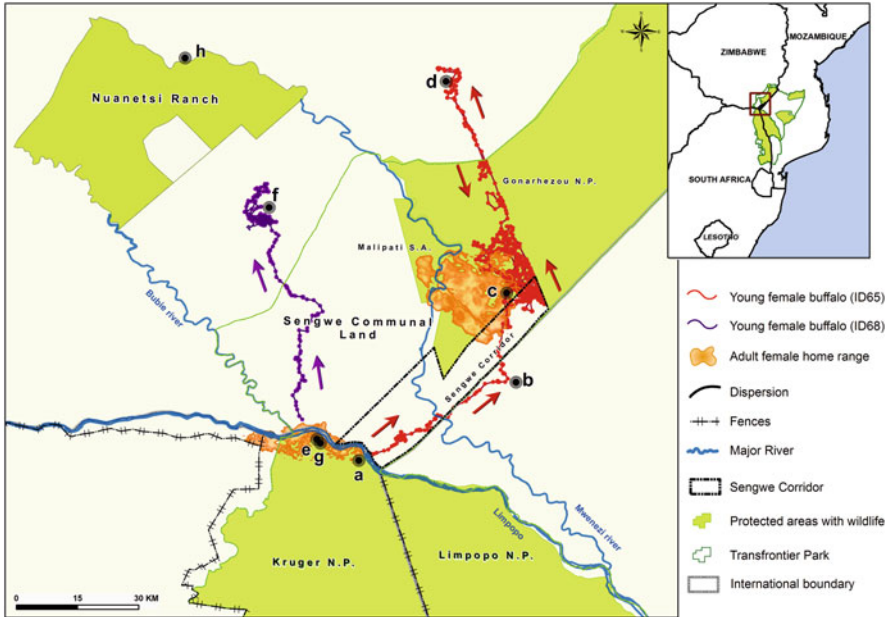


Fig. 3 Study area encompassing part of Mozambique, South Africa, and Zimbabwe. Inset map shows the location of the Great Limpopo Transfrontier Conservation Area within southern Africa. Orange areas represent the home ranges of 5 satellite collar-equipped adult female African buffaloes, representative of the five herds followed for the study in Kruger National Park (NP) ($n = 3$) and Gonarezhou NP ($n = 2$). Because of overlap among the herds, boundaries for the five herds cannot be seen. Data for the other adult female buffalo in the study are not represented. The home range of Kruger NP herds span the Limpopo River between South Africa and Zimbabwe. Long-distance movements of three subadult female buffalo are shown (letters from A to D, E to F and G to H). Arrows indicate the direction of movements for two buffalo; sites of capture and re-sighting are shown for the third buffalo. A complete description of the movements of these three buffalo is provided in the expanded figure legend online (<http://wwwnc.cdc.gov/EID/article/22/2/14-0864-F1.htm>). Reproduction from Caron et al. (2016)

range of adult female buffalo was relatively consistent across sites and years as can be seen in Fig. 3 (orange home ranges).

These home ranges were overlapping indicating an area of common use between buffalo groups, albeit limited. They also span moderately across the land-use boundary (i.e. the open interface between parks and communal land). Contact patterns between cattle herds and buffalo groups (as defined by adult female buffalo data) in this area was modelled and used to demonstrate the relationship between inter-species contacts and the incidence of foot-and-mouth disease in cattle (the African buffalo is a maintenance host for foot-and-mouth disease in Africa) (Miguel et al. 2013). Clearly, the contacts (as defined by the modes of transmission of foot-and-mouth disease) occurred in key foci in the available habitat as for example water point or grazing areas. Management of these key areas was then possible to mitigate contact and pathogen transmission to control disease spill-over. The story was

almost over. But during the last exercise of the telemetry study, informal communication by local stakeholders led to equipping 19 young females (subadults between 2.5 and 4.5 years, before their first reproductive cycle). In less than 3 months during the rainy season, 3 out of 19 (16%) of these young females engaged in movements much larger than any home range of adult females during the same protocol and during the previous 5 years of study. The three young females moved from 64 to 96 km in a few days. These results required the redefinition of the wildlife-livestock interface: the interface was initially defined using female adult buffalo and head of cattle data and spanned a couple of kilometres within the communal land; subsequently, the subadult movement data increased the area of potential overlap between buffalo groups and cattle herds by a band of more than 50 km. It has to be noted that even if a migration-type pattern would have been expected in this study site, most experts would have predicted a direction towards the South within the Kruger National Park where the anthropic impacts are much less; however, the reverse occurred with subadult female buffalo migrating (i.e. not just foraging) into an extensive farming area.

Theoretically, the risk of pathogen spill-over between buffalo and cattle was not homogenous across this newly defined interface: relatively high in the first few kilometres because of overlap between cattle herds and large buffalo groups, it decreased progressively as the distance to the protected area increased where only small groups of buffalo migrated rapidly. The lack of information about this type of behaviour in buffalo (e.g. how many animals did engage in these movement patterns? which age groups apart from young female, if any?) precluded any quantitative assessment of this risk. However, the risk of pathogen spill-over in the area is known (Caron et al. 2013) and the management of this risk had to be revisited. These results call for a better management of matrices of conservation and agricultural land-use and the coupling of movement and landscape ecology (Doherty and Driscoll 2018).

Macro-ecological Scale Assessment of Conflicts Between Alien and Native Species Linked to Anthropogenic Variables in a Mediterranean Hotspot

Characterising how species richness is spatially distributed and identifying the major drivers of that pattern is a relevant challenge as regards to the ecology of host species. In the context of understanding the distribution of alien species in relation to that of native species, this study exemplifies a macro-ecological scale approach that could be taken into account to evaluate the competition between native and invasive species at the wildlife-livestock interface. This study identified and characterised conflict areas among the Spanish alien fauna (59 vertebrate species: 5 amphibians, 15 reptiles, 6 mammals and 33 birds) and all native terrestrial vertebrate species in Spain (746 species: 29 amphibians, 62 reptiles, 111 mammals

and 544 birds), as a mean to provide directional indications with which to minimise the potential negative effects that the alien species may have on host ecosystems. To achieve this, the study applied spatially explicit predictive modelling in order to explain the diversity of vertebrate species. The modelling approach was calibrated based on climatic, topographic, ecological and land-use variables (Rahbek et al. 2007). The eco-geographical variables (EGVs) used for modelling were then selected on the basis of their significance as regards explaining the distribution of different taxa fauna. Two procedures were applied to transfer the EGVs to territorial units (10×10 km UTM grid squares): (1) the medium value of every climatic and topographic variable was calculated for each territorial unit; and (2) the percentage of the total area occupied by each type of land use within each territorial unit, thus enabling to obtain an independent variable for each type of land use. After checking for the predictive performance of the models, it was used to generate predicted richness of species for the whole country. The relative importance of the different factors was assessed using variation partitioning, and independent models for each factor (partial models) were developed. Overall, the main factor explaining the observed patterns of richness of alien species was the anthropogenic factor (80% of the total variation), which included urban land use and proximity to cities, which are mainly related to the introduction step in the invasive process and are known predictors of alien species distribution patterns (Luck 2007). The other important predictor of actual conflict areas was the number of native species, which is in accordance with “the rich get richer” acceptance hypothesis, which predicts a higher number of alien species in areas with high native species diversity. Alien species may therefore affect the invaded ecosystems to varying degrees, some resulting in substantial economic and health costs to human societies, along with causing the progressive substitution and elimination of native species through predation, hybridisation, the introduction of disease, habitat alteration and competition for resources or space. In this study, many of the actual conflict areas identified overlapped with protected areas, as is the case of Natural or National Parks, suggesting that additional conservation concerns could arise as a result of alien species spreading into these priority conservation areas, which are often inhabited by endangered species (Carpio et al. 2017).

A New “Science of the Interfaces”?

This chapter emphasised the importance of wildlife-livestock interfaces in health ecology in the current global context and how to characterise them to better understand, prevent and control infectious diseases in species and populations of interest. The emergence of shared infections among wildlife and livestock is largely a consequence of the colonisation and exploitation of novel host species and new biogeographic areas by pathogens (Lloyd-Smith et al. 2009). Overall, livestock constitutes on average 37% of the agricultural gross domestic product worldwide (Alexandratos and Bruinsma 2012) and is one of the most important and rapidly

expanding commercial agricultural sectors (Thornton 2010). Infections shared with wildlife cause direct losses to this sector through increased mortality and reduced livestock productivity, as well as indirect losses associated with cost of control, loss of trade, decreased market values and food insecurity (Dehove et al. 2012). Diseases also represent a potential burden to entire ecosystems, affecting biodiversity, and changing behaviour or composition of animal populations (Daszak et al. 2000). On one hand, anthropogenic land use, change of farming systems, conversion of natural habitats into production landscapes and intensification of international travel and wildlife trade continue to decrease or shift former geographical barriers between livestock and wildlife, likely facilitating exposure to novel pathogen communities (Patz et al. 2008). On the other hand, decreasing wildlife diversity and the isolation of ecological communities through habitat fragmentation may effectively increase the trends of pathogen transmission (Keesing et al. 2010) and have other yet to be realised consequences.

This global context underlines the fact that standard veterinary or public health approaches to disease (i.e. relationship between one host and one pathogen) are obsolete in most contemporary cases. Characterising wildlife-livestock interfaces has traditionally been through the investigation of epidemiological/ecological functions of local assemblages of wildlife species as static spill-over/spill-back or reservoir hosts (Siembieda et al. 2011). Currently though, wildlife-livestock interfaces are considered dynamic, truly diverse and bidirectional with pathogens transmitted freely within and between wildlife and livestock species (Wells et al. 2018). Health professionals are therefore required to transform their professions to adapt to these changes and the study of health issues at wildlife-livestock interfaces provides a good example. The recent development of integrated approaches to health (e.g. One Health, EcoHealth and more recently Planetary Health) expresses this need to change classical approaches (Buse et al. 2018; Lerner and Berg 2017). Most approaches consider that the linkages among humans, animals and their environments and their differences are mainly due to the academic definitions and political contexts. However, they often share a set of principles (below in italics) that have been well defined by Charron (2012) and that apply well to wildlife-livestock interfaces. Firstly, the various dimensions that need to be taken into account at wildlife-livestock interfaces include the ecological, socio-cultural, governance and economic contexts and require a *socio-ecosystem approach* (Ostrom 2009) to health issues. *Systems thinking* can help in connecting these different dimensions together and in addressing the multiple scales (spatial and temporal) that are often necessary to understand the ecology of particular diseases. The multiple scientific fields necessary to tackle health issues at wildlife-livestock interfaces call for *interdisciplinary research*. More and more, multi-stakeholder processes bringing different and non-academic actors in the problem resolution group provide much better efficiency at gathering academic and non-academic publics, including indigenous knowledge. *Local participation* (including farmers and community members) transforms interdisciplinarity into *transdisciplinarity* in research. Transdisciplinarity is initially more time-consuming and necessitates that researchers/managers accept that they are not the sole owners of knowledge and challenges their (biased) vision of the system; but

once reached, it translates into better-adapted and co-designed options for management that usually creates the necessary conditions for the sustainability of management. The objective is to reach a *knowledge to action* process involving many non-academic stakeholders, where research produces knowledge that is, after consultation with stakeholders, integrated into co-designed management options. Another principle, *social and gender equality* (including *environmental justice*) applies to wildlife-livestock interface issues when dealing with human health but also within transdisciplinary approaches. These principles provide guidelines for developing frameworks to tackle wildlife-livestock interface health issues and indicate the direction for future wildlife-livestock interface health studies. So far, examples integrating these various principles are few (Charron 2012).

Thinking outside health ecology, the principles presented above apply to a much broader range of disciplines than just animal and public health. In the introduction and examples, we have demonstrated how wildlife-livestock interfaces impact the relationship between local development and biodiversity conservation. The large field of ecosystem health (Rapport et al. 1998) (much older and larger than all integrated approaches to health combined) also addresses the interface of natural and anthropogenic habitats and characterises the services and disservices of ecosystems, their functional state and their resilience under the impact of global changes. This large field is often cited in the integrated approaches to health within the triptych of human, animal and ecosystem. It remains the poor parent of the trio though, ill-defined and often its principles are unknown to its users within the field of health. Within the field of social sciences, the dynamics of human populations, the social and cultural complexity and the depth of linkages between people and nature provides also a large field of interest at wildlife-livestock interfaces. Wildlife-livestock interfaces can also attract interest from other fields such as natural resource use and management and the associated fields of economics, food security and human nutrition. The development of the integrated approaches to health leads, therefore, to a much larger societal phenomenon impacting many academic fields and responding largely to the acknowledgement that natural systems are complex by nature and dynamic, and does so in abnormal ways recently due to global changes triggered by human activities.

In conclusion, it is of our belief that a “science of the interface” has its place in the spectrum of thematic fields. It is a necessity because of the context of global changes and the extensive wildlife-livestock-human interfaces created and impacting human societies and ecological processes, including epidemiological processes. The gradient of wildlife-livestock interfaces expands from cities to remote natural areas and includes challenges across sectors. It requires applying the principles presented above (systems thinking, transdisciplinarity, local participation, sustainability, gender and social equality and knowledge to action) to adapt to the novel nexus of people, animals and ecosystems at wildlife-livestock interfaces. Curricula will need to be adapted and made multidisciplinary to train scientists and managers who understand and apply these principles and embrace the fundamental and core concepts of these integrated approaches. This means producing individuals with multidisciplinary expertise and the ability to connect with other individuals from

other disciplines in interdisciplinary frameworks. With no doubt, the socio-ecological health framework presented in chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health” and the new tools available presented in chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife” will be dwarfed in power and efficiency by the ones developed in the near future and which will increase our capacity to characterise, understand and manage wildlife-livestock interfaces.

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Quantifying Transmission Between Wild and Domestic Populations



Beatriz Martínez-López, José Manuel Díaz-Cao, and Kim M. Pepin

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Why and How Quantifying Transmission Between Wild and Livestock Populations?

Recently there have been unprecedented increases in disease transmission at the wildlife-livestock interface due to land use and human activity changes that have increased contacts among wildlife and livestock species (Hassell et al. 2017; Wobeser 2002). Transmission at the wildlife-livestock and wildlife-livestock-human interface is recognized as one of the most important reasons for disease emergence or reemergence (i.e., pathogens adapting to new hosts, increased number of outbreaks and geographical spread) (Miller et al. 2013; Siembieda et al. 2011).

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Therefore, the quantification of transmission at these interfaces is key to not only understand disease dynamics and identify high-risk areas/time periods but also to be able to more cost-effectively allocate preventive and control interventions (Sokolow et al. 2018). Many methods have been developed aiming to better quantify the transmission between wildlife and livestock populations. This advance has been driven in part by the novel technologies and approaches to collect data about demographics, movements, and contacts within and between multiple populations and species (see chapters “Collecting data to assess the interactions between livestock and wildlife” and “Characterization of wildlife-livestock interfaces: the need for interdisciplinary approaches and a dedicated thematic field”) as well as the advances in computational science and analytical methods.

Box 1 Main Research Questions that Requires Quantifying Transmission Between Wild and Livestock Populations

1. **Conduct risk assessment:**
 - Characterize the main factors contributing to disease transmission
 - Define high-risk areas and time periods for transmission
 - Identify the most important transmission pathways
 - Evaluate the risk of introduction into a naïve population
2. **Predict pathogen spread:**
 - Understand transmission dynamics
 - Quantify transmission rates
 - Assess how contact network structure contributes to the pathogen spread
3. **Evaluate strategies for disease prevention and control:**
 - Evaluate multiple epidemiological scenarios and interventions
 - Propose more cost-effective strategies
 - Evaluate impact in the population

This chapter aims to provide a brief overview of the main modeling approaches available to quantify the multi-host disease transmission at the wildlife-livestock interface, illustrated with specific case studies. We are not trying to be exhaustive, but we will discuss the methods most popular/commonly used to address specific research questions (Box 1) and the benefits, uses, and limitations of each method. We also provide examples of their applications in each section of the text as well as in a summary table (Table 1). We will also cite those methods that, although not extensively used to quantify multi-host disease transmission, we believe they could be easily adopted from other disciplines (e.g., computer science, social sciences, economics, etc.) to provide valuable insights into wildlife epidemiology. Finally, we will discuss recommendations and future directions to better understand disease dynamics at the wildlife-livestock interface.

Different types of approaches are extensively used in epidemiology to evaluate pathogen transmission among individuals in one or more populations but considering wildlife-livestock or wildlife-livestock-human host groups is less common (Lloyd-Smith et al. 2009). Some of the reasons may be the complexity of gathering detailed/quality data on wildlife (see chapters “Collecting data to assess the

Table 1 Selected studies using different approaches to analyze disease transmission at the wildlife-livestock interface

Study	Approaches	Disease	Hosts	Study region	Description	References
Correlative approaches						
Characterizing African tick communities at a wildlife-livestock interface using repeated sampling protocols and models	Generalized linear mixed models with site occupancy models	Ticks-borne	Vegetation	Zimbabwe, Africa	Evaluate tick abundance in multi-host systems, identify factors influencing the density or the probability of detections of ticks, comparing different landscape compartments	Miguel et al. (2014)
Wildlife and domestic pig interactions at the wildlife-livestock interface of Murchison falls national park, Uganda, and the potential association with African swine fever outbreaks	Multiple correspondence analyses. Hierarchical clustering analysis	ASF	Wild and domestic pigs	Uganda, Africa	Investigate indirect wildlife-pig interactions and the associated human behavior and husbandry practices and evaluate their association with ASF outbreaks reported by farmers	Kukielka et al. (2016)
A Bayesian approach to study the risk variables for tuberculosis occurrence in domestic and wild ungulates in South Central Spain	Bayesian mixed-effects multivariable logistic regression	Bovine tuberculosis	Wild and domestic ungulates	Spain, Europe	Identify the nature and extent of the association between TB distribution and potential risk factors associated with cattle, wild ungulates, and the environment	Rodríguez-Prieto et al. (2012)
Estimating dynamic risk factors for pathogen transmission using community-level bird census data at the wild/domestic bird interface	Correlation analysis counting protocol, risk mapping	Avian influenza	Wild and domestic birds	Zimbabwe, Africa	Assess transmission risks in a complex epidemiological network that consists of spatiotemporally variable bird communities	Caron et al. (2010)

(continued)

Table 1 (continued)

Study	Approaches	Disease	Hosts	Study region	Description	References
One Health profile of a community at the wildlife-livestock interface, Mpumalanga, South Africa	Surveys and logistic regression analysis	Various	Wild and domestic	South Africa, Africa	Describe different aspects of health perception to develop a One Health profile of an agro-pastoralist population at the interface of wildlife areas in eastern South Africa	Berrian et al. (2016)
Influenza A H5N1 and H7N9 in China: A spatial risk analysis	Species distribution models (MaxEnt), Risk assessment	Avian influenza	Wild and domestic birds	China, Asia	Understand spread mechanisms and generate spatial risk profiles for the main Influenza subtypes in China	Bui et al. (2017)
Spatial modeling for low pathogenicity avian influenza virus at the interface of wild birds and backyard poultry	Species distribution models (MaxEnt), multicriteria decision analysis	Avian influenza	Wild and domestic birds	Argentina, South America	Generate space risk models of occurrence. Authors aim to develop a methodological approach for data-scarce scenarios	La Sala et al. (2019)
The wildlife-livestock interface modulates anthrax suitability in India	Species distribution models (MaxEnt)	Anthrax	Outbreaks in different species	India, Asia	Analyze contribution of the wildlife-livestock interface in the suitability of anthrax outbreaks	Walsh et al. (2018)
Spatially explicit modeling of animal tuberculosis at the wildlife-livestock interface in Ciudad Real province, Spain	Species distribution models (MaxEnt), logistic regression, cluster analysis	Bovine tuberculosis	Cattle and wild ungulates	Spain, Europe	Evaluate the influence of wildlife demographics and hunting management, land use, climatic, and environmental variables, and TB status in wildlife in TB breakdown, persistence, and new infection on cattle farms. Generate high-resolution predictive maps of TB occurrence to guide risk-based interventions	LaHue et al. (2016)

Spill-over of pH1N1 to swine in Cameroon: an investigation of risk factors	Random forest	Avian influenza	Wild birds, poultry, and swine	Cameroon, Africa	Assess how contact rates among different species in different managements influence transmission	Larison et al. (2014)
<i>Toxoplasma gondii</i> infection in wild mustelids and cats across an urban-rural gradient	Random forest, regression analysis	Toxoplasmosis	Cats and mustelids	Chile, South America	Analyze distribution in terrestrial/aquatic interfaces, risk factors, and contribution of variables to seropositivity	Barros et al. (2018)
Ecological indicators of mammal exposure to Ebola virus	Boosted regression trees, phylogenetic analysis	Ebola	119 mammal species	Africa	Identify predictors of exposure (BRT) and map presumptive phylogenetic distribution in Africa. Suggest species for priority sampling	Schmidt et al. (2019)
Spatial distribution and risk factors of highly pathogenic avian influenza (HPAI) H5N1 in China	Boosted regression trees, logistic regression	Avian influenza	Poultry	China, Asia	Analyze risk factors associated with outbreaks. Predict the geographical distribution of viral presence	Martin et al. (2011)
Spatiotemporal analysis of African swine fever in Sardinia (2012–2014): trends in domestic pigs and wild boar	Space-time cluster analysis, temporal evolution, maximum spatial distances	ASF	Wild boar and pigs	Italy, Europe	Evaluate the role of wild boar in the spatiotemporal patterns of ASF in Sardinia	Iglesias et al. (2017)
Mechanistic approaches						
Assessing disease risk at the wildlife-livestock interface: a study of Sierra Nevada bighorn sheep	Quantitative risk analysis	Various	Bighorn sheep	USA, North America	Assess risk disease for bighorn sheep in shared habitats with domestic sheep	Clifford et al. (2009)

(continued)

Table 1 (continued)

Study	Approaches	Disease	Hosts	Study region	Description	References
Rapidly assessing the risks of infectious diseases to wildlife species	Semi-quantitative risk analysis	Various	Antelope	Kazakhstan, Asia	Adapt risk assessment framework to rapidly assess and prioritize the risks of livestock pathogens for wildlife	Beauvais et al. (2019)
A model of animal–human brucellosis transmission in Mongolia	Compartmental model	Brucellosis	Sheep, cattle, and human	Mongolia, Asia	Develop a model of human/livestock transmission of brucellosis. Simulate epidemics with and without interventions	Zinsstag et al. (2005)
Threshold dynamics in a periodic three-patch Rift Valley fever virus transmission model	Multi-host SIR model	Rift Valley fever	Livestock	Africa and the Middle East	Develop a periodic three-patch model to describe the transmission of Rift Valley fever virus	Wen et al. (2019)
The metapopulation dynamics of an infectious disease: tuberculosis in possums	Multi-host SIR model	Tuberculosis	Possums	New Zealand, Oceania	Study temporal dynamics of tuberculosis in possums taking into account spatial variation. Different scenarios for disease control based on a larger number of habitat patches are compared	Fulford et al. (2002)
Understanding African Swine Fever infection dynamics in Sardinia using a spatially explicit transmission model in domestic pig farms	Simulation model (spatially explicit), Regression	ASF	Domestic pigs	Italy, Europe	Study dynamics and characteristics of ASF infections adapted to a specific scenario. Apply spread simulations to estimate the relative contribution of different species to ASF occurrence in the area	Mur et al. (2018)

Quantifying microbe transmission networks for wild and domestic ungulates in Kenya	Network analysis, genomic analysis	<i>Escherichia coli</i>	Cattle and wild ungulates	Kenya, Africa	Assess patterns of interspecific pathogen transmission among ten species of wild and domestic ungulates in Kenya	VanderWaal et al. (2014)
Cross-species transmission potential between wild pigs, livestock, poultry, wildlife, and humans: implications for disease risk management in North America	Network analysis (transmission-potential networks), descriptive statistics	84 pathogens	Wild pigs, livestock, poultry, wildlife, and humans	USA, North America	Identify potential sharing pathogens of economic importance among various species, Evaluate the reported prevalences in US wild pig populations to assess knowledge gaps and illustrate the importance of disease risk management	Miller et al. (2017)
A benefit–cost analysis decision framework for mitigation of disease transmission at the	Cost–benefit analysis	Rabies	Vampire bat	Mexico, Central America	Provide a decision framework for benefit–cost analyses of disease transmission mitigation at the wildlife–livestock interface	Shwiff et al. (2016)
Risk assessment and cost-effectiveness of animal health certification methods for livestock export in Somalia	Cost–effectiveness analysis	Various	Domestic ungulates	Somalia, Africa	Assess economic consequences of different health certification protocols for livestock exports in Somalia	Knight-Jones et al. (2014)
Expected utility of voluntary vaccination in the middle of an emergent Bluetongue virus serotype 8 epidemic: A decision analysis parameterized for Dutch circumstances	Cost–utility analysis	Bluetongue	Cattle	Netherlands, Europe	Assess farmer’s expected utility of vaccination and willingness to vaccinate	Sok et al. (2014)
Molecular approaches						

(continued)

Table 1 (continued)

Study	Approaches	Disease	Hosts	Study region	Description	References
Bluetongue virus spread in Europe is a consequence of climatic, landscape, and vertebrate host factors as revealed by phylogeographic inference	Phylogeography	Bluetongue	Various	Europe	Asses drivers of spread of Bluetongue	Jacquot et al. (2017)
Phylogeography of foot-and-mouth disease virus serotype O in Ecuador	Phylogeography, Molecular epidemiology	Foot-and-mouth disease	Cattle	Ecuador, South America	Spatial and epidemiological dynamics of FMDV serotype O in Ecuador	Fagundes de Carvalho et al. (2013)

interactions between livestock and wildlife” and “Characterization of wildlife-livestock interfaces: the need for interdisciplinary approaches and a dedicated thematic field”), livestock (and human) populations simultaneously as well as other methodological problems, including the need to incorporate multidisciplinary teams to achieve a well-balanced study design, obtain enough sample size and adequately design, parameterize, and interpret those models (Alexander et al. 2012; Allen et al. 2012; Huyvaert et al. 2018).

Transmission at the wildlife-livestock interface is driven not only by animal behavior, social structure, and spatial overlap but also by the pathogen characteristics (survival, transmission pathways) and environmental and climatic factors (landscape structure, weather, soil characteristics, etc.) (Plowright et al. 2017). Therefore, the selection and design of the type of modeling approach at the wildlife-livestock interface depends on multiple factors and likely will need to be adapted based on the disease and the epidemiological scenarios to be considered as well as the data available.

In this chapter, we will focus on what, for convenience here, we have classified into three groups of approaches: (1) correlative approaches; (2) mechanistic approaches; and (3) molecular approaches (Fig. 1). All those approaches can be used alone or in combination to study disease transmission at the wildlife-livestock interface across different spatio/temporal scales. The most appropriate method and scales to consider will depend on feasible/available data streams and objectives: e.g., designing surveillance at a national level (using a species distribution model for the entire region or country) or proposing protective measures regarding farms (quantifying wildlife visits at the farm/pasture level).

In the next section, we will describe the current methods applied to quantify multi-host transmission and their associated impact (economic impact, conservation, etc.). We also describe the bias/limitations of each technique and why it may be beneficial to combine them to have a more holistic view of the problem and/or improve accuracy.

Review of Most Commonly Used Approaches

Correlative Approaches

Here we refer to “correlative approaches” to all the data-driven approaches from statistical methods (regression, correlation, Bayesian networks, etc.) to machine learning algorithms that make use of data obtained through observational (genetic data, surveillance) or experimental (sentinel studies, intervention studies) studies for the purpose of estimation (i.e., calculating unknown parameters) or prediction (approximating outcomes for unseen data or future time periods).

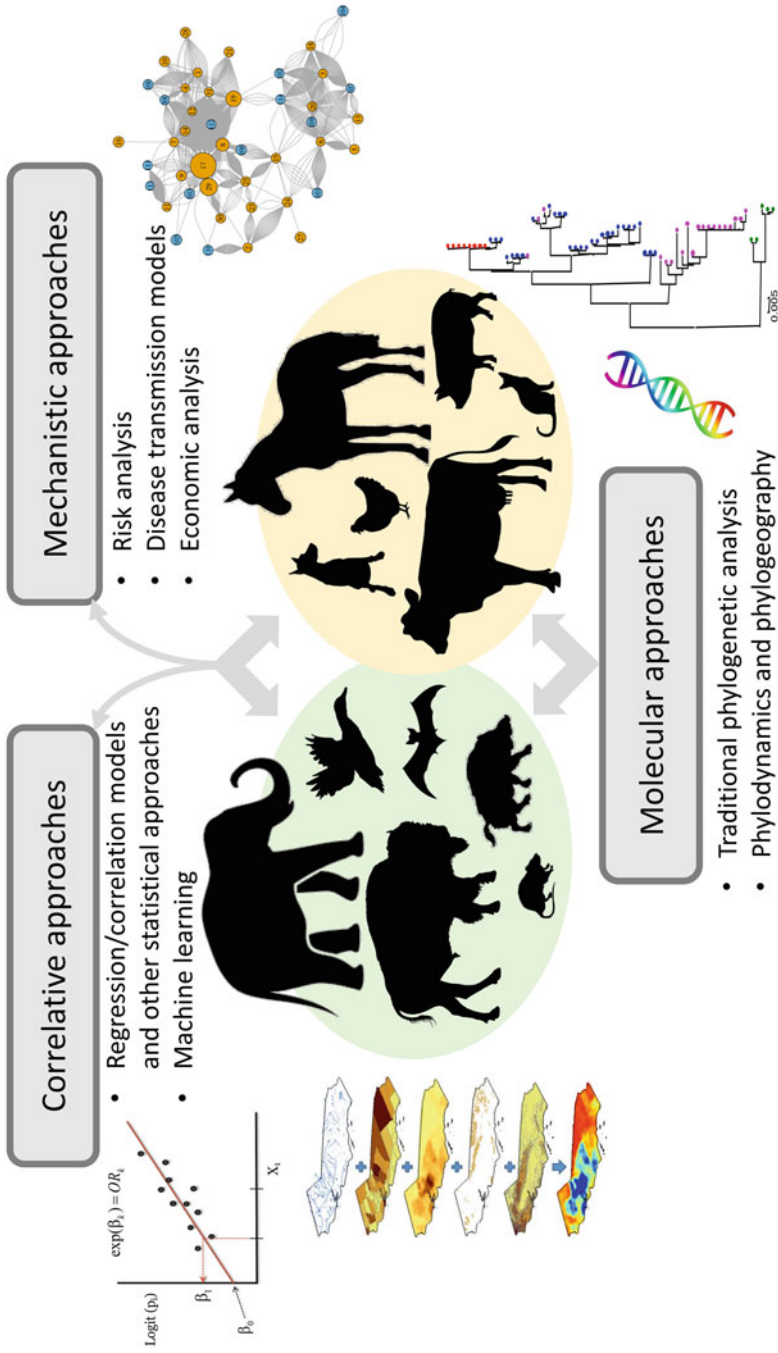


Fig. 1 Schematic figure of the main three groups of approaches to quantify multi-host transmission at the wildlife/livestock interface

Statistical Methods

Regression/Correlation of Observational Data

Regression models of disease surveillance data or other observational data are used to predict ongoing spatial disease spread, investigate effects of control strategies, perform risk analyses, or study the impact of diseases on population dynamics (Martínez-López et al. 2014; Rodríguez-Prieto et al. 2012; Berrian et al. 2016). These approaches involve defining a set of predictors that explain the patterns of cases reported in livestock over space, time, or both. Typical predictors include the distribution and movement patterns of host populations, host abundance, host social structure, and climatic and environmental conditions. The choice of predictors to evaluate depends on transmission mechanisms that are known to be important, for example, whether the transmission is direct, vector-borne, or environmentally mediated, and the array of host species that might be involved in reservoir dynamics or spill-over to livestock. Logistic, linear, and count data can be modeled with appropriate distributions (Binomial, Gaussian, Poisson, negative-binomial, zero-inflated, etc.) using Generalized linear or additive models and have been successfully and extensively applied in the literature to fulfill these goals. However, modeling disease transmission involving wildlife poses unique challenges (Cross et al. 2019). Information on wild hosts is collected at different spatial resolution and sampling intensity relative to that in livestock host populations and the wildlife-livestock interface is temporally and spatially dynamic, due to dynamic environmental conditions, seasonality, animal behavior, and anthropogenic activities. This variability should be included in modeling if findings are expected to be generalized. It is also not infrequent that contacts to assess disease transmission are measured in separate areas or sampling points that aggregate subjects/observations (e.g., by herd, area, enclosure). This can lead to autocorrelation and lack of independence among the observations that can affect interpretation of covariate effects if left accounted. When studies involve the comparison of collectives (e.g., groups in different areas), the different conditions of the environment may also act as modulators of the transmission of disease and a certain degree of correlation among the members of a collective may be expected. However, this usually results in complex datasets in which hierarchical dependencies among variables can be difficult to interpret and issues related to multicollinearity arise. The application of multilevel or random effects models allows accounting for correlation in a nonrandom sample and considers this clustering (Stryhn and Christensen 2014). Techniques such as principal component analysis (PCA), multiple factor analysis (MFA), multiple correspondence analysis (MCA), or factor analysis of mixed data (FAMD) may be helpful for reducing dimensionality into few posterior representative factorial components to run posterior models (Kukielka et al. 2013).

Box 2 Bayesian Versus Frequentist Statistical Frameworks for Modeling Disease Transmission at the Wildlife/Livestock Interface¹

✓ Main practical advantages

- Suitable for **small sample sizes** (do not require to assume an infinitely large sample)
- Easily deal with **missing data** (data augmentation)
- Incorporation of **Prior information** (previous knowledge, expert opinion, etc.)
- **Fit models** that are otherwise **difficult**, if not impossible, to fit using conventional methods, ex. hierarchical models with correlated (clustered) spatial and/or temporal information (time-series)
- **More intuitive interpretation of findings** (based on probabilities)
- It accounts for **two types of uncertainty** (one due to random variation and other due to imperfect knowledge of the phenomenon)

✗ Main challenges

- **Relative complexity in model construction** (not so much when using softwares such as WinBUGS, INLA, RJAGS, etc. but...usually requires some programming abilities)
- Difficulties to objectively define and integrate **prior knowledge** on proper/suitable informative prior distributions

Regression/Correlation of Experimental Data

While regression studies of observational data are mainly correlative and cannot disentangle causation, regression analysis of data from sentinel or experimental studies of interventions can be used to dissect factors that cause particular case patterns in livestock. A sentinel must always interact with both the pathogen and the host population of interest. The suitability of a candidate sentinel can be assessed using retrospective surveillance data. Network analysis may be especially useful for identifying subjects/areas (e.g., animals, hunters, wildlife managers, slaughterhouses or meat processors, etc.) that capture or concentrates a high amount of information about the whole system (Colman et al. 2019). Excessive variation within a sentinel population would greatly complicate the interpretation of findings and therefore, it is important to control members of the sentinel population regarding age, sex, or other relevant characteristics, depending upon the type of response measured. The value of

¹Frequentist approaches, from bivariate analysis to multivariate and multi-level models, have been extensively used to assess risk factors contributing to disease transmission at the wildlife-livestock interface. More recently, Bayesian analysis has been also proposed as a convenient and, many times, more robust and flexible framework.

a sentinel to define the status of a target population may be evaluated with properties that are analogous to diagnostic test sensitivity and specificity (e.g., Halliday et al. 2007). The use of sentinels is primarily focused on enabling timely detection and response to important livestock pathogens. However, combined with an appropriate experimental design and analytical framework, sentinel studies can improve our mechanistic understanding of spill-over and evolution of pathogens at the wildlife-livestock interface (Pepin et al. 2019). Ideally, early warning sentinels must allow detect response prior to the exposure or the appearance of cases in the target population. Syndromic monitoring of sentinels may be used to create decision trees to assess risks based on the frequency of appearance of determined clinical signs (Saegerman et al. 2016) which may be useful for predicting the transmission risk of certain pathogens in a community.

Frequentist Versus Bayesian Statistical Frameworks

All the regression/correlation approaches mentioned above could be conducted within a frequentist or a Bayesian framework (see Box 2).

Frequentist approaches, from bivariate analysis to multivariate and multilevel models, have been extensively used to assess risk factors contributing to disease transmission at the wildlife-livestock interface. More recently, Bayesian analysis has been also proposed as a convenient and, many times, more robust and flexible framework. Bayesian and frequentist methods present a philosophical difference in how probability is understood. In a frequentist approach, probability is considered as the frequency of events, while from a Bayesian point of view, it reflects the degree of certainty about an event. Bayesian analysis incorporates previous knowledge and the degree of certainty about the parameters to study and obtains posterior distributions based jointly on the likelihood and the prior distributions. This mixture of both sources of information allows less dependence on large sample sizes compared to frequentist requirements, which provides a practical advantage for quantifying disease transmission in the wildlife-livestock interface where large sample sizes are often not available. Furthermore, interactions at the wildlife-livestock interface are shaped by many factors: densities, abundance, behavioral differences, routes of pathogen transmission, host physiological condition, host immunological status, climatic conditions, and season of the year (Plowright et al. 2017). Uncertainty from the effects of these factors on spill-over is often due to a lack of previous knowledge rather than random variation. Bayesian statistics allow accounting for both types of uncertainties and incorporating them into modeling as random variables with assigned probability distributions.

Computational requirements of Bayesian analytics have traditionally inclined research toward the use of frequentist methods. Nowadays, Bayesian analytics may be implemented with relative ease using different widely available software or R-packages (OpenBugs, INLA, JAGS, CARBayes, etc.). This increasing accessibility has led to an explosive rise in the last decades of Bayesian frameworks in the wildlife-livestock interface research. However, Bayesian analysis is not exempt from

drawbacks. The proper establishment of priors is still a subjective step and may have a huge impact on the model outcome. Therefore, when Bayesian approaches are chosen, researchers should investigate the strength that prior assumptions have on their results and assess the sensitivity of posterior inferences. It can also be useful to compare Bayesian to frequentist results.

Other Statistical Approaches

Spatial and Spatiotemporal Cluster Analysis

Disease investigation may aim to identify areas at the wildlife-livestock interface and/or time periods at higher risk of disease occurrence (e.g., Fig. 2). There are a number of approaches to detect space–time clusters. One of the most popular and widely used is SaTScan (Kulldorff and Information Management Services 2009), which evaluates or “scans” a geographical area and identifies zones or “windows” with a higher (or lower) number of events (i.e., animals exposed or with disease) than expected (i.e., assuming a constant probability of an event). A temporal component may also be considered. Depending on the type of model selected, inputs may be the number of events/cases at a particular time (i.e., Permutation model), the number of cases and controls (i.e., Binomial model), or the cases and population at risk (i.e., Poisson Model) (Kulldorff 1997; Kulldorff et al. 2005). Hypothesis testing may be subsequently incorporated to examine the differences between observed occurrences and expected rates (or counts) inside/outside the window according to an assumed

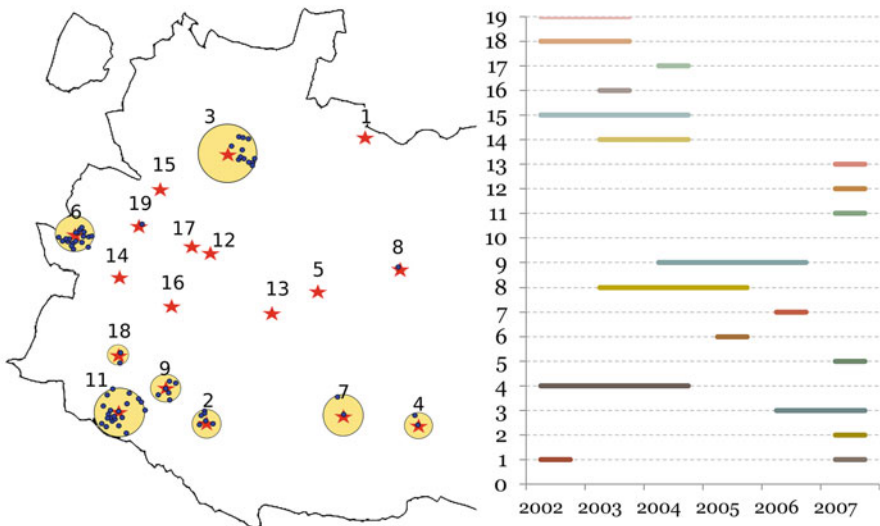


Fig. 2 Example of space–time cluster analysis to detect significant clusters of bovine tuberculosis prevalence in cattle in Spain

distribution. This approach is useful to identify high-risk areas as well as to detect spatiotemporal patterns of disease occurrence at the wildlife-livestock interface and generate hypotheses and testable explanations for the clusters detected. When a significant cluster is found, there are usually four possibilities that may have contributed to this increase in the number of events: (1) new introduction of the disease into an area, (2) changes in the frequency of disease occurrence (e.g., from endemic to epidemic), (3) higher notification of cases, or (4) increase in the sampling/effectiveness of surveillance in a specific time/space. One limitation is that the predefined morphology/shape of the scanning window (typically circular, although it could be also elliptical) may not match with the real shape of the risk area since clusters may not follow a precise geometry. Because of these constraints, negative cases may appear within high-risk windows. Efforts have been made to scan-based cluster analysis to detect irregular geometries (Tango and Takahashi 2012) but these approaches are usually computationally demanding.

Bayesian Belief Networks

A Bayesian network or Bayesian belief network is a probabilistic directed acyclic graphical model (a type of statistical model) that combines a set of variables and their conditional dependencies via a directed acyclic graph (DAG) in such a way that gives the best overall fit to the data while being probabilistically coherent (e.g., Fig. 3). It is a novel approach for structure discovery that has only been recently used in very few wildlife-livestock or wildlife-livestock/human interface studies (e.g., Mayfield et al. 2018), but it is well suited to investigate such a complex

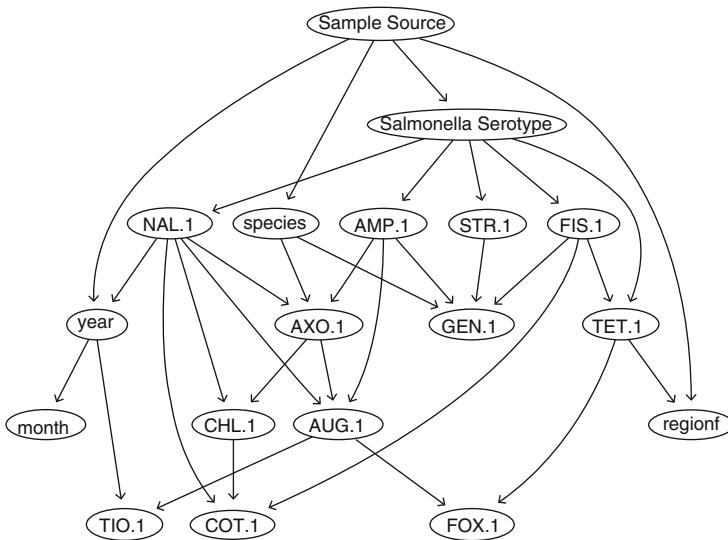


Fig. 3 Example of a Bayesian belief network of resistant Salmonella isolates found in multiple bird species

phenomenon. In this approach, we usually identify the best fitting model of all possible DAGs for exact Bayesian structure discovery (Koivisto and Sood 2004). Then, we address over-fitting by using a bootstrapping approach using Markov chain Monte Carlo (MCMC) simulation (Friedman et al. 1999). This multilevel approach allows to take into consideration the potential interdependences of all variables under study and can be easily updated and adapted as new data is available to more realistically model complex and rapidly evolving scenarios.

Machine Learning Algorithms

Regression approaches have been widely used for predictions, but these methods may present limitations when some of their assumptions cannot be accommodated. Alternatively, machine learning (ML) algorithms are flexible and free of many of the assumptions required in regression. Particularly, it is not necessary to specify the distribution of dependent or independent variables.

Machine learning will develop models based on input and output data (supervised learning), which may be used to predict responses. This means that ML will use two types of data sets: human-labeled input–output pairs (training data), to build the mathematical model, and the evaluation data to predict outcomes based on what the model learned from training data. ML may also interpret data considering solely input data (unsupervised learning), which may be used for clustering (detect hidden patterns or groupings). Some of the most commonly used ML methods, which aim to evaluate the risk of transmission at the wildlife–livestock interface, are what we refer to as disease distribution models (DDM).

The DDM model the relationship between the presence of disease and the environmental or spatial characteristics in a given site. The idea is that the disease is more likely in sites similar to others in which the disease has already been observed. We will use records of disease retrospectively (presence-only, presence/background, or presence/absence) as well as layers with environmental factors and other risk factors as inputs. Machine learning algorithms will learn from the relationships between them and interpolate suitability/risk maps (for now or projected to the future) for the unobserved areas that may be useful to inform control programs and surveillance. Results obtained with this approach may be combined with risk analysis to identify hot-spot areas (Bui et al. 2017) and it will be possible to break down the contribution of each factor to the outcome to propose risk-based strategies. Results obtained in these models may assist parameterization in mechanistic models that can be used for refining predictions of hotspots and identifying optimal control strategies. We are going to describe three commonly used ML algorithms: maximum entropy, random forest, and boosted regression trees.

Maximum Entropy (MaxEnt)

MaxEnt (Phillips et al. 2006) is probably the most widely DDM used in the wildlife-livestock interface (e.g., LaHue et al. 2016; Belkhiria et al. 2016). It only uses the presence of disease and background data which is convenient since sources of the presence of disease may be easily available (e.g., disease reports, health records, passive surveillance, etc.) but registers of absence of disease are difficult to obtain or unreliable in some contexts (true absence or low sampling effort?). This method takes a list of locations with observed disease and environmental predictors (e.g., precipitation, temperature) across a user-defined geographical window that constitutes the available background to determine the suitability to present disease in locations without observations (Fig. 4). Different models including different variables may be run to compare changes of predictability and AUC may be applied to assess predictions.

Overfitting is a potential concern with this methodology, limiting the capacity of the model to generalize well to independent data. This may be reduced by regularization. Multicollinearity and spatial autocorrelation are also issues that might lead to misinterpretations (Griffith 2010). As in other tools using occurrence records, different sampling efforts may be an issue. Spatial filtering, balancing of occurrence data, or background manipulation are suggested strategies to deal with this problem depending on the particular situation (Kramer-Schadt et al. 2013). The program MaxEnt has been widely used to implement models based on this algorithm (Merow et al. 2013).

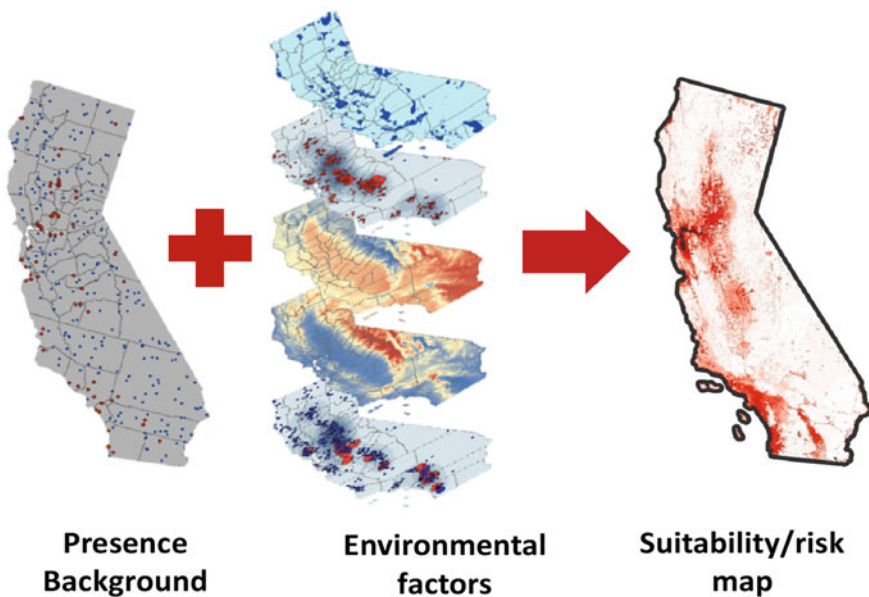


Fig. 4 Components of a disease distribution model

Random Forest

This algorithm is an extension of classification and regression trees. Decision trees are hierarchical and ramified dichotomous questions about the data that eventually lead to a predicted class. Random forest combines hundreds of randomly sampled decision trees to obtain averages of each individual tree. They may be used with presence/absence, pseudo-absence, or abundance data. The use of presence/absence offers us a possibility to estimate the probability of presence but requires representative sampling of absence. Random forest is also good to capture the influence of predictors in the outcome. They are very useful as graphical assessment of risks and supporting decision-taking. Overall estimations of the influence of a given predictor in the outcome are also possible by using partial dependence plots. A pre-classification assessment of correlation between variables is important since the algorithm may favor smaller groups over larger in correlated datasets. Specific implementations in R for random forest include the package `randomForest` (Liaw and Wiener 2002).

Boosted Regression Trees (BRT)

Also named as “gradient-boost trees.” Like random forest, BRT fits many random decision trees. Both methods differ in how random subset of data for new trees are selected since BRT uses boosting methods. This means that BRT additionally tries to look for an optimal linear combination of trees. Two key parameters need to be specified in BRT: tree complexity (number of splits in each tree) and learning rate (contribution of each tree to the growing model) that must be appropriately tuned since they will substantially influence results. BRT inputs must consist of presence and absence data for categorical data. Continuous data (as counts) may be used.

BRT models often perform better in terms of predictions, but they require a harder tuning and are more sensitive to overfitting if the data is noisy. BRT may be more appropriated to detect anomalies in data. Thus, they could be applied to manage data such as DNA sequences. Also, these ML algorithms are useful for real-time supporting the decision-making process. A specific package in R is `gbm` (Ridgeway 2005).

Mechanistic Approaches

Evaluating the risk of introduction, exposure, and spread of a disease is a challenging effort since it involves several factors that interact nonlinearly across multiple dimensions (space and time). First, one may want to find out the risk of a disease entering a population, but also “how will disease spread (i.e., what are the most important disease transmission pathways)?,” “how much is it expected to spread?,” “how fast is it going to spread?,” or “what will the economic impact be?” Although

these questions can be also partially addressed with the data-driven approaches we have discussed above, we usually need to combine data into knowledge-driven or mechanistic models to obtain a more holistic understanding of the magnitude and dynamics problem. Here, we describe some of the most commonly used knowledge-driven or mechanistic approaches to evaluate the risk of disease introduction and/or spread as well as to quantify the magnitude and economic impact of an epidemic at the wildlife-livestock interface.

Risk Analysis

Risk analysis in our context is defined as the scientific process to estimate the risk of occurrence of a disease event and the magnitude of its consequences (e.g., Arrijoja 2008). This approach identifies and mechanistically links relevant factors to this occurrence and assesses future scenarios based on the potential changes in these factors. For example, it has been used to evaluate the risk of import or export of transboundary animal diseases such as Foot-and-Mouth disease (e.g., Martínez-López et al. 2008), classical swine fever (e.g., Martínez-López et al. 2009a), or African swine fever (Jurado et al. 2019; Lu et al. 2019) into new countries (i.e., import risk analysis) or to assess risk points for rabies outbreaks (Abdrakhmanov et al. 2016). There is a well-accepted methodological framework composed of four interconnected phases in risk analysis applied to animal health (Fig. 5). Data inputs are factors with a potential role in the event occurrence. They may come from literature reviews, modeling, expert opinion, and direct knowledge of the species or ecosystem or obtained in samplings or surveillance.

Box 3 Some of the most popular software for Quantitative Risk Analysis

Software	URL	Availability
PopTools	www.poptools.org	Free
@Risk	www.palisade.com/risk	Purchase
OUTBREAK	www.cbsg.org	Free
Stella	www.iseesystems.com	Purchase
Vensim	www.vensim.com	Purchase
ModeRisk	www.vosesoftware.com	Free version

Risk analysis may be qualitative, quantitative, or semiquantitative, depending on the data collected/available and whether the likelihood of the outcome will be expressed with a term (e.g., high, medium, low), by assigning numbers (e.g., 1 outbreak/100 animal introductions) or categorized in scales. Qualitative analysis is faster and useful when data are limited and may be based on preliminary data, literature review, or expert opinion (USDA 2019). However, quantitative analysis allows a more accurate approach by assessing risks in terms of probability and providing variability and uncertainty estimates. A quantitative analysis will use

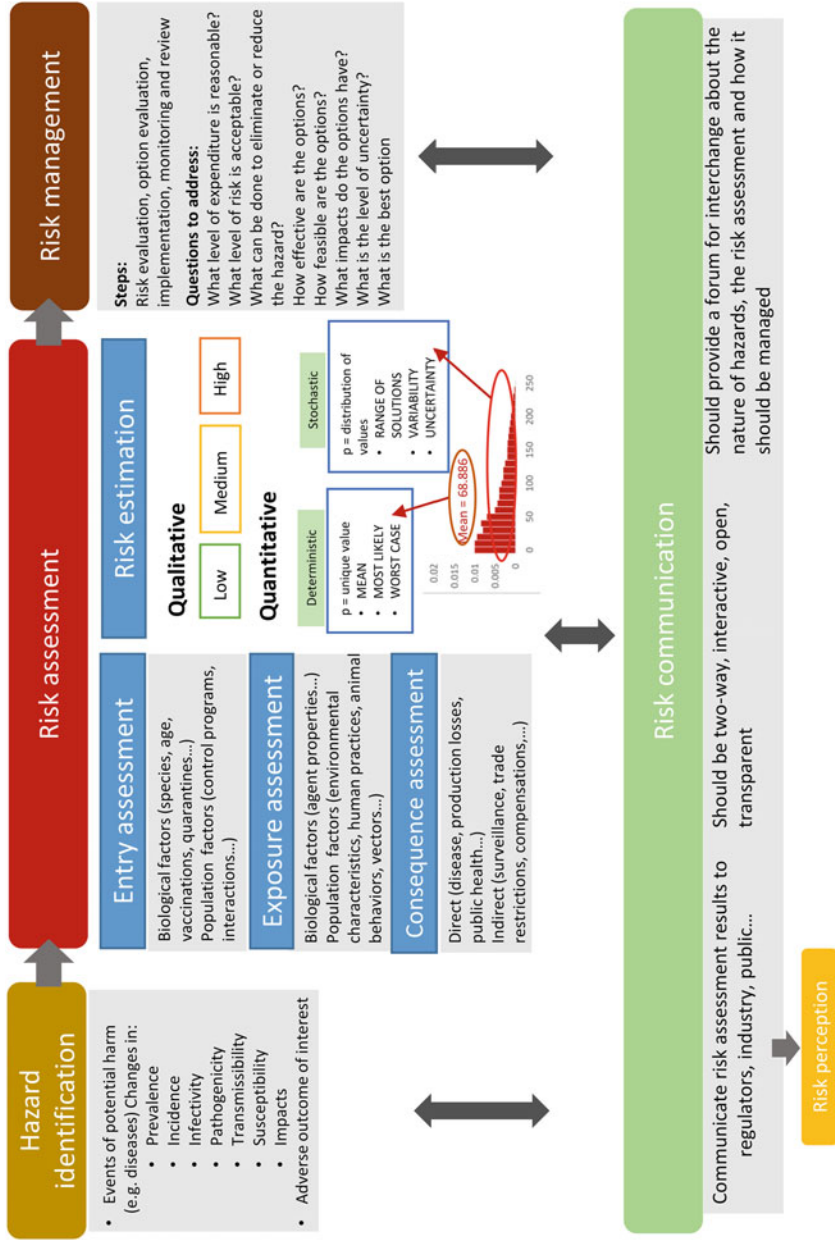


Fig. 5 Framework of a risk analysis (expanded from the proposed OIE Risk analysis framework, e.g., Arrijoja 2008)

probability distributions (e.g., normal, Poisson, hypergeometric, etc.) to describe the information available (as well as the uncertainty) regarding the input parameters and generates probabilities for the outcome using Monte Carlo (or Latin Hypercube) sampling. Different statements may be tested/explored to assess different scenarios in order to identify measures for prevention and control (i.e., scenario modeling) or evaluate the parameters that have the highest influence/impact in our model (i.e., sensitivity analysis). Box 3 details software for quantitative risk analysis.

Disease Transmission Models

Many times, we aim to predict and understand the mechanisms involved in the dynamics of pathogen transmission, quantify transmission rates, and assess how the population structure contributes to the pathogen spread. Only with a good understanding of those mechanisms we can identify optimal control strategies (Miller and Pepin 2019; Pepin et al. 2014). Disease transmission models can be particularly useful to address some of those issues as they can be used for numerical simulation (studying behavior of the system) or for analytics (deriving solutions that help to interpret the relationships of parameters). These models allow playing with variables in a way that would be impossible in the field to test hypotheses that would be too expensive/complex to test (e.g., simulate disease transmission in entire regions or countries) or logistically and ethically unfeasible (e.g., evaluate disease transmission in endangered populations). Here we briefly discuss the two main groups of disease transmission models used to study the wildlife-livestock interface: compartment-based models (SIR, SIR-extended) and agent-based models (network-based models, automata cell, coupled map lattice, and other spatially explicit agent-based models).

Compartment-Based Models

SIR Models

In compartmental models, a population of individuals is divided into disease-status states from which they can transition between at each time step, for example, susceptible, infectious, and removed (SIR) (Fig. 6). These can be modified by adding or subtracting states to accommodate the biological details of the host-pathogen system (e.g., exposed but not infectious, maternally derived temporary immunity, etc.) or the application of specific interventions (e.g., vaccinated, quarantined, etc.). Mathematical relationships for the compartments are defined by setting initial conditions (e.g., number of susceptible and infected, force of infection) and parameters representing relationships between compartments (e.g., reproductive number, duration of exposed and infected state). Deterministic or stochastic simulation of these mechanistic models allows visualization of how the number of hosts in each disease state changes over time (and space if desired).

Box 4 Assumptions of SIR models that may not be accomplished in epidemiological studies in the wild/domestic interface

ASSUMPTIONS OF SIR MODELS	WHY IS IT NOT ACCOMPLISHED?
Homogeneous population	Individuals are different (e.g. susceptibility)
Random mixing	Interactions between individuals are different
Static conditions	Parameters may change during an epidemic
Unique transmission mode	Pathogens may have different transmission routes
Closed population	No in W/D interface
Lifetime immune/recovering in subsequent time periods	Not true in most of the cases
Unique incubation period	Incubation period may be different between individuals

SIR or SIR-like (with additional states) models of a single host species is the starting point to expand to multi-host SIR models (next section) and explore the transient dynamics of pathogens that infect multiple hosts in a large population. They are certainly useful to estimate the average size of the affected population and to assess the effects of different interventions. However, they are usually inadequate to describe epidemics in the wildlife-livestock interface because heterogeneous transmission processes are important. These models are not good at representing interdependent processes (e.g., interactions of individuals with other individuals and with their environment in the space and time with different parameter values). Therefore, this modeling approach is only recommended when the characteristics to parameterize in the target populations are reasonably homogeneous among their individuals (see Box 4, which details the main assumptions of SIR models, and why they may not be accomplished in the wild/domestic interface).

SIR-Extended Models (Multi-host SIR Models)

Diseases may be maintained by several hosts and it is crucial to determine whether they act as a dead-end host (e.g., spill-over) or as active contributors to disease transmission. Multi-host models extend SIR-like models to model disease dynamics in multiple host species explicitly, rather than assuming dynamics in one species might correlate with dynamics in another species. By explicitly separating dynamics in different species, it is also possible to consider the same or different transmission mechanisms in each species, and spatial and environmental modulators of disease transmission (Fig. 6). Compared to a simple SIR-like approach, this approach further subdivides the disease status compartments into host species. For each host or vector species, there are independent processes that determine transitions among compartments (e.g., disease transmission, demographic dynamics; e.g., Manlove et al. 2019).

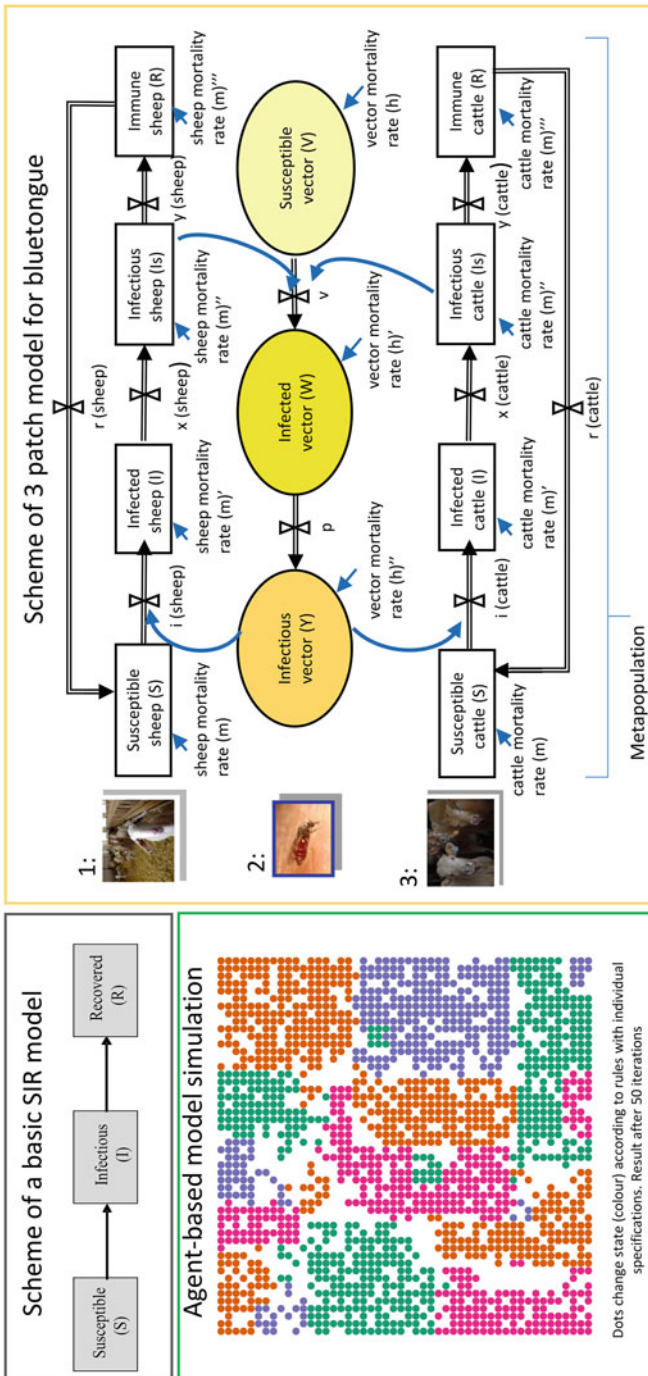


Fig. 6 Schematic representations of simple SIR, multi-host SIR, and ABM models

Then, compartments within host species are linked through the transmission of infectious individuals from one compartment to susceptible individuals in another compartment. By segregating dynamics in host species explicitly, differences in transmission rates within and between host species can be accounted for, thus accounting for a major source of transmission heterogeneity.

Network-Based Models

Compartmental mathematical models are inadequate to represent individual-level processes that might affect epidemic dynamics. The intricate network of contacts within and between species at the wildlife-livestock interface can be represented with diagrams (or graphs) in which each individual is represented by a node (or vertex) and their connections by edges (Fig. 7). Information about contacts at the wildlife-livestock interface can be obtained using either empirical observations or locational devices (e.g., surveys, GPS, camera traps, see chapter “Characterization of wildlife-livestock interfaces: the need for interdisciplinary approaches and a dedicated thematic field” for more details). Before studying disease transmission on networks, network analysis is recommended to better understand the structure and contact patterns among animals by analyzing the topological properties of a network (e.g., centrality, transitivity, etc.). For example, some networks may consist of sporadic random contacts while others may be highly heterogeneous or have scale-free properties where most of the nodes have few connections but few nodes have a high number of connections and can serve as super-spreaders (Martínez-López et al. 2009b; Lloyd-Smith et al. 2005). Identifying and understanding these

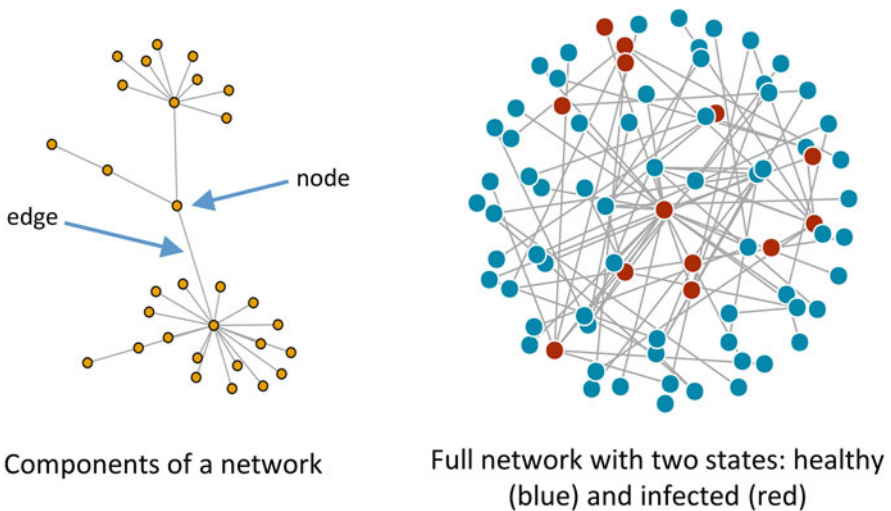


Fig. 7 Scheme of a network

differences is useful for evaluating and planning future measures such as vaccination or sampling. Similarly, network approaches can be useful for studying interactions between multiple species to identify which species might be most connected to livestock and thus an important management target (Wilber et al. 2019). For example, instead of surveying random individuals for detecting disease, one could select those that are more likely to be exposed to the disease based on their position in the network and allocate control efforts based on risk or how removal of particular nodes affects the spread of disease. Once the network analysis is conducted, network-based models can be used to simulate the disease transmission process taking into account the different contact structures (heterogeneities) within and between wildlife-livestock populations. They may be structured as individual- or population-based if there is not enough information at the individual level. In fact, network models are just extensions of the SIR-like framework (i.e., each node can be in “susceptible,” “infected,” or “recovered” state at each time step) to account for heterogeneities of contacts and can be used solely or combined with the other statistical methods (e.g., exponential random graph models), to improve the generalizability of results (Jenness et al. 2018). Exponential random graph models are particularly useful to explore which factors influence edge formation and dissolution, to identify risk factors, or to test hypotheses about disease origin (Robins et al. 2007) (i.e., contact tracing).

A significant limitation for these models is the registration of interactions. In the wildlife-livestock interface connections among individuals can be recorded through the use of satellite telemetry (GPS), collars, or camera-trapping (Clifford et al. 2009; Kukielka et al. 2013). These approaches may be applied in small areas with relative ease, providing useful information about disease spread locally but they may be more complicated at larger scales.

Agent-Based Models: Automata Cell, Coupled Map Lattice, and Other Spatially Explicit Agent-Based Models

More advanced computational models such as automata cell, coupled map lattice and other spatially explicit *agent-based models* (ABM) constitute a different approach that gives us a more detailed picture of disease spread by creating an entire synthetic population of cells or individuals. These approaches are especially useful in applied settings where control strategies need to be fine-tuned to real-world complexities. Characteristics of disease (e.g., infection rates), agents (attributes and behaviors), and also individual interactions with other agents and with the environment (defining how and between who) may be programmed with the desired detail, and rules are established to simulate the consequences of such interactions (e.g., Cissé et al. 2016). A richer representation of the environment may be obtained using GIS-derived data (e.g., Ward et al. 2015; Martínez-López et al. 2011). Furthermore, individuals may be organized in hierarchies or aggregates, so we can simulate disease spread differently for each agent or group or agents in the population. However, the main disadvantages of ABM models are that they can be

computationally intense, more difficult to replicate, and to fit to data for validation purposes. The model to choose will be determined by the complexity of the system we want to simulate and the questions we need to understand. In some circumstances, compartmental models may be enough to describe the spread of some diseases reasonably well, particularly when we do not have many heterogeneities (although again, that usually is not the case when studying wildlife-livestock interface systems) (see Box 5).

Box 5 Challenges of Modeling in Wildlife

- Multiple species → different characteristics
- Unknown population size
- Uncertainty in parameter values (e.g. incubation period, susceptibility, infectiveness, clinical signs, role of environmental factors, etc.) and difficult to estimate
- Hard to estimate contacts
- Co-morbidities and multiple pathogens → difficult to obtain an isolated value for a disease

Economic Analysis

Economic aspects of the disease are always a fundamental part in the impact of a disease in the society and in the livelihood of people and in the possible measures that may be carried out, but it is still largely underused to support decision-making at the wildlife-livestock interface. An approach is cost–benefit analysis, in which all the costs and benefits of the different interventions are listed and related by a conceptual model to be compared (Shwiff et al. 2016). We may also compare between disease (or different degrees) and non-disease scenarios and it may retrospective or prospective. All the listed factors need to be quantified in the same unit to obtain a monetary outcome per scenario. Also, discounts may be added to take into account, for example, the amortization of costs of a program in the long time. The key point is the right assignation of monetary values. Models can be adapted, though, to admit uncertainty by assigning probability distributions to the variables instead of point estimates and tools used in quantitative risk analysis may be applied here. Finally, a sensitivity analysis allows assessing the weight that our assumptions or estimations have in the model.

While the disease effects in production incomes might be relatively easy to quantify, sanitary, biological, or environmental impacts may be difficult or impossible to quantify. In this context, we can use a cost-effectiveness analysis (Rivière et al. 2017). This removes the need for a monetary output estimating instead the costs per unit of an objective and obtaining a cost-effectiveness ratio (e.g., \$100 per death prevented) for each intervention. Another alternative is the cost–utility analysis (Robinson 1993). This looks at the cost of the action regarding the increase in utility. A threshold to reflect the acceptable cost (willingness to pay) must be defined to

decide which intervention is the more appropriate. Outcomes of these analyses may be expressed in a decision tree to visualize the costs associated with each decision. These approaches may be enriched if combined with disease spread modeling to consider the economic impact under different epidemic scenarios. The economics of managing disease transmission at the wildlife-livestock interface are critical to support the decisions of resource managers and agricultural agencies. Certainly, there is an increasing interest to advance in this area and adapt economic approaches to inform decisions about disease mitigation efforts while optimizing financial resources.

Molecular Approaches

The epidemiological characterization of wildlife-livestock disease transmission is a difficult task that can be enhanced with genetic data. Molecular approaches are useful for identifying the source of transmission of infections (i.e., contact tracing at the wildlife-livestock interface) through analyzing genetic relationships in a set of samples from different species (Schmidt et al. 2019, see chapter “Characterization of wildlife-livestock interfaces: the need for interdisciplinary approaches and a dedicated thematic field”, section “Molecular approaches and genetics”). The emergence of new disciplines such as phylodynamics or phylogeography also allows inference about the spatial and temporal dynamics of wildlife-livestock diseases.

Traditional Phylogenetic Analysis

Molecular sequencing gives the possibility of comparing genetic strains between populations and represents the evolutionary relationships among various isolations with phylogenetic trees (see chapter “Natural and historical overview of the animal wildlife-livestock interface”). Therefore, we can cluster sequences regarding their similarity and track the chain of descents to infer potential sources for infection. This has been a main tool for determining disease origins at the wildlife-livestock interface (e.g., Schmidt et al. 2019; Fagundes de Carvalho et al. 2013). There is a number of different methods to build phylogenetic trees (see Box 6). The simpler of them is neighbor-joining (NJ), which builds the tree from the pairwise distances between the given sequences. NJ is a quick method, widely implemented in most of the phylogenetic tools and useful to explore sequences and generate hypotheses, but of limited value to infer real relationships. Phylogenetic reconstruction has been mainly made with two methods: maximum likelihood (ML) or Bayesian inference (BI). Under simple parameterizations, both methods often present similar results. Maximum likelihood has been widely used and it is quick and simple. However, BI allows incorporating previous knowledge as the prior distributions and has more capability to consider uncertainties offering large possibilities of parameterization. Bayesian can explicitly model substitution rates, clades in the tree, position of the

root, population sizes, and geographic diffusion. However, this turns back in terms of model complexity. The more parameters used, the more the time required to complete the analysis and unstable will be the estimates of the parameters.

Box 6 Maximum Likelihood Versus Bayesian Inference in phylogenetics

Maximum likelihood

- Search for the tree that best represent samples
- Confidence is assessed by running the analysis several times with bootstrap or jackknife
- No accurately account for uncertainty in relationship between isolates
- May have a spurious resolution
- Software: MEGA, PHYLIP, PhyML, RAxML

Bayesian inference

- Produces several trees and obtain a majority consensus tree
- Probability of clade being correct given the data and model
- Can account for uncertainty in the phylogeny. Slow with high parameterization.
- Can be unfeasible for large datasets
- May have low resolution at lower taxonomic levels
- Software: BEAST, MrBayes, PHYLOBAYES, revBayes

Phylogenetics and Phylogeography

The shapes and distances of the trees will reflect transmission dynamics of the pathogen as the evolutionary and genetic relationships between sequences are shaped by immunological (immune response is an actor of selective pressure) and epidemiological factors (modulating disease transmissions, e.g., demography). Phylogenetics combines these different actors to explain the evolutionary process of a pathogen (Grenfell et al. 2004) and phylogeography analyses the phylogenies over space and time to understand the processes (e.g., geological, climatic, or ecological conditions) that created their divergence. The combination of both approaches allows us to rebuild the processes that have led to the current genetic diversity of a pathogen and therefore, identify the drivers of their spread. This is particularly useful for RNA viruses, since their high mutation rates and short generation times favor that epidemiological and evolutionary changes occur at the same time scale. These tools become especially relevant when records of animal movements and contacts are not available and to offer an alternative for understanding parameters of importance in disease dynamics (e.g., reproduction number) which would be complicated to infer in wild populations by surveillance.

We can use these approaches to investigate epidemic spread, metapopulation dynamics, cross-species transmission, antigenic drift or tissue tropism (Volz et al. 2013), or understand factors that drive the evolutionary emergence of new pathogen strains (Pepin et al. 2010, 2019). Phylogenetic models may aid in dating epidemic and origins by inferring the date of the most common ancestor (Monne et al. 2011), inferring parameters of simple compartmental models, and combining them with more complicated simulation approaches (Volz et al. 2013; Volz and Siveroni 2018). Moreover, as sanitary interventions produce a selective pressure that affects genetic

diversity, it is possible to evaluate their efficiency by following the footprints of these measures in phylogenies. By combining genetic information with population-level information, it is possible to identify refractory groups, sources of maintenance of infection in a population or detect circulation patterns or quantify the hypothetical impact of different strategies (Dellicour et al. 2018). The incorporation of geographic information and analysis of a population structure allows revealing otherwise hidden transmission patterns, inferring the rates of movement of viral lineages between geographic locations and reconstructing the geographic origins of a pathogen. This has been useful to understand spatial dynamics of Foot-and-mouth disease in Ecuador (Fagundes de Carvalho et al. 2013), drivers of Bluetongue spread in Europe (Jacquot et al. 2017), or to investigate the evolutionary epidemiology of African swine fever in Eurasia and Africa (Alkhamis et al. 2018). Different software allows phylodynamic analysis (e.g., Beast, RevBayes) with different capabilities. Also, there are a number of implementations in R language (e.g., <https://cran.r-project.org/web/views/Phylogenetics.html>).

Case Studies

Bovine Tuberculosis

Bovine tuberculosis (TB) is a global multispecies disease caused by members of the *Mycobacterium tuberculosis* complex that still constitute an important threat to public and animal health (Byrne et al. 2019). A number of control programs are ongoing obtaining significant advances but total eradication is not achieved in many countries despite the dedication of efforts and investments carried out. The maintenance of wild reservoirs has been seen among the main causes for the resistance to eradication in different countries, but this occurs in very different epidemiologic contexts. For example, involving wild boar as maintenance hosts in the Iberian Peninsula or badgers in Great Britain as spill-overs and spill-backs or white-tailed deer in the USA (Palmer et al. 2012). This highlights the importance of surveillance and identification of risk factors for the exposure at the local level as a crucial point to suggest effective control measures.

Regression approaches have been very important in doing that and applied in several studies around the world (Broughan et al. 2016; Humblet et al. 2009). However, frequentist approaches may face some problems in the wildlife-livestock interface that hinder their use: spatial autocorrelation, dependence between covariates, or the variables with few observations among others. Bayesian regression models are then a good choice to solve these concerns. For example, they have been successfully applied in south-central Spain to predict TB occurrence in livestock or wild mammals (Rodríguez-Prieto et al. 2012). Another application of regression models has been quantifying the interactions between wildlife and livestock hosts and evaluating how they are influenced by spatial and seasonal factors (Kukielka et al. 2013). More insight may be gained combined this approach with other

methodologies. For example, Bouchez-Zacria et al. (2018) analyzed factors associated through different networks featuring different possible cattle contacts (trade, pasture, with badgers), which is important to characterize risks, and Wilber et al. (2019) used proximity logger data from cattle and multiple wildlife species to estimate contact networks at the wildlife-livestock interface and understand which wildlife species were most connected to cattle. By combining regression with species distribution models, LaHue et al. (2016) identified two areas with a high likelihood of TB occurrence in Spain, and with cluster analysis, Santos et al. (2018) detected areas of high exposure in Portugal. This makes it possible to develop risk maps for targeted control of the disease providing insights into TB management in endemic systems.

Foot-and-Mouth Disease and African Swine Fever

Both foot-and-mouth disease (FMD) and African swine fever (ASF) are highly infectious diseases that lead to important economic losses to infected countries and constitute a significant threat for free countries. Therefore, risk assessment has been performed to evaluate the main introduction and exposure pathways into free areas (Beltran-Alcrudo et al. 2019). The role of anthropogenic means such as the entrance of ASF by transport-associated routes in Europe (Lina Mur et al. 2012), smuggling of pork in air passenger luggage in the USA (Jurado et al. 2019), exporting of animal products (Lu et al. 2019) or of FMD through international live trade has been explored (Marcos and Perez 2019) and has relevance for assessing trade and movement politics. However, wild reservoirs, such as wild boar, may also constitute a risk for entrance, diffusion, or maintenance of disease if no proper measures are conducted. An example of modeling to address these questions is found in Taylor et al. (2019). The authors modeled wild boar movement and concluded that this species was only responsible for local transmission of ASF while other pathways are more determinant of medium- and long-distance spread.

Modeling may be used to understand how disease will or has spread and propose coherent and efficient ways of prevention or control. For example, Martínez-López et al. (2010) modeled the spread of FMD in Spain and evaluated the effects of different contingency measures, revealing that the official protocol would be greatly improved by including measures such as depopulation and vaccination of premises within a radius of <1 km and <3 km, respectively, from the outbreaks. Mechanistic models can also be used to evaluate how an introduction of FMD from livestock into wildlife might be prevented or controlled depending on the host ecology of the wildlife species (Pepin and VerCauteren 2016). Network analysis is also useful to analyze animal movements that may spread the disease. Ferdousi et al. (2019) applied this tool to evidence how farm operations (i.e., markets) play a critical role in ASF spread and vaccinations would be more effective to control an outbreak compared to centrality-based strategies. Even if livestock trade mainly introduces a disease, it can be passed to wildlife enhancing persistence and challenging

elimination. This was explored by Pepin et al. (2020) using ABM suggesting that autonomous persistence of ASF was only possible through carcass-based transmission or in high host densities by direct contact. Similarly, wild boar was estimated insufficient to maintain ASF in Denmark for more than a few months and the density of the population was identified as an important driver of the spread (Halasa et al. 2019). In contrast, FMD is becoming endemic in wildlife by spatial extent rather than density (Croft et al. 2019). As we see by these examples, modeling offers ways to understand different transmission mechanisms that can help to identify optimal management strategies across changing ecological conditions.

Avian Influenza

Genetic-Based Approaches

Avian influenza viruses in wild birds and poultry are one of the longest and most well-studied wildlife-livestock spill-over systems. These viruses evolve quickly due to their high mutation rates and capacity to reassort frequently, with different virus subtypes showing preferences for different poultry species and for particular coinfections. Thus, the selection landscape is complex driven both by host species and interactions with other viruses. These complex evolutionary genetics present a ripe opportunity for the development of phylogenetic and phylodynamic methods to inform spill-over at the wildlife-livestock interface (Ramey et al. 2016, 2018).

Phylogenetic analyses from poultry outbreaks and neighbor wild birds populations are commonly used to identify transmission events (e.g., Bouwstra et al. 2015; Haase et al. 2010; Lei and Shi 2012; Mulatti et al. 2017), the number of introductions from wild birds that seeded an outbreak in poultry (Lei and Shi 2012), or the wild bird population source(s) of poultry outbreaks (Bouwstra et al. 2015). For example, Haase et al. (2010) used phylogeographic techniques to show that introductions from wild birds drove two seasonal waves of H5N1 in poultry being able to distinguish both spill-over and spill-back events, which is important information for understanding mechanisms of viral persistence. Similarly, combining temporal phylogenetic analysis with phylogenetic network analysis (Bouwstra et al. 2015) reported that four of the five HPAI outbreaks of H5N8 in poultry in the Netherlands in 2014 were caused by separate introductions from wild birds rather than farm-to-farm spread. Methods for incorporating metadata such as sampling time, geographic location, and phenotypes (such as virulence) with phylogenetic inference (i.e., phylodynamics) have allowed estimation of the spatial dynamics of viruses (Zhou et al. 2016). When applied to the wildlife-livestock interface, these methodologies hold promise for understanding the mechanisms and spatial dynamics of spill-over, e.g., Lam et al. (2016), especially when phylodynamic results are tested experimentally for validation of transmission capacities, e.g., Cui et al. (2017).

Sentinel Host Approaches

Understanding the rate of spill-over to poultry and identifying genetic strains that are most likely to cause outbreaks, are two of the most fundamental knowledge gaps for managing wildlife-livestock spill-over systems such as avian influenza. The capacity to inform spill-over frequency of phylogenetic inference remains weak. This is partly due to poor sampling design as described by Haase et al. (2010), but adequate coverage could require infeasible amounts of sampling. Sentinel host studies are particularly useful for revealing spill-over dynamics in genetically diverse, generalist viruses such as avian influenza. They have allowed for direct measurement of spill-over rates to the livestock host (Halvorson et al. 1983), documentation of seasonal dynamics of spill-over (Halvorson et al. 1985), evaluation of vaccination effectiveness (Henning et al. 2011), and when combined with genetic analysis or strain-typing, they have allowed us to detect subtypes or genetic sequences that are most likely to lead to outbreaks in poultry (Halvorson et al. 1983). Because these approaches can be logistically, financially, and politically challenging to implement, they have been underused, especially at the wildlife-livestock interface. One way to circumvent some of the challenges has been to implement sentinel host studies in captivity (Achenbach and Bowen 2011). However, this still necessarily neglects some ecological (e.g., realistic contact dynamics) and genetic (full spectrum of strains) complexity, and thus should be validated in nature. Nevertheless, these and other (e.g., (Root et al. 2017)) types of simulated natural environments can be important first steps for feasibly identifying the most important sources and mechanisms of spill-over to poultry (or at least duck–chicken transmission, e.g., Claes et al. (2014), which has direct relevance to wild bird–poultry spill-over).

Bluetongue

Bluetongue (BT) is a viral disease of ruminants transmitted by biting midges (genus *Culicoides*). The disease is endemic in many countries but the expansion toward northern Europe has been noteworthy during the last decades, producing several outbreaks in the continent and important economic impacts. Due to its vector-borne nature, BT distribution is connected with the vector distribution and is limited by a number of environmental factors. Machine learning has been used to predict vector spatiotemporal distribution to identify zones at risk using algorithms for disease distribution modeling (Ciss et al. 2019; Cuéllar et al. 2018; Gao et al. 2017). This allows mapping the potential distribution of the vectors, which is crucial for planning health interventions. The temporal component is also important, since vector-borne diseases are continuously evolving particularly in the context of climatic change. Thus, climate-based ecological niches have found trends of increasing BT over time (Brand and Keeling 2017). In addition, disease distribution models may provide useful inputs for modeling spread, helping to reconstruct the dynamics of disease.

Using these models to identify major contributing factors to disease spread is helpful to infer key drivers of expansion and design contention measures.

However, not only climatic factors shape BT distribution. Bayesian regression models showed an important influence of livestock host composition in patterns of bluetongue disease in India (Chanda et al. 2019) and phylogeographic methods described virus spread in Europe as a consequence of climatic, landscape, and vertebrate host factors (Jacquot et al. 2017). Stochastic-dynamic networks models may be used to project future scenarios of disease considering animal movements (Jones et al. 2019). Though many models rely on transmission in domestic ruminants because of their contrasted importance, wild ruminants may also have a part in the spread. In endemic areas, BT virus circulation occurs in this species and they may play a role in the epidemiology of disease (Ruiz-Fons et al. 2014), so including the wild interface in the modeling may be important to fully understand the epidemiology of BT. For example, red deer has been suggested as a reservoir in endemic countries in southern Europe (García-Bocanegra et al. 2011). In fact, wild ruminants may be suitable for sentinel approaches, especially in areas where compulsory vaccination strategies to contain disease have limited serological surveillance. A current challenge to predict vector-borne diseases is integrate all the levels intervening in transmission: pathogen, diversity of hosts and vectors and how interact with their landscape, and regional variation of those interactions, incorporating landscapes as components of the functional habitat of vectors and hosts and so of the pathogen (Hartemink et al. 2015).

Conclusions and Future Directions

Modeling plays an important role to reproduce disease events and evaluate their dynamics and consequences at the wildlife-livestock interface. Along this chapter, we have explored different approaches that allow us to get insights into the epidemiology of infectious diseases in the wildlife-livestock interface. However, modeling wildlife-livestock is not always an easy task. Sometimes problems start for obtaining an accurate view of the extent of an infection. Underreporting of disease in livestock may occur and for several reasons: inability to recognize disease (i.e., mild unspecific clinical signs) fear of consequences, but it is usually a bigger problem in the wild side of the interface. In addition, wildlife sources of data are usually skewed to nonrandom samples due to convenience, or only based on detected cases. Surveillance in wildlife maybe also too sparse and limited to some diseases and hosts, and the accuracy of diagnostic tests may present some concerns since they are often only validated for livestock. This hinders the estimation of the real population affected.

There is also a need to increase our knowledge about how some wild populations are structured, not only regarding the number of individuals, but also social structure, movements, and interactions with other species, which are necessary to infer spread and few times available. This limits the accuracy of the predictions we can obtain.

Different efforts have been done into methods to estimate ecological characteristics of wildlife populations and provide this necessary information (Leopold 2019) but there are still considerable opportunities to make important contributions in this area.

Transmission in wildlife-livestock may imply systems in which different species may be interconnected presenting different roles in the transmission chain: reservoirs contributing to maintain disease, death-end hosts, etc. as well as susceptibility and vulnerability to the infection. Models that explicitly include contact networks and spatial structure have become increasingly used (Huyvaert et al. 2018). However, estimating contacts is challenging and usually only possible at small scales and factors influencing interactions may vary from one area to another. One must carefully define the scale. Sometimes sources of infection are distant and indirect, e.g., a species may be asymptotically infected and migrate from a distant endemic area to a naïve and transmit the infection to other more vulnerable animals. Molecular epidemiology provides a solution to track these interrelationships through phylogenies when networks cannot be directly identified. The suitability of disease may be mapped considering the environmental background. However, interpolations may be risky, if the scale is wrongly set, because suitable microhabitats for pathogens may exist surrounded by unsuitable larger zones. Zonification and local-scale approaches may be also useful to infer the right assessments of risk adjusted to a specific region, but at the same time, they lose generalizability.

In addition to multi-host interactions, different pathogens and strains may be present in the interface. This scenario is not abundantly explored in modeling, but concomitant infections may affect both clinical and epidemiological courses of the infection. Also, the interface is dynamic, and these relationships may vary along time. Agent-based models (ABM) may capture all this complexity and describe ecological processes as they actually occur. However, models may result so complex that estimating the parameters for all the processes and understanding how the systems change to the different parameter sets may be too complicated and overwhelming. The increasing complexity of a model does not necessarily ensure more credible results and more accurate descriptions of a subpopulation may fail to capture the population patterns. A model should not be more complex than necessary to fulfill its goals. Depending on the specific approaches, we have Bayesian and frequentist statistical approaches and machine learning for risk factor analysis and predictive inferences under a variety of data distribution scenarios. Risks may be assessed and quantified under a mathematical framework. Different spread models are available to our particular approaches: compartmental models to approximate estimates of the drivers of transmission and possible outcomes, patch models to increase the resolution of the estimations incorporating heterogeneities related, for example, with location or population, ABM to amplify the resolution to the individual level to assess how specific conditions affect to a cascade of events involved in transmission and network-based models that allow studying explicit relationships and integrate them into disease spread models. We can get a spatiotemporal view of the problem by using disease distribution models to predict suitable areas for disease, inform other modeling approaches to improve predictions, project scenarios for the future, and guide risk-based surveillance, and cluster analysis to detect

spatiotemporal aggregations over a map. This will allow us to discover points of special risks and generate hypotheses about why this is happening to increase our knowledge about the epidemiology of a disease. Phylodynamics and phylogeography are also revolutionizing our understanding of infectious disease dynamics by incorporating the molecular level to the disease spread level. However, more advances are expected in the future if changing mutation rates, selection, reassortment, and recombination, stochastic population dynamics, host population structure, and patterns at the within-host and between-host scales are more effectively accounted for (Frost et al. 2015).

The newly available technologies allow us to have more tools to assess disease spread. However, most of the actions that we are currently applying are reactive and sometimes carried out after high losses have already occurred. Moreover, treatment and control in wild animals is complicated, so there is a need to develop preventive approaches and early detections. One way might be to take advantage of the increased volume of data are generated daily from different sources, especially in the livestock side of the interface. Big Data analytical methods have proved been useful in different fields and have a promising value in veterinary epidemiology. When applied to integrate all the data generated by farms to support healthy plans and early detections of disease in livestock populations or to better understand wildlife habit use and movements, this will have a bidirectional impact on both sides of the interface. This will make more efficient and successful the management of infectious diseases at the wildlife-livestock interface, which will positively impact animal and public health as well as conservation efforts locally and globally.

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Part IV
Synthesis and Conclusions

Synthesis and Future Perspectives of the Study and Management of Diseases at the Wildlife-Livestock Interface



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Main Conclusions

The wildlife-livestock interface has proper ecological and epidemiological entity, with specific niches and epidemiological roles for wild, domestic, and environmental reservoirs. However, the study of this complex interface has a relatively short trajectory, experiencing an explosion of research contributions during the last decade. The wildlife-livestock interface had been often neglected and consequently, infection “spill over” between animal compartments, and also humans, had been largely underreported. Previous chapters illustrated how the world is experiencing unprecedented emergence and spread of diseases in livestock that have “spilled over” to wild populations and later “spilled back” to livestock (chapters “Host Community Interfaces: The Wildlife-Livestock” and “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”). One major conclusion that pervades all chapters is that the inclusion of the study of animal interfaces is a sine qua non condition to understand and address the establishment of newly shared emergent diseases. The control of increased exposure of human and animal populations to novel pathogens, especially those involving wildlife, is a challenging

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issue, which requires integral and interdisciplinary approaches, as evidenced by the present coronavirus disease (COVID-19) global pandemic.

Secondly, differences in the ecology, epidemiology, cultural background, and socioeconomical aspects of the wildlife-livestock interface matter (chapters “Host Community Interfaces: The Wildlife-Livestock”, “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”, and “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). Today, this interface occurs at multiple spatial scales, ranging from natural scenarios to human-instigated conditions for host interactions. The analyses of regional situations and diversity of contexts and characteristics of the interfaces (chapters “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Europe”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Asia”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Africa”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Oceania”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in North America”, and “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Central and South America”) drew an integrative perspective. Interestingly, different needs but similar approaches to understand and manage the interface were identified among regions of the globe: interfaces are interconnected centers for pathogen transmission giving rise not only to spatio-temporal disease emergence at local scales but stimulated by regional drivers associated with risk for emergence of pathogens are connected worldwide. Human expansion, technical development, trade, population growth, and growing interdependence of world economies have favored the increase of livestock spatial ranges, opportunities for animal pathogens to cross considerable geographic boundaries, and determined the characteristics of wildlife-livestock interfaces and subsequent opportunities for pathogen transfer (chapters “Host Community Interfaces: The Wildlife-Livestock” and “Natural and Historical Overview of the Animal Wildlife-Livestock Interface”). The capacity to modify and connect the interfaces that characterize humans has increased to an extent that, as mentioned in the first conclusion, improving health at the human, animal, and ecosystem interfaces is required to successfully address health challenges at a global scale. At finer scales, novel and intensifying anthropogenic (e.g., agricultural) practices need to be revised because they can lead to new host interactions at the interface and may trigger pathogen spill over. Particular attention to the neglected wildlife-livestock interface is needed in complex ecosystems in developing regions, characterized by high biodiversity, a complex interplay of ecological and human factors, and increased opportunities for pathogen emergence.

We also evidenced that human activities, of great impact on the environment and wildlife populations, present differences among continents (e.g., very intensive impacts in Europe). Therefore, current trends are different among regions (chapters “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Europe”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Asia”, “Characteristics and Perspectives of Disease at the Wildlife-

Livestock Interface in Africa”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Oceania”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in North America”, and “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Central and South America”). The wildlife impact, for instance, is reversing in vast regions of the Northern hemisphere, or contrary, deforestation, extension of urban areas and increasing human encroachment occurs in most tropical regions and developing countries. A difficult topic to address is the impact of deforestation at the wildlife-livestock interface, since it creates favorable conditions for some vectors, and allows the displacement and adaptation of others to new environments. This land transformation and its consequences need to be monitored, and structural national and regional solutions, based on regulatory policies, should be implemented. It is imperative that the development of sustainable initiatives and specific tools define effective interventions to reduce health risks and control of diseases. At the same time global changes, such as global warming and an increase of movement of humans, animals, and trade, represent a risk for the emergence/re-emergence of vectors or pathogens all over the world. Such trends, driven by different mechanisms, pose a serious threat to both animal and human health, and represent a good example of the need for a One Health approach (chapter “Host Community Interfaces: The Wildlife-Livestock”). Nowadays, there are common signs over different continents that indicate the need to change toward a more open and holistic approach.

In developing countries (chapters “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Asia”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Africa”, “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in North America”, and “Characteristics and Perspectives of Disease at the Wildlife-Livestock Interface in Central and South America”) many pathogens and hosts have not been listed because there is limited data/research about them. Though wildlife is the reservoir host for many shared diseases in Asia, Africa, and South America, the role of wild animals is still not very clear and there is a lack of adequate scientific information in such biodiverse continents, where on balance there are more questions than answers. This increasing recognition of the importance of wildlife in the dynamic of emerging infectious diseases is a big challenge for the countries in these regions. We can anticipate an exponential growth of interactions between wildlife, livestock, and people in these regions, with serious implications in the level of conflict and in disease emergence events. In this confrontation, wildlife is likely to suffer if no action is taken to highlight the potential value of wildlife and ecosystem services to improve human livelihoods and empower local rural economies. New formulas and approaches to promote cohabitation and resilience between natural ecosystems and farming systems need to be tested and successes disseminated at national, regional, and continental levels to promote new ways of thinking and acting. It is highly recommended to implement comprehensive continental programs involving integrated surveillance that could contribute to detect the presence of different pathogens either of the livestock population or among wildlife. The revision of surveillance strategies

needs to be accompanied with the strengthening of laboratory diagnosis capacities and biosecurity policies in farming.

We identified the targets and methods for integrating environment, population, and disease surveillance, which will allow a wiser allocation of resources in monitoring and control strategies in wildlife, and at their interface with livestock (chapter “The Ecology of Pathogens Transmission at the Wildlife-Livestock Interface: Beyond Disease Ecology, Towards Socio-Ecological System Health”). This means different disciplines should step up research cooperation and collaborative surveillance of animal and human pathogens to make the best-coordinated decisions for similar problems of global concern (chapter “Characterisation of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field”). The weaknesses of current wildlife disease and population monitoring and early warning systems acting at the origin of pathogen emergence indicate that we are often not able to notice in advance what is going on at the interface before pathogens spread. Consequently, it becomes too late to prevent their impacts. For instance, the lineage from which SARS-CoV-2, the causative agent of COVID-19, came has been circulating among bats for decades and is likely to include other viruses with the ability to infect humans. Monitoring trends in wildlife populations, large-scale surveillance efforts, and addressing the ecological and epidemiological study of the wildlife-livestock interface to identify epidemiologically relevant animal reservoirs are warranted to understand and prevent diseases of animal relevance, but also those potentially spreading to humans. Overall, on Earth, wildlife has been reduced by humans to their lowest levels ever. However, there are differences depending on the taxa and regions. Changes are taking place at high speed, with a few species benefitting and many others suffering the consequences of human-driven changes in land use and of climate change, with subsequent effects on pathogen distribution and disease emergence. Disease issues at the wildlife-livestock-human interfaces, though, are of increasing concern as they are leading to global pandemics and are far from being efficiently controlled or managed. The apparent increase in severity of human-wildlife conflicts, including shared diseases, is indicating that wildlife-livestock-human interfaces must be a crucial component in the formulation of modern wildlife management involving countries and international organizations. This will result in better targeting shared disease control programs and move toward eradication. Adaptive disease management principles can help integrate and prioritize surveillance activities along with the development and deployment of effective, practical, and economical mitigation measures designed to lower pathogen transmission risk. It is also strategic to promote research in collaboration with the medical sector to ensure we can make the best-coordinated decisions for current challenges in the interest of humanity.

The wildlife-livestock interface defines where the interaction between free ranging wildlife and livestock takes place. The need to identify interactions with the potential for pathogen transmission among the community of hosts at the wildlife-livestock interface has led to the development of multiple approaches in the field of epidemiology. These interactions among hosts are multiple and complex. We presented the different approaches employed to monitor animal interactions with a

potential risk of pathogen transmission (chapter “Collecting Data to Assess the Interactions Between Livestock and Wildlife”). These methods have mostly been developed and adapted from other fields, mainly in the last two decades. The specific definition of interaction and the selected properties under study are different in each work and are malleable to specific scenarios and objectives, considering the logistic constraints, target host species and pathogens, and the routes of transmission at the wildlife-livestock interface. However, There is a need to standardize and harmonize methods and approaches whenever possible. The approaches that are able to quantify real interactions (i.e., one individual close to another, or close to a commonly used resource) are always more precise than those that employ proxies (i.e., the presence of tracks of different species at a particular resource) and more easily allow for direct comparisons among studies. After we define the study methods; we must be aware that the correlation between interaction and transmission is not straightforward.

The quantification of transmission at the wildlife-livestock interface is key to understand disease dynamics and identify high-risk areas/time periods but also to be able to more cost-effectively allocate preventive and control interventions (chapter “Quantifying Transmission Between Wild and Domestic Populations”). The evaluation of pathogen transmission among individuals has been rarely assessed at the wildlife-livestock or wildlife-livestock-human interface because of the complexity of gathering detailed/quality data on wildlife, livestock (and human) populations simultaneously and the need to set up multidisciplinary teams to achieve a well-balanced study design, obtain enough sample size and adequately design, parameterize, and interpret those models. Transmission at the wildlife-livestock interface is driven not only by animal behavior, social structure, and spatial overlap but also by the characteristics of pathogens (e.g., survival and transmission pathways) and environmental and climatic factors (landscape structure, weather, soil characteristics, etc.). All this must therefore be considered in the selection and design of modelling approaches at the wildlife-livestock interface. Obtaining an accurate view of the extent of an infection is often challenging. Underreporting of disease in livestock may occur and for several reasons: inability to recognize disease (i.e., mild unspecific clinical signs) or fear of consequences, but it is usually a bigger problem on the wild side of the interface. In addition, sources of data on wildlife are often skewed to nonrandom samples due to convenience, or only based on detected cases. Surveillance in wildlife may also be too sparse and limited relative to some diseases and hosts, and the accuracy of diagnostic tests may present some concerns since they are often only validated for domestic animals. All this hinders the estimation of the real proportion of a population affected. Some models explicitly including contact networks and spatial structure have become increasingly employed. However, estimating contacts is challenging and usually only possible at small scales as factors influencing interactions may vary from one area to another. Therefore, there is a need to increase our knowledge about how wild populations are structured, not only regarding the number of individuals, but also social structure, movements and interactions with other species, which are necessary to infer spread but only rarely available. The success of disease control in wildlife depends on many factors, including disease ecology, natural history, characteristics of specific pathogens,

availability of suitable diagnostic tools, characteristics of domestic and wildlife host (s) and vectors, geographical spread of the problem, scale of the control effort, and stakeholders' attitudes.

The control of diseases shared with wildlife requires the development of strategies that will reduce pathogen transmission between wildlife and both domestic animals and human beings. Ideally, tools from several fields of study need to be combined in an integrated control strategy. We note that options currently applied (or researched) to control disease at the interface were not specifically addressed in the present book and a future volume will describe wildlife disease control perspectives.

What Is Next?

There are essential gaps that prevent us from better understanding and managing disease dynamics at the wildlife-livestock interface. As a first step relative to many interfaces, it is still necessary to describe the hosts and their pathogens, their distributions and behavioral characteristics with epidemiological consequences; and then, what the pathways and transmission rates are among these compartments. Then the effects of pathogens exert at both population and community level must be addressed. As indicative, for more than 50% of OIE listed pathogens present in North America (the region leading the study of the wildlife-livestock interface) there have been no studies assessing their prevalence in wildlife. Next, we detail our view on how to tackle wildlife-livestock interface health issues, and we indicate the direction for future wildlife-livestock interface health studies.

That spill-over and spill-back events do not occur with the same frequencies and intensities is probably a widespread phenomenon ("asymmetric interfaces"). This should be explored more thoroughly, with potentially huge implications for the management of diseases in interface areas. Understanding how any barriers are functionally and quantitatively linked, and how they interact in space and time, will substantially improve our ability to predict or prevent spill-over and spill-back events.

The integration of ecological, biomedical, and social sciences into a single discipline of "disease socio-ecology" remains a major research frontier for improved management of wildlife-livestock interfaces. Disease ecology is an emerging discipline essential to improve our understanding and management of diverse and complex wildlife-livestock interfaces across the globe. The main challenge ahead for improved wildlife-livestock disease management is not merely technical or even conceptual. It will necessitate a radical shift in attitudes toward wildlife, which should be considered more as an integral asset than a problem to be controlled.

Despite many challenges, there remain opportunities to develop new collaborations and leverage new technologies to mitigate disease risks at the wildlife-livestock interface. The principles of adaptive management offer the greatest opportunities to

formulate a framework from which collaborations can be developed and progress made.

The ever-increasing role of the anthropogenic drivers of change suggests a future exponential growth in the interactions among wildlife, domestic animals and humans, with important implications, including additional disease emergence at the interfaces. The recent COVID-19 pandemic increases our certainty that a systems-wide holistic perspective on pathogen dynamics at the wildlife-livestock-human interface based on interdisciplinary approaches to the examination of biological, ecological, economic, and social drivers of pathogen emergence is required. Simply, we cannot look at any compartment in isolation from others as they are ineludibly and functionally linked through ecological and evolutionary processes underlying host jumps by pathogens. The implementation of actions (ranging from local to holistic) under this principle across the animal health, human health and environment sectors remains a challenge. We need to understand, predict, prevent, and control disease emergence at their main origin, the animal interfaces. Detecting early warning signs at the origin of pathogen emergence is imperative so they can be halted before they lead to dramatic local, regional, or global consequences.

Thinking in the global context underlines the fact that standard veterinary or public health approaches to disease (i.e., relationship between one host and one pathogen) are obsolete in most contemporary cases. The recent development of integrated approaches to health (e.g., One Health, EcoHealth, and more recently Planetary Health) expresses this need to change classical approaches. Local participation (including farmers and community members) must transform interdisciplinarity into transdisciplinarity in research. The objective is to reach knowledge to action process involving many nonacademic stakeholders, where research produces knowledge that will be, after consultation with stakeholders, integrated into science-based, co-designed management options.

Chapter “Characterisation of Wildlife-Livestock Interfaces: The Need for Interdisciplinary Approaches and a Dedicated Thematic Field” claimed that a “science of the interface” has its place in the spectrum of thematic fields. It is a necessity because of the context of global changes and the extensive wildlife-livestock/human interfaces created and impacting human societies and ecological processes, including epidemiological processes. The gradient of wildlife-livestock interfaces expands from cities to remote natural areas and includes challenges across sectors. It requires applying the principles presented above (e.g., systems thinking, transdisciplinarity, local participation, sustainability, gender and social equality, and knowledge to action) to adapt to the novel nexus of people, animals, and ecosystems at wildlife-livestock interfaces. We argue for a dedicated field focusing on wildlife-livestock interfaces that have particular characteristics and implications in disease ecology. A conceptual model, as a basis to understand the details of the interface under study was presented. The representation of the wildlife-livestock interface will always require a priori definition of the study site, comprising a set of items: (1) wild and domestic species of interest; (2) key environmental features such as the presence of a “visible” land use boundary that could influence the type and extent of the interface; the presence of key resources that could influence the behavior of wild species and

livestock husbandry practices; (3) key local actors involved in activities at and/or in the management of the interface area; and, (4) this a priori knowledge will help in framing a conceptual model for the wildlife-livestock interface.

There is a need to improve and develop technologies to be able to accurately assess the real situation around the interaction between wildlife and livestock. New technologies are increasingly allowing us to better assess disease spread. However, most of the interventions that are currently applied are reactive and sometimes carried out after high losses have already occurred. Moreover, treatment and control in wild animals is complicated, so there is a need to develop preventive approaches and early detection methods. One way might be to take advantage of the increased volume of data that are generated daily from different sources, especially in the livestock side of the interface. Big Data analytical methods have proven useful in different fields and have a promising value in veterinary epidemiology. When applied to integrate all the data generated by a farm to support health plans and early detection of disease in livestock populations or to better understand wildlife habitat use and movements, they will have bidirectional impact in both sides of the interface. This will make the management of infectious diseases at the wildlife-livestock interface more efficient and successful, which will hopefully impact animal and public health as well as conservation efforts locally and globally.

Though some assessments exist for specific diseases, more research evaluating the economics of diseases at the interface is needed. The same is true relative to human dimensions and the need to educate the gamut of publics in democratic societies to help ultimately lead to sound, long-term disease management choices.

To sum, the future health of humanity and other beings on Earth is at risk due to the continual, eminent presence of established and emerging pathogens. Our knowledge base though, as outlined in this book, is sound and establishes the foundation needed to build from to succeed when facing these challenges. The outlook requires swift action but is not dire, cooperative research, management, and communication involving expertise from several fields of study and capitalizing on emerging tools and technologies can and will serve to address these issues of pathogen transmission at the wildlife-livestock/human interface (Fig. 1).

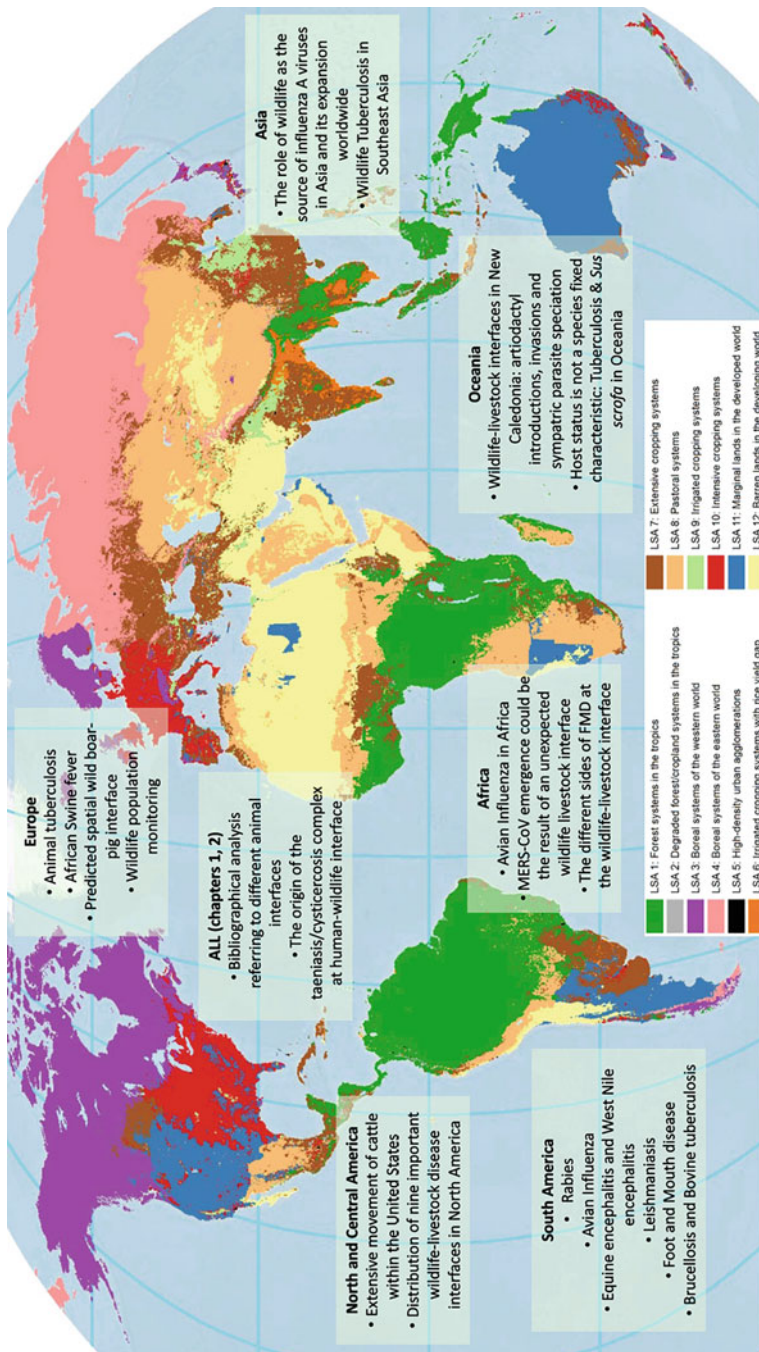


Fig. 1 The wildlife-livestock interface is present in most pastoral systems and this book contains examples on its ecology and epidemiology from all around the world (see boxes and figures in respective chapters) (global land use map for 2005, Helmholtz Centre for Environmental Research, UFZ)