

REVIEW

Emerging zoonotic diseases originating in mammals: a systematic review of effects of anthropogenic land-use change

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ABSTRACT

1. Zoonotic pathogens and parasites that are transmitted from vertebrates to humans are a major public health risk with high associated global economic costs. The spread of these pathogens and risk of transmission accelerate with recent anthropogenic land-use changes (LUC) such as deforestation, urbanisation, and agricultural intensification, factors that are expected to increase in the future due to human population expansion and increasing demand for resources.
2. We systematically review the literature on anthropogenic LUC and zoonotic diseases, highlighting the most prominent mammalian reservoirs and pathogens, and identifying avenues for future research.
3. The majority of studies were global reviews that did not focus on specific taxa. South America and Asia were the most-studied regions, while the most-studied LUC was urbanisation. Livestock were studied more within the context of agricultural intensification, carnivores with urbanisation and helminths, bats with deforestation and viruses, and primates with habitat fragmentation and protozoa.
4. Research into specific animal reservoirs has improved our understanding of how the spread of zoonotic diseases is affected by LUC. The behaviour of hosts can be altered when their habitats are changed, impacting the pathogens they carry and the probability of disease spreading to humans. Understanding this has enabled the identification of factors that alter the risk of emergence (such as virulence, pathogen diversity, and ease of transmission). Yet, many pathogens and impacts of LUC other than urbanisation have been understudied.
5. Predicting how zoonotic diseases emerge and spread in response to anthropogenic LUC requires more empirical and data synthesis studies that link host ecology and responses with pathogen ecology and disease spread. The link between anthropogenic impacts on the natural environment and the recent COVID-19 pandemic highlights the urgent need to understand how anthropogenic LUC affects the risk of spillover to humans and spread of zoonotic diseases originating in mammals.

INTRODUCTION

Three quarters of emerging human pathogens are zoonotic, that is they are transmitted from other vertebrate animals to humans (Taylor et al. 2001). Zoonoses have a

considerable ecological and socio-economic impact, as well as being a burden on global economies (Cascio et al. 2011). Emerging infectious diseases (EIDs) are newly recognised or reappearing diseases that have been detected

in a population for the first time and are rapidly increasing in prevalence or geographic range (Lederberg et al. 1992). Zoonoses account for nearly two thirds of EIDs, and the majority of zoonoses originate in wild animals (Jones et al. 2008). For new emergences, it is important to identify the source of the outbreak and the epidemiological factors that allow it to spread, but many methods for collecting these data are still under development (DiEuliis et al. 2016). A major scientific challenge in EID research is developing realistic and cost-effective ways to predict, prevent, and respond to outbreaks (Lendak et al. 2017).

The advancement of diseases has been described as "a side effect of the growth of civilisation" (Dobson & Carper 1996), and zoonoses are no exception. Recent unprecedented rates of anthropogenic land-use change (LUC), including urbanisation, agricultural conversion or intensification, deforestation, and habitat fragmentation, have led to run-away loss of natural environments to human development. LUCs that alter the local environment and human-wildlife interactions can be a prominent source of zoonotic diseases because they remove or reduce the natural habitats and home ranges of many species, forcing them to live in closer proximity to humans. This becomes an issue if the species is a host for a zoonotic disease (Jones et al. 2013). Pathogen transmission tends to increase in response to anthropogenic change, but this effect is not universal (Gottdenker et al. 2014).

Although not all zoonotic pathogens are strongly associated with particular types of non-human hosts (Woolhouse & Gowtage-Sequeria 2005), the interactions at the host-pathogen interface are still important for understanding how a disease may spread if populations are affected by anthropogenic LUC. Therefore, it is important to consider the differences between taxa of zoonotic pathogens and hosts, because changes in the dynamics of the interface may be partly responsible for disease emergence (Ko et al. 2009). Mammals are particularly important hosts of zoonotic EIDs. High mammal species richness in combination with anthropogenic LUC in forested tropical areas has been identified as a key predictor of risk of zoonotic disease emergence (Allen et al. 2017). Hence, this review addresses the effects of anthropogenic LUC on the spread of zoonotic diseases, focusing on analysing trends in the literature, identifying key mammalian reservoirs and pathogen taxa, assessing emerging threats, and highlighting avenues for future research.

METHODS

Search terms for the systematic review were identified through pilot searches of 'Web of Science', with initial keywords and phrases 'land-use change', 'zoonotic diseases', and 'emergence' to gain an overview of important topics

covered in the literature. From this, the most important anthropogenic LUCs identified were urbanisation, deforestation, habitat fragmentation, and agricultural intensification, leading to the following search pattern carried out in 'Web of Science' for the years 1970–2019: TOPIC: (*zoonotic diseases OR zoonoses OR rodent-borne diseases OR bat-borne diseases*) AND TOPIC: (*anthropogenic land-use change OR anthropogenic land cover change OR deforestation OR urbanisation OR urbanization OR agricultural intensification OR agriculture expansion OR agriculture conversion OR urban expansion OR urban sprawl OR land conversion OR fragmentation*). The final search was carried out in October 2019.

Of the 357 papers recovered from the final search (Appendix S1), 276 were retained following application of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA; Moher et al. 2009). The decision to reject papers was independently revised by two people. Initially, seven duplicate papers, book chapters, and conference abstracts were omitted. After reading the abstracts of the remaining papers, 74 papers were removed because they did not directly study either anthropogenic LUC (58 papers) or zoonotic diseases (15). These include studies that only mentioned LUC or zoonotic diseases as a potential future problem. Trends in the literature were analysed in the 276 papers that were retained, focusing primarily on a subset of 136 papers that specifically studied mammalian hosts. The following parameters were recorded: publication year, study region(s), study type (review, modelling, and empirical, including observation and experimental studies), host taxa, LUC, pathogen type, and whether or not it was a study of vector-borne disease (in which a vector, such as an insect or tick, transmits the pathogen between hosts; Appendix S2). Chi-square tests were used to identify associations between the different parameters (five tests), and *P* values were adjusted for multiple testing.

RESULTS AND DISCUSSION

General trends in the literature

We compiled a total of 276 studies on zoonotic diseases and anthropogenic LUC, published between 1990 and 2019 (Appendix S2). Of the 276 studies included in the first step of this review, nearly half (136 studies; 49%) were focused on mammals, while 42% were not focused on a specific host taxon. The remaining 9% of studies either were focused on or included birds (12 studies), arthropods (12 studies), or frogs (one study). The first four studies, published 1990–1996, were review papers that did not focus on specific host taxa. The first mammal paper was published in 1997 and was an empirical study (Pavlovic

et al. 1997). Similar to Gottdenker et al. (2014), we found a trend of increased rates of publication with time, which continued in the last seven years. Overall rate of publications increased in 2006 from 1 to 3 papers to > 5 papers, in 2012 to > 18 papers, and in 2017 to > 33 papers per year. Mammal papers followed a similar trend, with the exception of a dip in publications in 2007 and 2011 (Fig. 1). The two major points of increase in publication rates (2012 and 2017) appeared to follow periods of discovery or outbreaks of major zoonotic diseases, such as the discovery of Middle East respiratory syndrome coronavirus in Saudi Arabia (2012) and the major Ebola outbreak in Africa (2014–2016; WHO 2019). However, the increase in number of publications may simply reflect the general increase in scientific publications over that period. Furthermore, like any comparative study, this systematic search may have missed pertinent papers; therefore, results should be considered as a sample of the broader literature.

Nearly a quarter of studies of mammals were global (24%, 33 studies), 20% were carried out in each of South America and Asia, and around 10% in each of Europe, Africa, and North America (Fig. 2a). Significant associations were identified between mammalian hosts and geographic region, whereby carnivores were studied more in Europe, primates in Africa, rodents in North America, and livestock globally ($\chi^2 = 80.08$, d.f. = 25, $P < 0.001$). Of the LUCs, urbanisation was studied more in Europe and agricultural intensification globally ($\chi^2 = 50.1$, d.f. = 15, $P < 0.001$).

The majority of non-host specific studies were reviews (72%, 84 studies), while the majority of studies of mammals were empirical (63%, 85 studies). Only 4% of

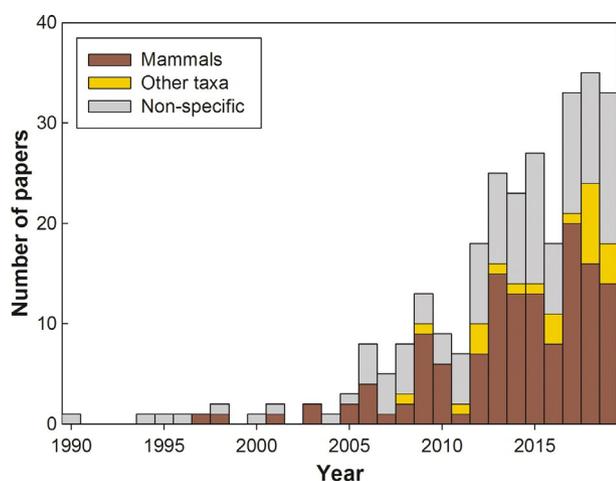


Fig. 1. Increase in the number of publications addressing the effect of anthropogenic land-use change on the spread of zoonotic diseases with time (year of publication), divided into mammal, other taxa (birds, arthropods, and amphibians), and non-specific papers.

overall studies used modelling approaches (5% of studies of mammals). In the mammal dataset, empirical studies were mainly carried out in South America (31%) and Asia (22%), studied rodents (34%), and focused on urbanisation (53%). In contrast, review studies were mostly global (57%), studied livestock (54%), and focused on agricultural intensification (54%; Fig. 3).

Significant associations were identified between LUC categories and mammalian host taxa ($\chi^2 = 98.02$, d.f. = 15, $P < 0.001$; Fig. 4a). Primarily, livestock were studied more within the context of agricultural intensification, but less with urbanisation, while carnivores were studied more with urbanisation, bats with deforestation, and primates with habitat fragmentation. Pathogen taxa were not associated with LUC categories ($\chi^2 = 12.55$, d.f. = 9, $P > 0.05$; Fig. 4b). However, we did find associations between pathogens and mammalian hosts ($\chi^2 = 63.88$, d.f. = 15, $P < 0.001$; Fig. 4c), whereby bats were studied more with viruses, carnivores with helminths, and primates with protozoa.

Most-studied hosts of zoonotic pathogens under land-use change

Different animal hosts can have life-history traits or life cycles that impact disease spread and determine whether the pathogen can overcome the species barrier. It is important to understand both sides of the host–pathogen interface in order to be able to predict spillover to humans, amplification, and spread of zoonotic diseases (Johnson et al. 2015). The most frequently studied mammalian taxon was rodents (36 studies; 27%), closely followed by livestock (34; 25%) and carnivores (33; 24%). The remaining studies focused on non-human primates (18; 13%), bats (13; 10%), and other wild mammals (13; 10%; Fig. 2b). Eleven studies covered more than one mammalian group.

RODENTS

Rodents are important reservoirs of emerging zoonotic viruses because they come into close contact with livestock in the agricultural setting and humans in urban areas (Luis et al. 2013). We found that the main LUC covered in the rodent studies was urbanisation (21 studies; 58%), followed by deforestation (8; 22%). Only two studies covered the impacts of agricultural intensification and three covered habitat fragmentation (Fig. 4a). The main pathogens studied were bacteria (13 studies; 36%) and helminths (7; 19%). Viruses and protozoa were included in three studies each, and fungi and parasites in one. A quarter of rodent studies did not focus on a specific pathogen (Fig. 4c).

Rats have been reported to harbour an expansive range of zoonoses in both developing and developed countries, such as bartonella in *Rattus norvegicus* in Canada

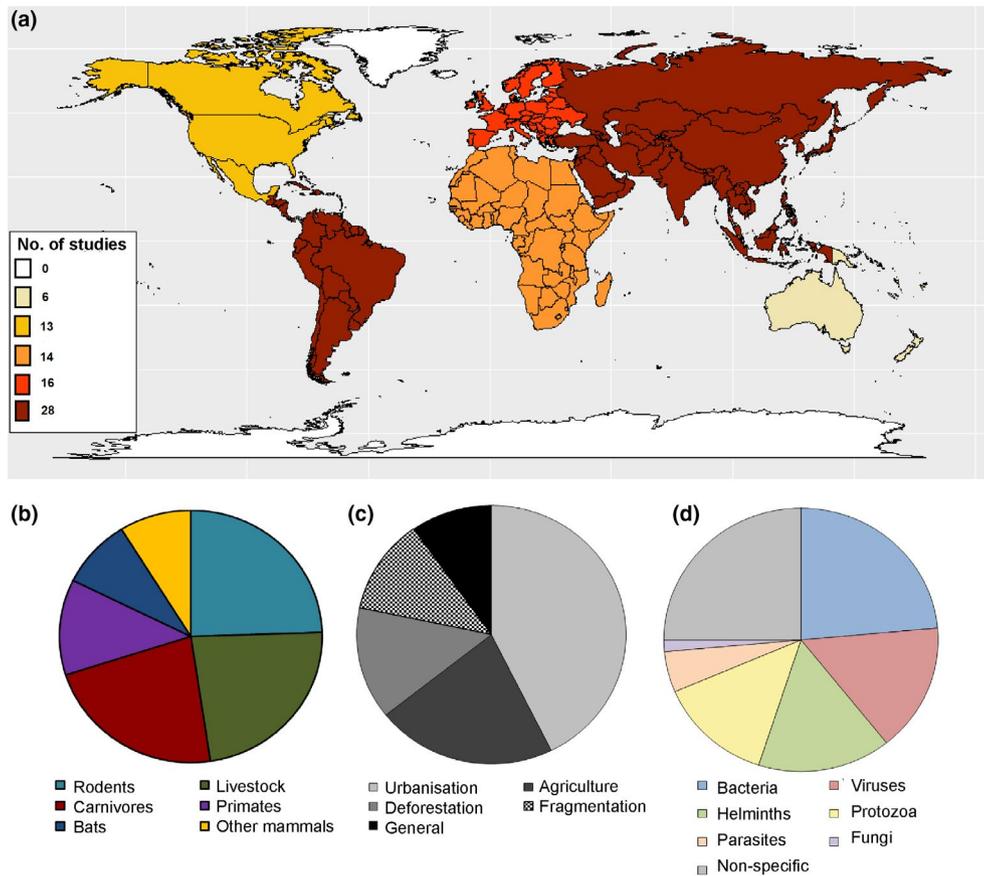


Fig. 2. Trends in the publications on anthropogenic land-use change and mammalian zoonotic diseases: colour-coded numbers of papers per key geographic region (a), overall proportion of papers including different host taxa (b), land-use change categories (c), and pathogens (d).

(Rothenburger et al. 2018), *Leptospira* spp. in Malaysian Borneo (Blasdell et al. 2019), and helminths in Argentina (Hancke & Suarez 2018). Furthermore, *Yersinia pestis* (black plague) circulates at low levels in rodent populations. Deforestation and urbanisation increase the risk of re-emergence of this disease in humans, because these LUCs can result in the emergence of new vectors, expansion of rodent habitats, and modification of population dynamics (Duplantier et al. 2005). Recent studies considering diseases associated with non-*Rattus* rodents include intestinal helminths in Japanese field mice *Apodemus speciosus* (Anders et al. 2019), infections from *Nosopsyllus fasciatus* ticks in mice and voles in Berlin (Maaz et al. 2018), and cutaneous leishmaniasis in the fat sand rat *Psammomys obesus*, and the Libyan jird *Meriones libycus*, in Saudi Arabia (Abuzaid et al. 2017).

LIVESTOCK

Livestock are prevalent zoonotic reservoirs. LUC factors promoting transmission are usually associated with farming

conditions and practices and their demographic consequences (Tomley & Shirley 2009). Of the 34 livestock studies reviewed, 77% covered the impacts of agricultural intensification, and six studies (18%) covered urbanisation (Fig. 4a). The main pathogens covered in livestock studies were bacteria (10 studies; 29%) and viruses (5; 15%); 44% of studies did not cover a specific pathogen. Other pathogens covered were protozoa and parasites (1 study; Fig. 4c).

Bovine leptospirosis was found in 13% of dairy cows in urban and peri-urban Tajikistan, including in areas where large numbers of human and animals co-exist (Rajala et al. 2017). Brucellosis is another emerging threat from cattle, particularly in Africa, and is a prominent issue for developing economies (Ducrottoy et al. 2014). Viral diseases from livestock also pose threats in the developing world, with increased risk of infection potentially associated with deforestation (Bayry 2013). Clark and Soares Magalhães (2018) show that the prevalence of Q fever, caused by a bacterium that attaches to dust and is spread by sheep or goats, is partly associated with urbanisation level and stocking density, which increases greatly when agriculture

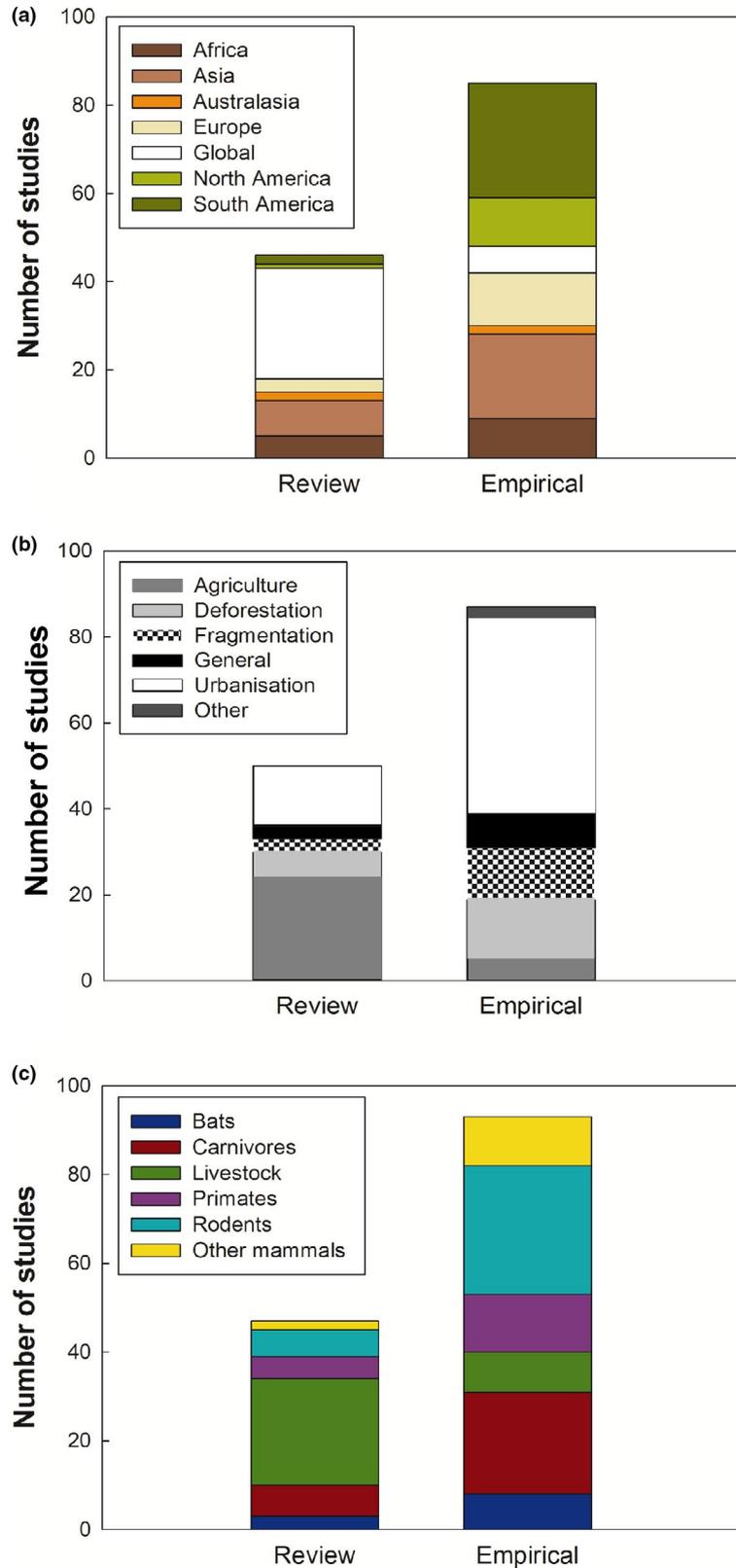


Fig. 3. Number of review papers and empirical studies in the mammalian dataset divided according to geographic regions (a), anthropogenic land-use change categories (b), and mammalian hosts (c).

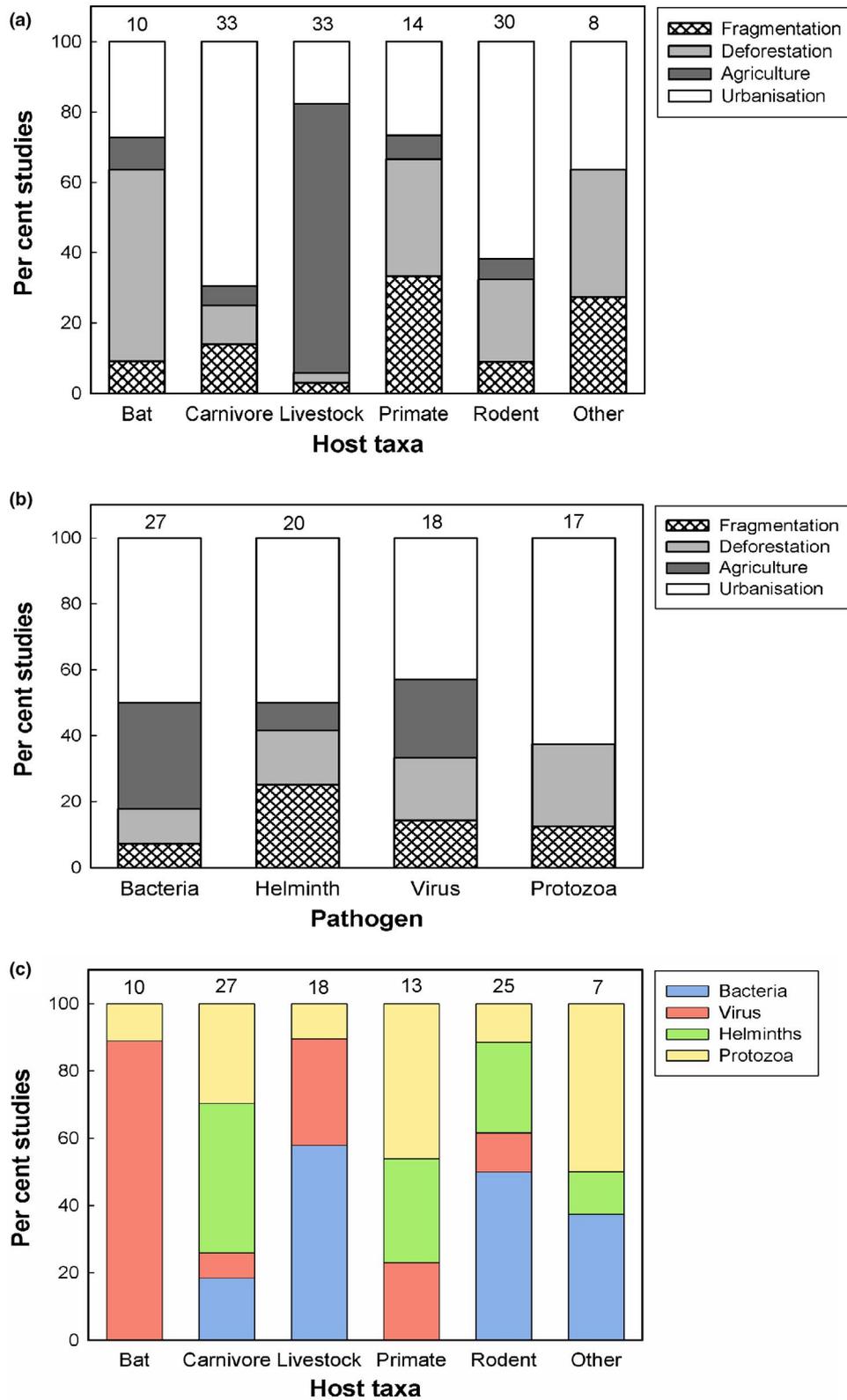


Fig. 4. Associations between mammalian host taxa and land-use change categories (a), pathogens and land-use change categories (b), and mammalian host taxa and pathogens (c), based on the per cent of published studies covering each category. The number of studies included in each category is shown above each bar.

is intensified. There are many zoonoses associated with pigs in Asia, including leptospirosis, *Trichinella*, and hepatitis E virus, and the lack of epidemiological studies into these diseases may allow spread to increase as agriculture becomes more intensive (Okello et al. 2015). Reducing global consumption of animal-based food products is a way to reduce zoonotic disease spread associated with agriculture, as there would be reduced reliance on agricultural intensification. The literature covers the main livestock zoonoses identified by the UK government (HSE 2019); however, epidemiology and surveillance studies of rarer diseases, such as *Erysipeloid* bacterial infection and anthrax, are still lacking.

CARNIVORES

The majority of the 33 carnivore studies included in our review (76%) were focused on impacts of urbanisation. Impacts of deforestation and habitat fragmentation were covered in four studies each, while agricultural intensification featured in only two studies (Fig. 4a). The main pathogens covered in carnivore studies were helminths (12 studies; 36%) and protozoa, primarily *Leishmania* (8; 24%). Bacteria and parasites were covered in three studies each (Fig. 4c). Despite the role of carnivores in transmission of rabies to humans (Abera et al. 2015), only a single study covered viruses.

Zoonotic diseases associated with canines emerge in urbanised areas across the world, caused by, for example, *Echinococcus multilocularis* in medium-sized cities in France (Umhang et al. 2014), *Brucella canis* in urban Argentina (Marzetti et al. 2013), and vector-borne *Ehrlichia* spp. and *Babesia* spp. in Costa Rica (Springer et al. 2019). Dingoes in urban Australia are associated with the transmission of parasitic zoonoses, as they can reach higher population densities in urban areas than in their natural habitats (Mackenstedt et al. 2015). Domestic dogs are prominent reservoirs for visceral leishmaniasis, a disease caused by an obligate intracellular protozoan parasite (de Oliveira et al. 2015). A study investigating leishmaniasis in dogs and other wild mammals in protected areas in Brazil found evidence of outbreak foci becoming established following environmental modifications (Donalisio et al. 2017). Other carnivores associated with zoonotic diseases include genets with *Bartonella* spp. and *Coxiella burnetii* in Spain (Millán et al. 2016), wild and domestic carnivores and Brazilian spotted fever in fragmented forests in São Paulo (Scinachi et al. 2017), and giant pandas and hookworm in urbanised areas in China (Xie et al. 2017). Although some of the studies were focused on parasitic nematodes in specific locations, the immense impact of human activities and politics on zoonotic helminths in carnivores around the globe (Otranto & Deplazes 2019) is under-represented in the literature.

NON-HUMAN PRIMATES

Of the 18 non-human primate studies reviewed, five each looked at impacts of deforestation and habitat fragmentation (27% each) and four at urbanisation (22%; Fig. 4a). The main pathogens covered were protozoa (6 studies; 33%), helminths (4; 22%), and viruses (3; 17%; Fig. 4c). Several viral and parasitic infections can naturally transmit between non-human primates and humans (Parker et al. 2007, Salyer et al. 2012). While parasites of macaque monkeys *Macaca* sp. are a prominent issue, only three papers cover this. Some species have been found to have a higher prevalence of plasmodium hosting as a result of forest fragmentation, including disturbed forest areas and forest edges (Moyes et al. 2016), and habitat fragmentation increases the prevalence of *Oesophagostomum* and *Trichuris* helminth eggs in suburban areas in Japan (Arizono et al. 2012). Other primates associated with LUC and parasites are vervet and proboscis monkeys *Chlorocebus pygerythrus* and *Nasalis larvatus* (Klaus et al. 2017, Thatcher et al. 2018). Viruses spreading in response to LUC were not associated with a particular group of primates, and only dengue fever was specifically covered in the studies (Twiddy et al. 2003, Rey et al. 2010). However, other viruses, including pox, Marburg, and Ebola, can be indirectly transmissible to humans via insect vectors or rodents (Taku et al. 2007), highlighting another gap in the literature.

BATS

Although bats are regarded as important hosts of zoonotic pathogens (e.g. Allocati et al. 2016), only 13 studies so far have addressed the effects of anthropogenic LUC on zoonotic diseases emerging from bats. These studies have mainly been focused on the impacts of deforestation (6 studies; 46%) and to a lesser extent urbanisation (3; 23%; Fig. 4a), and primarily covered viruses (8; 62%). Other pathogens included were protozoa, parasites, and fungi, with one study each (Fig. 4c).

Bats have diverse and unique life-history traits that allow the spread of pathogens, including the ability to migrate long distances and their tendency to aggregate in crowded roosts, which facilitates both intraspecific transmission and interspecific transmission of microbes (Hayman et al. 2012, Luis et al. 2015). Due to their long lifespan and adapted intracellular processes that enable survival of some types of infection (Brook & Dobson 2015), bats are natural reservoir hosts of over 200 viruses, bacteria, and fungi (Allocati et al. 2016). Prevalence of pathogens can be affected by LUC, for example mucocutaneous leishmaniasis and parasites by urbanisation (Shapiro et al. 2013, Nunes et al. 2017) and henipaviruses by deforestation (Field 2009,

Pernet et al. 2014). The risk of henipaviruses emerging from Old World fruit bats increases due to anthropogenic forest disturbance, which results in changes to resource provisioning and behaviour of these hosts (Kessler et al. 2018).

Emergences of bat-borne viruses are challenging to predict in an environment that has been subject to extensive LUC. The high number of pathogens associated with bats, especially bacteria, has not been represented in the reviewed literature, indicating that further studies are required to allow a comprehensive understanding of bats and zoonoses under LUC.

OTHER MAMMALIAN HOSTS

Of the 136 studies of mammals, 13 covered wild mammals other than rodents, carnivores, primates, and bats. Changes in zoonotic bacteria in deer reservoirs have been associated with LUC, such as Lyme disease, *Ehrlichia chaggeensis*, and *Anaplasma phagocytophilum* (Manangan et al. 2007, Millins et al. 2017). Furthermore, grey seals *Halichoerus grypus*, have been associated with *Campylobacter* in Europe (Baily et al. 2015), and pika *Ochotona princeps*, with *Echinococcus multilocularis* in Asia (Marston et al. 2014a).

Studies of vector-borne disease

The full dataset included 47 studies of vector-borne disease, 45% of which did not focus on a specific host, while 28% (13 studies) covered mammals. The studies of mammalian disease covered the impacts of urbanisation (5 studies; 39%) and bacterial pathogens (6; 46%). Swei et al. (2020) found that the majority of emerging vector-borne zoonoses are transmitted by ticks and mosquitoes, and that the most common pathogens are *Rickettsiaceae* bacteria and RNA viruses. Although the driver for an emergence is not always known, these studies indicate LUC is likely to play an important role.

Most-studied pathogens and parasites under land-use change

Understanding how the type of pathogen affects the epidemiology of the zoonotic disease is necessary for the development of treatments and prediction of outbreaks (Morse et al. 2012). To become zoonotic, a pathogen must overcome a hierarchical series of barriers (Plowright et al. 2017) and eventually be able to adapt successfully to fluctuating environments posed by the human immune response (Regoes et al. 2012). It must acquire new characteristics to overcome host species barriers, thus transmitting to and between humans.

The most common pathogens and parasites studied within the context of anthropogenic LUC and mammalian hosts are bacteria (33 studies; 24%), viruses (22; 16%), helminths (22; 16%), and protozoa (20; 15%). A quarter of mammalian studies reviewed (35 studies) did not focus on a specific pathogen (Fig. 2d). While studies of bacteria were distributed relatively evenly across the globe, studies of protozoa were more common in South America (50%) and studies of helminths and viruses in Asia (36% and 27%, respectively). Bacterial pathogens were most commonly studied in rodents (13 studies; 39%) and livestock (11; 33%), viruses in bats (8; 36%), and helminths and protozoa in carnivores (55% and 40% respectively; Fig. 4c). We identified four emerging zoonoses associated with anthropogenic LUC that have received most research attention thus far, possibly due to global concern or public health impacts: the bacteria *Leptospira* causing leptospirosis and *Bartonella* causing bartonellosis, the parasitic tapeworm *Echinococcus*, and the intracellular protozoa *Leishmania* causing leishmaniasis.

BACTERIA

All types of anthropogenic LUCs considered here (i.e. urbanisation, agricultural conversion/intensification, deforestation, and fragmentation) have the potential to increase the risk of an emergence of a bacterial zoonotic disease across the globe. For example, the relative abundance of *Bartonella* in rodents has been correlated with the increasing level of land disturbance and deforestation in Peru (Cortez et al. 2018), risk of brucellosis increases with agricultural intensification (Ducrottoy et al. 2014), and the incidence of *Borrelia* spp. in mammals increases with habitat fragmentation across Europe (Millins et al. 2018). *Borrelia* spp., the cause of Lyme disease, was only studied in three papers, despite its known association with changes in land-use patterns (CDC 2019). *Leptospira*, hosted by rodents and livestock, causes leptospirosis in humans and spreads particularly well in tropical regions (Levett 2001). It has been identified as a worrying emerging zoonotic disease associated with urbanisation (Rajala et al. 2017, Blasdel et al. 2019).

Antibiotic resistance in livestock continues to be a pressing issue worldwide, for example the emergence of methicillin-resistant *Staphylococcus aureus* (MRSA; Mehndiratta & Bhalla 2014). Antibiotics need to be used judiciously (Tilman et al. 2002) to reduce the risk of rapid outbreaks of antibiotic-resistant zoonotic EIDs that could spread extremely quickly. Despite this potentially major global issue, the link between antibiotic resistance and zoonotic disease emergence due to agricultural intensification is not well reported in the literature.

VIRUSES

Viruses can generate *de novo* diversity over a short period due to their ability to mutate rapidly (Duffy et al. 2008). Despite recent technological developments allowing the discovery of novel zoonotic viruses (Marston et al. 2014b), our understanding of how a zoonotic virus emerges and spreads is still incomplete. RNA viruses are particularly likely to emerge as they can adapt quickly to new environmental pressures through rapid replication times and mutation rates (Domingo & Holland 1997). Their risk of emergence can increase under LUC, for example Ross River virus under agricultural intensification (Carver et al. 2009) and SARS coronavirus from bats under several LUCs (Field 2009). However, surveillance is poor, with only a few studies focused on high-risk environments, such as tropical countries. Numerous zoonotic viruses are emerging alongside agricultural intensification in the developing world (Bayry 2013). While some are considered in association with specific hosts, such as Nipah virus with bats and Ross River virus with sheep (Carver et al. 2009, Pulliam et al. 2012), the number of studies in this area is not sufficient to understand the range of potential outbreaks, such as influenza, Hendra, Newcastle disease virus, and more (Bayry 2013).

HELMINTHS

Helminths are parasitic worms that are usually transmitted via food or faeces. Infection is reported all around the world, with a number of papers focusing on urbanisation impacting *Echinococcus multilocularis* spread by carnivores, for example foxes *Vulpes vulpes* in Switzerland (Otero-Abad et al. 2017) and dogs in France (Umhang et al. 2014). A change in landscape dynamics resulting from deforestation was found to affect disease distribution of human alveolar echinococcosis following changes in rodent host distribution (Giraudoux et al. 2003). The strong link between LUC and rodent and carnivore-borne *Echinococcus* infection highlights the need for improved mitigation techniques. In South-East Asia, helminth sharing among rodents becomes harder to contain under conditions of habitat fragmentation due to a less connected and more modular rodent–helminth network (Bordes et al. 2015). Only a few of the studies reviewed were focused on the spread of helminths in South America, where stray dogs often roam freely in urban areas and are known for spreading other zoonotic pathogens, suggesting there may be unreported helminth outbreaks.

PROTOZOA

Instances of zoonotic infections caused by protozoa (obligate intracellular parasites) have been linked with many

types of anthropogenic LUC. Giardiasis is a diarrhoeal disease caused by *Giardia* spp. in the gastrointestinal tract. It has been described as re-emerging, has multiple hosts, and transmission can occur when contact is made with excrement (Thompson 2000). Deforestation has been associated with outbreaks of *Giardia* spp. from many hosts, including livestock, *Coendou villosus*, *Oligoryzomys* sp., *Didelphis aurita*, and *Marmosops incanus* (Lallo et al. 2009).

Leishmania, the protozoan causing leishmaniasis, is hosted by bats and rodents (cutaneous; Shapiro et al. 2013, Abuzaid et al. 2017) or canines (visceral; de Oliveira et al. 2015). Prevalence of visceral vector-borne leishmaniasis was found to increase with urbanisation in Brazil (de Oliveira et al. 2015). Visceral, as opposed to cutaneous infections, can severely affect several organs in humans. The severity of this disease means that surveillance needs to continue as urbanisation increases, to prevent this from becoming a neglected zoonotic disease. An increased risk of infection by plasmodium, the malaria parasite, has been associated with disturbed forests and the presence of non-human primates, such as *Macaca* sp. monkeys (Moyes et al. 2016). This is a particular problem in Malaysian Borneo, where a risk map was developed to visualise land use and assess malaria risk distributions (Sato et al. 2019). Such mapping approaches can help determine the risk factor for vector-spread protozoa under LUC, enabling people to predict and mitigate outbreaks.

Anthropogenic land-use changes

Incursions into wild habitats expose humans to new pathogens if they come into contact with wild animals or hunt, butcher, and consume wild meat (Cantlay et al. 2017). Agricultural land can be used for food-animal production, which brings domestic animals physically closer to other individuals and into frequent contact with humans. If biosecurity methods are not applied, this can impact the rate and pattern of zoonotic disease spread (Jones et al. 2013). Some forms of land use can alter entire ecosystems. Responding to these changes demands fast adaptations of wild animals' foraging strategies and use of space (Jung & Kalko 2010), which often bring wildlife into closer and more frequent contact with humans, thus increasing the chance of pathogen transmission and changing patterns of zoonotic EID spread. Resource provisioning in human-dominated habitats can also affect infection outcomes in wildlife, increasing levels of infection by helminths and viruses (Becker et al. 2015).

The most commonly studied LUC in the mammalian dataset was urbanisation (61 studies; 45%), followed by agricultural intensification (31; 23%), deforestation (20; 15%), and habitat fragmentation (17, 13%; Fig. 2c). Of the remaining studies, 14 discussed LUC in general and

three covered impacts of other LUCs, including woodland expansion (Millins et al. 2017) and watershed development (Walker et al. 2008).

URBANISATION

More than half of the human population inhabits urban settlements, and cities are projected to increase in both size and number as the human population expands (United Nations 2016). This rapid LUC will lead to new challenges for global health and epidemiology of zoonotic EIDs, given evidence of increased transmission in urban-adapted hosts, such as rodents. Urbanisation can provide favourable eco-epidemiological conditions for rodent-borne *Leptospira* spp. that is becoming an emerging risk and a serious threat in urbanised areas in both developing and developed countries (Kurucz et al. 2018, Blasdel et al. 2019). Rats and urbanisation have also been associated with increased spread of bartonella in North America (Peterson et al. 2017, Rothenburger et al. 2018) and leishmaniasis in Borneo and Brazil (Shapiro et al. 2013). Moreover, helminths from foxes are spreading partly as a result of urbanisation in Europe (Pavlovic et al. 1997, Otero-Abad et al. 2017). It remains unclear whether this occurs globally, but it has been reported in other carnivores (Otranto & Deplazes 2019). The 2006 influenza A H1N1 (swine flu) urban pandemic shows just how fast a zoonotic disease can spread and become uncontrollable in the absence of containment provisions (Fasina et al. 2007). This is an example of how outbreaks could be a greater threat in the future, as new megacities could become incubators of zoonotic diseases that will allow them to spread faster and become a worldwide threat (Neiderud 2015). The association between carnivores and zoonotic helminths also increases in urban areas (Field 2009). Bats can form large roosts even in dense urban centres (Hayman et al. 2012), yet only three of the studies reviewed addressed impacts of urbanisation on bat pathogens (Field 2009, Shapiro et al. 2013, Pernet et al. 2014). As bats are important reservoirs for zoonotic diseases (Allocati et al. 2016), it is essential to understand how urbanisation may affect the risk of disease spread.

AGRICULTURAL INTENSIFICATION

The most important infectious human diseases have come into existence since the advent of agriculture, and in particular since the domestication of animals (Carroll et al. 2010). As the human population continues to rise, there will be an increasing dependency on agricultural systems to provide food and other resources. Rapid growth in meat consumption increases the chance of exposing consumers to food-borne pathogens, particularly from chickens and pigs (CIWF 2013, Gilbert et al. 2015). Industrial food

animal production systems increase animal and public health risks as they create diverse wildlife–livestock–human interfaces (Jones et al. 2013, Hassell et al. 2017), increasing the risk of zoonotic emergence as agriculture intensifies. These industrial systems involve keeping a large number of animals confined to a small space in close physical contact, where pathogens can easily be transmitted. Risks are particularly high for large-scale livestock farm workers and neighbouring residents, who can be exposed to harmful bacteria and viruses (Smit & Heederik 2017).

In developed countries, tuberculosis outbreaks are mitigated by strict animal control, elimination programmes and milk pasteurisation, as well as access to veterinary services, which reduces the chances of transmission to humans (Cosivi et al. 1998). However, in Indian dairy farms, it has been found that selling or abandoning infected animals, lack of education about bovine tuberculosis, and only consulting veterinarians as a last resort worsens the problem (Chauhan et al. 2019). As industrial food-animal production becomes increasingly common in developing countries, agricultural intensification is likely to increase the risk of zoonotic disease emergence and spread. Differences in farming practices between countries as a result of culture or income can lead to differences in outbreak patterns, posing challenges for research (Gilbert et al. 2015).

DEFORESTATION AND HABITAT FRAGMENTATION

Deforestation is considered the most immediate contributor to the likelihood of zoonotic disease emergence and spread, as natural forest ecosystems are disrupted through habitat destruction, habitat fragmentation, and conversion into anthropogenic environments (Sehgal 2010). An estimated 1.6 billion people rely on forests for survival (Anonymous 2018), and risks can occur when humans come into contact with wildlife and are exposed to new pathogens. In addition, the formation of forest edges affects the ecology of zoonotic diseases by providing the opportunity for local epidemic expansions (Sharma & Kondrashin 1991).

The purpose of deforestation is often logging activities. The mechanisms of pathogen transmission are complex and differ with logging method. The low contact rate between humans and wildlife during clear-cut logging reduces the chance of zoonotic emergence compared with selective extraction, the favoured method used in Central African logging (Fa et al. 1995). However, regardless of the method, the removal of trees still drastically reshapes the environment, transforming whole ecosystems, and consequently affecting disease emergence and transmission (Taylor 1997). Conversion of forests to agricultural land results in decreased diversity of zoonotic microparasites

and rodent-borne pathogens in South-East Asia; however, the consequent increase in synanthropic rodents favours pathogen spread (Morand et al. 2019). In South America, where deforestation rates are high, there are instances of zoonotic EIDs including microsporidia (Pereira et al. 2009), *Bartonella*, and *Leptospira* (Cortez et al. 2018). However, it is not clear whether microsporidia spores found in wild mammal faeces are always the result of an infection, rather than simply passing through the gastrointestinal tract (Pereira et al. 2009), and the methodology used for *Bartonella* and *Leptospira* identification has limitations (Cortez et al. 2018). Therefore, the prevalence of these zoonoses in areas with deforestation is not yet well understood.

Deforestation has been associated with the increased emergence of pathogens in bats around the world, due to the creation of patches of habitat that isolate or divide populations, alter behaviour, reduce biodiversity, and compromise ecosystem functions (Willig et al. 2019). Viruses of notable concern include henipaviruses in Africa (Pernet et al. 2014), Hendra virus in Australia (Wild 2009), and Nipah virus in Malaysia (Field 2009). Likewise, non-human primates show an increase in zoonotic parasites with fragmentation of forests (Gillespie 2006); parasites include plasmodium (Moyes et al. 2016, Sato et al. 2019) and a range of helminth species (Klaus et al. 2017). In Sri Lanka, habitat fragmentation from deforestation has led to wild animals roaming in nearby neighbourhoods, increasing the exposure of residents to ticks and the risk of tick-borne infections (Liyanaarachchi et al. 2015).

There is further uncertainty about how vector-borne disease emergence will change with forest clearance. Some studies show that the loss of forests may eliminate local vector species (Molyneux 2003), whereas woodland expansion was found to increase suitable habitat for hosts and the tick vectors of Lyme disease, and may therefore increase risk of emergence (Millins et al. 2017). Other researchers warn of a higher risk of infection for people residing near fragmented forests because vector species find new breeding sites by reshaping ecosystem boundaries, which are often points of contact between humans and pathogens (Gottwalt 2015). For example, Brazilian spotted fever, caused by the bacterium *Rickettsia rickettsia* and spread by the tick *Amblyomma cajennense*, is associated with habitat fragmentation and lower abundance and richness of wild vertebrates (Scinachi et al. 2017).

MULTIPLE LAND-USE CHANGES

The spread of some zoonoses has been associated with the impacts of multiple LUCs. The spread of *Bartonella*, the bacterium causing bartonellosis, increases with

deforestation (Cortez et al. 2018, Neves et al. 2018) and urbanisation (Peterson et al. 2017, Rothenburger et al. 2018), and outbreaks associated with these LUCs have been identified in South America, North America, and Asia. Similarly, the prevalence of the helminth *Echinococcus multilocularis* in hosts increases with both deforestation (Giraudoux et al. 2003) and urbanisation (Fischer et al. 2005).

Comparison with previous reviews

A previous review by Gottdenker et al. (2014) covering changes in spread of EIDs under anthropogenic LUC up to the year 2012 identified, similar to our review, agricultural development, urbanisation, and deforestation or habitat fragmentation as key LUCs. Although both reviews identified leishmaniasis and Lyme disease as commonly studied pathogens, our focus on mammals meant that *Echinococcus* and leptospirosis studies were more common than malaria and Chagas disease studies. Our review further considers the region where each study took place, and found differences in study frequency of each pathogen or land-use type between continents. We also consider the host taxon for each paper and find that this changes between pathogen type, LUC type, and region, whereas Gottdenker et al. (2014) only identify whether the pathogen studied was multi-host or single host. Other previous reviews were focused on specific land-use types. For example, Hassell et al. (2017) reviewed the link between urbanisation and disease emergence dynamics at the wildlife–livestock–human interface. They showed that most urban disease transmission studies were focused on a single species and pathogen or on a small number of species and pathogens, which alone may not be suitable for understanding epidemiology. Finally, Han et al. (2016) present a more general review of zoonotic disease in mammals, mapping global patterns of disease risk, identifying rodents, carnivores, and ungulates (especially livestock) as having highest zoonotic potential, and associating carnivores with zoonotic bacteria pathogens, rodents with helminths, and ungulates with protozoa. However, they do not review the link between zoonotic disease spread and anthropogenic LUC, though they do mention the importance of understanding extrinsic pressures that influence disease outbreaks in humans.

Future research needs

Predicting how zoonotic diseases emerge and spread in response to anthropogenic LUC requires a comprehensive understanding of how these changes will influence both the hosts and the pathogens. For each of the identified LUCs, the recognition of patterns and consistency of

emergences require reliable surveillance and an understanding of transmission, but our results show that this information is not yet available for all hosts and pathogens. Multiple pathogens in rodent reservoirs identified by the Centre for Disease Control and Prevention have not been the subject of research, such as Lassa fever (CDC 2017). Similarly, some key zoonoses hosted by bats have been understudied within the context of impacts of LUC, including coronaviruses (only two studies). Rarer diseases in livestock are also missing epidemiology and surveillance data, for example anthrax, and emerging diseases such as Q fever require more attention.

Our results show that it is not fully understood how parasitic nematodes in carnivores are spread globally, particularly in urban environments. In contrast, primate studies predominantly covered infections by nematodes (Arizono et al. 2012, Klaus et al. 2017, Rondon et al. 2017), and less research attention has been given to pathogens such as viruses. In fact, the epidemiology of many zoonotic viruses is yet to be considered in relation to LUC. In addition, studies into both reforestation and habitat fragmentation identified an increased risk of Lyme disease (Millins et al. 2017), suggesting that further investigation is needed into the best way to mitigate outbreaks following deforestation.

Understanding how zoonotic diseases emerge and spread in response to LUC requires adequate identification of the incidence of infection. As noted in the papers collected, appropriate tests to identify infection are not always available. For example, the frequently used test for microsporidia infection, the presence of eggs in faecal matter, is not necessarily indicative of infection (Pereira et al. 2009).

Our review highlights new emerging approaches to the study of effects of LUC on the spread of mammalian zoonotic diseases, such as risk maps developed for malaria (Sato et al. 2019). Similarly, modelling approaches are promising tools for identifying general trends and predicting future consequences, yet we found that they are underutilised.

There is an urgent need for empirical studies that link host ecology and responses to LUC with epidemiology and patterns of disease spread. Although the majority of mammalian studies reviewed were empirical, more than 80% of studies looking at impacts of agriculture, a major driver of LUC, were reviews. Moreover, there is a need for data synthesis studies, such as global-scale meta-analyses or applications of data science methods, to identify whether the different LUCs have consistent impacts, in terms of either the pathogen groups or host taxa studied.

CONCLUSIONS

This systematic review identified key hosts, pathogens, and LUC categories covered in the literature on the effect of

anthropogenic LUC on the spread of mammalian emerging zoonotic diseases, and their geographic distribution and interactions. The studies we reviewed suggest that the direct and knock-on effects of anthropogenic LUC are likely to increase the spread of EIDs. Yet, several gaps in the literature limit our understanding of how zoonotic disease spread and host–pathogen interactions may change in response to LUC. Gaining a more comprehensive understanding of how anthropogenic LUC affects the spread of emerging zoonotic diseases is essential for predicting and mitigating future emergences through fine-tuning surveillance and control measures towards particular locations and reservoirs. The link between anthropogenic impacts on the natural environment and the recent COVID-19 pandemic (Zhang & Holmes 2020) highlights the urgent need to increase understanding of how anthropogenic LUC affects the risk of spillover to humans and spread of zoonotic diseases.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. List of papers obtained from the systematic review search string.

Appendix S2. Data extracted from the papers for analysis.