Reviews of Geophysics

REVIEW ARTICLE
10.1029/2022RG000785

Land Use Change and Infectious Disease Emergence

M. Cristina Rulli[1], Paolo D'Odorico[2], Nikolas Galli[1], Reju S. John[3], Renata L. Muylaert[3], Monia Santini[4], and David T. S. Hayman[3]

[1]Department of Civil and Environmental Engineering, Politecnico di Milano, Milano, Italy, [2]Department of Environmental Science, Policy, & Management, University of California at Berkeley, Berkeley, CA, USA, [3]Massey University, School of Veterinary Science - Tāwharau Ora, Molecular Epidemiology and Public Health Laboratory, Palmerston North, New Zealand, [4]Institute for Climate Resilience, CMCC Foundation - Euro-Mediterranean Center on Climate Change, Lecce, Italy

Key Points:

- Zoonotic and vector-borne disease outbreaks are on the rise, particularly in the tropics
- "New" emerging disease outbreaks are often favored by natural habitat destruction and human contact with wildlife from land use change
- The study of sustainable food systems and land use change typically overlooks outcomes related to emerging disease outbreak risk

Correspondence to:

M. C. Rulli,
cristina.rulli@polimi.it

Citation:

Rulli, M. C., D'Odorico, P., Galli, N., John, R. S., Muylaert, R. L., Santini, M., & Hayman, D. T. S. (2025). Land use change and infectious disease emergence. *Reviews of Geophysics*, *63*, e2022RG000785. https://doi.org/10.1029/2022RG000785

Received 22 JUL 2024
Accepted 5 APR 2025

Author Contributions:

Conceptualization: M. Cristina Rulli, Paolo D'Odorico, Nikolas Galli, David T. S. Hayman
Writing – original draft: M. Cristina Rulli, Paolo D'Odorico, Nikolas Galli, Reju S. John, Renata L. Muylaert, Monia Santini, David T. S. Hayman

Abstract Major infectious diseases threatening human health are transmitted to people from animals or by arthropod vectors such as insects. In recent decades, disease outbreaks have become more common, especially in tropical regions, including new and emerging infections that were previously undetected or unknown. Even though there is growing awareness that altering natural habitats can lead to disease outbreaks, the link between land use change and emerging diseases is still often overlooked and poorly understood. Land use change typically destroys natural habitat and alters landscape composition and configuration, thus altering wildlife population dynamics, including those of pathogen hosts, domesticated (often intermediary) hosts, infectious agents, and their vectors. Moreover, land use changes provide opportunities for human exposure to direct contact with wildlife, livestock, and disease-carrying vectors, thereby increasing pathogen spillover from animals to humans. Here we explore the nexus between human health and land use change, highlighting multiple pathways linking emerging disease outbreaks and deforestation, forest fragmentation, urbanization, agricultural expansion, intensified farming systems, and concentrated livestock production. We connect direct and underlying drivers of land use change to human health outcomes related to infectious disease emergence. Despite growing evidence of land-use induced spillover, strategies to reduce the risks of emerging diseases are often absent from discussions on sustainable food systems and land management. A "One Health" perspective—integrating human, animal, and environmental health—provides a critical yet often-overlooked dimension for understanding the health impacts of land use change.

Plain Language Summary Many dangerous contagious illnesses are transmitted to people from animals like mammals and insects. Recently, new cases of both known and previously unknown diseases have increased, especially in the tropics. Despite growing awareness that altering natural habitats can lead to new cases of infections, how these two things are interconnected is still being studied. Land use change, the transformation of natural land into other types of land - mainly agricultural or urban - changes the composition of landscapes and the behavior of wild and domesticated animals that live there, including those carrying pathogens like viruses, bacteria or parasites. Moreover, land use change increases the possibility of contact between animals and humans, and thus the potential flow of pathogens between them. In this review we explore the interconnections between land use change and human health, looking at the many pathways that connect emerging infectious diseases to deforestation, urbanization, and agriculture, for example, We connect the dots between underlying and direct drivers of land use change, the different types of land use change, and the emergence of infectious diseases. We highlight the importance of looking at the health of humans, animals and ecosystems as a single concept, to tackle related issues more effectively.

1. Introduction

Infectious diseases have been a significant threat to human health throughout history (e.g., Karesh et al., 2012; Wolfe et al., 2007). They are caused by a range of pathogenic microorganisms, including viruses, bacteria, fungi, as well as proteins (prions) and eukaryotic organisms, such as single celled protozoa or multicellular parasites. Following the advent of modern antibiotics and vaccinations, the impact of infectious diseases on people has been reduced globally, if unequally (Naghavi et al., 2024). Simultaneously, there have been dramatic demographic, social and economic changes that have driven local, regional and global environmental and ecological changes (IPBES, 2019) (Figure 1). In recent years, there has been a growing recognition of the link between land use change and the emergence of infectious diseases (Daszak et al., 2001; Gottdenker et al., 2014; Gottwalt, 2013;

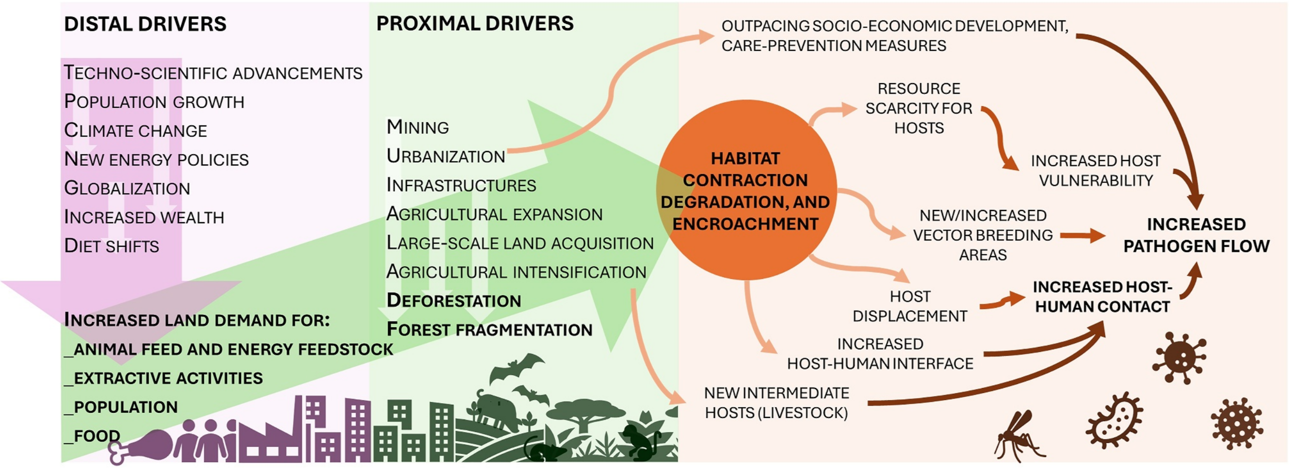

Figure 1. Simplified schematization of distal drivers, proximal drivers and mechanisms connecting land use changes to emerging infectious diseases risk (connections made by arrows are not exhaustive).

Mahon et al., 2024; Wallace et al., 2014) (Figure 1). The alteration of *natural habitats*, that is *where living and non-living things exist and interact without significant human influence*, can disrupt ecosystems and lead to the loss of biodiversity, which can trigger changes in the dynamics of infectious agents and their vectors (Mahon et al., 2024; Molyneux, 2003; Suzán et al., 2008; Taylor, 1997). Additionally, land use changes often bring humans into closer contact with wildlife (Sections 6.1 and 6.2), livestock (Section 5.2.1), and pathogen-carrying vectors (Table 1), increasing the likelihood of zoonotic pathogen transmission (aka "spillover") from animals to humans (Daszak et al., 2001; Gibb, Franklinos, et al., 2020; Pinzon et al., 2004; Rulli et al., 2017, 2021).

Land use change refers to the alteration of the way the Earth's surface is used by human activities, as a result of processes such as deforestation, urbanization, agricultural expansion, irrigation, or the transition from extensive to intensive farming (Geist & Lambin, 2022; Jones et al., 2013; Myers et al., 2013; Naylor, 2011; Runyan & D'Odorico, 2016; Wallace et al., 2014). While these activities have been essential for economic development and human well-being, they can have unintended consequences on the environment and its health, damaging its integrity and the balance of natural systems, including air, water, soil, and biodiversity, that sustain life, ecosystem functions, and public health (Galaz et al., 2023; McElwee et al., 2024; Yang et al., 2021). One of the significant repercussions is the emergence and spread of infectious diseases (Jones et al., 2013; Myers et al., 2013; Wallace et al., 2014), which have risen in the last decade (Figure 2).

Deforestation, in particular, has been associated with numerous infectious diseases (Section 6.1). As forests are cleared for agriculture (Section 5.2.1), mining (Section 5.2.4), or urban expansion (Section 5.2.2), the habitats of various animal species are disturbed, forcing them to migrate or adapt to new environments to survive (Muylaert et al., 2023; Pigott et al., 2014). This displacement can lead to increased contact between wildlife, livestock, and humans, facilitating the transmission of pathogens, particularly where exposed people are unable to minimize risks due to their livelihoods, overall unawareness, and health and safety conditions at home or work (Keesing et al., 2010). For example, the loss of forest cover has been linked to the emergence of Ebola virus disease (Rulli et al., 2017), while agricultural expansion increases the risk of hantavirus disease (Muylaert, Bovendorp, et al., 2019) and roads influence Yellow fever virus circulation (Pigott et al., 2014; Ribeiro Prist et al., 2022).

Urbanization is another critical factor contributing to the emergence of infectious diseases (Munster et al., 2018) (Section 5.2.2). As cities expand, natural habitats are converted into built environments, creating breeding grounds for some disease vectors that are able to adapt to urban environments, such as some mosquitoes and some rodents. Moreover, densely populated urban areas can facilitate the rapid spread of infections due to increased human-to-human contact. Examples of urban-associated diseases include dengue fever, tuberculosis, pneumonia and diarrhea from various causes (Alirol et al., 2010; Gao et al., 2021). This burden is particularly true for scenarios where urbanization occurs without a proportional increase in health care access and disease prevention and control strategies (Muylaert et al., 2023), though it is difficult to distinguish between outbreak detection that

Table 1
Overview of Key Zoonotic Infectious Diseases and Current Human Infections and Their Ancestors Discussed in the Text

Disease	Region	Symptoms and clinical signs in people	Human case fatality[a]	Agent(s)	Infectiousness (R0) among people[b]	Non-human hosts (vertebrate); except where now maintained among humans (e.g. HIV, SARS-CoV-2)	Vectors (invertebrates)/transmission
Marburg virus disease	Sub-Saharan Africa	Fever, chills, headache, myalgia, maculopapular rash, hemorrhage	~23%–90% (Brauburger et al., 2012; Kortepeter et al., 2020)	Virus: Marburg marburgvirus	~0.5–1.5 (Ajelli & Merler, 2012)	Fruit bats (Rousettus aegyptiacus)	None/direct contact transmission
Ebola virus disease	Sub-Saharan Africa	Fever, severe headache, muscle pain, fatigue, diarrhea, vomiting, hemorrhage	~25%–90% (Shears & O'Dempsey, 2015)	Virus: Ebolavirus (several species)	~1.5–2.5 (Althaus, 2014)	Fruit bats, non-human primates and duiker (small antelope) (intermediate hosts)	None/direct contact transmission
Simian immunodeficiency virus infection (SIV) & human only HIV/AIDS	Central and West Africa (SIV) Worldwide (HIV)	Symptoms: Typically asymptomatic in natural host species; in some cases can cause an AIDS-like illness (SIV); Acute phase - fever, rash, swollen lymph nodes; Chronic phase - weight loss, opportunistic infections (HIV/AIDS)	Variable, often low in natural hosts, higher in species not adapted to the virus (SIV); Variable, untreated progression to AIDS can be fatal (HIV) (Williams & Gouws, 2013; (Croxford et al., 2017)	Virus: Simian immunodeficiency viruses (various strains); HIV-1, HIV-2 (people only)	Median ~3 (2.1–4.3 95% Credible intervals) (SIV in mandrills) (Roussel et al., 2014) Median ~4.6 (range 2.3–8.9) (HIV)	Non-human primates (e.g., sooty mangabeys, African green monkeys, chimpanzees SIV); Humans only (HIV)	None/transmitted primarily through direct contact, including blood and bodily fluids, SIV; None/sexual contact, blood transfusion, HIV
Nipah virus disease	Southeast Asia	Fever, headache, respiratory issues, encephalitis	Approx 40%–75% (Epstein et al., 2006)	Virus: Nipah henipavirus	~ <1 (varies) (S. P. Luby, 2013)	Fruit bats (Pteropus species), pigs (intermediate hosts)	None/direct contact transmission
Hendra virus disease	Australia	Influenza-like symptoms, encephalitis, respiratory issues	~50%–75% (Powell et al., 2017)	Virus: Hendra henipavirus	~<1 (varies)	Fruit bats (Pteropus species), horses (intermediate hosts))	None/direct contact transmission

Table 1
Continued

Disease	Region	Symptoms and clinical signs in people	Human case fatality[a]	Agent(s)	Infectiousness (R0) among people[b]	Non-human hosts (vertebrate); except where now maintained among humans (e.g. HIV, SARS-CoV-2)	Vectors (invertebrates)/ transmission
Lassa fever	West Africa	Symptoms: Fever, headache, sore throat, muscle pain, nausea, vomiting, diarrhea, abdominal pain, severe cases can involve hemorrhage, respiratory distress, and neurological problems	~1%–15% among hospitalized patients, can be higher in epidemics (Dwalu et al., 2024)	Virus: Lassa mammarenavirus	~1–2 (J. Wang et al., 2021)	Multimammate rats (Mastomys natalensis), some other rodents	None/transmission primarily through direct contact with urine, feces, or saliva of infected rodents, or person-to-person transmission via bodily fluids
Coronavirus diseases including COVID-19, SARS and MERS	Worldwide (varies by specific coronavirus)	Fever, cough, shortness of breath, fatigue, in severe cases acute respiratory distress syndrome (ARDS)	Varies by virus (e.g., SARS-CoV-2 ~0.5%–3% (Horita & Fukumoto, 2022), MERS-CoV ~35%) (Pustake et al., 2022)	Virus: SARS-CoV, MERS-CoV, SARS-CoV-2	~SARS-CoV-2 ~2–3.5 (Liu et al., 2020)	Bats (ancestral viruses), civets, raccoon dogs (SARS-CoV, possibly SARS-CoV-2 intermediate hosts), dromedary camels (MERS), humans (all, but SARS-CoV-2 now endemic), deer (SARS-CoV-2, from people)	None/respiratory droplets, direct contact
Mpox	Central and West Africa	Fever, headache, muscle aches, lymphadenopathy, rash	~1%–10% (Yinka-Ogunleye et al., 2023)	Virus: Monkeypox virus	~1.2 (Al-Raeei, 2023)	Rodents, non-human primates (intermediate hosts), humans	None/direct contact, respiratory droplets
Hantavirus Pulmonary Syndrome (HPS) and Hemorrhagic Fever with Renal Syndrome (HFRS)	HPS primarily in the Americas; HFRS in Asia and Europe	HPS: Early symptoms include fever, fatigue, muscle aches, headache, and abdominal problems. Late symptoms include pulmonary signs and symptoms. HFRS: Fever, chills, headache, muscle pain, inflammation or redness of the eyes, and rash. Severe cases may	HPS: Approximately 36%; HFRS: 1%–15%, depending on the hantavirus strain (Duchin et al., 1994; Vial et al., 2006)	Virus: Various hantaviruses (e.g., Sin Nombre virus for HPS, Hantaan virus for HFRS)	~ Low (human-to-human transmission is rare) (L. J. S. Allen et al., 2006)	Rodents (different species for different hantaviruses, e.g., deer mice, rats)	None/transmitted primarily through inhalation of aerosolized virus from rodent urine, droppings, or saliva

Table 1
Continued

Disease	Region	Symptoms and clinical signs in people	Human case fatality[a]	Agent(s)	Infectiousness (R0) among people[b]	Non-human hosts (vertebrate); except where now maintained among humans (e.g. HIV, SARS-CoV-2)	Vectors (invertebrates)/transmission
		include hemorrhage and kidney failure					
Zika virus disease	Tropical and subtropical regions	Mild fever, rash, conjunctivitis, muscle and joint pain	Low, severe outcomes in pregnancy (microcephaly) (Hills et al., 2017)	Virus: Zika virus	~1.4–6 (Lessler et al., 2016)	Non-human primates	Aedes mosquitoes
Rift Valley fever	Africa, Middle East	Fever, weakness, back pain, dizziness, severe cases include hemorrhagic fever	~27.5% (Ebogo-Belobo et al., 2023)	Virus: Rift Valley fever virus	~2.5–4 (Tennant et al., 2021)	Livestock (cattle, sheep, goats), possible wildlife hosts	Mosquitoes (Aedes, Culex)
Japanese encephalitis	Southeast Asia, Western Pacific	Fever, headache, vomiting, seizures, encephalitis	~20%–30% (Turtle & Solomon, 2018)	Virus: Japanese encephalitis virus	~1–1.4 (Ladreyt et al., 2022)	Birds, pigs	Culex mosquitoes
Crimean-Congo hemorrhagic fever	Africa, Balkans, Middle East, Asia	Fever, myalgia, dizziness, neck pain, hemorrhage	~10%–40% (Atwan et al., 2024; Perveen & Khan, 2022; Rasikh et al., 2023)	Virus: Crimean-Congo hemorrhagic fever orthonairovirus	~Low (Hawman & Feldmann, 2023)	Livestock (cattle, goats, sheep), humans	Hyalomma ticks
Malaria	Tropical and subtropical regions	Fever, chills, sweats, headaches, nausea, vomiting	Varies by species and treatment (P. falciparum can be high if untreated in people) (Olliaro, 2008)	Eukaryote: *Plasmodium falciparum*, *P. vivax*, *P. ovale*, *P. malariae*, *P. knowlesi*	~Varies (D. L. Smith et al., 2007)	Non-human primates, humans	Anopheles mosquitoes
Lyme disease	North America, Europe, Asia	Erythema migrans (bullseye rash), fever, chills, headache, fatigue, joint pain	Low, if treated (Kugeler et al., 2010)	Bacteria: *Borrelia burgdorferi*	~0, there is no current evidence of humans being the sources of Lyme infection	Rodents, deer, other wildlife	Ixodes ticks

Note. The infections here include current zoonoses and current human-only infections that were derived from zoonoses. Examples include human immunodeficiency viruses (HIV) and their ancestors simian immunodeficiency virus infection (SIV), or vector-borne equivalents, such as Zika virus, which were initially zoonotic infections that are now not considered zoonoses because people are now reservoir hosts and these infections perpetuate among people (HIV) or people and vectors (Zika virus). The SIV R0 estimate is from mandrills, a monkey species, and not chimpanzees, which are the likely reservoir host for the ancestor of pandemic HIV1-M and other HIV1 viruses in people. [a]The proportion of people who die from a disease among all individuals infected. [b]Reproduction number (R0) indicates the average number of secondary infections from one person in a totally naive population. For example, an $R0 = 2$ means one infected individual will on average infect two other people in an entirely susceptible population. Note that R0 will necessarily be greater than one in the reservoir systems the infection is maintained in, but here we focus on R0 in people.

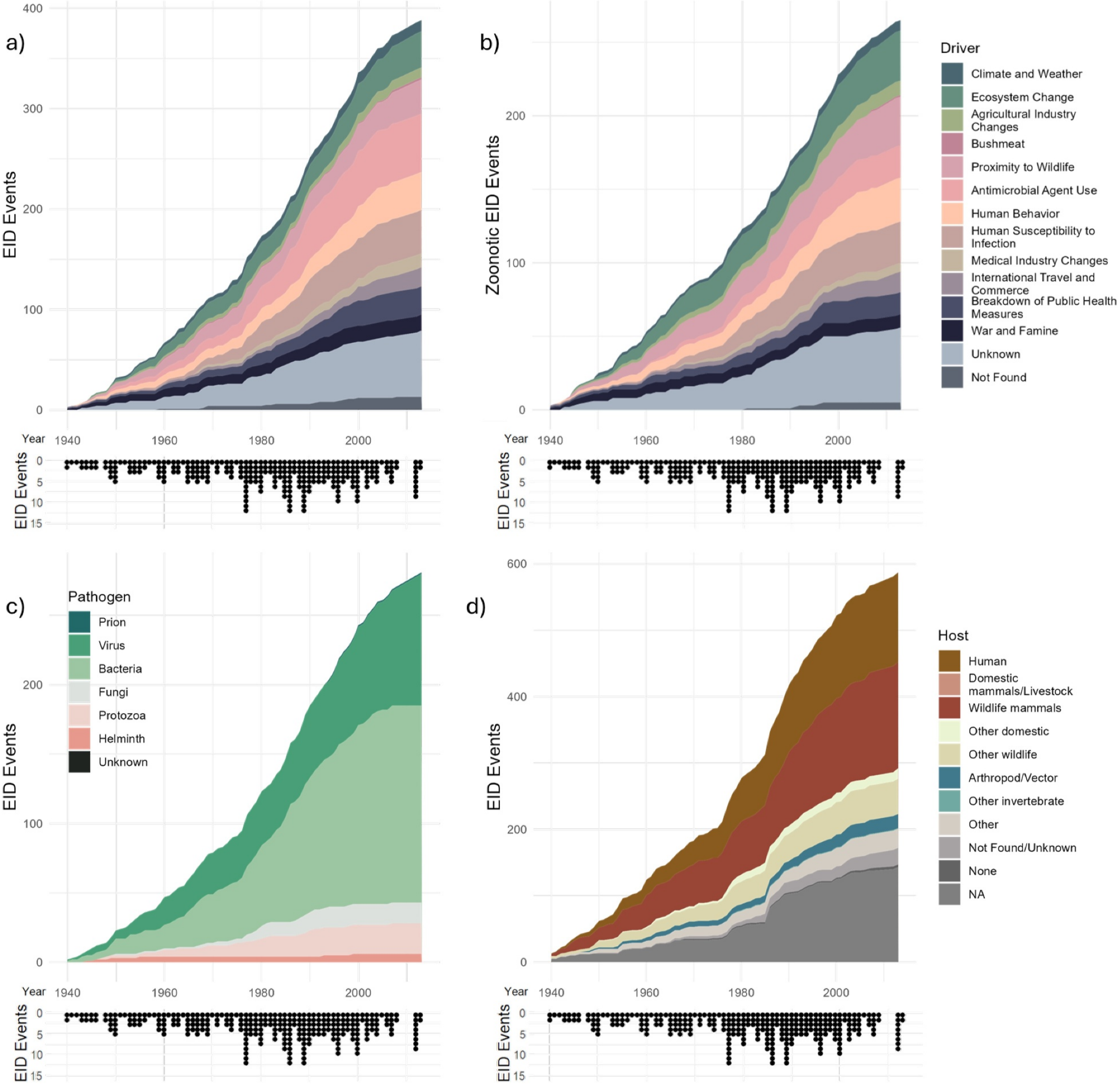

Figure 2. Temporal changes of emerging infectious disease (EID) events reported since 1940. (a) Reports all EID events classified by drivers, (b) reports zoonotic EID events classified by drivers, and (c, d) report EID events classified by pathogen and by host, respectively. Adapted from (Rohr et al., 2019). Data from the EID Repository, EcoHealth Alliance (2025; https://www.ecohealthalliance.org/program/eidr). Cumulative sums reach different values because events with multiple drivers/hosts/pathogens are counted once for each driver/host/pathogen, and because the classification of the diseases into zoonotic and non-zoonotic is not based exclusively on the host but also on the type of transmission.

occurs in urban areas and the role of urbanization itself as a driver of infectious disease emergence (Gibb et al., 2024). These processes likely happen simultaneously across space and time but are difficult to model.

Agricultural expansion and intensification also play a key role in infectious disease emergence (Morand, 2022) (Section 5.2.1). The conversion of natural landscapes into agricultural land often involves the use of pesticides and other chemicals, which can have unintended consequences on the environment and human health (Fuller et al., 2022). Additionally, intensive farming practices, such as factory farming, can increase the risk of disease transmission among animals and facilitate the spillover of pathogens to humans (Hayek, 2022), especially if there is poor biosecurity. Examples include the emergence of Nipah virus in pig farms in Malaysia (Pulliam et al., 2011), the emergence of highly pathogenic avian influenza viruses in poultry (Kuiken & Cromie, 2022), and transmission of SARS-CoV-2 among farmed mink in Europe during the Covid-19 pandemic (Oude Munnink et al., 2021) along with the potential emergence of SARS-CoV-2 among other related farmed carnivores (WHO, 2021). In agriculturally dominated areas, cases are also less likely to present at clinics due to less access to healthcare. An analysis of >50,000 disease reporting instances worldwide has shown that, on average, reporting of infectious disease outbreaks drops by a third for each additional hour of travel time to the nearest hospital or clinic (Gibb et al., 2024).

Understanding the complex relationship between land use change and infectious disease emergence is crucial for developing effective strategies to mitigate and prevent future outbreaks (Markotter et al., 2023). It requires consistent interdisciplinary collaboration among scientists, policymakers, and stakeholders to identify sustainable land management practices that balance human needs with environmental and public health considerations (McElwee et al., 2024). By addressing the drivers of land use change and promoting ecosystem conservation, we can work toward minimizing the risks associated with infectious disease emergence and safeguarding global health.

Here we review recent advances in the understating of the nexus between land use change and zoonotic infectious disease emergence in humans. Specifically, we focus on pathways of pathogen transfer from wildlife to humans that are related to land use change. We examine the direct and underlying drivers of land use changes conducive to zoonotic infections and evaluate modeling and multisectoral and integrative approaches that have been used to predict and understand zoonotic disease emergence in humans under climate and land use change (Figure 1). While we focus on the transmission pathways from non-human species to people, it is also very valuable to remember that the reverse also happens (Fagre et al., 2022), and these pathways can allow other species to be infected by humans (Tan et al., 2024). We also highlight, where relevant, how key changes that led to animal to human transmission can facilitate also ongoing human to human transmission.

2. Ecology of Host and Vector Species Populations and Their Impact on Infectious Disease Dynamics

The ecology of the populations of host (Section 2.1) and vector species (Section 2.3) of emerging infectious diseases, along with their biophysical environment, plays a crucial role in shaping the dynamics of infectious diseases. For convenience, arthropod hosts such as mosquitoes, flies, biting midges, ticks, mites, fleas, and lice are typically referred to as vectors, and vertebrate hosts typically just *hosts*, though both may be the "vector" of infection to another and play a role as reservoir hosts in maintaining infection in a system (Haydon et al., 2002) (Section 2.1). The complex interactions between hosts, vectors, and their environments influence the transmission, spread, and persistence of these infectious diseases. The study of underlying ecological factors is essential for predicting and managing disease outbreaks effectively (Gibb, Franklinos, et al., 2020).

Host populations, which can include humans, wildlife, and domestic animals, serve as reservoirs of infectious agents (Figure 2d; Section 2.1) (Haydon et al., 2002). The size, density, and distribution of these host populations influence the likelihood of pathogen transmission (Johnson et al., 2020). Factors such as host behavior, immune response, and genetic diversity can also affect disease susceptibility and resistance (Hayman, 2019b). Changes in host population dynamics (Eby et al., 2023), such as with migration (Altizer et al., 2011), or due to urbanization (Costa et al., 2015) or alterations in social structures, including from host culling in attempts to control infectious diseases (Amman et al., 2014; Bielby et al., 2016; Donnelly et al., 2006; Mariën et al., 2024; Viana et al., 2023), can have profound implications for disease transmission patterns (Appendix A).

Vector species, such as mosquitoes, ticks, and flies, play a crucial role in transmitting many pathogens from hosts to humans. The abundance, distribution, and competence of vector populations are key factors in disease transmission dynamics (Kraemer et al., 2015, 2019; Messina et al., 2019; Pepin et al., 2015). Vector biology, including feeding habits, reproductive cycles, and vector lifespan, influences the rate and efficiency of pathogen transmission. Environmental factors, such as temperature, humidity, and vegetation cover, impact vector populations and their ability to transmit diseases.

Natural ecosystems, such as forests, wetlands, or grasslands, can provide suitable habitats for natural hosts and vectors, influencing their population dynamics and contact rates (Dobson, 2004) (Appendix A). Within these environments, ecological processes such as predation, competition, and parasitism, also influence infectious disease dynamics (Thieltges et al., 2024). Interactions between species within ecological communities can affect the abundance and behavior of hosts and vectors, indirectly impacting disease transmission (Luis et al., 2018).

2.1. Reservoir Hosts of Infectious Diseases

Many infectious diseases affecting humans are caused by pathogens that originate from animals or are transmitted to humans (Wolfe et al., 2007).

Here, we consider reservoir hosts as a species or group of species in which a pathogen can persist long-term, maintaining transmission even in the absence of other hosts (Haydon et al., 2002). Reservoir hosts do not necessarily experience high mortality or severe disease, allowing the pathogen to circulate stably, though disease may also occur, such as for rabies. For a species to be considered a true reservoir, it must be capable of sustaining the infection over time and serve as a source of transmission to other susceptible hosts. Other hosts that are infected are sometimes called dead end hosts if they do not infect another host or vector, and sometimes amplifying or intermediate hosts, where a species might contribute to transmission through high levels of pathogen replication (amplifying) or become infected and transmit infection to another species (such as a person; intermediate), yet unlike true reservoirs, amplifying and intermediate hosts may not maintain the pathogen long-term without continuous introduction from reservoirs (Haydon et al., 2002).

Reservoir hosts can include a wide range of animals, such as rodents, bats, birds, and non-human primates (Olival et al., 2017), as well as people (Tan et al., 2024) for infections of other species. The ability of reservoir hosts to carry and transmit pathogens is often due to their unique biological characteristics (Luis et al., 2013, 2015; Olival et al., 2017). They may have developed co-evolutionary relationships with the infectious agents, allowing them to tolerate the presence of the pathogen without succumbing to illness (Guito et al., 2021; Hayman, 2019b). Additionally, reservoir hosts may have specific physiological, immunological, or behavioral traits that enable them to carry and shed the pathogen for an extended period (Hayman, 2019b).

Many of the emerging infectious diseases that are currently thought to pose a threat to human health are directly transmitted zoonotic diseases (Jones et al., 2008), meaning they originate in animals and can be transmitted to humans through direct or in-direct contact (Section 2). Several notable recent emerging infectious viruses include Marburg virus, Ebola virus, human immunodeficiency viruses (HIV), Nipah virus, Hendra virus, coronaviruses, and Monkeypox virus (Grange et al., 2021) (Table 1). These infections have animal reservoirs, and transmission to people has been either through direct contact with people or following contact with other intermediate hosts before people, such as farmed or other hunted wildlife or domestic animals (Table 1). Identifying and studying these animal reservoirs and their interactions with people and domestic species, along with the land use changes that increase direct and indirect contacts may explain the natural history of these infectious diseases and their transmission dynamics, and enable the development of effective prevention and control strategies (Markotter et al., 2023).

2.2. Directly Transmitted Emerging Infectious Diseases

Marburg virus and Ebola virus are members of the Filoviridae family (hereon, filoviruses) and are known to cause severe and often fatal hemorrhagic fever with cases being intermittently detected in Africa since the 60s (Emanuel et al., 2018). Fruit bats are suspected to be the natural reservoirs for both viruses, as they carry and shed these or related viruses without exhibiting symptoms (Olival & Hayman, 2014). However, there are multiple different filoviruses and their hosts are widely distributed in the Old World (Biedenkopf et al., 2024; Han et al., 2016), yet there have not been serious human disease outbreaks reported outside of Africa. For example, Reston virus outbreaks have been limited to The Philippines or are linked to the region via animal trade (Section 6.6), with no evidence of symptomatic human disease. Land use changes that lead to forest fragmentation are linked to Ebola virus disease outbreaks (Section 6.2) (Rulli et al., 2017) and to interconnected and urbanized populations (Section 5.2.2) (WHO Ebola Response Team, 2014). Marburg virus disease outbreaks have been directly linked to mining activities (Section 5.2.4) (Bausch et al., 2003, 2006).

HIVs, the viruses (Table 1) that cause AIDS, are believed to have originated from non-human primates, particularly chimpanzees, in Central Africa (D'arc et al., 2015; Gao et al., 1999; Keele et al., 2006; Sharp & Hahn, 2011). There are several different HIVs and many more simian immunodeficiency viruses (SIVs) in primates. The HIVs likely crossed over to humans through the hunting and consumption of animals infected with simian immunodeficiency virus (SIV) (Kurpiers et al., 2016). Subsequently, the HIV twentieth century pandemic largely spread in humans primarily through sexual contact, blood transfusions and the sharing of contaminated hypodermic needles. How viruses adapt to hosts and spread is dependent on multiple factors (Lloyd-Smith et al., 2009), but other lentiviruses (retroviruses like HIV) have repeatedly infected people from other primates, yet remain as individual or local infections (Mossoun et al., 2017). However, it is direct contact with animals that causes the spillover events and the increasingly urbanized and interconnected populations (Sections 5.1.7 and 5.2.2) that led to the global pandemic (Quinn, 1996).

Nipah virus and Hendra virus are both zoonotic viruses that can cause severe respiratory and neurological diseases (Luby & Broder, 2023) in Asia and Australasia (Table 1). Fruit bats, specifically those of the *Pteropus* genus, are the natural reservoirs for these viruses and have wide geographical distribution. Infected bats shed the virus in their saliva, urine, and droppings, and transmission to humans can occur through direct contact with infected bats or consumption of contaminated food (Luby & Broder, 2023). Both viruses are archetypal examples of how land use changes (Section 4) lead to viral disease emergence, with land use change being implicated in several outbreaks among people and domestic species (Section 6) (Eby et al., 2023; Pulliam et al., 2011).

Coronaviruses (Table 1), including the severe acute respiratory syndrome coronavirus (SARS-CoV), Middle East respiratory syndrome coronavirus (MERS-CoV), and, more recently, SARS-CoV-2 (the virus responsible for COVID-19), are believed to have originated in bats in Asia; (Boni et al., 2020; Corman et al., 2015; Li et al., 2005; Xiong et al., 2022). Other animal species, including farmed wild animals such as civets (infected with SARS-CoV-1 (Wang et al., 2005) and susceptible to SARS-CoV-2) (Sections 5.1.2 and 5.2.1), and domesticated dromedary camels (infected with MERS-CoV), have also been implicated as intermediate hosts in the transmission of coronaviruses to humans, with camels the likely maintenance hosts of MERS-CoV with the virus perpetuating in the domesticated dromedary populations (Mohd et al., 2016). These outbreaks highlight how changing human diets and animal use can interact with changing landscapes and human connectivity to cause large epidemics and pandemics (Section 4.1).

Monkeypox, a viral disease similar to smallpox, is primarily found in Central and West African countries and first detected in humans in the 70s (Breman et al., 1980). Various animals, including rodents, monkeys, and squirrels, have been identified as potential reservoirs for the monkeypox virus (Mitjà et al., 2023). This virus' pandemic potential was highlighted during the 2000s (Rimoin et al., 2010), before it began to spread globally, causing thousands of cases instead of hundreds from 2022 (Mitjà et al., 2023; Thornhill et al., 2022). Lassa virus and hantaviruses (Table 1) are two other groups of rodent-borne zoonotic viruses that can cause severe illnesses in humans. Lassa virus is responsible for Lassa fever, a viral hemorrhagic fever, with thousands of cases annually in West Africa (Fichet-Calvet & Rogers, 2009; Kenmoe et al., 2020; Redding et al., 2021). Hantaviruses, on the other hand, are distributed globally (Holmes & Zhang, 2015) and can cause various diseases, including hantavirus pulmonary syndrome (HPS) caused by New World hantaviruses and hemorrhagic fever with renal syndrome (HFRS) caused by Old World hantaviruses (Vial et al., 2023). Both Lassa virus and hantaviruses are typically transmitted to humans through contact with infected rodents or their excreta. Land use change and the diversity of rodent hosts allows hantavirus to circulate in a wide spectrum of habitats (Muylaert et al., 2019a), particularly rural areas in the Americas (García-Peña & Rubio, 2024). Understanding the transmission dynamics and implementing appropriate preventive measures particularly for the most vulnerable population sectors are crucial for mitigating the impact of these viruses on human health (Haby et al., 2021; John, Fatoyinbo, & Hayman, 2024; Luis, Douglass, et al., 2015; Muylaert et al., 2019a, 2019b; Redding et al., 2016). Many rodent hosts of zoonotic diseases are expected to thrive in more modified landscapes, highlighting how changes in biodiversity can increase the risk of zoonotic human infection (Gibb, Redding, et al., 2020).

2.3. Vector-Borne Diseases

Vector-borne diseases are caused by pathogens that are transmitted to humans primarily through the bites of infected arthropods, such as mosquitoes, ticks, and flies (Weaver & Reisen, 2010). These infections pose a significant public health threat globally and are responsible for a range of diseases. Notable vector-borne viruses include Zika virus, Rift Valley fever (RVF) virus, Japanese encephalitis virus (JEV), Crimean-Congo hemorrhagic fever (CCHF) orthonairovirus, vector-borne protozoa including *Plasmodium* (malaria) parasites, and bacteria including *Borrelia burgdorferi*, the cause of Lyme disease (Table 1). Transmission patterns, prevention, mitigation, and control measures for these vector-borne viruses and diseases differ from directly transmitted infections in that the infections life cycles are dependent on the arthropod hosts, which themselves are dependent of a range of environmental factors that can differ to other species involved in maintaining the infections. For example, female *Anopheles* mosquitoes transmit *Plasmodium falciparum* to people, the other reservoir host of *P.*

falciparum. Yet, out of hundreds of *Anopheles* mosquitoes, *Anopheles gambiae* complex is a particularly efficient vector and distributed across parts of Africa, therefore impacting the distribution on *P. falciparum* malaria and increasing the risk to vulnerable people in sub-Saharan Africa (Sinka et al., 2010). Efforts to understand vectors, their life cycles, and land use changes that affect the risk of vector-borne disease are important for limiting infection alongside raising awareness and developing effective vaccines and treatments to reduce the burden of these diseases and prevent new events (Table 1).

2.3.1. Notable Emerging Vector-Borne Diseases

Zika virus (Table 1) gained worldwide attention during the 2015–2016 outbreak, primarily in the Americas. However, the virus it was first detected in Zika Forest in Uganda, Africa in 1947 (Musso & Gubler, 2016; Petersen et al., 2016). Transmitted by *Aedes* mosquitoes, urbanized mosquitoes that can also transmit Dengue, Chikungunya, Yellow Fever and RVF viruses, Zika virus can cause mild flu-like symptoms in infected individuals. However, it poses a significant risk to some, especially pregnant women and their children, as severe abnormalities in Zika infection-related births are reported, including microcephaly (Nascimento et al., 2022). Zika virus highlights how an infection that circulated in forests in East Africa can emerge and spread around the world due to the combined impacts of human encroachment into forest habitats (Sections 6.1 and 6.2), urbanization (Section 5.2.2) and human connectivity (Section 6.7).

Rift Valley Fever virus (RVFV) is predominantly found in Africa and the Middle East, with mosquitoes (often *Aedes* and *Culex*) acting as the primary vectors. Infection with RVFV can cause a range of symptoms in humans, from mild flu-like illness to severe hemorrhagic fever (Anywaine et al., 2022). It also poses a significant threat to livestock (Bird et al., 2009). The sporadic outbreaks have been linked to environmental and climatic factors that alter the infection dynamics (Anyamba et al., 2009; Linthicum et al., 1999) (Sections 5.1.8 and 7).

Japanese encephalitis virus is a leading cause of viral encephalitis in Asia (van den Hurk et al., 2009; Solomon et al., 2003; Wang & Liang, 2015). It is transmitted by mosquitoes, particularly the *Culex* species. Infection with JEV can result in neurological complications and, in severe cases, can be fatal (Wang & Liang, 2015). The virus has a complex life cycle, involving numerous mosquito and host species, including farmed species who are often linked to human infection (Lord et al., 2015).

Crimean-Congo hemorrhagic fever orthonairovirus is transmitted to humans through ticks, primarily from the *Hyalomma* genus (Lord et al., 2015). The virus can cause a severe hemorrhagic fever with a high fatality rate (Whitehouse, 2004). The virus is widespread across Africa, Asia, and Europe (Messina et al., 2015), with many non-human vertebrate hosts likely playing a role in its epidemiology, including farmed domestic species (Spengler et al., 2016). Land use change (Section 4), climate (Sections 5.1.8 and 7) and domestic animal distributions have been linked to changing CCHF risk (Chanda et al., 2023).

Plasmodium parasites are responsible for malaria, an ancient life-threatening disease prevalent in tropical and subtropical regions (Cibulskis et al., 2016; Llanos-Lizcano et al., 2024), with a consistent burden of around 249 million malaria cases estimated globally, with over half a million deaths in 2022 (Venkatesan, 2024). Female *Anopheles* mosquitoes transmit the parasites, leading to recurring cycles of fever, chills, and flu-like symptoms. There are multiple *Plasmodium* species, with both similarities and differences (Escalante et al., 2022). African apes host at least twelve *Plasmodium* species (Kaiser et al., 2010; Rich et al., 2009; Sharp et al., 2020) some of which switch hosts to become human infections, including *Plasmodium falciparum* from gorillas, and with different potential pathways for *P. vivax* (Sharp et al., 2020) and *P. malariae* (Plenderleith et al., 2022). *Plasmodium knowlesi* is an increasingly diagnosed cause of zoonotic human malaria in Asia, with increased cases linked to land use change (Byrne et al., 2021; Tobin et al., 2024).

Dengue virus is transmitted by *Aedes* mosquitoes and is a major global health concern (Bhatt et al., 2013; Guzman & Harris, 2015; Messina et al., 2019), endemic in more than 100 countries (Paz-Bailey et al., 2024), with deaths related to dengue increasing by around 65% in the last 20 years. Dengue virus is believed to have originally emerged from non-human primates in forests of Southeast Asia or Africa, where it circulated in a sylvatic ("jungle") cycle involving mosquitoes and primates. It can cause a spectrum of symptoms, ranging from mild dengue fever to severe dengue hemorrhagic fever, which can be fatal (Guzman & Harris, 2015). Dengue virus is an archetypal example of how urbanization (Section 5.2.2) and climate change (Section 7) (Gibb et al., 2024) have and will likely dramatically change the risk of infectious diseases.

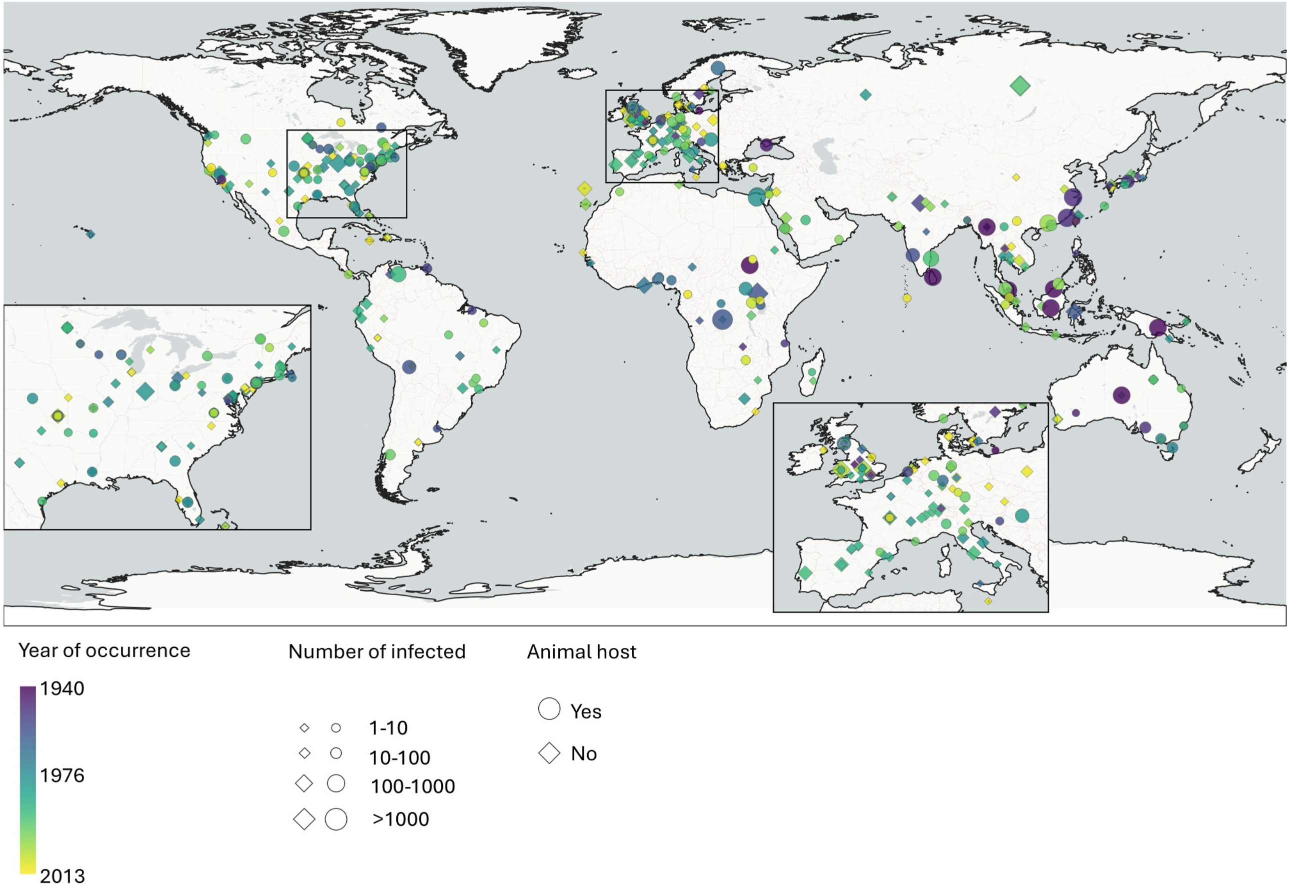

Figure 3. Geographic distribution of emerging infectious disease (EID) events reported from 1940 to 2004. Data from the EID Repository, EcoHealth Alliance (https://www.ecohealthalliance.org/program/eidr).

Lyme disease is caused by the bacterium *Borrelia burgdorferi* and is transmitted to humans through the bites of infected ticks, primarily *Ixodes*, and is the most commonly diagnosed arthropod-borne infectious disease in the temperate regions of the northern hemisphere (Dong et al., 2022). It can lead to various symptoms, including rash, joint pain, and neurological problems if not treated promptly. *Borrelia* and ticks have complex life cycles, often with multiple species of host, and people are at risk due to tick contact, which is related to land use (Section 4.1), climate (Section 7) and human behaviors (Diuk-Wasser et al., 2021).

3. Biogeography of Emerging Zoonotic Pathogens

The biogeography of viruses and other pathogens associated with emerging zoonotic diseases is a complex field of study that explores the geographical distribution and ecological factors influencing the emergence and spread of these pathogens (Figure 3). It involves examining the interplay between biodiversity patterns, climate, and land cover/use and their impact on the distribution and dynamics of zoonotic diseases (Carlson et al., 2022; Gibb et al., 2024; Murray et al., 2018; Wilkinson et al., 2018).

Biodiversity change plays a crucial role in the emergence of zoonotic diseases (Mahon et al., 2024) Ecosystems with high biodiversity harbor a wide range of host species coexisting within their habitat, and when humans encroach in that habitat, the chances of potential cross-species transmission increase (Jones et al., 2008; Murray et al., 2015). The loss or fragmentation of natural habitats due to land use changes can disrupt biodiversity patterns (Alkemade et al., 2013; Crist et al., 2017), leading to increased contact between humans, domestic animals, and wildlife, and facilitating the spillover of pathogens (Gibb, Franklinos, et al., 2020; Wilkinson et al., 2018). Global studies point out that land use conversion, agricultural expansion, biodiversity hotspots and global travel are widely associated with hotspots of infectious disease emergence (Allen et al., 2017; Gibb et al., 2024; Jones et al., 2008). However, data on emergence events are biased toward better-resourced settings where novel infections are more likely to be reported, rather than rural and remote areas (Figure 3) (Gibb et al., 2024). Due to evidence gaps and heterogeneity across systems, driven by differences in pathogen life cycles, host and vector ecology, and variation in biodiversity, the links between EID risk and biodiversity loss vary depending on the context across diseases and locations (Salkeld et al., 2013). While recent meta-analysis suggest that loss of pre-existing biodiversity is associated with large increases in infectious disease outcomes (Mahon et al., 2024), global models corrected by geospatial effects and detection-related covariates showed that observed infectious disease hotspots are created by outbreak event observation and reporting biases (Gibb et al., 2024; Jones et al., 2008), exceeding the effect of any individual driver. These findings highlight that bias-adjusted and disease system-specific analyses are necessary understand the role of biodiversity and biodiversity loss as drivers of infectious disease emergence. The apparent exceptions for that are highly studied diseases such as Lyme disease, for which risk decreases as an effect of higher biodiversity intactness (Gibb et al., 2024; LoGiudice et al., 2003; Ostfeld & Keesing, 2000). Moreover, nonlinearity and interaction effects are expected when it comes to modeling the effects of biodiversity in disease risk emergence (Faust et al., 2018; Wilkinson et al., 2018). Ultimately, global models tend to agree that emerging infectious diseases are associated with areas at the interface between people (Section 5.1.1), livestock (Section 5.2.1), and highly biodiverse ecosystems, such as tropical forests (Allen et al., 2017; Gibb et al., 2024; Jones et al., 2008; Morand, 2022; Murray et al., 2018).

Climate is a significant factor shaping the biogeography of zoonotic pathogens, because pathogen biodiversity tends to be influenced by host biodiversity, which is impacted by the climate (Murray et al., 2015, 2018) (Section 5.1.5). Climate influences the distribution and abundance of host and vectors, such as mosquitoes and ticks, which play a vital role in transmitting many zoonotic diseases (Section 2) (Kraemer et al., 2015, 2019). Changes in temperature, rainfall patterns, and seasonal variations can impact vector populations, altering their geographical ranges and potentially expanding the transmission zones of diseases (Kraemer et al., 2015, 2019).

Land cover and land use practices also contribute to the biogeography of zoonotic pathogens (Gibb, Franklinos, et al., 2020). Deforestation, urbanization, and agriculture (Sections 5.2.1, 5.2.2, and 6.1) can both remove and create ecological niches that favor certain vector species, changing their abundance and proximity to human populations (Tucker Lima et al., 2017). Additionally, agricultural intensification, including the use of pesticides, can disrupt ecological balance, potentially leading to the emergence or amplification of zoonotic diseases (Pulliam et al., 2011). While these factors have been shown to influence the emergence of infectious diseases less than biodiversity loss and the introduction of new species (Mahon et al., 2024) these mechanisms are interconnected, and context-specific effects of landscape transformation on infectious disease emergence, mediated by ecological alterations, remain important.

By mapping the distribution of pathogens, identifying key hotspots, and analyzing the underlying eco-evolutionary (Forero-Muñoz et al., 2024) and environmental factors, scientists can develop targeted surveillance and control strategies (Murray et al., 2018; Muylaert et al., 2023).

4. Land Use Change

Land use change is one of the main ways in which humankind has modified the Earth system and altered its ecosystems, with important impacts on local and global climate, biogeochemical cycles, biodiversity, and human health (Foley et al., 2005; McElwee et al., 2024; Newbold et al., 2015; Runyan & D'Odorico, 2016; Steffen et al., 2015). Land use change entails a wide range of modifications in the activities humans perform on the land and its vegetation cover (Liang et al., 2012). It has been estimated that land use change has affected almost one third (32%) of the global land area in just six decades (1960–2019), accounting for 43 million square kilometers (Winkler et al., 2021) (Figure 4). From 2000 to 2020, roughly 1 million square kilometres of forest have been lost, mainly to agricultural lands, timber production and human settlement expansion, while another million square kilometres of cropland have been converted to other uses or abandoned (Potapov et al., 2022).

The relationship between land use change and pathogen transmission from wildlife hosts to humans depends on the type of land use change that occurs and on its consequences on natural habitat. It also depends on how the host and/or the vector species react to those impacts, and on the presence of domesticated, potentially intermediate animal hosts. Thus, next we provide a broad overview of the nexus of land use change and zoonotic disease emergence (Section 4.1), describe different drivers of land use change (Section 5) and then explain in more detail how the differing types of land use change may increase zoonotic disease emergence (Section 6).

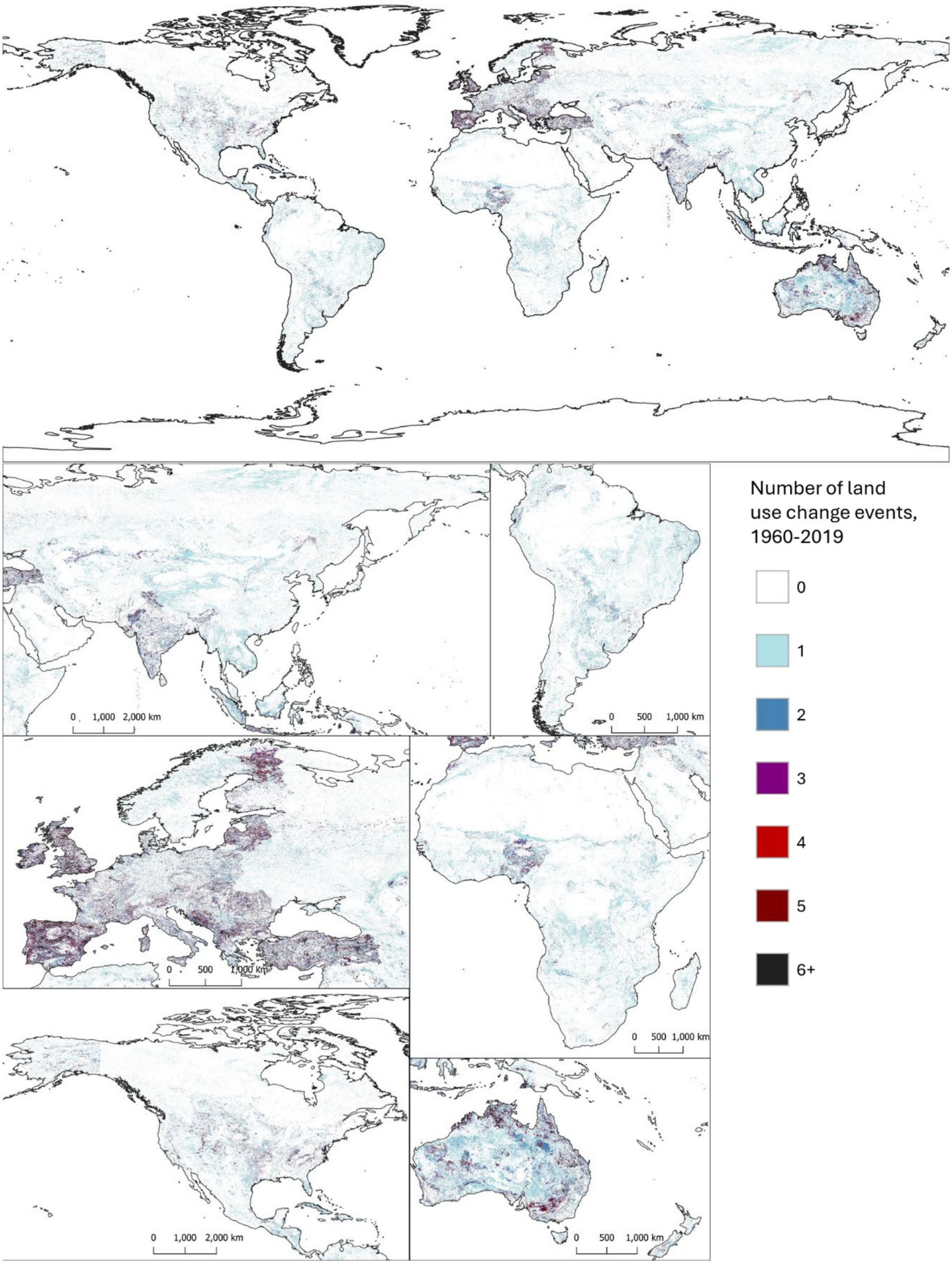

Figure 4. Spatial extent of global land use/cover change (from Winkler et al., 2021). Number of land use change events for six major land use/cover categories (urban area, cropland, pasture/rangeland, forest, unmanaged grass/shrubland, non-/sparsely vegetated land) in 1960–2019, as the number of times a pixel has changed status between any two categories in the time period. The panels show, counterclockwise from the top left corner: Asia, Europe, North America, Oceania, Africa, South America.

4.1. The Nexus Between Land Use Change and Risk of Zoonotic Infection

How does global land use change affect pathogen transmission from wildlife to humans? A large share of the land conversion globally occurs at the expense of natural areas such as forests, savannas, grasslands, or shrublands (Hansen et al., 2022), leading to the destruction or the degradation of natural habitats for a variety of wildlife species. It has been estimated that on average land use change has contributed to a 14% decrease in natural habitat area for each species worldwide (Semenchuk et al., 2022). The dynamics of habitat contraction often starts with human intrusion into wildlife habitat, typically to build roads for resource extraction or logging activities (Napolitano Ferreira et al., 2021). The land use conversion that occurs afterward increases the amount of edge habitat areas, that is, portions of natural habitat bordering anthropized land (Napolitano Ferreira et al., 2021), and thus increases the likelihood of contact between humans and wildlife pathogen hosts (Wilkinson et al., 2018). The interaction between humans and wildlife pathogen hosts can occur both at the edge of their respective habitats or within one of them, through the direct encroachment of one of the two species into the other species' adjacent habitat (Figure 1) (Faust et al., 2018). These mechanisms are favored by land use change dynamics that not only reduce the spatial extent of natural habitat, but fragment it, thus creating an environment characterized by longer, more complex edges (Ribeiro Prist et al., 2022; Wilkinson et al., 2018) between natural and anthropized lands, and by patches of natural land isolated within anthropized land (Faust et al., 2018). Forest fragmentation, as a specific form of forest cover modification, has often been presented as a driver of zoonotic spillover (Rulli et al., 2017, 2021; Wilkinson et al., 2018), requiring specific consideration in the study of EID under environmental change. Also, the role of habitat contraction and fragmentation in zoonotic diseases spillover is enhanced for pathogens having a vector species and/or a domesticated intermediate host (Morand et al., 2014). Land use change can increase human exposure to disease vectors (de Castro et al., 2006), while the introduction of livestock in newly converted areas creates additional environmental pathways for zoonotic spillover (Jones et al., 2013; Pulliam et al., 2011). Other emerging infectious diseases are transmitted to humans through a spillover from wildlife hosts such as rodents, bats or other species (Gibb, Franklinos, et al., 2020), because some of these species (but not all) are generalist species that can survive in more urbanized environments and whose abundance may be even enhanced by forest disturbance and forest fragmentation (Delaval & Charles-Dominique, 2006; Galindo-González, 2014; Gibb, Franklinos, et al., 2020; Klingbeil & Willig, 2009; Meyer et al., 2016; Meyer & Kalko, 2008; Muylaert et al., 2019b; Sampaio et al., 2003). Importantly, after an event of land use change, wildlife host populations might also be subjected to stress and food scarcity, having to move to find food and shelter, and stress may lead to increased shedding for certain pathogens (Eby et al., 2023), increasing spillover risk, a phenomenon called land-use induced spillover (Plowright et al., 2021).

5. Drivers of Land Use Change

Drivers of land use change are often classified either as proximate (or “direct”) or distal (or also “distant,” “underlying,” or “indirect”) (Geist & Lambin, 2022). Both proximate and distal drivers interact with each other to form the observed patterns of land use change. Proximate drivers of land use, such as agricultural expansion/intensification (Section 5.2.1), urbanization (Section 5.2.2), and infrastructural development (Sections 5.2.3, 5.2.4, and 5.2.5), are frequently the outcome of direct human actions and are determined by social, economic, and political factors (IPBES, 2019). Distal drivers of land use change (Section 5.1) include population growth, dietary shifts, policy changes, economic development, changes in global markets, technical advancements, and cultural shifts, described below.

Land use changes conducive to infectious zoonotic disease emergence are often driven by the need to sustain increasing demand for agricultural commodities (mostly for food production). Such an increasing demand is contributed by the increase in global population (i.e., “more mouths to feed”) (5.1.1) and the shift to resource-intensive diets (i.e., increase in per capita consumption) (Section 5.1.2) typically occurring with increasing income levels (Bennett, 1941) (Figure 5). Both factors play a comparable role and indirectly contribute to agricultural expansion and the associated land use change (van Dijk et al., 2021; Whitnall & Pitts, 2019). A third factor is associated with biomass production to be used as feedstock for bioethanol and biodiesel production or in negative emission systems to address new energy policies (Section 5.1.3). Thus, population growth, dietary shifts, and externalities of some energy policies are important underlying drivers of land use changes (e.g., deforestation, forest fragmentation, urbanization, agricultural expansion) potentially favoring pathogen spillover from wildlife to humans.

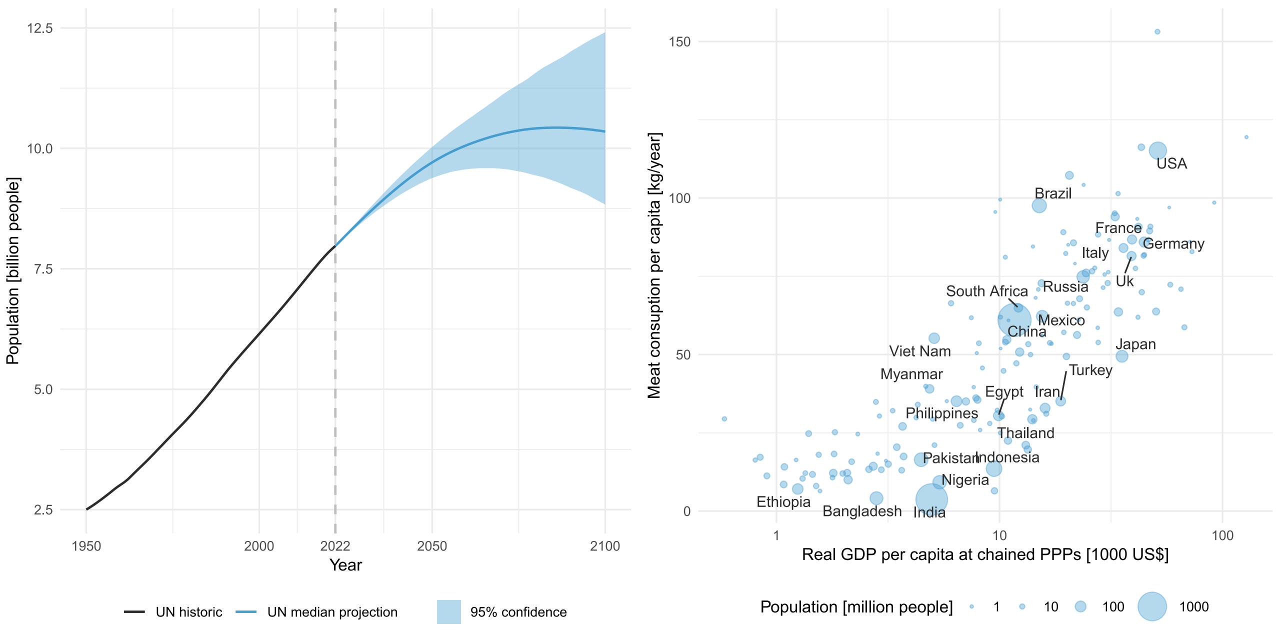

Figure 5. (a) Temporal dynamics of human population growth (UN, 2022; UN DESA, 2024). (b) Per capita meat consumption as a function of national GDP (Modified after D'Odorico et al., 2018). Chained purchasing power parities are the rates of currency conversion that try to equalize the purchasing power of different currencies, considering the inflation over time.

5.1. Distal Drivers of Land Use Change

5.1.1. Human Population Growth

The global population has increased through the history of humanity, undergoing an unprecedented acceleration in the last three centuries (e.g., Warren, 2015). The threefold growth from about 190 million people around the year 0, to 600 million by the beginning of the XVIII century was followed by a thirteen-fold increase to today's 8 billion people. Such an acceleration has been attributed to major technological, economic, and social changes brought about by the industrial revolution and the large-scale European colonization in the previous two centuries. Progress in science and medicine allowed mortality rates to drop significantly, contributing to a sharp increase in global population size. Life expectancy started to increase in the mid-1800s and accelerated in the twentieth century, when more significant progress in the field of medicine provided the first cures (especially antibiotics) or vaccines against major infectious diseases (Sakai & Morimoto, 2022). New advances in agriculture, known as the "second agricultural revolution" increased food supply, with the introduction of new adaptable and nutritious crops from the Americas such as maize and potatoes, technological improvements in crop rotation and tillage techniques in the 1700s, and the first introduction of fertilizers in the 1800s. The green revolution (or "third agricultural revolution"), took place after WWII with the increase in crop yields through the introduction of mechanization, the expansion of irrigation, the use of the first industrial fertilizers and pesticides, and the adoption of new cultivars (e.g., Borlaug, 1972; DeBlij, 2012). The consequent unprecedented increase in food production led to the emergence of agricultural surplus in technologically advanced and productive regions of North America. Such surpluses were partly placed on the global market and exported to food scarce regions (Section 7), and partly diverted to the livestock sector, with the use of food crops as feed and the development of grain-fed concentrated livestock farms (Section 5.2.2). Known as "livestock revolution," this phenomenon contributed to zoonoses and pathogen transfer to humans (Delgado et al., 1999).

In the last few decades, economically wealthier parts of world have seen a demographic slowdown, or "demographic transition" driven by a decrease both in mortality and fertility rates (average number of children women have) due to simultaneous improvements in education and living standards and increases in cost of living, leading to an aging and declining population (Lee, 2011). Conversely, in poorer parts of the world, birth rates have remained high (UN, 2022). Together, the world human population has, therefore, kept increasing and some projections indicate that the planet will reach 10 billion between 2050 and 2100 (Figure 5a). Population growth often correlates with a number of inequalities or social stress factors that compound with the effects of environmental degradation (De Blij, 2011, 2012). In fact, countries with higher demographic growth rates tend to have higher fractions of the population living below the poverty line, and countries with younger populations struggle in providing youth with adequate levels of education. Dietary shifts and the adoption of resource intensive diets in economically wealthier or emerging economies and population growth in low- and middle-income countries are major contributors to the increasing demand for agricultural products, an important underlying driver of land use change through agricultural intensification and expansion (Section 5.2.1).

5.1.2. Diets and Dietary Shifts

Food systems are dynamic and undergo changes in response to socioeconomic drivers such as demographic trends, affluence, technological development, urbanization, globalization, and associated cultural transformations. Human diets affect human health and wellbeing as well as the anthropogenic pressure on the environment (Davis et al., 2016). Presently, the land and water footprints of the global food system are 0.85 ha per capita (ha cap^{-1}) and 776 m^3 H_2O y^{-1} cap^{-1} respectively. On average, plant-based diets have smaller land and water footprints (0.31 ha cap-1 and 615 m^3 H_2O y^{-1} cap), similar to those of pescetarian diets (0.33 ha cap^{-1} and 630 m^3 H_2O y^{-1} cap^{-1}) (Davis et al., 2016). Thus, a reduction in reliance on plant food and seafood and an increasing consumption of meat and animal products are expected to have a strong impact on the land and water use for agriculture, which explains why agriculture (and specifically livestock farming) is the major driver of land use change and deforestation worldwide (Runyan & D'Odorico, 2016). Indeed, if we combine global grazing land with the amount of cropland used for animal feed, livestock accounts for 80% of agricultural land use (Ritchie & Roser, 2019). To be noted, cropland used to grow feed for livestock is related to livestock intensive systems, as they often require large-scale monocultures to supply the high feed demands of confined animals (Steinfeld et al., 2006). This contributes to land-use change and often results in deforestation and biodiversity loss (Sections 5.2.1 and 6.1). Conversely, extensive livestock systems in specific contexts such as in savannas or other semi-natural landscapes cannot imply significant land-use conversion for feed production and have more positive ecological outcomes (Steinfeld et al., 2006).

In response to increasing income and urbanization trends, the last five decades have seen the emergence of a dietary transition worldwide (Tilman & Clark, 2014), with trends consisting of increasing the total per capita calorie demand, as well as the consumption of meat and other animal products. Specifically, animal-based protein consumption increased from 61 g per person per day in 1961 to 80 g per person per day in 2011 (Sans & Combris, 2015). Projections for the next decade show an additional 14% increase in global meat protein consumption with respect to the 2018–2020 baseline period (OECD & FAO, 2021). Drivers of global meat consumption are several and interlinked with each other, including consumers' demography, income, religious beliefs, tradition, health and environmental education.

Meat consumption is particularly influenced by income levels and its growing trends have been related to economic development. Meat is an expensive protein source that becomes increasingly accessible as income increases, as represented by the Bennett's law (Bennett, 1941) (Figure 5b), which shows strong trends in meat consumption with increasing affluence, particularly in emerging economies. Over the past 50–60 years, the global production of meat has more than tripled at the global scale (FAO, 2024). Cattle heads increased by 50%, exceeding 1.5 billion heads in 2020. In the same period pigs have tripled and chickens have increased eight times, exceeding 1.3 and 4.4 billion (in 2020), respectively (FAO, 2024). These estimates show that most of the increasing meat demand is being met by pork and poultry and to a lesser extent by beef. Indeed, beef is expected to account for a decreasing share of global livestock production, a phenomenon often termed "the livestock transition" that is slightly reducing the growth of the land footprint of livestock production (Davis et al., 2015, 2016).

The demand for animal products is overall predicted to rise by as much as 50% by 2050, likely driven by growth in southern Asia and Africa (FAO, 2024). Despite productivity improvements, livestock-induced land use conversion is on the rise thus raising major environmental and social concern in some areas (Herrero & Thornton, 2013). Population growth is also increasing the consumption of wild meat (Section 6.6) (Kurpiers et al., 2016). In regions of Central Africa, wild meat consumption often becomes a necessity because of the cost of rising livestock and the limited access to alternative protein sources through the market (Karesh & Noble, 2009; Kurpiers et al., 2016). Indeed, in the near future wild meat may become fundamental to regional food security (Friant et al., 2020) with an important trade-off between securing access to protein sources and increasing the exposure to emerging zoonotic infectious disease associated with wild meat consumption (Van Vliet et al., 2017). On the other hand, urban dwellers and people from more economically wealthy countries are increasing the global demand for wild meat as a delicacy, personal taste preference, traditions, and status quo (Kurpiers et al., 2016). For instance, the urban and southern regions of China import significant amounts of wild meat through internal bushmeat trade and from Southeast Asia as an exotic food and/or traditional medicine (Karesh & Noble, 2009).

Bushmeat hunting and the trade of wild animals and meat play a crucial role in land use change, particularly in tropical regions where biodiversity is richest. The demand for bushmeat, driven by local consumption and international trade, has led to the over-exploitation of wildlife and the degradation of ecosystems (Lindsey et al., 2013). In many areas, the need for hunting has contributed to deforestation as forested areas are cleared for farming, logging, and infrastructure to support hunting activities (Wilkie et al., 2000). The expansion of roads and settlements to facilitate the bushmeat trade further accelerates land conversion and habitat destruction (Laurance et al., 2009). Additionally, the growing global demand for exotic meats has led to unsustainable hunting practices, contributing to the loss of wildlife populations and altering natural landscapes (Harrison et al., 2016). As habitats are disrupted and wildlife populations decline, land use patterns shift, often resulting in the expansion of agricultural activities or the development of new infrastructure to support the bushmeat trade (Ripple et al., 2016). Ultimately, the unsustainable nature of bushmeat hunting and the wildlife trade exacerbate land use changes, intensifying environmental pressures and threatening biodiversity (Lindsey et al., 2013). As explained in Section 6.6, bushmeat consumption is also a direct pathway for pathogen transfer from wildlife to humans and associated human exposure to zoonotic infection.

5.1.3. New Energy Policies

The adoption of new energy policies has often led to unintended environmental impacts associated with land use change, a phenomenon often known as “leakage” (Balmford et al., 2025). For instance, the European Union and the USA promoted the production of biofuels as an approach to combat climate change (EU, 2012), thus leading to an increase in the global demand for biofuel crops often displaced through international trade and land investments (Davis et al., 2015; D’Odorico et al., 2017; de Gorter et al., 2013; Janda et al., 2012; Rulli et al., 2019). Indeed, biofuel production in Southeast Asia is largely (30%–40%) for the export market (Rulli et al., 2016), and recent work has connected the dots between biodiesel demand and deforestation in oil palm concessions in Indonesia and Malaysia (Davis et al., 2015; D’Odorico et al., 2017; Rulli et al., 2016, 2019). Some of these land use changes affected peat forests in the Kalimantan, where peat soil drainage and oxidation is contributing to major carbon emissions (Carlson et al., 2013), thus leading to the paradox that energy policies aiming at a reduction in greenhouse gas (GHG) emissions induced have increased such emissions, in addition to habitat destruction and biodiversity loss (Rulli et al., 2019), thus leading to a “carbon debt” that would take decades of biodiesel consumption to pay off (Fargione et al., 2008). In response to these unintended environmental impacts of energy policies, the EU adopted subsequent directives that ensured the protection of primary forests and other ecosystems (European Parliament & Council of the European Union, 2009). However, the impact of biofuel production on natural habitat and biodiversity loss can be indirect and difficult to track, with biofuel crop production expanding into pastureland, and livestock grazing encroaching into formerly forested land (Hermele, 2014).

Indirect drivers of land use change partly related to urbanization are also associated with growing and shifting energy demand, particularly by the renewable sector, which relies on technologies such as biofuels and solar and wind energy, that are relatively land-intensive (van de Ven et al., 2021). The material needs of decarbonization and energy transition proposals (Ali et al., 2022) are expected be met by mineral extraction activities that will further induce forest loss, human encroachment into wildlife habitat, let alone the exploitation of indigenous and local communities and of their land (Kara, 2023; Klinger, 2023; Owen et al., 2023).

5.1.4. Globalization

Globalization is the growing interdependence among economies and cultures around the world as a result of information flows, transnational investments, connectivity-enabling technology (e.g., internet), and cross-border trade of goods and services. The contribution of international trade to the global GDP has roughly doubled since the 1970s, and by 2021 accounted for about 57% of the world GDP (The World Bank Group, 2025). About 8.5% of the traded value is in agricultural products (D’Odorico et al., 2014; FAO, 2022). Around 86% of the global value of agricultural products is contributed by food and feed products, while the rest by biofuels, fibers, and other non-edible products. Presently, 13% of biodiesel and 8% of bioethanol are globally traded (OECD-FAO Agricultural Outlook 2023-2032, 2023). Globalization strongly interacts with the land use, driving changes in land cover and land use, and in land management practices across the globe, a phenomenon known as "land use displacement" (Meyfroidt et al., 2013). As global markets expand and demand for resources increases, agricultural production, urbanization, and industrial development have intensified, often at the expense of natural ecosystems. The spread of multinational corporations and foreign investments has led to large-scale land conversions, such as the expansion of monoculture crops, deforestation, and infrastructure development. Additionally, globalization has facilitated the movement of people and capital, resulting in the rapid growth of cities and towns, which in turn accelerates land consumption for housing, commercial, and industrial purposes. While globalization has spurred economic growth in many regions, it has also contributed to environmental degradation, loss of biodiversity, and altered local land-use patterns, often leading to unsustainable land management practices and increased pressure on already fragile ecosystems (Davis et al., 2017; Meyfroidt et al., 2013, 2024; Rulli et al., 2013). In Section 6.7 we analyze globalization directly in the context of emerging disease infections.

5.1.5. Climate Change Induced Land Use Conversion

Climate change is both an underlying driver and a consequence of land use change, in complex and reciprocal relationship between the two (IPBES, 2019). As an underlying driver, climate change alters weather patterns, temperatures, and precipitation with wide-ranging effects on both natural ecosystems and human activities that depend on land-based resources. As global temperatures continue to rise and precipitation patterns become more unpredictable, both ecosystems and agricultural systems are undergoing significant transformation. These changes often compel shifts in land use as communities and industries adapt to the new climatic conditions. For example, in many regions experiencing higher temperatures and altered rainfall, agricultural productivity has been compromised due to reduced water availability, with direct impacts on crop yields. In response, farmers are adapting by switching to drought-resistant crops, adopting more efficient irrigation systems, or altering planting schedules to better match shifting climate conditions (Lal, 2004). In more severe cases, however, agricultural land may be abandoned entirely if it becomes unproductive due to prolonged droughts, heat waves, or other climate-related stresses, which forces rural populations to either shift their farming practices or relocate to more fertile areas.

In addition, climate change might result in the exacerbation of the frequency and intensity of extreme weather events such as floods, hurricanes, and wildfires, which can cause widespread destruction to infrastructure, homes, and farmlands. These catastrophic events often result in the displacement of populations and the need for rebuilding, which leads to the conversion of agricultural land for post-disaster recovery or the construction of temporary housing and flood defenses (Adger et al., 2003; Smit et al., 2001). For example, in coastal regions, rising sea levels—another consequence of climate change—threaten to inundate low-lying areas, requiring the conversion of agricultural lands for the construction of flood defenses like sea walls or reclamation projects to protect urban areas and infrastructure (Nicholls et al., 2007). These adaptations to rising seas often result in the loss of valuable agricultural land, which further drives land use changes and alters local economies.

On the other hand, some regions may initially see short-term benefits from climate change, as higher temperatures and increased carbon dioxide levels can enhance agricultural productivity in certain areas by extending growing seasons or boosting crop yields. However, these gains are often localized, and they come with their own set of challenges. The long-term effects of climate change, such as more frequent droughts, unpredictable rainfall, and extreme weather, can undermine these short-term benefits, leading to inconsistent or unsustainable agricultural outcomes. As a result, land that was traditionally used for crop cultivation may shift toward other uses, such as forestry or livestock farming, as farmers attempt to adapt to changing climatic conditions (Yang et al., 2024). In some cases, as rural areas become less viable due to climate impacts, urbanization may increase, with populations migrating to cities in search of more stable living conditions. This migration can drive the expansion of urban areas, further converting agricultural and forest land into residential, commercial, or industrial spaces.

The conversion of land for urban development and infrastructure projects not only reduces the amount of land available for agriculture but also increases pressures on ecosystems and biodiversity. Deforestation, habitat fragmentation, and the loss of natural resources such as water, soil fertility, and wildlife are common outcomes of these land use changes. Furthermore, the complex interactions between climate change and land use create a feedback loop that exacerbates the environmental challenges faced by both human societies and the natural world (McElwee et al., 2024). For instance, unsustainable land use practices such as deforestation contribute to climate change by releasing stored carbon into the atmosphere, while the impacts of climate change—such as more frequent floods, droughts, and wildfires—can further degrade land and exacerbate the pressures on ecosystems. Climate change also has several more direct impacts on infectious disease emergence, which are analyzed in Section 7.

5.2. Proximate Drivers of Land Use Change

5.2.1. Agriculture

Land use change is for the most part driven by the increasing demand for agricultural products (food, fibers, and bioenergy) by the growing and increasingly demanding global population (Sections 5.1.1 and 5.1.2) (Ramankutty et al., 2018; Runyan & D'Odorico, 2016). Presently, agriculture has a footprint of about 4.7 billion hectares, accounting for temporary and permanent croplands (1.6 billion ha), and pasturelands and permanent rangelands (3.1 billion ha), corresponding to 12.5% and 40% of the global terrestrial land areas, respectively (D'Odorico et al., 2018; Sachs, 2024). Livestock production relies on fodder from grasslands and rangelands as well as feed cultivated on roughly 71% (i.e., ∼1.1 billion ha) of the global cropland (Govoni et al., 2023). Presently, according to FAO estimates, livestock contributes to 40% of the value of agricultural output globally, supports the livelihoods and food and nutrition security of around 1.3 billion people, and supplies 34% of food protein production. The environmental footprint greatly varies with the type of livestock and production practice (e.g., grass-fed vs. feed-fed). The largest footprint is typically associated with the production of beef and other ruminants, followed by pork, poultry, eggs, and milk (de Vries & de Boer, 2010). For instance, the land footprint of beef is more than 26 times greater (on a per Calorie basis) than that of pulses (Hong et al., 2021).

Agricultural expansion and agricultural intensification are the two main strategies to address the growing demand for agricultural products by increasing production (Zabel et al., 2019). Through agricultural intensification productivity is achieved by increasing crop yields without changing the cultivated area. Conversely, agricultural expansion increases the cultivated area without affecting crop yields. In particular, a sharp increase in cultivated area occurred starting from 1700 when the extent of agricultural land was around 1 billion hectares (Bha) (Figure 6a). By 1960 it had increased fourfold, peaking in 2000 when it reached 4.9 Bha. After the year 2000 global agricultural production became decoupled from global agricultural expansion because of an increase of intensification. Presently, global croplands are still expanding in some countries (Potapov et al., 2021), often at the expense of biodiversity and carbon rich habitats (FAO, 2024; Klein Goldewijk et al., 2011; Taylor & Rising, 2021). In particular, in the twenty-first Century agriculture has been expanding especially in Africa and South America, though a slight slowdown was recently observed in South America (Potapov et al., 2021). Central and South America, Southeast Asia and tropical Africa are regions where agricultural expansion is likely to affect biodiversity the most, because these regions have the highest biodiversity (Shah et al., 2019; Zabel et al., 2019). Moreover, land use change is an important contributor to global GHG emissions, due to the reduction in CO_2 sequestration associated with photosynthesis, increase in CO_2 emissions from respiration from plant and soil biomass, and other GHG emissions associated with land management (Chiriacò et al., 2024, 2025; Hong et al., 2021). As of 2019, land use change and forestry accounted for 3.2% of the global GHG emissions, which have increased from 11 to 14.6 gigatonnes CO_2-equivalent between 2001 and 2017 (Hong et al., 2021). While globally land use change is the second contributor to GHG emissions (after fossil fuel burning), it is the largest in countries affected by high rates of land use change such as the Democratic Republic of Congo, Paraguay and Indonesia (Our world in Data & ClimateWatch, 2023). Deforestation and other forms of land use change have other major environmental impacts on global biogeochemical cycles, regional water balance, microclimate, soil erosion, as well as the provision of ecosystem services and functions that are crucial to rural livelihoods and the subsistence of land-based economies.

5.2.1.1. Agricultural Expansion

The geography of agricultural expansion is typically complex (Figure 6b) and causes the loss and fragmentation of natural habitat (Sections 6.1 and 6.2) (Hansen et al., 2022; Potapov et al., 2022; Vancine et al., 2024). This phenomenon now primarily affects lower-income countries in tropical regions of the globe often to the benefit of higher income countries (the "Global North") (Davis et al., 2020; Naylor, 2011; Zabel et al., 2019). Indeed, the

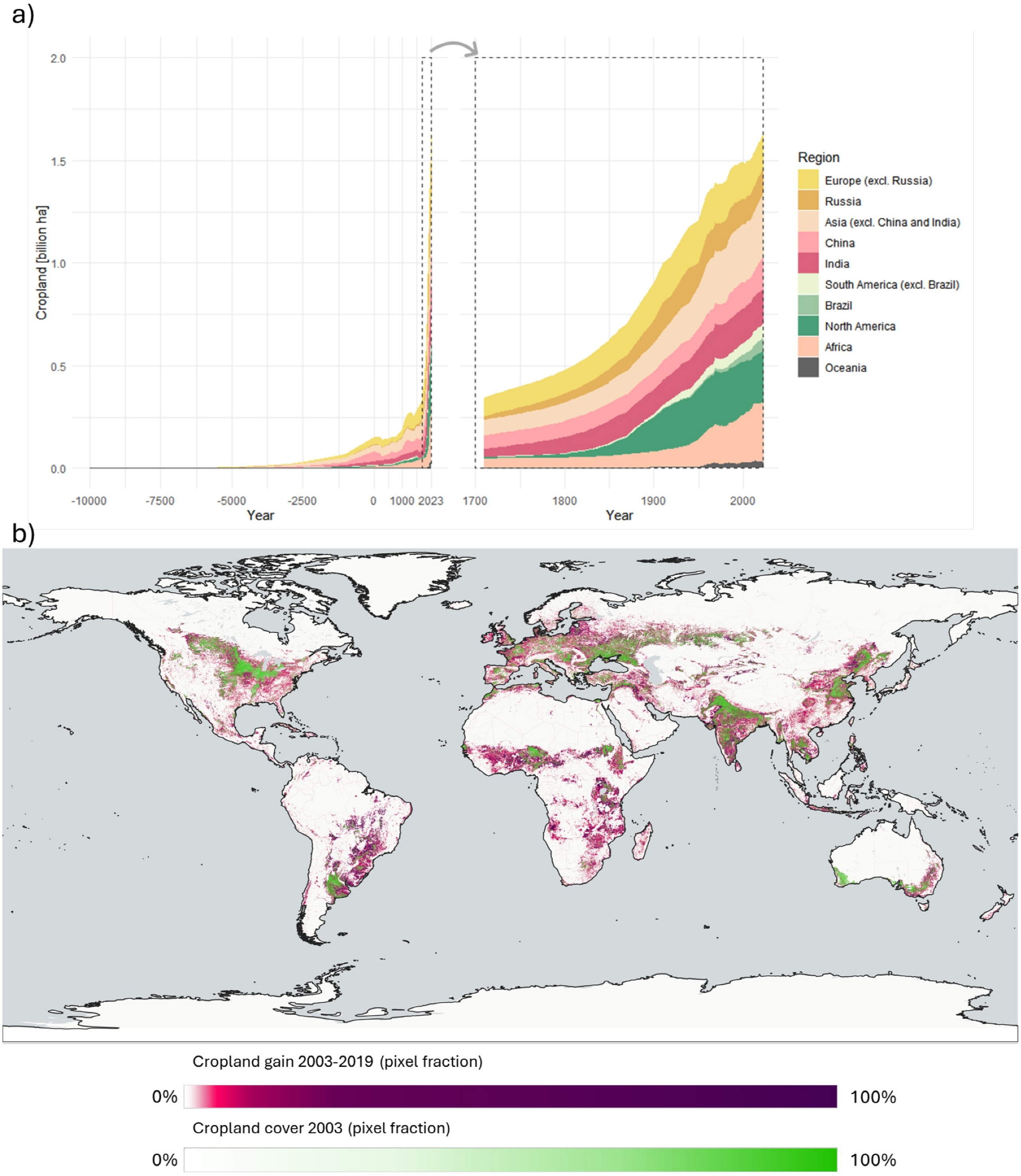

Figure 6. (a) Historical trend of global cropland extent from the HYDE 3.2 data set (Klein Goldewijk et al., 2017). (b) Cropland distribution across the world in a nominal 30-m resolution. This is the baseline product of the GFSAD30 Project (https://glam1.gsfc.nasa.gov/api/doc/cropmask/v1/GFSAD30-CE_2015_crops).

food and energy demands that agricultural expansion is set to satisfy are often distant from the areas affected by agricultural expansion (Meyfroidt et al., 2013; Rulli et al., 2019). This distance is not only geographic, but also socio-economic and environmental in the sense that agricultural expansion often impacts the environment and those people who have no voice in the decision process leading to land use conversion and entails a cost shift to the environment and the most marginalized, poor, and least powerful rural populations (Balmford et al., 2025; Martinez-Alier, 2003).

While half of the recent global cropland expansion has occurred directly at the expenses of forests or woodlands, the other half has affected pasturelands (Potapov et al., 2021). Interestingly, croplands have been recently encroaching into pastureland in the arid and temperate regions, while in the wet and humid tropics the increasing demand for beef production is driving grazing land expansion into forested areas (McAlpine et al., 2009; Vale et al., 2019). Many carbon-dense and biodiversity-rich tropical forest biomes have been converted to pasture and feed crop production for the livestock sector (FAO and UNEP, 2020). Moreover, pastureland is being converted to cropland, a land use change that is directly affecting agricultural land but that can induce an indirect loss of natural habitats and of ecosystem services through pasture encroachment in forest areas. For instance, soybean expansion at the expenses of pasturelands in South America has led to the establishment of new grazing grounds at the expenses of natural habitats (Song et al., 2021).

5.2.1.2. Agricultural Intensification

Agricultural intensification can apply to both crop and livestock production systems. It consists of a set of techniques, interventions and practices aimed at increasing agricultural productivity without increasing the extent of agricultural land (Foley et al., 2011; Herrero et al., 2023). Pathways to intensified crop production include the selection of higher yield crop varieties, fertilization, irrigation, the use of pesticides and other chemicals, and the implementation or improvement of other agronomic practices (Tilman et al., 2011). Livestock intensification entails a switch from free range, mostly grass-fed, production to an increasing reliance on feed, which historically coincided with the redirection of surplus crop production resulting from the green revolution to the livestock sector, a phenomenon known as the “livestock revolution” (Delgado et al., 1999). Therefore, in the last few decades a lot of beef production has moved from open pasture grazing toward more intensive farming systems because grain-fed livestock is often more land-efficient than pasture-fed livestock (Vale et al., 2019).

Agricultural intensification is often regarded as a more sustainable alternative to agricultural expansion, because, if correctly implemented, it avoids the negative effects of land clearing associated with agricultural expansion such as losses of habitat, biodiversity, and increase in CO_2 emissions (Alkemade et al., 2013; Lowder et al., 2021; Tilman et al., 2011). Agricultural intensification is thus expected to be on the rise especially in regions of the world with relatively large yield gap (i.e., the difference between max potential and actual yield) and limited land availability for agricultural expansion, such as India (Zabel et al., 2019). Agricultural intensification, however, often requires the expansion of irrigation to rainfed areas, including areas affected by water scarcity (Rosa et al., 2018). Moreover, it often requires technological investments that subsistence farmers in lower income countries might be unable to make. Thus, without adequate safeguards, intensification would entail the displacement of subsistence or semi-subsistence agriculture by large-scale commercial farming with important implications for rural livelihoods, food security, and migration to urban centers (Davis et al., 2020; D'Odorico et al., 2017, 2018; D’Odorico & Rulli, 2013; Meyfroidt, 2024; Rulli et al., 2019). The direct impacts of agricultural intensification and expansion on emerging disease infections are reviewed in Section 6.3.

5.2.2. Urbanization

Urbanization acts both as a proximate driver of land use change through the encroachment of human settlement into natural habitat, and indirectly, to build the infrastructure (e.g., power generation, industrial facilities), as well as to intensify and expand agriculture to meet the needs of the growing urban population and its increasingly natural resource-demand (Goldstein et al., 2022; Nova et al., 2022). The share of the global population that lives in urban areas has been steadily increasing over the past half century, moving from one third in 1960 to more than half today, while 7 people out of 10 are expected to live in cities by 2050 (Chen et al., 2020; The World Bank Group, 2025) The drivers explaining this trend are complex, including the mechanization and industrialization of agriculture, quest for better paid jobs, land grabbing, access to employment, social services, and economic opportunities (Gerten et al., 2019). Urbanization drives land use change, as the rapid expansion of cities and towns requires the conversion of natural landscapes and agricultural land into built environments. As populations grow and migrate from rural areas to urban centers in search of better economic opportunities, the demand for housing, infrastructure, and services increases, leading to the conversion of forests, wetlands, and agricultural lands into residential, commercial, and industrial spaces. This transformation often results in the fragmentation of ecosystems, loss of biodiversity, and the depletion of natural resources (Seto, Güneralp, & Hutyra, 2012). Urban sprawl, characterized by the spread of cities into surrounding rural areas, exacerbates land use change by encroaching on fertile agricultural lands, leading to a reduction in food production capacity and the loss of valuable ecosystems. Moreover, urbanization often leads to increased demand for energy, water, and raw materials, further intensifying land use changes through the expansion of infrastructure like roads, power lines, and factories (Seto, Güneralp, & Hutyra, 2012). The growth of urban areas also alters local climates, contributing to the urban heat island effect, where built-up areas experience higher temperatures than surrounding rural zones due to the concentration of buildings, concrete, and asphalt (Oke, 1982). In addition, urbanization can lead to changes in land ownership patterns, with large-scale real estate development and investments driving land use decisions that prioritize economic growth over environmental sustainability (Güneralp et al., 2015). While urbanization can promote economic development and improve living standards, its environmental impacts, including habitat destruction, pollution, and resource depletion, highlight the need for sustainable urban planning and land management practices to mitigate the negative consequences of urban sprawl and ensure the long-term health of ecosystems and communities. Some of the impacts of urbanization on infectious disease emergence are discussed in Section 6.5.

5.2.3. Road Construction

Roads are often built to provide access to previously remote and ecologically sensitive areas, leading to profound transformations in both landscapes and ecosystems. The construction of roads typically involves the direct conversion of natural habitats such as forests, wetlands, and agricultural lands into infrastructure, which in turn contributes significantly to deforestation and the fragmentation of ecosystems (Sections 6.1 and 6.2) (Laurance et al., 2009). As roads expand into these previously inaccessible areas, they open up opportunities for human activities such as logging, agriculture, and settlement, which can result in further land degradation. Roads also favor the spread of pathogens and emergent disease infections in humans. Roads are also linked to illegal activities, including illegal logging and mining, as they facilitate access to regions that are often legally protected or contain high biodiversity. These activities are particularly problematic in biodiversity-rich regions, such as the Amazon rainforest, where roads enable exploitation of previously undisturbed natural resources, further threatening fragile ecosystems (Barber et al., 2014).

In addition to opening up new areas for exploitation, roads serve as key catalysts for urbanization (Section 5.2.2). As cities and towns grow, the construction of roads enables the expansion of urban areas into rural landscapes, leading to the phenomenon of urban sprawl. Urban sprawl typically results in the conversion of agricultural lands into residential, commercial, and industrial zones, reducing the land available for food production and contributing to further land use change and to the depletion of natural resources. This shift also places increased demand on surrounding ecosystems, which are often transformed to accommodate new infrastructure. This urban expansion often leads to additional land conversions, such as the development of commercial and residential areas, which further degrade the natural landscape (Lambin et al., 2001). Roads not only affect land use directly, but they also influence the movement of people and goods, thus leading to additional infrastructure development such as power lines, railways, and factories, which in turn require further land conversion. The impact of roads is particularly severe in tropical and remote regions, where road construction is often associated with an increase in deforestation and environmental degradation. In these areas, roads provide access to previously inaccessible natural resources, such as minerals, timber, and agricultural land. The expansion of roads into these regions is often associated with increased pressures on local biodiversity (e.g., by favoring biological invasions, the spread of plant pathogens, and the extraction of timber and other biological materials), further intensifying the challenge of conserving natural habitats (Nepstad et al., 2008). Roads also increase human settlement and economic activities in these areas, which can lead to irreversible changes to ecosystems and the displacement of indigenous populations.

5.2.4. Mining Activities

Mining, that is the extraction of valuable geological materials and minerals from the surface of the Earth, including the seas, is a crucial component of the global economy, providing essential raw materials for industries such as construction, energy production, technology, and manufacturing. The sector has evolved significantly over the years, with modern mining practices enabling the extraction of minerals and metals from increasingly remote and challenging environments. However, the status of mining activities today is marked by a complex interplay of technological advancements, environmental concerns, and social impacts raising serious environmental and social challenges. The environmental degradation caused by mining, including deforestation, soil erosion, water contamination, and loss of biodiversity, has prompted global calls for more sustainable practices (Bebbington & Bury, 2009). In some regions, particularly in tropical and biodiversity-rich areas, illegal mining operations continue to thrive, driven by high demand for minerals like gold, diamonds, and rare earth elements (Fearnside, 2005). Furthermore, the demand for mineral resources has surged with the rise of technologies like electric vehicles, renewable energy infrastructure, and electronics, driving further expansion of mining operations in areas such as lithium, cobalt, and graphite (Arrobas et al., 2017). Despite efforts to improve mining regulations and promote responsible sourcing, the sector continues to face significant challenges, including labor rights violations, displacement of indigenous communities, and conflicts over land use (Galli et al., 2022).

Mining operations, including open-pit mining, strip mining, and underground mining, directly convert forests, wetlands, and agricultural lands into mining pits, waste dumps, and industrial zones. This transformation results in the destruction of natural habitats, fragmentation of ecosystems, and the loss of biodiversity, as well as soil erosion and the contamination of local water sources due to the release of toxic substances such as heavy metals and chemicals. At the same time, these land use changes may create habitats for some reservoir species including some bat species which thrive in caves and tunnels from underground mines. Mining is a significant driver of land use change, as the extraction of natural resources often requires large tracts of land to be cleared and transformed into industrial sites, leading to long-term environmental degradation. The conversion of land for mining activities also disrupts local agricultural practices, leading to a reduction in food production and the degradation of the soil's ability to support crops.

The expansion of mining areas often requires the construction of supporting infrastructure, such as roads, railways, and power plants, which further accelerates land use changes. Roads, in particular, play a critical role in the expansion of mining activities by providing access to previously remote areas. The construction of roads facilitates the movement of heavy machinery, workers, and resources to mining sites, while also making it easier for goods and mined materials to be transported to markets. These roads, however, can have profound environmental consequences, as they open up previously inaccessible areas to logging, agriculture, and urbanization, further contributing to deforestation and habitat fragmentation (Laurance et al., 2009) (Section 5.2.3).

The growth of the mining industry can also drive deforestation in areas with rich mineral deposits, such as the Amazon rainforest, where illegal mining activities are widespread, especially in remote and protected regions (Fearnside, 2005). The expansion of roads and industrial infrastructure into these regions often accelerates illegal mining, further contributing to the degradation of forest ecosystems and the loss of biodiversity.

Moreover, mining activities can displace local communities, forcing them to relocate and resulting in changes to land ownership patterns, as large mining companies acquire vast areas of land for resource extraction. As mining operations deplete resources, they often leave behind barren landscapes that are difficult to rehabilitate, compounding the challenges of land restoration and long-term environmental recovery (Worlanyo & Jiangfeng, 2021).

5.2.5. Dam Construction

Dams are structures built across a stream, a river, or an estuary to retain water so crating a water impoundment to be used for different purposes such as irrigation, energy production, human consumption, industrial use, aquaculture, and navigability. Dam building has evolved significantly over the past several decades, with ongoing projects and the expansion of hydropower development playing an important role in global energy production, water management, and economic growth. However, the practice has become increasingly controversial due to the environmental, social, and economic consequences associated with large-scale dams. The flooding of large areas of land, the alteration of river ecosystems, and the associated infrastructure developments can lead to long-term environmental degradation and social issues. The creation of reservoirs behind dams leads to the inundation of vast tracts of forests, wetlands, and agricultural land. This flooding directly results in the loss of biodiversity, as entire ecosystems are submerged, and many species, particularly those adapted to specific habitats, are either displaced or face extinction. In addition to the direct environmental impacts, dam construction can also cause significant disruption to river ecosystems. The alteration of water flow and sediment transport can impact water quality, change the composition of riverbeds, and disrupt the migratory patterns of aquatic species, particularly fish populations (McCully, 2001). These changes in river dynamics often have cascading effects on the land use patterns in the surrounding areas, as they influence the availability of resources for agriculture, fishing, and other land-based activities. For instance, the construction of large dams can benefit agricultural development, thus contributing to land use change with the expansion of agriculture and/or irrigation.

Furthermore, the construction of dams typically spurs the development of significant infrastructure, including roads, power lines, and urban settlements, which can further accelerate land use changes in both the immediate and surrounding areas (Dams WCO, 2016).

The social impacts of dam building are also substantial in term of land use change, as the displacement of local communities is a common consequence. Large-scale dam projects often require the relocation of thousands of people, leading to the loss of homes, livelihoods, and access to traditional land and resources. These displaced communities often face challenges in rebuilding their lives and adapting to new environments, which can lead to social tensions and long-term economic instability. Changes in land ownership patterns also accompany dam construction, as large areas of land are acquired by developers, governments, or corporations for the purpose of building the dam or its associated infrastructure, or the adjacent land that will benefit from access to new irrigation infrastructure (Tatlhego & D'Odorico, 2022), which can disempower local populations and reduce their control over the land they once occupied. Importantly, dams and irrigation infrastructure such as canals, tanks and reservoirs provide humid environments that can offer the ideal habitat for mosquitoes and other arthropod vectors (Table 2), thus increasing the exposure of local populations to emerging infectious diseases such as malaria or dengue (Kibret, 2018).

6. Land Use Change Types and Zoonotic Infection Exposure

6.1. Deforestation and Zoonotic Infection Exposure

Deforestation is a specific type of land use change that is strictly connected to the loss of forest cover and has been defined as "The conversion of forest to another land use or the long-term reduction of the tree canopy cover. Deforestation implies the long-term or permanent loss of forest cover and its transformation into another land use" (FAO, 2007). Deforestation is mainly now affecting tropical forests (Hoang & Kanemoto, 2021; Jayathilake et al., 2021; Runyan & D'Odorico, 2016) and is predominantly driven by the need to make room for agriculture, including both commercial agriculture and subsistence farming (Section 5.2.1) (Jayathilake et al., 2021) (Figure 7). Other important drivers of deforestation include urbanization and human settlement in general, mining, logging, and infrastructure development (Sections 5.2.2–5.2.5). Even though deforestation is primarily driven by agriculture, followed by human settlement and infrastructure, the typical deforestation dynamics follow the opposite sequence: first, tree cover is cleared to accommodate new transportation infrastructure (e.g., roads, railways), which is typically built to support some extractive activity (e.g., logging or mining) (Napolitano Ferreira et al., 2021). Then, settlements are built, typically as lodging and dorms for workers hired by such extractive activities. Lastly, the surrounding areas are cleared for agricultural purposes (Ellwanger et al., 2020; Napolitano Ferreira et al., 2021). There is evidence, however, that, despite agriculture being the main driver of deforestation, only around a third to half of deforested areas results into actively managed crop production productive livestock farming areas (Parker et al., 2024; Pendrill et al., 2022).

With deforestation typically happening in tropical areas, the pathogen host species that are most impacted by this land use change are tropical forest dwellers. A very important pathway through which deforestation impacts pathogen hosts involves the decline of biodiversity associated with forest loss (Mahon et al., 2024). Intact forests typically exhibit extremely high levels of biodiversity, which are matched by the likely presence of a high number of unknown pathogens (Ellwanger et al., 2020). As the high diversity of co-existing and coevolving pathogens-host creates a shield against the transmission of pathogens, the loss of biodiversity forms new opportunities for pathogen hosts and vectors (Ellwanger et al., 2020). Thus, deforestation overall increases the transmission of pathogens hosted by reservoir species or carried by vector species able to adapt to degraded environments (Gibb, Franklinos, et al., 2020). Bats and rodents are among the most diverse reservoir hosts known to be affected by deforestation (Mollentze & Streicker, 2020). Bats in particular exhibit some key characteristics that make them prone to survive and spread infections such as the tendency to aggregate into colonies, the ability to travel long distances, the adaptability to forest disturbance, and the tolerance of infections (White & Razgour, 2020). These traits explain why some bat-borne diseases have been observed following deforestation and more specifically habitat and roost disturbance (Rulli et al., 2017).

Table 2
Examples of Observed Causal Mechanisms Between Land Use Changes and Zoonotic Disease Spillovers

Driver	Mechanism(s)		Human diseases/pathogens[a] (genus or species; invertebrate vector; non-human vertebrate reservoir hosts)	Ref.
Deforestation	Pathogen flow from generalist host species		Bat-borne diseases	White and Razgour (2020), Rulli et al. (2017)
			Rodent-borne diseases	White and Razgour (2020)
			Primate-borne diseases	Wolfe et al. (2007)
Forest fragmentation	Increased host-human interface		Ebola virus disease (*Ebolavirus*; reservoir: bats)	Rulli et al. (2017)
			Hantavirus Pulmonary Syndrome/Hemorrhagic Fever with Renal Syndrome (*Hantavirus*; reservoir: rodents)	Muylaert et al. (2019b), Prist et al. (2017)
	Hosts/vectors enter anthropized areas	Increased contacts with vectors and parasites	Chagas disease (*Trypanosoma cruzi*; vector: triatomine insects; hosts: mammals)	Trovo et al. (2024)
			Yellow fever (*Yellow fever virus*; vector: *Aedes* mosquitoes; hosts: primates)	Mancini et al. (2024)
			Malaria (*Plasmodium spp.*; vector: *Anopheles* mosquitoes; hosts: primates)	Mancini et al. (2024)
			Lyme disease (*Borrelia burgdorferi*; vector: *Ixodes* ticks; hosts: mammals, birds, reptiles)	Allan et al. (2003)
		Overlap with risky activities in anthropized areas	Coronaviruses (*Betacoronavirus*; hosts: bats)	Rulli et al. (2021)
			Henipaviruses (*Hendra virus*; hosts: bats)	Eby et al. (2023)
Agricultural intensification	Intensive farming	Low biodiversity and biosecurity	Nipah virus (*Nipah virus*; host: bats)	Pulliam et al. (2011)
			Avian influenza (*Influenza A viruses*; hosts: birds)	Kuiken and Cromie (2022)
			Covid-19[b] (*SARS-CoV-2*; host: mink)	Oude Munnink et al. (2021)
	Agrochemicals	Favor life cycle of parasitic hosts	Trematode infections (*Schistosoma spp.*; hosts: freshwater snails, fish, mammals)	Hoover et al. (2020)
			Fungi	Lekberg et al. (2021)
	Irrigation	Breeding area for vectors	Malaria (*Plasmodium*; vector: *Anopheles* mosquitoes; hosts: primates)	Gottdenker et al. (2014)
			Dengue (*Dengue virus*; vector: *Aedes* mosquitoes; hosts: primates)	Brady and Hay (2020)
Urbanization	Impermeabilization, ponding		Zika (*Zika virus*; vector: *Aedes* mosquitoes; hosts: primates)	Nova et al. (2022)
			Chikungunya (*Chikungunya virus*; vector: *Aedes* mosquitoes; hosts: primates)	Nova et al. (2022)

[a] Some analyses were on diseases (the outcome of infection) and some on the causal infections (hantaviruses). [b] Mink were infected with SARS-CoV-2 following transmission from infected people (see Oude Munnink et al., 2021). Multiple other species such as white-tailed deer have been infected with ongoing animal-to-animal transmission (https://www.nature.com/articles/s41586-021-04353-x).

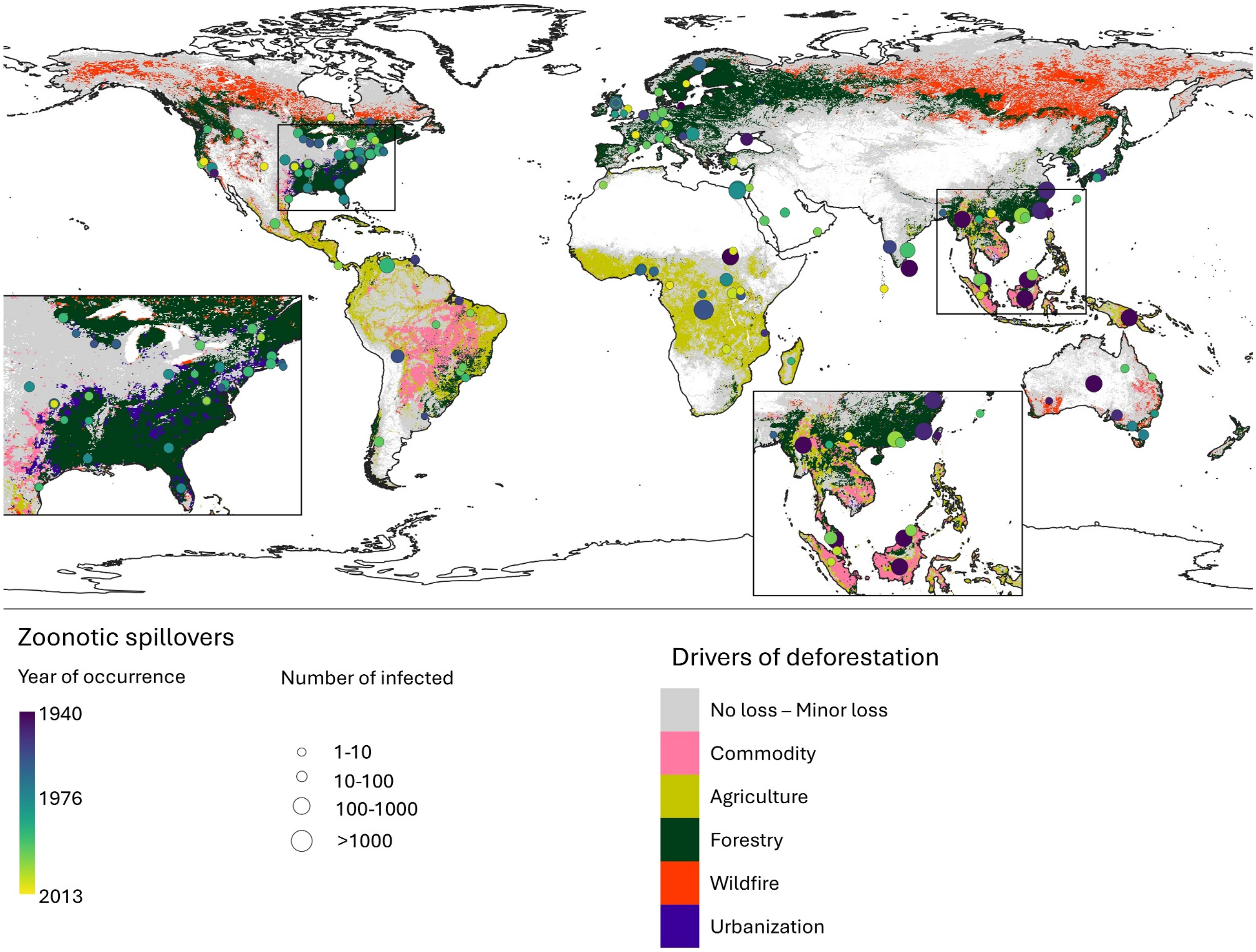

Figure 7. Primary drivers of forest cover loss for the period 2001 to 2015 and zoonotic spillovers (forest cover loss drivers from Curtis et al. (2018), zoonotic spillovers from the Emerging Infectious Disease Repository, EcoHealth Alliance https://www.ecohealthalliance.org/program/eidr).

Bat-borne viruses are more studied than bat-borne bacteria (Brook & Dobson, 2015; Huang et al., 2022). Examples of bat-hosted viral families whose spillover to humans might be increased due to deforestation include coronaviruses (Muylaert et al., 2023; Ribeiro et al., 2022; Rulli et al., 2021) and paramyxoviruses, such as Hendra and Nipah henipaviruses (Eby et al., 2023; Hahn, Epstein, et al., 2014; McKee et al., 2021) (Tables 1 and 2). In the case of Hendra virus, pathogen transmission from bats to humans relies on domestic species as intermediary, whereby bats leave their forest habitat to source food in agricultural areas, where they infect horses, the intermediate hosts for the spillover to humans (Eby et al., 2023). In the case of Nipah virus, zoonotic spillover from bats to humans is connected to both deforestation and human encroachment into wildlife habitats, as the typical pathogen pathway from bats to humans in Bangladesh is through palm sap directly collected from palm trees by humans and infected by bats (Daszak et al., 2013; Hahn, Epstein, et al., 2014; Hahn et al., 2014, 2014; Islam et al., 2016). Ebola virus disease outbreaks in humans have also been associated with deforestation, but even more strongly with forest fragmentation (Rulli et al., 2017; Wilkinson et al., 2018) (Section 6.2).

Rodents are other mammal hosts that have been studied in connection with deforestation. Indeed, they share some traits with bats, such as being highly diverse (with more known species than bats) and with several species adaptable to habitat degradation. Moreover, like bats, rodents have a range of social behaviors, yet they have very different life history traits with considerably shorter lifespans and larger litter size than bats (Han et al., 2016; Luis et al., 2013; Luis, O'Shea, et al., 2015; Morand et al., 2015). The emergence of rodent-borne bacterial infections such as the plague and, to a lesser extent, bartonella, has been associated with deforestation (White & Razgour, 2020), but through complex mechanisms and interrelationships with other changes and risk factors for other rodent-borne infections (Muylaert et al., 2019a, 2019b). Finally, primates constitute a hazardous forest-dwelling pathogen host, mainly because of their strong phylogenetic proximity with humans (Wolfe et al., 2007). Like bats and rodents, some species of primates exhibit synanthropism, which is the ability to adapt well to heavily anthropized environments, and to close proximity to humans (Humle & Hill, 2016; Lappan et al., 2020). However, sensitive species of primates, usually highly forest-dependent species, have been severely impacted by deforestation and changes that increase the risk of infectious diseases for them. This is not limited to the changing ecology of hosts and viruses, as it is the case for ebolaviruses, for insance, but includes also the risk of infection from human viruses (Hayman, 2019a; Köndgen et al., 2008; Leroy et al., 2004; Walsh et al., 2003).

6.2. Habitat Fragmentation and Zoonotic Infection Exposure

Forest fragmentation, or more in general habitat fragmentation, can be seen as a further mechanism of land use change that drives zoonotic spillover. It is often regarded as the way in which land use change creates “hazardous landscapes” that favor zoonotic spillovers (Dobson et al., 2020; Wilkinson et al., 2018). Cropland expansion is one of the main drivers of forest fragmentation (Potapov et al., 2021; Zabel et al., 2019). In some regions, this is often associated with the acquisition of large tracts of land for agribusiness development projects, such as the expansion or establishment of oil palm plantations (Rulli et al., 2019). Thus, relevant hotspots of forest fragmentation broadly coincide with hotspots of deforestation and cropland expansion at the margins of tropical forests (Dobson et al., 2020) and dividing larger portions of forest into millions of smaller/shrinking patches, from European colonization times and pervasive to date (Vancine et al., 2024), as observed in Sub-Saharan Africa (Rulli et al., 2017; Wilkinson et al., 2018), South East Asia (Brock et al., 2019; Muylaert et al., 2023; Rulli et al., 2021) and the Neotropics (Prist et al., 2017). For instance, in the Atlantic Forest of South America, characterized by both high biodiversity and high forest fragmentation, 97% of forest fragments are small (<0.5 km^2) and 50%–60% of the vegetation is within 90 m from the forest fragment edges (Vancine et al., 2024).

The mechanisms that determine habitat fragmentation patterns can be traced back to the dynamics underlying land use change. When land use change happens, landscape composition (the amount of land use types present) and landscape configuration (how patches are spatially arranged and (dis)connected) is changed, with great impacts for populations survival and ecology. For instance, deforestation typically evolves in a forest-fragmenting pattern, creating checkerboard and fishbone-like landscapes with the interface between forest and cleared areas increasing in size over time (Dobson et al., 2020), often measured through different types of landscape and patch-based metrics.

From a methodological point of view, forest fragmentation (Brock et al., 2019) can be analyzed and quantified through the classification of forested and cleared areas, based on their mutual spatial relationships. For instance, common methodologies distinguish between isolated forest patches, edge amount of forested patches and perforations within forest cores. These distinctions are important because different fragmentation features can differ in their accessibility by humans or likelihood of pathogen transmission to humans (Shapiro et al., 2016; Wilkinson et al., 2018). Therefore, the analysis of the spatio-temporal transitions across fragmentation features and levels can better unravel the transient mechanisms of deforestation or cropland expansion (Shapiro et al., 2016) because the highest spillover risk has been found in association with intermediate levels of habitat loss (Faust et al., 2018).

In fact, pathogen transmission depends, among other factors, on the contact rate between pathogen hosts and susceptible individuals, which in turn depends on the magnitude of the interface between wild habitat and the land converted to agriculture or other anthropic use (Dobson et al., 2020). Thus, the dynamic geometry of habitat loss is a key factor affecting spillover risk because it alters this interface, potentially affecting pathogen flow from wildlife to humans even more than complete habitat loss from forest clearcut (Wilkinson et al., 2018). Indeed, fragmentation can increase contact opportunities between wildlife hosts and humans even without major reductions in forest cover and host habitat extent (Figure 8) (Rulli et al., 2017). Moreover, an increase in forest cover is not necessarily associated with a reduction in forest fragmentation. In fact, reforestation projects focusing on monocultures and/or planned without accounting for the pre-existing vegetation structure have been shown to possibly further increase the degree of forest fragmentation (Rulli et al., 2021).

Beside the purely geometric aspect of fragmentation, ecological alterations play a relevant role. For instance, fragmentation can alter movement patterns of hosts (Mancini et al., 2024) that migrate, relocate or commute between fragmented patches, thus crossing cleared areas and increasing transmission opportunities (Gottdenker et al., 2014). Fragmentation also decreases resource availability to wildlife hosts, thereby inducing behavioral

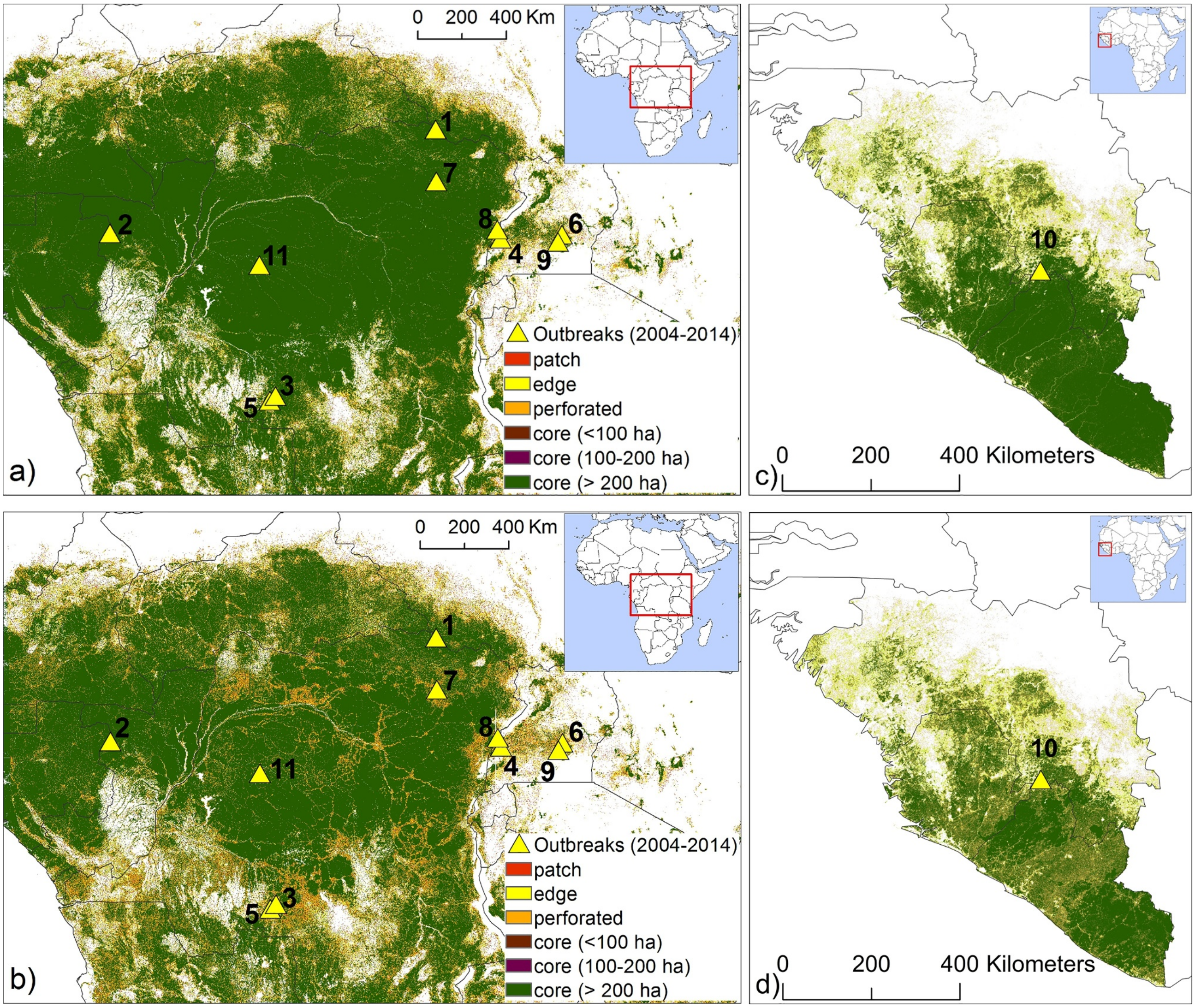

Figure 8. Forest fragmentation in Central and West Africa and centers of first infection (yellow triangular markers) (from Rulli et al., 2017). Within areas in the surroundings (<25 km) of points of first infection forest fragmentation was significantly greater (*p*-value 0.032) than in comparable areas in the same region with a fragmentation index of 0.32 versus a regional average of 0.20. The increase in fragmentation (338%) between 2000 (panels a; c) and 2014 (panels b; d) was also significantly larger than the regional average (145%).

changes as alternative food and shelter opportunities are identified, while simultaneously increasing host susceptibility to pathogens or pathogen shedding (Gottdenker et al., 2014; Plowright et al., 2021). Consequently, fragmentation typically has negative effects on the population of forest-specialist species, while favoring habitat generalists, which can better adapt to degraded environment (Muylaert et al., 2019b; Prist et al., 2017; Rulli et al., 2021). For instance, fragmentation increases the presence of frugivorous bats (Plowright et al., 2021; Rulli et al., 2017) and other mammals such as rodents (Prist et al., 2017), which host a range of pathogens (Table 1) (Prist et al., 2017). Conversely, a decrease in non-human primates has been associated with the first stages of forest fragmentation, while a rebounding increase has been observed in subsequent phases of fragmentation (Rulli et al., 2017). Therefore, forest fragmentation has been associated with a number of diseases that are believed to have these species as putative hosts. Ebola virus disease outbreaks due to probable viral spillover from fruit bats in Western Africa have been found to be more strongly associated with highly fragmented forest landscapes than with large, deforested areas (Rulli et al., 2017). Likewise, in South America, the increased connectivity in the landscape of generalist rodent populations resulting from habitat fragmentation has been shown to be an important driver of hantavirus spillovers (Muylaert et al., 2019b; Prist et al., 2017) and forest fragmentation has been linked to the increase in risk for other diseases such as Chagas disease (Trovo et al., 2024), yellow fever, and malaria (Mancini et al., 2024). Similarly, *Plasmodium knowlesi*, a zoonotic malaria, has been more frequently detected in the most fragmented areas of Southeast Asia (Brock et al., 2019). A number of other parasitic diseases have also been associated with forest fragmentation (Patz, Graczyk, et al., 2000), including tick-borne diseases (Gottdenker et al., 2014) such as Lyme disease (Allan et al., 2003). The transmission of such diseases can be further facilitated by the interaction of fragmentation with other activities taking place in the cleared areas within forest fragments, as concentrated livestock farming can further increase spillover risk when livestock act as intermediate hosts (Kuiken & Cromie, 2022; Pulliam et al., 2011; Rulli et al., 2021).

6.3. Agricultural Expansion and Intensification and Zoonotic Infection Exposure

Beside habitat loss and fragmentation, agricultural expansion drives other mechanisms that can increase the spillover risk of zoonotic infections. The loss of bat habitat due to deforestation for agriculture expansion in east Australia has resulted in changes in the location, size, and structure of bat colonies as well as in their foraging areas (Eby et al., 2023), thus ultimately linking the emergence of three bat-associated viruses, namely, Menangle virus, Australian bat lyssavirus, and Hendra virus to agricultural expansion (Plowright et al., 2021). While this increase in vulnerability mainly acts through the co-occurrence of new or increased host interactions, the often unsafe and unregulated “socio-economic frontier” that develops concurrently with agricultural expansion, as well as other activities encroaching into previously non-anthropized environments, creates another set of vulnerabilities to different infectious diseases, including exposure to sexually transmitted diseases imported through hired labor from other regions (Ellwanger et al., 2020; Faas et al., 1999; Minter, 2021; Rohr et al., 2019).

Likewise, agricultural intensification, particularly, the transition of animal husbandry to more concentrated and industrialized production, can alter pathogen transmissions thereby increasing spillover risk (Kuiken & Cromie, 2022; Perfecto et al., 2023). Indeed, while agricultural intensification typically affects less extended areas than expansion, these more local impacts should not be overlooked, as they imply, for instance, the direct reduction of biodiversity within agricultural areas, affecting both species native to these areas and species of the surrounding natural habitats (Rohr et al., 2019; Zabel et al., 2019), as documented in the case of Sub-Saharan Africa and Brazil (Zabel et al., 2019). The contamination of water, soil, and air from animal waste, biomass burning, fertilizers and pesticides can increase spillover risk by shifting the range of vector species or increasing human vulnerability to infectious diseases (Ferraguti et al., 2023; Rohr et al., 2019). In the Tropics, the use of agrochemicals could be associated with the increase of infectious pathogens with complex life cycles, such as trematodes, because their intermediate hosts have higher chance of survival in nutrient rich environment (Hoover et al., 2020) and favor some pathogenic fungi (Lekberg et al., 2021). In addition, fertilizer made of manure has the potential to be a source of fecal pathogens, such as verotoxigenic *E. coli* and *Salmonella* (Mukherjee et al., 2004; Ongeng et al., 2015; Tran et al., 2020).

Moreover, the expansion of irrigated areas onto pre-existing croplands alters the behavioral patterns of water-dwelling arthropod vectors, such as mosquitoes carrying malaria (Gottdenker et al., 2014), as well as increasing the risk of many waterborne diseases (Gebremichael, 2018; Huang & Manderson, 1992; Perez-Saez et al., 2016). The building of hydraulic infrastructures for irrigation, such as dams (Section 5.2.5) and irrigation canals have been associated with the occurrence of Rift Valley virus epidemics (Sang et al., 2016). More generally, a broad range of viral, bacterial and protozoan pathogens have been associated with agricultural intensification, especially in “developing countries” (White & Razgour, 2020). On the other hand, agricultural intensification can also come with a set of socio-economic benefits that can reduce transmission risks through the increase of human preparedness and decrease in vulnerability (Ijumba & Lindsay, 2001).

Lastly, there is a significant sector that farms non-domesticated animal species and relatively high densities, whether for fur or meat. Multiple infectious diseases are thought to have the capacity to emerge through these pathways as they often bring together multiple different species with different infections together in farms or in markets (Milbank & Vira, 2022; WHO, 2021; Zhao et al., 2024).

6.4. Wetlands and Zoonotic Infection Exposure

Wetlands are recognized for their important environmental functions, such as carbon sequestration, provision of natural habitat, and flood mitigation (Mitsch et al., 2013). Inland and coastal wetlands have historically been targets of land use change, driven by the goal of land reclamation for agricultural or residential uses. In the last

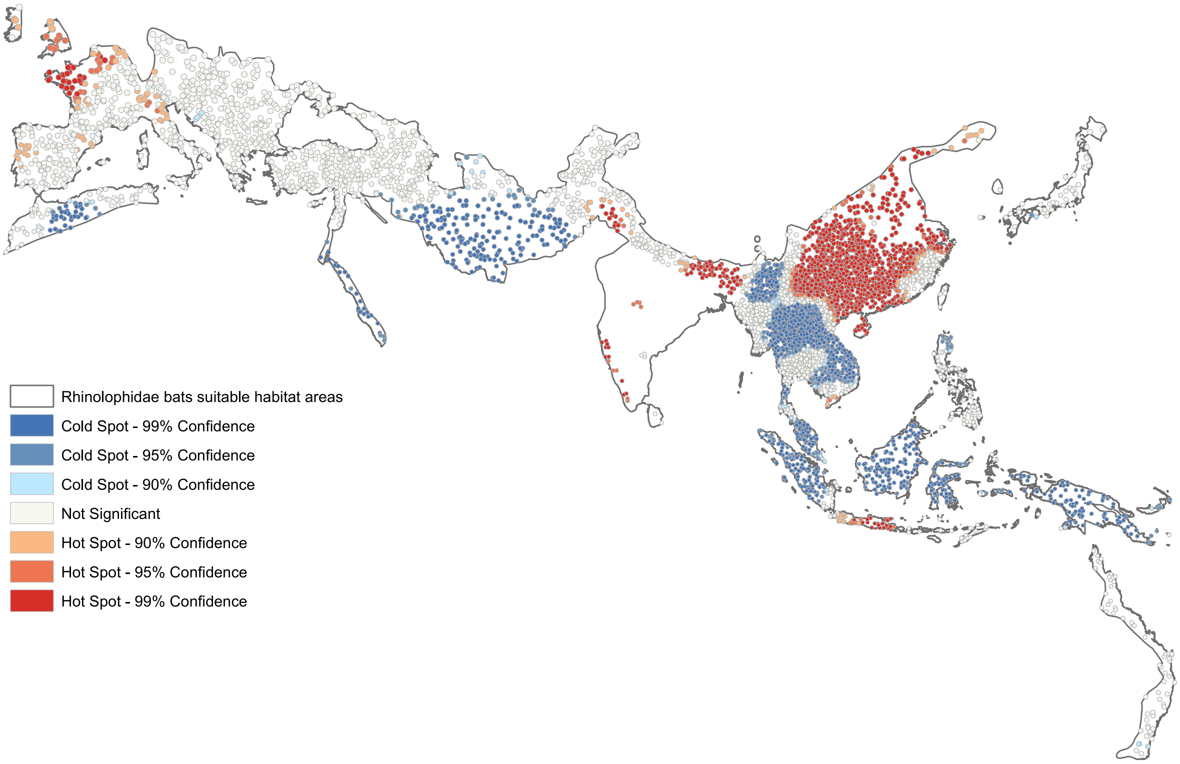

Figure 9. Multivariate spatial analysis of coronavirus outbreak drivers. A hotspot analysis has been performed on forest fragmentation, livestock density (cattle, goats, pigs, sheep) and human settlement presence data using the Getis-Ord Gi* test, which standardizes data applying a spatial clustering algorithm. Hot spots are defined as points belonging to spatial clusters characterized by values significantly higher than the sample average, and cold spots are points with spatial clusters significantly lower than the sample average. The multivariate hotspot analysis shown in the map is obtained by averaging the standardized values of the analyzed data (from Rulli et al., 2021).

three centuries, wetland areas are estimated to have decreased by 16%–23% (Flouet-Chouinard et al., 2023), though some estimates are considerably higher (Davidson, 2014). In this process, wetlands are typically drained, thereby losing their most defining attribute: the presence of standing water (or a water table close to the ground surface). Land drainage, altered plant community compositions, triggered major CO2 emissions by turning carbon sinks into sources, and favoring human settlement, agricultural or urban development. Such changes have historically affected the exposure to mosquito-borne infections that cause diseases such as malaria or dengue fever (Rey et al., 2012). Indeed, the loss of wetlands was typically followed by a decline in mosquitoes with beneficial impacts on human health (e.g., De Blij, 2011). Such impacts have repeatedly been invoked to justify new wetland reclamation projects.

Recent years have seen the opposite process, namely, the restoration of wetland environments because of their importance as habitat for diverse wildlife, as natural water filters, improving water quality by trapping pollutants, buffers against floods and droughts, storing and slowly releasing water, and support for fisheries and agriculture, providing livelihoods and food for millions (McElwee et al., 2024). Additionally, wetlands are crucial for climate regulation, as they store vast amounts of carbon, helping to mitigate climate change (Temmink et al., 2022). However, restoration efforts can reestablish pools of stagnant water and impoundments, providing the preferred habitat for mosquitoes (Willott, 2004). Therefore, wetland restorations are often followed by an increase in mosquito populations (Dworrak et al., 2022) and new insurgence of mosquito-borne infectious pathogens such as Plasmodium spp. (which causes malaria), Dengue virus, West Nile virus, or the eastern equine encephalitis virus (Medlock & Leach, 2015; Rey et al., 2012). Therefore, wetland restoration efforts started to be evaluated considering the impacts on mosquitoes, leading to the development of mosquito managements practices such as the Integrated Mosquito Management approach (IMM), which aims at controlling mosquito breeding habitats (Jackson et al., 2009), fostering surveillance, and improving conditions for mosquito predators (Dale & Knight, 2008; Dworrak et al., 2022).

6.5. Urbanization and Zoonotic Infection Exposure

The potential for zoonotic spillover evolves with urbanization, as some pathogens and their spillover to humans are favored by fully urbanized environments (Himsworth et al., 2013), while many others by intermediate degrees of urbanization (Gibb, Franklinos, et al., 2020). Indeed, the fringe of urban expansion is often a hazardous ecotone for zoonotic spillover. Peri-urban areas may exhibit high degrees of natural habitat fragmentation, favor the interaction between humans and wildlife (Patz, Graczyk, et al., 2000), including arthropod vectors (Hendy et al., 2020), and provide opportunities for their coexistence with high livestock concentrations (Alarcon et al., 2017), potentially acting as intermediate hosts (Saksena et al., 2014). The co-occurrence of landscape fragmentation, urbanization and livestock intensification is a recurrent pattern in regions of Southeast Asia that have already been prone to diverse zoonotic spillovers (Goldstein et al., 2022; Rulli et al., 2021) (Figure 9). Indeed, urbanization, and especially peri-urbanization, often comes hand-in-hand with the industrialization of agriculture (Goldstein et al., 2022; Nova et al., 2022), and this combination creates spillover-driving mechanisms that go beyond the increase in contact rates between humans and pathogen hosts/vectors typically associated with land use change (de Melo Ximenes et al., 2020). The increased presence and density of humans, for instance, increases a series of potential transmission factors such as movements of people and goods, including rural-urban trade and migration, as well as inequalities including in the access to safe and clean water resources, which can be conceptualized as a network of human-pathogen interfaces (Brady & Hay, 2020; Hassell et al., 2017). This can create a risk not only for transmission of pathogens from animal hosts to humans but also reverse spillover, from humans to animals, putting wildlife at further risk (Hassell et al., 2017). While urbanization can also decrease human vulnerability through improved access to prevention and care, especially in lower income countries, the urbanization process often outpaces socioeconomic development, creating new risks (Goldstein et al., 2022; Sun et al., 2020). Moreover, urbanization can alter pathogen transmission by creating significant ecological changes also at the host/vector community level (Hassell et al., 2017). Urban areas can become clusters of resources, increasing the density of hosts, creating new sources of food for urban-adaptive hosts, or creating new breeding sites for vectors (Hassell et al., 2017; Jones et al., 2013). These feeding and breeding opportunities are also highly diversified, potentially reducing inter- and intraspecific competition for hosts/vector species and thus increasing their populations (Brady & Hay, 2020). The diversity of mechanisms connecting urbanization to zoonotic spillover risk leads to different pathogens to be associated with different levels of urbanization. For instance, arboviruses hosted by *Aedes aegypti* mosquitoes, such as Dengue, Chikungunya and Zika viruses thrive in fully urbanized areas (Brady & Hay, 2020; Nova et al., 2022), while Lyme disease and arboviruses hosted by ticks and *Aedes albopictus* mosquitoes are favored by peri-urban environments (Nova et al., 2022). In general, vector-borne diseases are most frequently associated with urbanization, including malaria (Ferraguti et al., 2023; Patz, Graczyk, et al., 2000). However, other pathogens carried by synanthropic vertebrates increase in urban contexts, as in the case of rodents carrying leptospirosis, plague, and hantavirus, and livestock, carrying leptospirosis and other bacterial infections (Hassell et al., 2017; White & Razgour, 2020). High density poultry farming in the urban context has been associated with the emergence of avian influenza (Saksena et al., 2014). Also, generalist species of carnivores and omnivores have been extensively investigated as pathogen hosts favored by urbanization, including, but not limited to, domestic animals (Földvári et al., 2011, 2014; White & Razgour, 2020). Some bat species can also survive or benefit from urban and peri-urban areas (Hassell et al., 2017; Jones et al., 2013).

6.6. The Role of Wildlife Hunting and Wild Animal and Meat Trade in Zoonotic Infection Exposure

Even though it is not a form of land use change in a strict sense, wild animal or bushmeat hunting directly involves the encroachment of humans into wildlife habitats and is driven by processes that contribute to land use change (Wegner et al., 2022). Wild animal meat from the tropics is mostly referred to as bushmeat in the African context (Karesh & Noble, 2009). Wildlife hunting and trading is also facilitated by deforestation, as bushmeat supply chains can build up along the infrastructures created by the logging industry (Karesh & Noble, 2009). In this case, bushmeat can also become an alternative source of income, and thus an instrument of access to food, in addition to being a food item itself (Kurpiers et al., 2016). Moreover, in situations of conflict, the de-regulation and lack of enforcement of wildlife conservation laws has been shown to favor bushmeat hunting and trading (Karesh & Noble, 2009). This also translates into the diffusion of zoonotic risk due to wild meat hunting, processing, trading and consuming (World Organisation for Animal Health, 2024).

The consumption of wild meat is one of the main mechanisms of zoonotic spillover (Choo et al., 2023). While Central America and central Africa are the main hotspots of zoonotic risk from wild meat, if we account for trade

Southern Africa becomes a hotspot, while China has very high zoonotic exposure from wild meat both directly and through trade (Choo et al., 2023). The globalization of trade networks has led to a globalization of wild meat consumption and of the associated zoonotic spillovers. In fact, zoonotic spillovers from wild meat rose in the 2000s, with a similar trend as increase in bushmeat consumption (Karesh & Noble, 2009; Milbank & Vira, 2022). Yet, the country with the most reported cases of zoonotic spillover from wild meat is the USA, with a prevalence of bacterial infections, followed by the predominantly viral spillovers in Congo and Japan (Milbank & Vira, 2022). Interestingly, women are more affected by such spillovers, likely because the highest transmission risk is during meat butchering, which is when there is the most direct human contact with animal body fluids (Kurpiers et al., 2016). This activity is predominantly performed by women (Kurpiers et al., 2016; Magouras et al., 2020). Wild meat consumption involves a wide range of animal species and allows for a very direct contact between humans and animals. Thus, the number of diseases that can be transmitted this way is high. Spillover events attributed to bushmeat and wild meat hunting, processing, trading or consuming include SIVs and Monkeypox virus from primates, ebolaviruses from bats, primates and duiker, Lassa virus from rodents, Hepatitis E from pigs and deer, and a wide range of bacterial and parasitic infections involving an equally wide range of species (Cantlay et al., 2017; Kurpiers et al., 2016; Milbank & Vira, 2022).

6.7. Globalization and Infectious Disease Emergence Through Trade and International Land Acquisitions

The globalization of food and bioenergy has been rapidly increasing in the last few decades, in terms of both traded volumes, which have more than doubled since the mid-1980s, and interconnectedness, with an increasing number of countries being integrated in the agricultural trade network (Carr et al., 2013; D'Odorico et al., 2014; FAO, 2022; Tu et al., 2019). The increased interconnectedness of food systems across national and international borders has transformed the way food is produced, distributed, and consumed worldwide. Nearly one quarter of food for human consumption is traded across international borders as both plant, animal and processed food (D'Odorico et al., 2014; FAO, 2022). Trade enables the movement of agricultural products across borders, along with pests, pathogens, and invasive species (Roy et al., 2023).

Globalization is also associated with international investments, including Large Scale Land Acquisitions (LSLAs) targeting large tracts of land in lower income countries. Large Scale Land Acquisitions, which are often termed "land grabs" when they take place under unbalanced power conditions, in disregard of prior land users and their rights, can contribute to EID spillovers because they are drivers of major land use change, overuse and degradation of natural resources, and habitat destruction (Morand & Lajaunie, 2021; Rulli et al., 2017; Wallace et al., 2014). Large Scale Land Acquisitions results in an alteration of the environment that in turn leads to changes in human-wildlife interactions. Large Scale Land Acquisitions often target forested (tropical) areas and in most of the cases land investments are followed by deforestation (Davis et al., 2015, 2020) for timber extraction, agriculture, mining, or infrastructure development, leading to forest fragmentation (Rulli et al., 2019) and potential biodiversity loss (Davis et al., 2023). Land deals for agricultural purposes are associated with both an expansion and intensification of crop production, promoting the cultivation of export-oriented crops for the global market and the agrarian transition from subsistence/smallholder farming to large-scale commercial agriculture (Müller et al., 2021). The associated changes in agricultural practices and land management often lead to large-scale monoculture, overuse of agrochemical inputs and irrigation, thus impacting local ecosystems, their biodiversity, and wildlife. Moreover, LSLAs can impact land tenure security, displace local land users and/or dispossessing them of their land (Nolte et al., 2022), thus determining circular labor migration, intensified interactions between rural communities and urban dwellers, and altered land-livelihood dynamics displace people from newly acquired land (Kelley et al., 2020).

The interconnectedness of global trade, travel, and urbanization facilitates the movement of people, animals, and goods across distances and multiple ecosystems at unprecedented speed. This increased connectivity creates opportunities for pathogen spillover, through wildlife trade, livestock farming practices, or encroachment into natural habitats. Climate change further exacerbates the interconnectedness dynamics by altering the ecosystems and when species do not tolerate local conditions for survival, they move to new distributions (Muylaert et al., 2022), bringing humans into closer contact with hundreds of novel pathogens (Carlson et al., 2022) (Section 7). Effective prevention of zoonotic spillover and zoonotic outbreaks in a globalized world requires coordinated international efforts to monitor, regulate, and mitigate the range of factors contributing to disease emergence, ensuring both human health and environmental sustainability (Section 9) (Hayman et al., 2023; Markotter et al., 2023).

7. Direct and Land-Mediated Impact of Climate Change on Emerging Infectious Disease Risk

Land use change and climate change are closely interconnected (IPCC, 2022; Pörtner et al., 2023). The expansion of both urban and cultivated lands contributes to deforestation altering the Earth's surface energy and water balance and reduces the capacity of global ecosystems to sequester carbon, thus leading to increased atmospheric greenhouse gas (GHG) levels and global warming. Moreover, the conversion of forests and wetlands to agricultural land releases significant amounts of GHGs, including carbon dioxide (CO2), methane (CH4), and Nitrous oxide (N2O), due, for example, to fires, livestock intensification, and fertilizer applications (Friedlingstein et al., 2024; Saunois et al., 2024; Tian et al., 2024).

In addition to altering global biogeochemical cycles, land use changes also impact regional and local climate and weather patterns by altering surface albedo, roughness and evapotranspiration rates (Perugini et al., 2017). In turn, climate change influences land cover and use modifications as rising temperatures and shifting precipitation patterns modify the range of vegetation suitable habitats, alters disturbance regimes (e.g., drought stress, wildfire, storminess), and reshapes the distribution of cultivated and irrigated areas (Altman et al., 2024; Mottl et al., 2021), impacting the suitable habitats for pathogen hosts and vectors, necessitating to rethink land management strategies. This feedback loop underscores the importance of both sustainable and climate smart land use practices to mitigate climate change and enhance the resilience of ecosystems to its impacts, respectively.

Climate change, the natural environment and land use also affect public health through their effects on disease emergence patterns (Gibb et al., 2025; Mora et al., 2022). While improved sanitation, health care, and preventive and clinical medicine have reduced the vulnerability to and consequences of several infectious diseases in many regions from 2010 to 2016, this trend reversed between 2016 and 2018, indicating that other factors, including climate change, continue to challenge disease control efforts (Watts et al., 2021).

Climate per se is becoming increasingly beneficial to the transmission of various infectious diseases (Carlson et al., 2022). More erratic weather and stronger extreme events have profound consequences on the incidence, distribution, intensity and derived risks of infectious diseases, especially vector- and water-borne, but also rodent-borne, food-borne and air-borne (Bhattachan et al., 2021; Gibb et al., 2024; Rupasinghe et al., 2022). Models tracking dengue, malaria, and pathogenic *Vibrio* bacteria, the cause of cholera and vibriosis, show increased climate suitability for disease transmission since the 1950s (Watts et al., 2021). However, the frequency of disease outbreaks is likely to increase due to the complex and combined effects of average to extreme climate conditions on pathogens (like viruses and bacteria), animals (acting as vector, carrier host or reservoir host), human population, and ecosystems (Liao et al., 2024), requiring generalizable approaches to timely cover a wide spectrum of diseases and planning horizons (Bartlow et al., 2019; Head et al., 2022).

Higher temperatures and modified precipitation patterns, as well as air pollution, influence the lifecycle and distribution of mosquitoes, ticks and flies—usually prospering in warm, humid environments - thereby affecting the transmission dynamics of diseases like malaria, dengue, yellow fever, Lyme disease, West Nile encephalitis and leishmaniasis (Bal & Sodoudi, 2020; Ochida et al., 2022; Schönherr, 2023; Wang et al., 2024a, 2024b). Modes of natural climate variability, like El Nino Southern Oscillations (ENSO), are also associated with higher risk (frequency and severity) of infectious diseases (Flahault et al., 2016), for instance in the Horn of Africa, for the RVF, cholera, and malaria during El Nino, and for the dengue, chikungunya, and yellow fever during La Nina.

A review of studies from 2015 to 2020 on climate change and infectious diseases found several biases. Most research focused on mosquito-borne diseases, with tropical areas receiving less attention than temperate areas (Van de Vuurst & Escobar, 2023). However, studies on climate change impacts and adaptation strategies related to malaria and dengue reveal strong impacts in Africa and Southern Asia, respectively Kulkarni et al. (2022).

Between 2015 and 2019, suitability for malaria transmission in highland areas rose by 38.7% in the African region and 149.7% in the Western Pacific region compared to the 1950s baseline (Watts et al., 2021). Predictions for 2050 suggest a 50% higher probability of malaria cases threatening some previously unexposed areas worldwide (Cella et al., 2019), especially in Asia, sub-Saharan Africa, and South America (Semenza et al., 2022).

Spreading into temperate zones and prolongation of the transmission season is expected for the *Aedes* mosquitoes that carry dengue, significantly increased in 2018, especially in Europe, and from 1950 to 2018 at global level (Watts et al., 2021). Rocklöv and Tozan (2019) mentioned the increase also of other viruses brought by

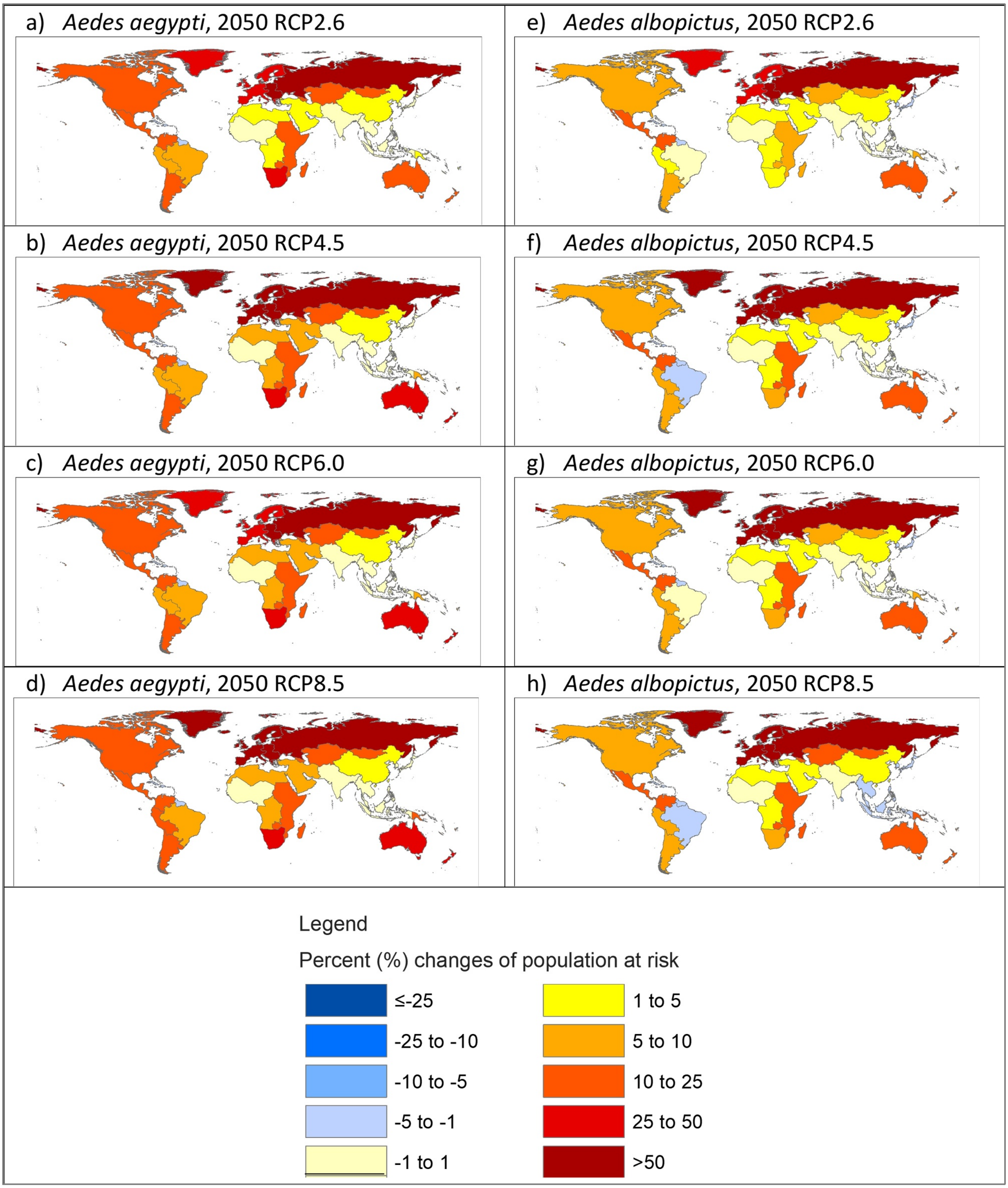

Figure 10. Percent (%) changes of population at risk for 2050 in global health regions due to temperature suitability for virus transmission. Projections are averaged across four GCMs, broken down by vector and RCP: *Aedes aegypti* in (a) RCP2.6; (b) RCP4.5; (c) RCP6.0; (d) RCP8.5; and *Aedes albopictus* in panel (e) RCP2.6; (f) RCP4.5; (g) in RCP6.0; (h) RCP8.5. RCPs (Representative Concentration Pathways) from 2.6 to 4.5, 6.0 and 8.5 refer to different levels of mitigation efforts leading to different thermal and moisture regimes (Authors' elaboration from Ryan et al., 2019). RCP2.6 assumes ambitious mitigation strategies leading to low emissions andRCP8.5 represents a high-emissions, business-as-usual scenario.

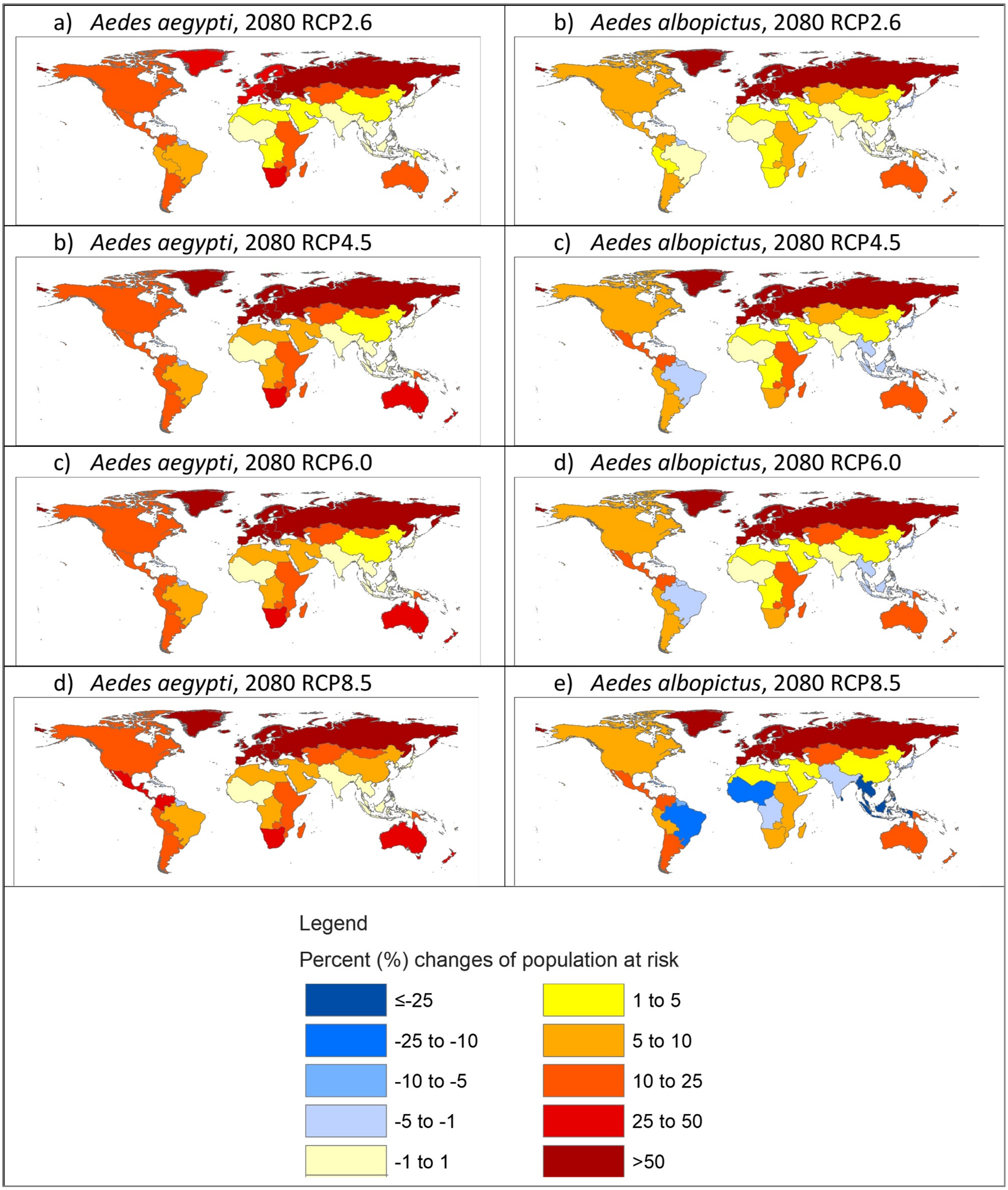

Figure 11. Percent (%) changes of population at risk for 2080 in global health regions due to temperature suitability for virus transmission. Projections are averaged across four GCMs, broken down by vector and RCP: *Aedes aegypti* in (a) RCP2.6; (b) RCP4.5; (c) RCP6.0; (d) RCP8.5; and *Aedes albopictus* in (e) RCP2.6; (f) RCP4.5; (g) in RCP6.0; (h) RCP8.5. RCPs (Representative Concentration Pathways) from 2.6 to 4.5, 6.0 and 8.5 refer to different levels of mitigation efforts leading to different thermal and moisture regimes (Authors' elaboration from Ryan et al., 2019). RCP2.6 assumes ambitious mitigation strategies leading to low emissions andRCP8.5 represents a high-emissions, business-as-usual scenario.

mosquitoes, like Zika, chikungunya, and the West Nile, as happened in Europe in 2018 (Semenza et al., 2022). Vector movement, climate change and immunization levels have all contributed to the re-emergence of yellow fever during the sporadic outbreak in 2019–2020 in Sub-Saharan Africa (Uchenna Emeribe et al., 2021). Therefore, alongside landscape changes shown to influence spillover risk, increased precipitation and temperatures are likely to expand many mosquitoes' habitat suitability with poleward shifts of *Aedes*-borne viruses, with different patterns across regions, but with nearly a billion people newly exposed to these viruses in the worst-case scenario (Ryan et al., 2019) (Figures 10 and 11).

However, climate change has been linked to a range of diseases favored by other vectors, including lice, fleas, mites, and ticks (Mojahed et al., 2022) and to water-related diseases such as cholera and other enteropathogens, helminthic infections and leptospirosis (Kim et al., 2023).

Semenza et al. (2022) reinforce the causal link between climate change and the spread of tick-borne diseases like Lyme (a bacterial disease) and tick-borne encephalitis (a viral disease), particularly in North America and Europe, with other arthropod vector-borne diseases expected to expand their distribution toward Northern latitudes (Omazic et al., 2019).

Climate change is likely to impact not only the vectors but even the hosts of transmitted diseases (Carlson et al., 2022; Muylaert et al., 2022). Douglas et al. (2021) found strong evidence for Latin America and Caribbean of hantavirus disease (a directly transmitted disease; Table 1) association with precipitation and habitat types, but mixed evidence was observed for temperature and humidity, revealing complex climate-virus interactions due to still unknown host reservoirs, circulation of multiple virus strains, agricultural practices, climate conditions and challenged public health systems.

Concerning water-borne diseases, although they have been decreasing over the last decades due to socioeconomic development and public health measures, changes in climate can reverse some of these positive developments, as water heating and flooding foster the transmission of water-borne pathogens. Higher average temperatures and out-of-normalclimate conditions (ENSO, floods, cyclones, droughts) favor cholera, also indirectly through displacement dynamics, and leptospirosis, as well as various diarrheal pathogens (Kim et al., 2023; Semenza et al., 2022). The distribution of water-borne diseases like schistosomiasis in Africa, Latin America, the Middle East, and Southeast Asia is likely to alter with climate change, for example, through impacts on the snail hosts (Glidden et al., 2024; Perez-Saez et al., 2016; Stensgaard et al., 2019). Pathogenic *Vibrio* infections have also become more likely, with suitable coastal areas in northern latitudes increasing by 50.6% compared to the 1980s baseline (Watts et al., 2021).

Some of the above-mentioned elements, from agricultural practices to people relocation - or concentration—in urban and coastal areas, suggest that climate change does not act alone, but it influences and is strictly interrelated to land cover/use modifications, also connected to socio-economic drivers and human dynamics. Despite climate projections for future horizons already embed global-scale land use transitions consistent with GHG concentrations and socio-economic pathways, the role of climate-landscape interactions on infectious diseases involves more regional to local dynamics.

Degradation of habitats, natural resource exploitation, as well as infrastructure deterioration or disruptions caused by climate trends or by slow-to fast-onset extremes - like warming, heatwaves, drought, storms, floods, wildfires - facilitate interactions between pathogens, carrier, reservoirs, and people.

Biodiversity losses can be due to long term modification in climate trends, or abrupt climate events, such as droughts, fires, floods, and windstorms, and can either increase (lose the dilution effect on) or decrease the disease exposure and incidence, function of the surviving host species, if having or not a role in the transmission (Civitello et al., 2015; Halliday et al., 2020; Keesing & Ostfeld, 2021; Luis et al., 2018). In turn, degraded areas become less resilient to subsequent climate hazards, which further affect infrastructure, livelihoods and infection risks and potentially further increase pressure, with such feedback potentially generating self-sustaining rural "poverty traps" (Gibb et al., 2025). However, the biodiversity, climate and infectious disease nexus is more complex and not unidirectional (Pfenning-Butterworth et al., 2024).

Looking at human-dominated landscapes, a plethora of example arises in literature. Impacts of hot temperature on malaria transmission in Venezuela are more pronounced in gold mining areas (Fletcher et al., 2022). In densely populated and poorer settlements, urban heat island effects and low-quality water and sanitation systems can increase both thermal suitability and breeding site availability for mosquito reproduction and vector competence, thereby increasing the risk of disease for already vulnerable - marginalized - communities (Gibb et al., 2023; Romeo-Aznar et al., 2024). Both stagnating water sources remained after droughts and those created after floods force mosquitoes and birds closer for breeding and favoring the array of pathogens that they transmit, like West Nile virus (Myaing, 2011; Quarles, 2017), leishmaniasis, malaria, and dengue (Dayrit et al., 2018), RVF (Mills et al., 2010), yellow fever (Gage et al., 2008). Similarly, wild species like bats, rodents, primates (Charron et al., 2008; Kontra, 2017) search new areas for habitats and food resources after droughts—also ENSO-related - or wildfires, favoring spillover from Nipah, Hendra, or Ebola Virus, for example, (Eby et al., 2023; Nagy et al., 2016; Patz et al., 2004). In other cases, warming and intense precipitation increased food and habitat resources, which reinforce rodent populations associated with plague (Mills et al., 2010) and hantaviruses (Gubler et al., 2001). Heavy rainfall was supposed to increase dengue incidence more markedly in rural than urban area of Brazil, probably due to better urban drainage infrastructure reducing vector breeding sites (Lowe et al., 2021). But when storms and floods cause overflow from wastewater systems, they can trigger both direct and food-borne transmission of noroviruses (Semenza et al., 2012), hantavirus (Patz, Graczyk, et al., 2000), hepatitis (Yavarian et al., 2019), *Cryptosporidium* (Boxall et al., 2009). Besides extremes, overall warming reduces snow, ice, and permafrost surfaces forcing voles to take shelter within human settlements, triggering hantavirus outbreaks (Butler & Harley, 2010), or exposure to - previously frozen - pathogens (Gross, 2019; Wu et al., 2022).

In addition to moving vectors or their hosts close to human-dominated landscapes, some climate regimes or extremes facilitate people approaching pathogens' concentration areas. For example, recreational water-related activities increase during heatwaves and have been associated with water-borne diseases such as *Vibrio*-associated infections (Baker-Austin et al., 2016), encephalitis (Ghanchi et al., 2017) and gastroenteritis (Waits et al., 2018). Storms, floods (de Azevedo et al., 2024), and sea level rise affected human displacements associated with leptospirosis (Oskorouchi et al., 2018) and gastroenteritis (Ivers & Ryan, 2006), among others. Drought and heavy precipitation were involved in the movement of livestock to suitable areas, which in turn led to pathogen exposure and disease outbreaks (Gale et al., 2009; Munang'andu et al., 2012).

Finally, climate-driven prolonged displacement, traveling, and global trade, favor novel host contacts, increasing the possibility for transmission and degrading the overall health of susceptible host populations (Khatib, 2023; Liao et al., 2024; Semenza et al., 2022; Van de Vuurst & Escobar, 2023).

8. Models of Zoonotic Infection Transmission

The emergence of infectious diseases is a multi-step, complex process. To understand this requires consideration of the infection, the infection hosts and the environment. Beyond the biophysical aspects, the environment can encompass social, cultural, economic, and historical components (Bedson et al., 2021; Heesterbeek et al., 2015). Various models contribute to this, because they allow us to simplify complex systems (Heesterbeek et al., 2015; Keeling & Rohani, 2011). These may be conceptual, statistical and/or mathematical. The types of models include compartmental dynamic models, ecological models, spatial models, evolutionary models, social network models, and economic and integrative models applied to governance. After defining these concepts, we explore classical mathematical models for pathogen spillover and spread in Appendix A.

Transmission dynamics models aim to understand how infectious agents spread within or between populations. They incorporate parameters like the reproduction number ($R0$), indicating the average number of secondary infections from one person in a totally naive population (Table 1). This understanding guides interventions during outbreaks (Tian et al., 2020) and they can be used to understand how environmental changes might impact infection dynamics (Faust et al., 2018; John, Fatoyinbo, & Hayman, 2024).

Ecological models focus on interactions within ecosystems, including factors influencing pathogen prevalence in wildlife, their diversity and distribution. These models may include the agent-host-environment models that emphasize the interconnectedness of infectious agents, hosts, and the environment (Rinaldo et al., 2020; Rohani et al., 2009). They highlight how broader issues, like land use and climate change, impact infection host switches and emergence (Faust et al., 2018; Hayman et al., 2016). Spatial models analyze geographical factors affecting disease spread taking into account neighborhood influences through spatial autocorrelation functions (Mergenthaler et al., 2022). Spatial models are useful to identify high-risk regions and guide control measures (Lawson, 2018). Evolutionary models explore how pathogens evolve within host populations based on processes including mutation, recombination, and selection (Holland, 1992), and providing insights into transmission potential and control strategies (Smith et al., 2009). Network models (Craft & Caillaud, 2011) study how interaction patterns (e.g., contact, social) facilitating disease spread, aiding outbreak prediction and intervention design (John, Fatoyinbo, & Hayman, 2024). And economic models assess the societal and economic impacts of outbreaks, informing policymakers about investing in prevention and response strategies (Heesterbeek et al., 2015). Models can be integrated to include different components of these, depending on the purpose and data available.

These diverse modeling approaches offer a comprehensive understanding of pathogen interactions, aiding in preventing and controlling zoonotic diseases and promoting public health and One Health initiatives. For a more detailed introduction of mathematical models of spillovers and spread, see Appendix A.

9. Integrated Approaches for Global Health

Addressing land use change and factors such as climate change impacts on health requires coordinated actions at both global and local levels (Carlson et al., 2025; McElwee et al., 2024; Patz et al., 2004; Rulli et al., 2024). At the international level, for example, on one side, policy frameworks such as the Paris Agreement play a crucial role in mitigating climate change; on the other side, amendments to the International Health Regulations are needed to include climate risk assessments. Moreover, countries need to tailor their public health strategies to anticipate and react to specific challenges, for example, by investing in vector control programs or public education to reduce exposure to disease vectors, by activating new plans that did not yet prioritize disease control in disease-free regions, and by ensuring infrastructure to ensure clean water and sanitation during extreme weather events. Continued, international and multi-disciplinary collaboration in research, sustained public health funding for surveillance and treatments, and adaptive strategies all will be vital to develop effective solutions (McElwee et al., 2024), including those that consider the interconnected issues related to water and food systems (Ricciardi et al., 2024).

There are several integrated approaches for global health which do this and conceptually overlap but have different epistemological and ontological assumptions, typically classified into Planetary health, EcoHealth and One Health (Harrison et al., 2019; Khan et al., 2018; Lerner & Berg, 2017; Talukder et al., 2024). They all consider it important to mitigate the health impacts of climate change, such as extreme weather events, rising temperatures, changing disease patterns, and food insecurity, as well as recognizing the importance of preserving biodiversity and ecosystems for human health, including the potential for emerging infectious diseases and the loss of natural resources. They then tend to focus on different aspects, relating to the effects of air, water, and soil pollution on human health and identifying strategies to reduce exposure and mitigate harm; promoting sustainable practices in agriculture, energy, transportation, and urban planning to improve public health outcomes; social justice and equity, through addressing health inequities caused by environmental degradation and ensuring that interventions prioritize the needs of vulnerable populations. These approaches are interdisciplinary by design and can influence high-level policy decisions through advocating for evidence-informed actions that prioritize planetary health and promote sustainable development goals. Recent efforts have aimed to bring together these approaches to the health of humans, animals, and the environment into one working framework to address the complex health challenges we face in the modern world. A One Health High Level Expert Panel has aimed to integrate the different perspectives under the One Health term and there is now an agreed working model accepted and used by the quadripartite of intergovernmental agencies, FAO, WHO, WOAH and UNEP (Adisasmito et al., 2022) (https://www.who.int/news/item/27-03-2023-quadripartite-call-to-action-for-one-health-for-a-safer-world).

One Health is now defined as "an integrative approach to health that recognizes the health of people is connected to the health of animals and the environment" (Adisasmito et al., 2022). The definition underscores the importance of considering the health of all three domains and acknowledges that the well-being of humans, animals, and the environment are intertwined. The interconnectedness between humans, animals, and the environment means that health issues cannot be viewed in isolation. Rather, a comprehensive understanding of the complex interactions and shared risks is necessary to develop sustainable and effective solutions. One Health initiatives encourage collaboration between professionals from various fields, including human medicine, veterinary medicine, environmental science, public health, and wildlife conservation. This multidisciplinary approach enables a broader perspective, facilitates knowledge sharing, and promotes joint efforts to prevent, detect, and respond to health threats (Hayman et al., 2023; Markotter et al., 2023). This approach is particularly valuable in identifying high-risk interfaces where human-animal-environment interactions elevate the likelihood of spillover

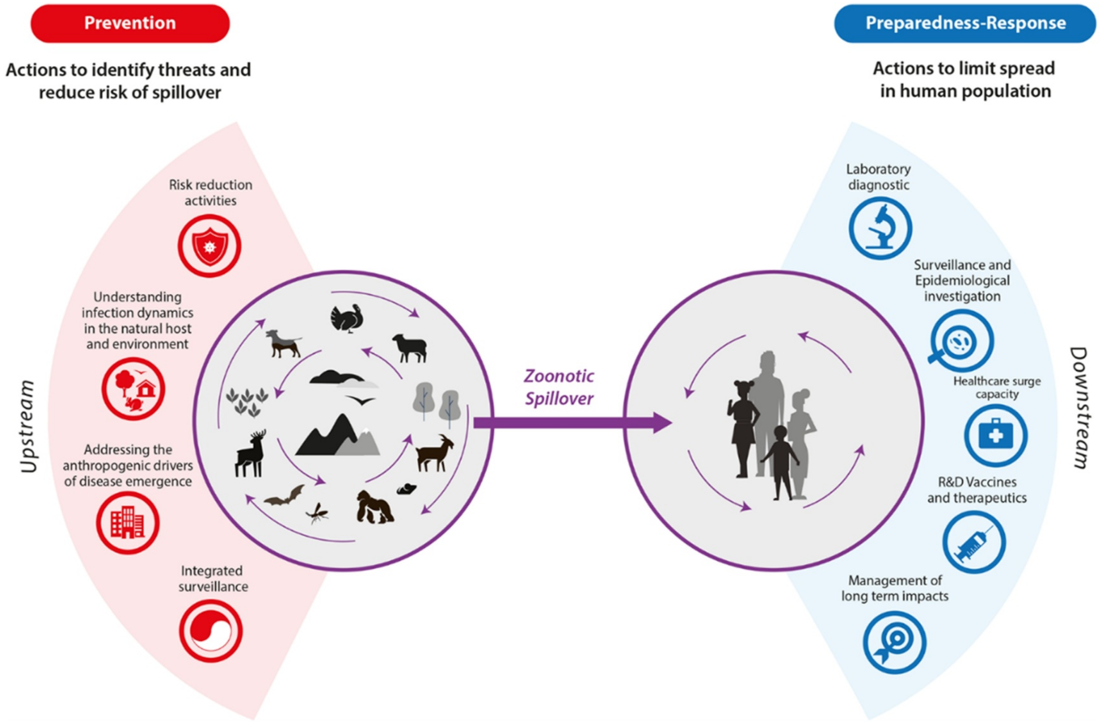

Figure 12. Prevention of zoonotic spillover to humans requires shifting the infectious disease control paradigm from reactive responses (right) to proactive primary upstream prevention (left). Prevention includes addressing the ecological, meteorological, and anthropogenic drivers of disease emergence to reduce the risk of human infection. From Markotter et al., 2023 (https://journals.plos.org/plospathogens/article?id=10.1371/journal.ppat.1011504). All activities in the "Upstream" left section require land use change to be considered. Risk reduction may include changing land use or preventing change to current systems; understanding infection dynamics in the natural host and environment is important to understand risks from land use change; addressing anthropogenic drivers includes addressing land use change as a driver, and integrated surveillance will include understanding spatial and temporal changes in land use for infection risk, surveillance and mitigation purposes.

(Jones et al., 2008; Wilkinson et al., 2018). Recognizing that human, animal, and environmental health are closely intertwined allows for proactive and preventive measures (Markotter et al., 2023) (Figure 12). This new framework for the study and mitigation of EID concentrates on identifying the root causes and the risk factors associated with land use change, habitat destruction, climate change, and wildlife trade (Daszak et al., 2020). It is expected that such an integrated One Health approach will allow for improvements in infectious zoonotic disease mitigation, human health and well-being. Most recently, an IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) global assessment aiming to tackle together five interlinked global crises in biodiversity, water, food, health and climate change offered more than 70 response options that were assessed to maximize the co-benefits across the cascading and compounding challenges impacting the biodiversity, water, food, health and climate change nexus (McElwee et al., 2024). These approaches will increasingly recognize the impact of land use change on infectious disease emergence, reviewed in this work, and the need to address land use change drivers, simultaneously accounting for their impacts on the quality and distribution of biodiversity, including pathogens, and the likelihood of pathogen transfer to humans, balancing the direct and indirect interactions between these (McElwee et al., 2024).

Appendix A

A1. Mathematical Models of Spillovers and Spread

Mathematical models are a key tool used to help understand and predict the spread of infectious diseases. While developing simple models of spillovers of emerging zoonotic diseases, we can make the following assumptions to start with: (a) The animal population controls the infection dynamics; (b) The human population determines the contact rates and disease's impact once there has been transmission. These can be altered by various land use changes and adjusted accordingly.

A1.1. Directly Transmitted Infection

To understand the dynamics of zoonotic diseases the model must include both the animal reservoirs and humans. Here we develop a generic model that could be adapted to many directly transmitted zoonoses with appropriate parameterization, where direct transmission here implies the absence of an arthropod vector such as a mosquito or tick (Section 2.2). We will assume the infection progresses through stages, where a host is susceptible (S), infected (I), and then recovered (R) (SIR), where R class are initially considered immune (Keeling & Rohani, 2011). The model considers both the human (*h*) and animal (*a*) host populations as separate but interconnected hosts of the infectious disease. The change in the number of susceptible animals, *S*, in the animal population over time is given as:

$$\frac{dS_a(t)}{dt} = \nu_a N_a(t) - \beta_a S_a(t)\, I_a(t) - \mu_a S_a(t)$$

where $S_a(t)$, $I_a(t)$, $R_a(t)$ represent the number of susceptible, infected, and recovered animals at time *t* and $N_a = S_a + I_a + R_a$, is the total number of animals. ν_a and μ_a represent the birth and death rates, respectively, per animal per unit time for the animal population. The dynamics of ν_a (birth) and μ_a (death) may be influenced by seasonal changes, dependence on population density, and random fluctuations. The term $\nu_a N_a$ represents the number of newborn animals per unit time, all of which will belong to the susceptible class (assuming no maternal antibodies are present). The term $\mu_a S_a(t)$ represents the number of susceptible animals that die per unit time, and the negative sign before the term represents their removal from the susceptible compartment. The probability of infected animals transmitting the disease to susceptible animals is assumed to be proportional to the number of susceptible animals ($S_a(t)$) and the number of infected animals ($I_a(t)$); therefore $\beta_a S_a(t) I_a(t)$ represents the number of susceptible animals that will become infected per unit time at time *t,* with β_a being the rate of infection (or transmission rate) from infected animals to susceptible animals. The transmission term ($\beta_a S_a(t) I_a(t)$) assumes that as the population size, or more accurately, the density of individuals increases, so does the contact rate (Begon et al., 2002). This approach is called the density-dependent approach. We introduce an alternative, frequency-dependent transmission, below. Land use changes can significantly impact the density of individuals, so impacting infection transmission dynamics, frequently be increasing or decreasing resources so impacting population densities.

The negative sign in front of the term $\beta_a S_a(t) I_a(t)$ shows that as the number of infected hosts increases, the number of susceptible hosts decreases. Using a similar line of reasoning and considerations, we can express the change in the number of infected ($I(t)$) and recovered ($R(t)$) animals over time as:

$$\frac{dI_a(t)}{dt} = \beta_a S_a(t)\, I_a(t) - \mu_a I_a(t) - \gamma_a I_a(t)$$

$$\frac{dR_a(t)}{dt} = \gamma_a I_a(t) - \mu_a R_a(t)$$

where γ_a represents the recovery rate, per animal per unit time. Detailed descriptions are elsewhere (Diekmann et al., 2013; Hayman et al., 2022; John, Miller, et al., 2024; Keeling & Rohani, 2008; Kermack & McKendrick, 1991).

To model the dynamics of infection in humans we need to consider the fact that human-human interactions may be frequency-dependent. This means that the number of contacts is not influenced by the population size, like density dependent transmission, but rather by social factors and, classically, applied to sexually transmitted infections. The distinction, however, is typically not so clear in reality and transmission is likely a combination of both density and frequency dependent transmission, but this simplification suffices here (Begon et al., 2002; Lloyd-Smith et al., 2004; Luis et al., 2018). The probability of an infected individual transmitting the disease to a susceptible individual is proportional to the number of susceptible individuals, $S_h(t)$ at time *t* and the fraction of the total population that is infected, $\frac{I_h(t)}{N_h(t)}$ (Hayman et al., 2022). This relationship can be expressed as $S_h(t)\,\frac{I_h(t)}{N_h(t)}$. If new infections from within-species (human-to-human) transmission are not possible, this term, $S_h(t)\,\frac{I_h(t)}{N_h(t)}$ can be discarded when calculating the rate of change of the susceptible human population, $\frac{dS_h(t)}{dt}$. On the other hand, the human-animal interaction can be modeled using a density-dependent approach. If ε represents the rate of infection (or transmission rate) from infected animals to susceptible humans, then $\epsilon S_h(t)\,I_a(t)$ represents the number of susceptible humans who will become infected in a unit of time due to between-species (zoonotic) transmission. In this expression, $S_h(t)$ is the number of susceptible humans at time t, and $I_a(t)$ is the number of infected animals at time t. This term captures the impact of zoonotic spillover events on the human population, where the pathogen is transmitted from an animal reservoir to humans. Thus, the change in the number of susceptible human individuals in the population over time is

$$\frac{dS_h(t)}{dt} = \nu_h N_h(t) - \beta_{ah} S_h(t)\,I_a(t) - \mu_h S_h(t)$$

Where β_{ah} represent the rate of infection (or transmission rate) between the animals and people. With similar reasoning and considerations, the change in the number of infected ($I_h(t)$) and recovered ($R_h(t)$) individuals over time can be expressed as:

$$\frac{dI_h(t)}{dt} = \beta_{ah} S_h(t)\,I_a(t) - \mu_h I_h(t) - \gamma_a I_h(t)$$

$$\frac{dR_h(t)}{dt} = \gamma_h I_h(t) - \mu_h R_h(t)$$

for cases where all the human infection is derived from an animal reservoir, that is, the spillover stage. Changes in land use that increase human-animal contacts also impact the likelihood of transmission, altering β_{ah}.

Where there is continued human infection and spillover this then may become:

$$\frac{dS_h(t)}{dt} = \nu_h N_h(t) - \beta_h \frac{S_h(t)\,I_h(t)}{N_h(t)} - \beta_{ah} S_h(t)\,I_a(t) - \mu_h S_h(t)$$

$$\frac{dI_h(t)}{dt} = S_h(t)\left(\beta_h \frac{I_h(t)}{N_h(t)} + \beta_{ah} I_a(t)\right) - \mu_h I_h(t) - \gamma_a I_h(t)$$

$$\frac{dR_h(t)}{dt} = \gamma_h I_h(t) - \mu_h R_h(t)$$

Where β_h represents the rate of infection (or transmission rate) from infected humans to susceptible humans.

A1.2. Vector-Borne Infection

Many diseases are spread by arthropods, known as vectors (Section 2.3). These diseases cannot typically be directly transmitted between people or animals, only through the vector, though again there are exceptions. The spread of vector-borne diseases follows a specific cycle. First, an infected animal or person (the primary host) is bitten by an arthropod vector (a mosquito in our example). The vector then becomes infected with the pathogen, which can be a virus, bacteria, or parasite (Table 1). After a period of time, the infected vector can transmit the pathogen to a new susceptible host when it bites again. This cycle continues, allowing the disease to spread. To model this, we need to introduce additional compartments for the vector population. The compartmental model of vector-borne infection transmission from animals to humans typically involves a system of differential equations. One such equation can represent the rate of change of infected humans over time, which depends on various factors such as the rate of infection from vectors (e.g., mosquitoes) and the recovery rate of infected individuals.

So a simplified differential equation model for malaria transmission, for example, may include the total human population, $H(t)$, split into susceptible humans $S_h(t)$, and infected and infectious humans, $I_h(t)$, and the total mosquito population $V(t)$, which is similarly divided into susceptible mosquitoes, $S_v(t)$, with infectious mosquitoes $I_v(t)$. The model takes the following form:

$$\frac{dI_h(t)}{dt} = ab\frac{I_v(t)}{H(t)}[H(t) - I_h(t)] - \gamma I_h(t)$$

$$\frac{dI_v(t)}{dt} = ac\frac{I_h(t)}{H(t)}[V(t) - I_v(t)] - \mu I_v(t)$$

where

a: Average number of bites on humans by a single mosquito per unit time.
b: Probability of a susceptible human becoming infected by a single bite from an infectious mosquito.
c: Probability of a susceptible mosquito becoming infected by a single bite from an infectious human.
γ: Rate at which infected humans recover from malaria.
μ: Mortality rate of mosquitoes.

The fraction $\frac{I_v(t)}{H(t)}$ in the first equation represents the proportion of infectious mosquitoes relative to the total human population at time t. The number of infectious mosquitoes, $I_h(t)$ is important, but it is more relevant to consider this number in relation to the total human population, $H(t)$ that the mosquitoes can potentially bite and infect. In other words, the transmission of the disease from mosquitoes to humans depends not only on the number of infectious mosquitoes but also on the probability of a mosquito encountering a susceptible human. This probability is higher when there is a larger fraction of infectious mosquitoes relative to the human population size, thus land use changes that favor increases in mosquito infections can increase human infection. The term $[H(t) - I_h(t)]$ represents the number of susceptible humans available for infection.

The fraction $\frac{I_h(t)}{H(t)}$ represents the proportion of infected and infectious humans relative to the total human population at time t. This fraction is used in the above second equation for the rate of change of infected mosquitoes, $\left(\frac{dI_v(t)}{dt}\right)$ to capture the probability that a susceptible mosquito will encounter and bite an infectious human. The transmission of the disease from humans to mosquitoes depends not only on the number of infectious humans $(I_h(t))$ but also on the probability of a mosquito encountering and biting an infectious human during its feeding cycle. By dividing $I_h(t)$ by $H(t)$, the model accounts for the relative abundance of infectious humans compared to the total human population size. And the term $[V(t) - I_v(t)]$ represents the number of susceptible mosquitoes available for infection.

To incorporate more complexity or additional factors into the model, such as the dynamics of the vector population or the effects of interventions like vector control measures, additional equations can be added and the system can be solved using numerical methods (Keeling & Rohani, 2008).

Data Availability Statement

Data availability does not apply to this article, as no new data set was created in this study. All data from all Figures are taken from previously published and freely available data sets. Emerging infectious disease records are retrieved on May 2024 from The EcoHealth Alliance Emerging Infectious Diseases Repository (2025) at https://eidr.ecohealthalliance.org/events. Drivers of deforestation maps are taken on May 2024 from Curtis et al. (2018). Global cropland cover and gain between 2003 and 2019 are taken on May 2024 from Potapov et al. (2022) and available at https://glad.umd.edu/dataset/croplands. The number of land use change events map is taken on May 2024 from Winkler et al. (2021). Global cropland extent from 10000BCE to date is taken on May 2024 from Klein Goldewijk et al. (2017). Global population historical and projection data are taken from the United Nations World Population Prospects (2022) at https://population.un.org/wpp/. Data on changes of population at risk for climate change scenarios in global health regions due to temperature suitability for virus transmission are taken in June 2024 from Ryan et al. (2019).

Acknowledgments
M.C.R. and N.G. were supported by RETURN Extended Partnership, funded by the European Union Next-GenerationEU (National Recovery and Resilience Plan NRRP, Mission 4, Component 2, Investment 1.3 D.D. 1243 2/8/2022, PE0000005). P.D. was funded by the USDA Hatch Multistate project #W5190 capacity fund. D.T.S.H., R.L.M. and R.S.J. were supported by Bryce Carmine and Anne Carmine (née Percival), through the Massey University Foundation. D.T.S.H. was supported by the Percival Carmine Chair in Epidemiology. R.L.M. thanks the Massey University Foundation and the Morris Trust.

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