

1 **REVIEW**

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

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16 **ABSTRACT**

17 **1.** Zoonotic pathogens and parasites that are transmitted from vertebrates to humans are  
18 a major public health risk with high associated global economic costs. The spread of these

19 pathogens and risk of transmission accelerates with recent anthropogenic land-use  
20 changes (LUC) such as deforestation, urbanisation and agricultural intensification, factors  
21 that are expected to increase in the future due to human population expansion and  
22 increasing demand for resources.

23 **2.** We systematically review the literature on anthropogenic LUC and zoonotic diseases,  
24 highlighting the most prominent mammalian reservoirs and pathogens, and identifying  
25 avenues for future research.

26 **3.** The majority of studies were global reviews that did not focus on specific taxa. South  
27 America and Asia were the most-studied regions, while the most-studied LUC was  
28 urbanisation. Livestock were studied more within the context of agricultural intensification,  
29 carnivores with urbanisation and helminths, bats with deforestation and viruses, and  
30 primates with habitat fragmentation and protozoa.

31 **4.** Research into specific animal reservoirs has improved our understanding of how the  
32 spread of zoonotic diseases is affected by LUC. The behaviour of hosts can be altered  
33 when their habitats are changed, impacting the pathogens they carry and the probability  
34 of disease spreading to humans. Understanding this has enabled the identification of  
35 factors that alter the risk of emergence (such as virulence, pathogen diversity and ease  
36 of transmission). Yet, many pathogens and impacts of LUC other than urbanisation have  
37 been under-studied.

38 **5.** Predicting how zoonotic diseases emerge and spread in response to anthropogenic  
39 LUC requires more empirical and data synthesis studies that link host ecology and  
40 responses with pathogen ecology and disease spread. The link between anthropogenic

41 impacts on the natural environment and the recent COVID-19 pandemic highlights the  
42 urgent need to understand how anthropogenic LUC affects the risk of spillover to humans  
43 and spread of zoonotic diseases originating in mammals.

44 **KEYWORDS:** anthropogenic land-use change, deforestation, epidemic, global change,  
45 mammals, urbanisation, zoonotic diseases

46 **Running head:** anthropogenic land use change and zoonotic diseases

## 48 INTRODUCTION

49 Three quarters of emerging human pathogens are zoonotic, i.e. they are transmitted from  
50 other vertebrate animals to humans (Taylor et al. 2001). Zoonoses have a considerable  
51 ecological and socio-economic impact, as well as being a burden on global economies  
52 (Cascio et al. 2011). Emerging infectious diseases (EIDs) are newly recognised or  
53 reappearing diseases that have been detected in a population for the first time and are  
54 rapidly increasing in prevalence or geographic range (Lederberg et al. 1992). Zoonoses  
55 account for nearly two thirds of EIDs, and the majority of zoonoses originate in wild  
56 animals (Jones et al. 2008). For new emergences, it is important to identify the source of  
57 the outbreak and the epidemiological factors that allow it to spread, but many methods  
58 for collecting these data are still under development (DiEuliis et al. 2016). A major  
59 scientific challenge in EID research is developing realistic and cost-effective ways to  
60 predict, prevent and respond to outbreaks (Lendak et al. 2017).

61 The advancement of diseases has been described as “a side effect of the growth of  
62 civilisation” (Dobson & Carper 1996), and zoonoses are no exception. Recent  
63 unprecedented rates of anthropogenic land-use change (LUC), including urbanisation,  
64 agricultural conversion or intensification, deforestation and habitat fragmentation, have  
65 lead to run-away loss of natural environments to human development. LUCs that alter the  
66 local environment and human-wildlife interactions can be a prominent source of zoonotic  
67 diseases because they remove or reduce the natural habitats and home ranges of many  
68 species, forcing them to live in closer proximity to humans. This becomes an issue if the  
69 species is a host for a zoonotic disease (Jones et al. 2013). Pathogen transmission tends

70 to increase in response to anthropogenic change, but this effect is not universal  
71 (Gottdenker et al. 2014).

72 Although not all zoonotic pathogens are strongly associated with particular types of non-  
73 human hosts (Woolhouse & Gowtage-Sequeria 2005), the interactions at the host-  
74 pathogen interface are still important for understanding how a disease may spread if  
75 populations are affected by anthropogenic LUC. Therefore, it is important to consider the  
76 differences between taxa of zoonotic pathogens and hosts because changes in the  
77 dynamics of the interface may be partly responsible for disease emergence (Ko et al.  
78 2009). Mammals are particularly important hosts of zoonotic EIDs. High mammal species  
79 richness in combination with anthropogenic LUC in forested tropical areas have been  
80 identified as key predictors of risk of zoonotic disease emergence (Allen et al. 2017).  
81 Hence, this review addresses the effects of anthropogenic LUC on the spread of zoonotic  
82 diseases, focusing on analysing trends in the literature, identifying key mammalian  
83 reservoirs and pathogen taxa, assessing emerging threats and highlighting avenues for  
84 future research.

## 85 **METHODS**

86 Search terms for the systematic review were identified through pilot searches of 'Web of  
87 Science', with initial keywords and phrases 'land-use change', 'zoonotic diseases', and  
88 'emergence' to gain an overview of important topics covered in the literature. From this,  
89 the most important anthropogenic LUCs identified were urbanisation, deforestation,  
90 habitat fragmentation and agricultural intensification, leading to the following search  
91 pattern carried out in 'Web of Science' for the years 1970-2019: TOPIC: (*zoonotic*

92 *diseases OR zoonoses OR rodent-borne diseases OR bat-borne diseases*) AND TOPIC:  
93 *(anthropogenic land-use change OR anthropogenic land cover change OR deforestation*  
94 *OR urbanisation OR urbanization OR agricultural intensification OR agriculture expansion*  
95 *OR agriculture conversion OR urban expansion OR urban sprawl OR land conversion*  
96 *OR fragmentation)*. The final search was carried out in October 2019.

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

## 113 **RESULTS AND DISCUSSION**

## 114 **General trends in the literature**

115 We compiled a total of 276 studies on zoonotic diseases and anthropogenic LUC,  
116 published between 1990 and 2019 (Appendix S2). Of the 276 studies included in the first  
117 step of this review, nearly half (136 studies; 49%) were focused on mammals, while 42%  
118 were not focused on a specific host taxon. The remaining 9% of studies either were  
119 focused on or included birds (12 studies), arthropods (12 studies) or frogs (one study).  
120 The first four studies, published 1990-1996, were review papers that did not focus on  
121 specific host taxa. The first mammal paper was published in 1997 and was an empirical  
122 study (Pavlovic et al. 1997). Similar to Gottdenker et al. (2014) we found a trend of  
123 increased rates of publication with time, which continued in the last seven years. Overall  
124 rate of publications increased in 2006 from 1-3 papers to >5 papers, in 2012 to >18  
125 papers, and in 2017 to >33 papers per year. Mammal papers followed a similar trend,  
126 with the exception of a dip in publications in 2007 and 2011 (Fig. 1). The two major points  
127 of increase in publication rates (2012 and 2017) appeared to follow periods of discovery  
128 or outbreaks of major zoonotic diseases, such as the discovery of Middle East Respiratory  
129 Syndrome coronavirus in Saudi Arabia (2012) and the major Ebola outbreak in Africa  
130 (2014-2016; WHO 2019). However, the increase in number of publications may simply  
131 reflect the general increase in scientific publications over that period. Furthermore, like  
132 any comparative study, this systematic search may have missed pertinent papers,  
133 therefore results should be considered as a sample of the broader literature.

134 Nearly a quarter of studies of mammals were global (24%, 33 studies), 20% were carried  
135 out in each of South America and Asia, and around 10% in each of Europe, Africa and  
136 North America (Fig. 2a). Significant associations were identified between mammalian

137 hosts and geographic region, whereby carnivores were studied more in Europe, primates  
138 in Africa, rodents in North America and livestock globally ( $\chi^2=80.08$ ,  $df=25$ ,  $P<0.001$ ). Of  
139 the LUCs, urbanisation was studied more in Europe and agricultural intensification  
140 globally ( $\chi^2=50.1$ ,  $df=15$ ,  $P<0.001$ ).

141 The majority of non-host specific studies were reviews (72%, 84 studies), while the  
142 majority of studies of mammals were empirical (63%, 85 studies). Only 4% of overall  
143 studies used modelling approaches (5% of studies of mammals). In the mammal dataset,  
144 empirical studies were mainly carried out in South America (31%) and Asia (22%), studied  
145 rodents (34%), and focused on urbanisation (53%). In contrast, review studies were  
146 mostly global (57%), studied livestock (54%) and focused on agricultural intensification  
147 (54%; Fig. 3).

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

## 156 **Most-studied hosts of zoonotic pathogens under land-use change**

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

## 165 **RODENTS**

166 Rodents are important reservoirs of emerging zoonotic viruses because they come into  
167 close contact with livestock in the agricultural setting and humans in urban areas (Luis et  
168 al. 2013). We found that the main LUC covered in the rodent studies was urbanisation  
169 (21 studies; 58%), followed by deforestation (8; 22%). Only two studies covered the  
170 impacts of agricultural intensification and three covered habitat fragmentation (Fig. 4a).  
171 The main pathogens studied were bacteria (13 studies; 36%) and helminths (7; 19%).  
172 Viruses and protozoa were included in three studies each, and fungi and parasites in one.  
173 A quarter of rodent studies did not focus on a specific pathogen (Fig. 4c).

174 Rats have been reported to harbour an expansive range of zoonoses in both developing  
175 and developed countries, such as bartonella in *Rattus norvegicus* in Canada  
176 (Rothenburger et al. 2018), *Leptospira* spp. in Malaysian Borneo (Blasdell et al. 2019),  
177 and helminths in Argentina (Hancke & Suarez 2018). Furthermore, *Yersinia pestis* (black  
178 plague) circulates at low levels in rodent populations. Deforestation and urbanisation

179 increase risk of re-emergence of this disease in humans, because these LUCs can result  
180 in the emergence of new vectors, expansion of rodent habitats and modification of  
181 population dynamics (Duplantier et al. 2005). Recent studies considering diseases  
182 associated with non-*Rattus* rodents include intestinal helminths in Japanese field mice,  
183 *Apodemus speciosus* (Anders et al. 2019), infections from *Nosopsyllus fasciatus* ticks in  
184 mice and voles in Berlin (Maaz et al. 2018), and cutaneous leishmaniasis in fat sand rat,  
185 *Psammomys obesus*, and Libyan jird, *Meriones libycus*, in Saudi Arabia (Abuzaid et al.  
186 2017).

## 187 **LIVESTOCK**

188 Livestock are prevalent zoonotic reservoirs. LUC factors promoting transmission are  
189 usually associated with farming conditions and practices and their demographic  
190 consequences (Tomley & Shirley 2009). Of the 34 livestock studies reviewed, 77%  
191 covered the impacts of agricultural intensification, and six studies (18%) covered  
192 urbanisation (Fig. 4a). The main pathogens covered in livestock studies were bacteria (10  
193 studies; 29%) and viruses (5; 15%); 44% of studies did not cover a specific pathogen.  
194 Other pathogens covered were protozoa and parasites (1 study; Fig. 4c).

195 Bovine leptospirosis was found in 13% of dairy cows in urban and peri-urban Tajikistan,  
196 including in areas where large numbers of human and animals coexist (Rajala et al. 2017).  
197 Brucellosis is another emerging threat from cattle, particularly in Africa, and is a prominent  
198 issue for developing economies (Ducrottoy et al. 2014). Viral diseases from livestock also  
199 pose threats in the developing world, with increased risk of infection potentially associated  
200 with deforestation (Bayry 2013). Clark and Soares Magalhães (2018) show that the

201 prevalence of Q fever, caused by a bacterium that attaches to dust and is spread by  
202 sheep or goats, is partly associated with urbanisation level and stocking density, which  
203 increases greatly when agriculture is intensified. There are many zoonoses associated  
204 with pigs in Asia, including leptospirosis, *Trichinella* and hepatitis E virus, and the lack of  
205 epidemiological studies into these diseases may allow spread to increase as agriculture  
206 becomes more intensive (Okello et al. 2015). Reducing global consumption of animal-  
207 based food products is a way to reduce zoonotic disease spread associated with  
208 agriculture, as there would be reduced reliance on agricultural intensification. The  
209 literature covers the main livestock zoonoses identified by the UK government (HSE  
210 2019); however, epidemiology and surveillance studies of rarer diseases, such as  
211 *Erysipeloid* bacterial infection and anthrax, are still lacking.

## 212 **CARNIVORES**

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

220 Zoonotic diseases associated with canines emerge in urbanised areas across the world,  
221 caused by, for example, *Echinococcus multilocularis* in medium-sized cities in France  
222 (Umhang et al. 2014), *Brucella canis* in urban Argentina (Marzetti et al. 2013), and vector-

223 borne *Ehrlichia* spp. and *Babesia* spp. in Costa Rica (Springer et al. 2019). Dingoes in  
224 urban Australia are associated with the transmission of parasitic zoonoses, as they can  
225 reach higher population densities in urban areas than in their natural habitats  
226 (Mackenstedt et al. 2015). Domestic dogs are prominent reservoirs for visceral  
227 leishmaniasis, a disease caused by an obligate intracellular protozoal parasite (de  
228 Oliveira et al. 2015). A study investigating leishmaniasis in dogs and other wild mammals  
229 in protected areas in Brazil found evidence of outbreak foci becoming established  
230 following environmental modifications (Donalisio et al. 2017). Other carnivores associated  
231 with zoonotic diseases include genets with *Bartonella* spp. and *Coxiella burnetii* in Spain  
232 (Millán et al. 2016), wild and domestic carnivores and Brazilian spotted fever in  
233 fragmented forests in São Paulo (Scinachi et al. 2017), and giant pandas and hookworm  
234 in urbanised areas in China (Xie et al. 2017). Although some of the studies were focused  
235 on parasitic nematodes in specific locations, the immense impact of human activities and  
236 politics on zoonotic helminths in carnivores around the globe (Otranto & Deplazes 2019)  
237 is underrepresented in the literature.

## 238 **NON-HUMAN PRIMATES**

239 Of the 18 non-human primate studies reviewed, five each looked at impacts of  
240 deforestation and habitat fragmentation (27% each) and four at urbanisation (22%; Fig.  
241 4a). The main pathogens covered were protozoa (6 studies; 33%), helminths (4; 22%)  
242 and viruses (3; 17%; Fig. 4c). Several viral and parasitic infections can naturally transmit  
243 between non-human primates and humans (Parker et al. 2007, Salyer et al. 2012). While  
244 parasites of macaque monkeys, *Macaca sp.*, are a prominent issue, only three papers  
245 cover this. Some species have been found to have a higher prevalence of plasmodium

246 hosting as a result of forest fragmentation, including disturbed forest areas and forest  
247 edges (Moyes et al. 2016), and habitat fragmentation increases the prevalence of  
248 *Oesophagostomum* and *Trichuris* helminth eggs in suburban areas in Japan (Arizono et  
249 al. 2012). Other primates associated with LUC and parasites are vervet and proboscis  
250 monkeys, *Chlorocebus pygerythrus* and *Nasalis larvatus* (Klaus et al. 2017, Thatcher et  
251 al. 2018). Viruses spreading in response to LUC were not associated with a particular  
252 group of primates, and only dengue fever was specifically covered in the studies (Twiddy  
253 et al. 2003, Rey et al. 2010). However, other viruses, including pox, Marburg and Ebola,  
254 can be indirectly transmissible to humans via insect vectors or rodents (Taku et al. 2007),  
255 highlighting another gap in the literature.

## 256 **BATS**

257 Although bats are regarded as important hosts of zoonotic pathogens (e.g. Allocati et al.  
258 2016), only 13 studies so far have addressed the effects of anthropogenic LUC on  
259 zoonotic diseases emerging from bats. These studies have mainly been focused on the  
260 impacts of deforestation (6 studies; 46%) and to a lesser extent urbanisation (3; 23%; Fig.  
261 4a), and primarily covered viruses (8; 62%). Other pathogens included were protozoa,  
262 parasites and fungi, with one study each (Fig. 4c).

263 Bats have diverse and unique life history traits that allow the spread of pathogens,  
264 including the ability to migrate long distances and their tendency to aggregate in crowded  
265 roosts, which facilitates both intraspecific and interspecific transmission of microbes  
266 (Hayman et al. 2012, Luis et al. 2015). Due to their long lifespan and adapted intracellular  
267 processes that enable survival of some types of infection (Brook & Dobson 2015), bats

268 are natural reservoir hosts of over 200 viruses, bacteria and fungi (Allocati et al. 2016).  
269 Prevalence of pathogens can be affected by LUC, for example, mucocutaneous  
270 leishmaniasis and parasites by urbanisation (Shapiro et al. 2013, Nunes et al. 2017) and  
271 henipaviruses by deforestation (Field 2009, Pernet et al. 2014). The risk of henipaviruses  
272 emerging from Old World fruit bats increases due to anthropogenic forest disturbance,  
273 which results in changes to resource provisioning and behaviour of these hosts (Kessler  
274 et al. 2018).

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

## 280 **OTHER MAMMALIAN HOSTS**

281 Of the 136 studies of mammals, 13 covered wild mammals other than rodents, carnivores,  
282 primates, and bats. Changes in zoonotic bacteria in deer reservoirs have been associated  
283 with LUC, such as Lyme borreliosis, *Ehrlichia chaggeensis* and *Anaplasma*  
284 *phagocytophilum* (Manangan et al. 2007, Millins et al. 2017). Furthermore, grey seals,  
285 *Halichoerus grypus*, have been associated with *Campylobacter* in Europe (Baily et al.  
286 2015), and pika, *Ochotona princeps*, with *Echinococcus multilocularis* in Asia (Marston et  
287 al. 2014a).

## 288 **Studies of vector-borne disease**

289 The full dataset included 47 studies of vector-borne disease, 45% of which did not focus  
290 on a specific host, while 28% (13 studies) covered mammals. The studies of mammalian  
291 disease covered the impacts of urbanisation (5 studies; 39%) and bacterial pathogens (6;  
292 46%). Swei et al. (2020) found that the majority of emerging vector-borne zoonoses are  
293 transmitted by ticks and mosquitoes, and that the most common pathogens are  
294 *Rickettsiaceae* bacteria and RNA viruses. Although the driver for an emergence is not  
295 always known, these studies indicate LUC is likely to play an important role.

### 296 **Most-studied pathogens and parasites under land-use change**

297 Understanding how the type of pathogen affects the epidemiology of the zoonotic disease  
298 is necessary for the development of treatments and prediction of outbreaks (Morse et al.  
299 2012). To become zoonotic, a pathogen must overcome a hierarchal series of barriers  
300 (Plowright et al. 2017) and eventually be able to adapt successfully to fluctuating  
301 environments posed by the human immune response (Regoes et al. 2012). It must  
302 acquire new characteristics to overcome host species barriers, thus transmitting to and  
303 between humans.

304 The most common pathogens and parasites studied within the context of anthropogenic  
305 LUC and mammalian hosts are bacteria (33 studies; 24%), viruses (22; 16%), helminths  
306 (22; 16%) and protozoa (20; 15%). A quarter of mammalian studies reviewed (35 studies)  
307 did not focus on a specific pathogen (Fig. 2d). Whilst studies of bacteria were distributed  
308 relatively evenly across the globe, studies of protozoa were more common in South  
309 America (50%) and studies of helminths and viruses in Asia (36% and 27%, respectively).  
310 Bacterial pathogens were most commonly studied in rodents (13 studies; 39%) and

311 livestock (11; 33%), viruses in bats (8; 36%), and helminths and protozoa in carnivores  
312 (55% and 40%, respectively; Fig. 4c). We identified four emerging zoonoses associated  
313 with anthropogenic LUC that have received most research attention thus far, possibly due  
314 to global concern or public health impacts: the bacteria *Leptospira* causing leptospirosis  
315 and *Bartonella* causing bartonellosis, the parasitic tapeworm *Echinococcus*, and the  
316 intracellular protozoa *Leishmania* causing leishmaniasis.

### 317 BACTERIA

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

330 Antibiotic resistance in livestock continues to be a pressing issue worldwide, e.g. the  
331 emergence of methicillin-resistant *Staphylococcus aureus* (MRSA; Mehndiratta & Bhalla  
332 2014). Antibiotics need to be used judiciously (Tilman et al. 2002) to reduce the risk of

333 rapid outbreaks of antibiotic-resistant zoonotic EIDs that could spread extremely quickly.  
334 Despite this potentially major global issue, the link between antibiotic resistance and  
335 zoonotic disease emergence due to agricultural intensification is not well reported in the  
336 literature.

### 337 **VIRUSES**

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

### 353 **HELMINTHS**

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

### 368 **PROTOZOA**

369 Instances of zoonotic infections caused by protozoa (obligate intracellular parasites) have  
370 been linked with many types of anthropogenic LUC. Giardiasis is a diarrhoeal disease  
371 caused by *Giardia* spp. in the gastrointestinal tract. It has been described as re-emerging,  
372 has multiple hosts, and transmission can occur when contact is made with excrement  
373 (Thompson 2000). Deforestation has been associated with outbreaks of *Giardia* spp. from  
374 many hosts, including livestock, *Coendou villosus*, *Oligoryzomys* sp., *Didelphis aurita* and  
375 *Marmosops incanus* (Lallo et al. 2009).

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

### 389 **Anthropogenic land-use changes**

390 Incursions into wild habitats expose humans to new pathogens if they come into contact  
391 with wild animals or hunt, butcher and consume wild meat (Cantlay et al. 2017).  
392 Agricultural land can be used for food animal production, which brings domestic animals  
393 physically closer to other individuals and into frequent contact with humans. If biosecurity  
394 methods are not applied, this can impact the rate and pattern of zoonotic disease spread  
395 (Jones et al. 2013). Some forms of land-use can alter entire ecosystems. Responding to  
396 these changes demands fast adaptations of wild animals' foraging strategies and use of  
397 space (Jung & Kalko 2010), which often bring wildlife into closer and more frequent

398 contact with humans, thus increasing the chance of pathogen transmission and changing  
399 patterns of zoonotic EID spread. Resource provisioning in human-dominated habitats can  
400 also affect infection outcomes in wildlife, increasing levels of infection by helminths and  
401 viruses (Becker et al. 2015).

402 The most commonly studied LUC in the mammalian dataset was urbanisation (61 studies;  
403 45%), followed by agricultural intensification (31; 23%), deforestation (20; 15%) and  
404 habitat fragmentation (17, 13%; Fig. 2c). Of the remaining studies, 14 discussed LUC in  
405 general and three covered impacts of other LUCs, including woodland expansion (Millins  
406 et al. 2017) and watershed development (Walker et al. 2008).

#### 407 **URBANISATION**

408 More than half of the human population inhabits urban settlements, and cities are  
409 projected to increase in both size and number as the human population expands (United  
410 Nations 2016). This rapid LUC will lead to new challenges for global health and  
411 epidemiology of zoonotic EIDs, given evidence of increased transmission in urban-  
412 adapted hosts, such as rodents. Urbanisation can provide favourable eco-epidemiological  
413 conditions for rodent-borne *Leptospira* spp. that is becoming an emerging risk and a  
414 serious threat in urbanised areas in both developing and developed countries (Kurucz et  
415 al. 2018, Blasdell et al. 2019). Rats and urbanisation have also been associated with  
416 increased spread of bartonella in North America (Peterson et al. 2017, Rothenburger et  
417 al. 2018), and leishmaniasis in Borneo and Brazil (Shapiro et al. 2013). Moreover,  
418 helminths from foxes are spreading partly as a result of urbanisation in Europe (Pavloic  
419 et al. 1997, Otero-Abad et al. 2017). It remains unclear if this occurs globally, but it has  
420 been reported in other carnivores (Otranto & Deplazes 2019). The 2006 influenza A H1N1

421 (swine flu) urban pandemic shows just how fast a zoonotic disease can spread and  
422 become uncontrollable in the absence of containment provisions (Fasina et al. 2007).  
423 This is an example of how outbreaks could be a greater threat in the future, as new  
424 megacities could become incubators of zoonotic diseases that will allow them to spread  
425 faster and become a worldwide threat (Neiderud 2015). The association between  
426 carnivores and zoonotic helminths also increases in urban areas (Field 2009). Bats can  
427 form large roosts even in dense urban centres (Hayman et al. 2012), yet only three of the  
428 studies reviewed addressed impacts of urbanisation on bat pathogens (Field 2009,  
429 Shapiro et al. 2013, Pernet et al. 2014). As bats are important reservoirs for zoonotic  
430 diseases (Allocati et al. 2016), it is essential to understand how urbanisation may affect  
431 the risk of disease spread.

#### 432 **AGRICULTURAL INTENSIFICATION**

433 The most important infectious human diseases have come into existence since the advent  
434 of agriculture, and in particular since the domestication of animals (Carroll et al. 2010).  
435 As the human population continues to rise, there will be an increasing dependency on  
436 agricultural systems to provide food and other resources. Rapid growth in meat  
437 consumption increases the chance of exposing consumers to food-borne pathogens,  
438 particularly from chickens and pigs (CIWF 2013, Gilbert et al. 2015). Industrial food animal  
439 production systems increase animal and public health risks as they create diverse  
440 wildlife–livestock–human interfaces (Jones et al. 2013, Hassell et al. 2017), increasing  
441 the risk of zoonotic emergence as agriculture intensifies. These industrial systems involve  
442 keeping a large number of animals confined to a small space in close physical contact,

443 where pathogens can easily be transmitted. Risks are particularly high for large-scale  
444 livestock farm workers and neighbouring residents, who can be exposed to harmful  
445 bacteria and viruses (Smit & Heederik 2017).

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

#### 456 **DEFORESTATION AND HABITAT FRAGMENTATION**

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

465 The purpose of deforestation is often logging activities. The mechanisms of pathogen  
466 transmission are complex and differ with logging method. The low contact rate between  
467 humans and wildlife during clear-cut logging reduces the chance of zoonotic emergence  
468 compared with selective extraction, the favoured method used in Central African logging  
469 (Fa et al. 1995). However, regardless of the method, the removal of trees still drastically  
470 reshapes the environment, transforming whole ecosystems, and consequently affecting  
471 disease emergence and transmission (Taylor 1997). Conversion of forests to agricultural  
472 land results in decreased diversity of zoonotic microparasites and rodent-borne  
473 pathogens in Southeast Asia; however, the consequent increase of synanthropic rodents  
474 favours pathogen spread (Morand et al. 2019). In South America, where deforestation  
475 rates are high, there are instances of zoonotic EIDs including microsporidia (Pereira et al.  
476 2009), *Bartonella*, and *Leptospira* (Cortez et al. 2018). However, it is not clear if  
477 microsporidia spores found in wild mammal faeces are always the result of an infection,  
478 rather than simply passing through the gastrointestinal tract (Pereira et al. 2009), and the  
479 methodology used for *Bartonella* and *Leptospira* identification has limitations (Cortez et  
480 al. 2018). Therefore, the prevalence of these zoonoses in areas with deforestation is not  
481 yet well understood.

482 Deforestation has been associated with the increased emergence of pathogens in bats  
483 around the world, due to the creation of patches of habitat that isolate or divide  
484 populations, alter behaviour, reduce biodiversity and compromise ecosystem functions  
485 (Willig et al. 2019). Viruses of notable concern include henipaviruses in Africa (Pernet et  
486 al. 2014), Hendra virus in Australia (Wild 2009), and Nipah virus in Malaysia (Field 2009).  
487 Likewise, non-human primates show an increase in zoonotic parasites with fragmentation

488 of forests (Gillespie 2006); parasites include plasmodium (Moyes et al. 2016, Sato et al.  
489 2019) and a range of helminth species (Klaus et al. 2017). In Sri Lanka, habitat  
490 fragmentation from deforestation has led to wild animals roaming in nearby  
491 neighbourhoods, increasing the exposure of residents to ticks and the risk of tick-borne  
492 infections (Liyanaarachchi et al. 2015).

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

#### 504 **MULTIPLE LAND-USE CHANGES**

505 The spread of some zoonoses has been associated with the impacts of multiple LUCs.  
506 The spread of *Bartonella*, the bacterium causing bartonellosis, increases with  
507 deforestation (Coretz et al. 2018, Neves et al. 2018) and urbanisation (Peterson et al.  
508 2017, Rothenburger et al. 2018), and outbreaks associated with these LUCs have been  
509 identified in South America, North America, and Asia. Similarly, the prevalence of the

510 helminth *Echinococcus multilocularis* in hosts increases with both deforestation  
511 (Giraudoux et al. 2003) and urbanisation (Fischer et al. 2005).

## 512 **Comparison with previous reviews**

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

532 helminths and ungulates with protozoa. However, they do not review the link between  
533 zoonotic disease spread and anthropogenic LUC, though they do mention the importance  
534 of understanding extrinsic pressures that influence disease outbreaks in humans.

### 535 **Future research needs**

536 Predicting how zoonotic diseases emerge and spread in response to anthropogenic LUC  
537 requires a comprehensive understanding of how these changes will influence both the  
538 hosts and the pathogens. For each of the identified LUCs, the recognition of patterns and  
539 consistency of emergences require reliable surveillance and an understanding of  
540 transmission, but our results show that this information is not yet available for all hosts  
541 and pathogens. Multiple pathogens in rodent reservoirs identified by the Centre for  
542 Disease Control and Prevention have not been the subject of research, such as Lassa  
543 fever (CDC 2017). Similarly, some key zoonoses hosted by bats have been understudied  
544 within the context of impacts of LUC, including coronaviruses (only two studies). Rarer  
545 diseases in livestock are also missing epidemiology and surveillance data, e.g. anthrax,  
546 and emerging diseases such as Q fever require more attention.

547 Our results show that it is not fully understood how parasitic nematodes in carnivores are  
548 spread globally, particularly in urban environments. In contrast, primate studies  
549 predominantly covered infections by nematodes (Arizono et al. 2012, Klaus et al. 2017,  
550 Rondon et al. 2017), and less research attention has been given to pathogens such as  
551 viruses. In fact, the epidemiology of many zoonotic viruses is yet to be considered in  
552 relation to LUC. In addition, studies into both reforestation and habitat fragmentation

553 identified an increased risk of Lyme disease (Millins et al. 2017), suggesting that further  
554 investigation is needed into the best way to mitigate outbreaks following deforestation.

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

560 Our review highlights new emerging approaches to the study of effects of LUC on the  
561 spread of mammalian zoonotic diseases, like risk maps developed for malaria (Stato et  
562 al. 2018). Similarly, modelling approaches are promising tools for identifying general  
563 trends and predicting future consequences, yet we found that they are under-utilised.

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

## 571 **CONCLUSIONS**

572 This systematic review identified key hosts, pathogens and LUC categories covered in  
573 the literature on the effect of anthropogenic LUC on the spread of mammalian emerging  
574 zoonotic diseases, and their geographic distribution and interactions. The studies we  
575 reviewed suggest that the direct and knock-on effects of anthropogenic LUC are likely to  
576 increase the spread of EIDs. Yet several gaps in the literature limit our understanding of  
577 how zoonotic disease spread and host-pathogen interactions may change in response to  
578 LUC. Gaining a more comprehensive understanding of how anthropogenic LUC affects  
579 the spread of emerging zoonotic diseases is essential for predicting and mitigating future  
580 emergences through fine-tuning surveillance and control measures towards particular  
581 locations and reservoirs. The link between anthropogenic impacts on the natural  
582 environment and the recent COVID-19 pandemic (Zhang & Holmes 2020) highlights the  
583 urgent need to increase understanding of how anthropogenic LUC affects the risk of  
584 spillover to humans and spread of zoonotic diseases.

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- 929

930 **Figure legends**

931

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

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

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

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

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948 **SUPPORTING INFORMATION**

949

950 Additional supporting information may be found in the online version of this article at the  
951 publisher's website.

952

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

954 **Appendix S2.** Data extracted from the papers for analysis.

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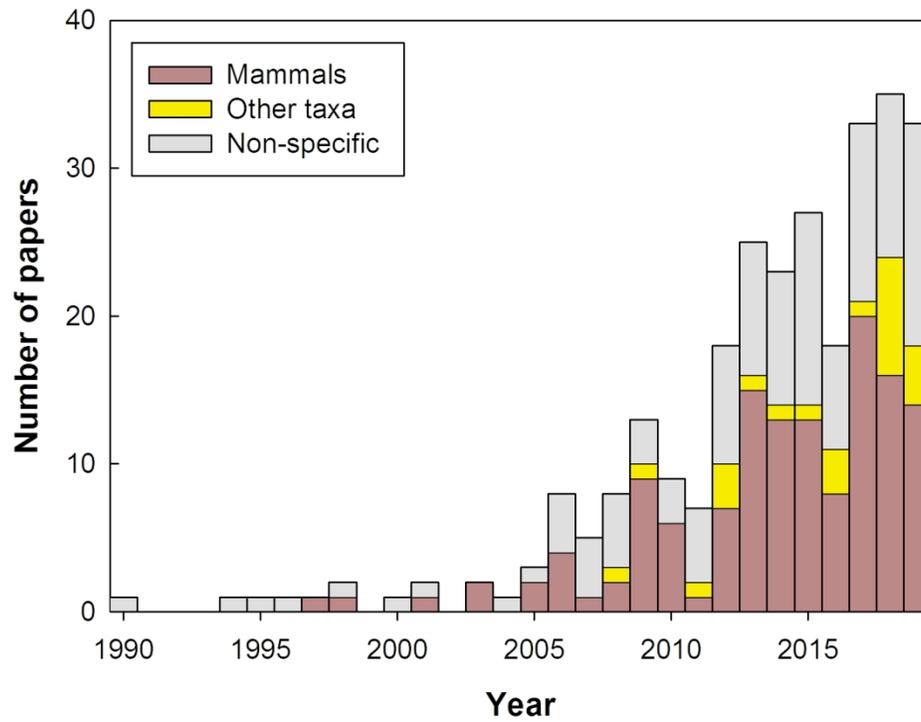


Fig. 1 - Increase in the number of publications addressing the effect of anthropogenic land-use change on the spread of zoonotic diseases with time, divided into mammal, other taxa (birds, arthropods and amphibians) and non-specific papers.

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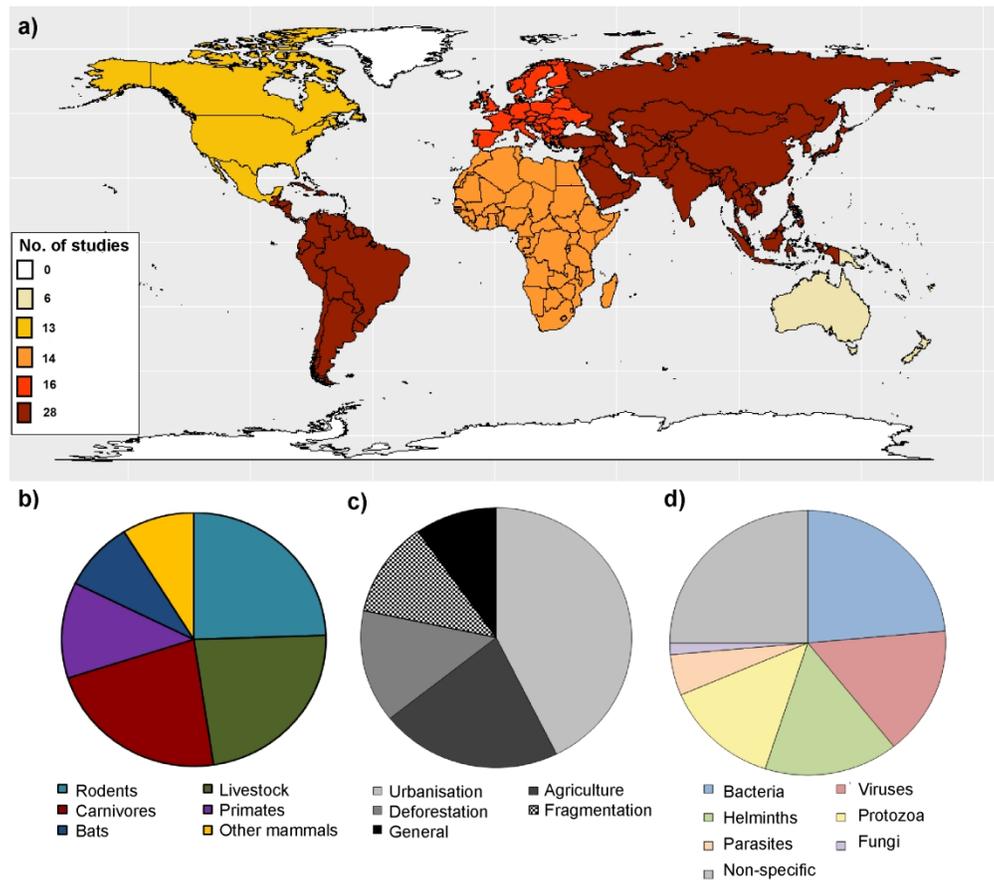


Fig. 2 - Trends in the publications on anthropogenic land-use change and mammalian zoonotic diseases: colour-coded number of papers per key geographic regions (a); overall proportion of papers including different host taxa (b), land-use change categories (c), and pathogens (d).

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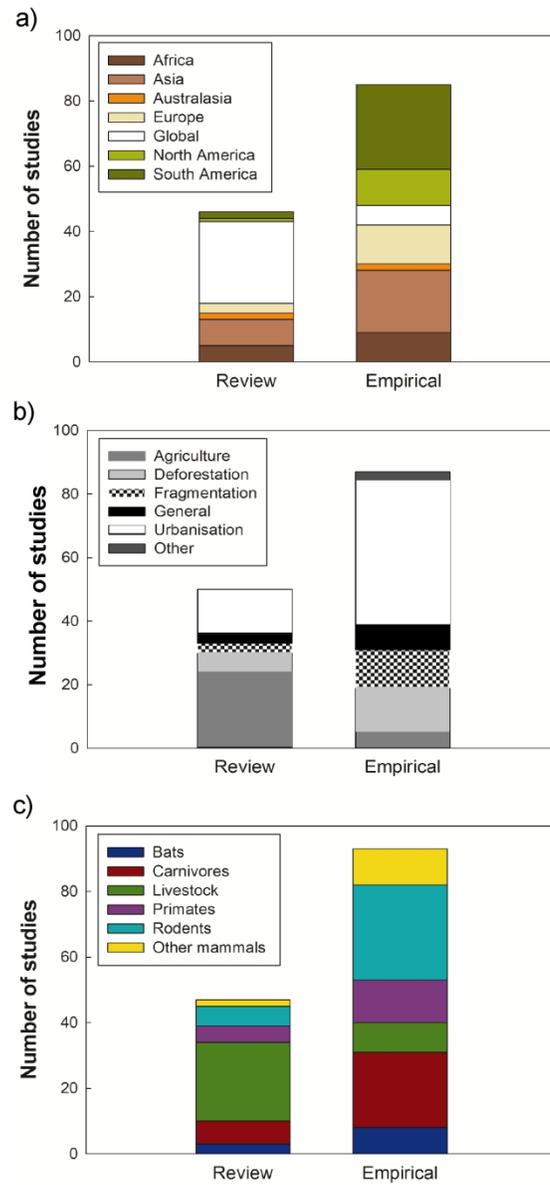


Fig. 3 - Number of papers in review versus empirical studies in the mammalian dataset divided according to geographic regions (a), anthropogenic land-use change categories (b), and mammalian hosts (c).

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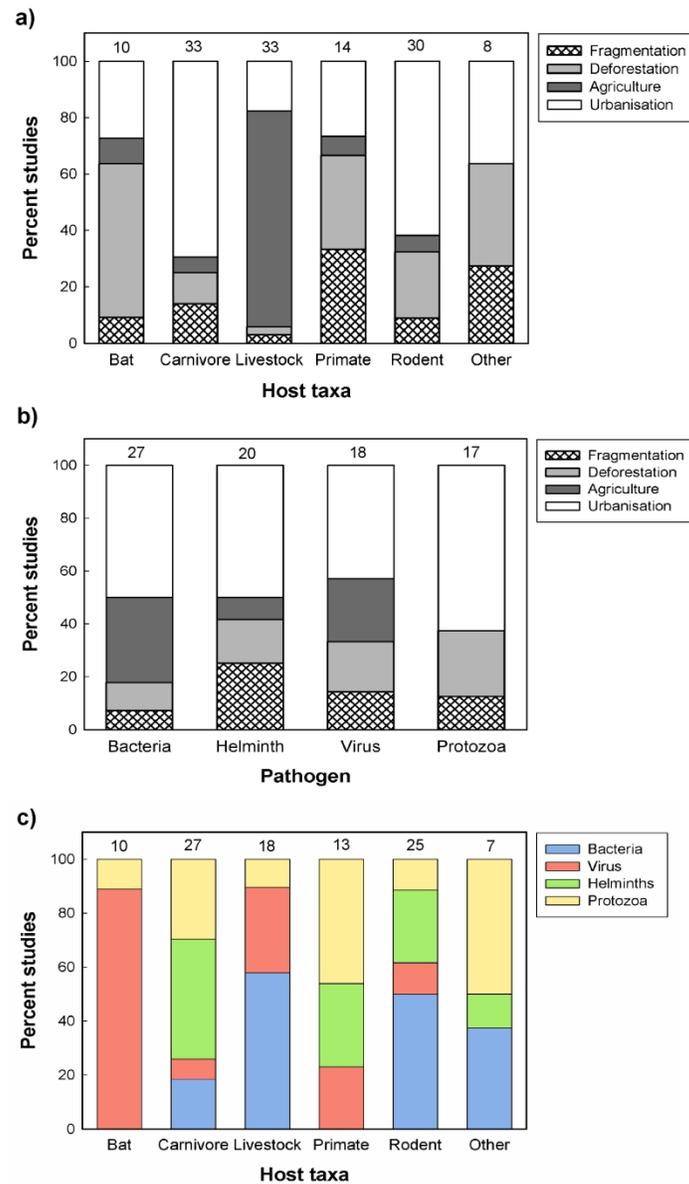


Fig. 4 - Associations between mammalian hosts and land-use change categories (a), pathogens and land-use change categories (b), and mammalian hosts and pathogens (c) based on the percent of published studies covering each category. Number of studies included in each category is presented above the bars.

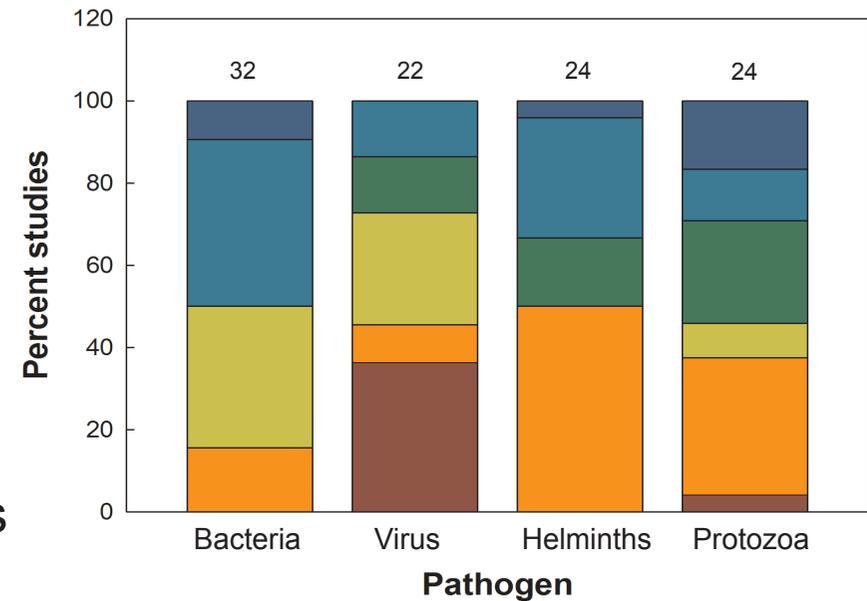
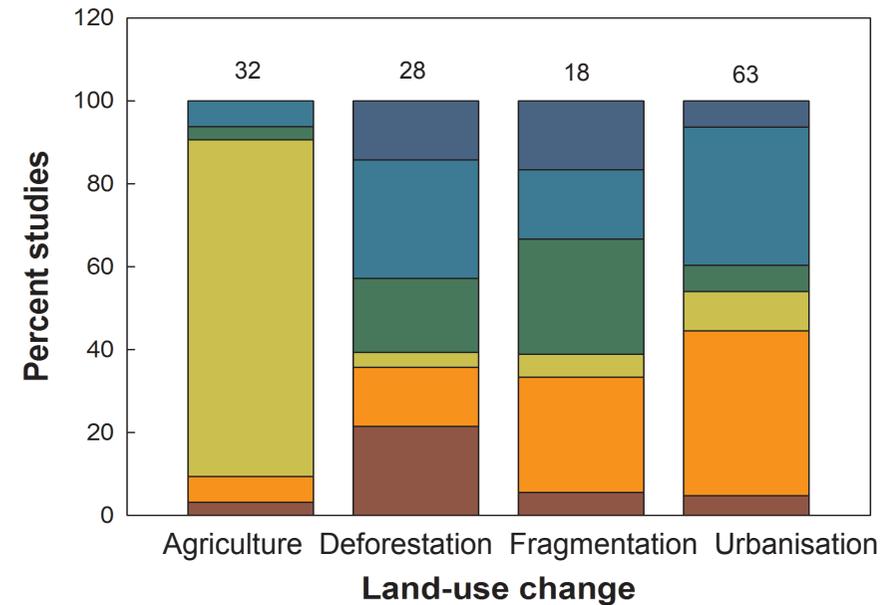
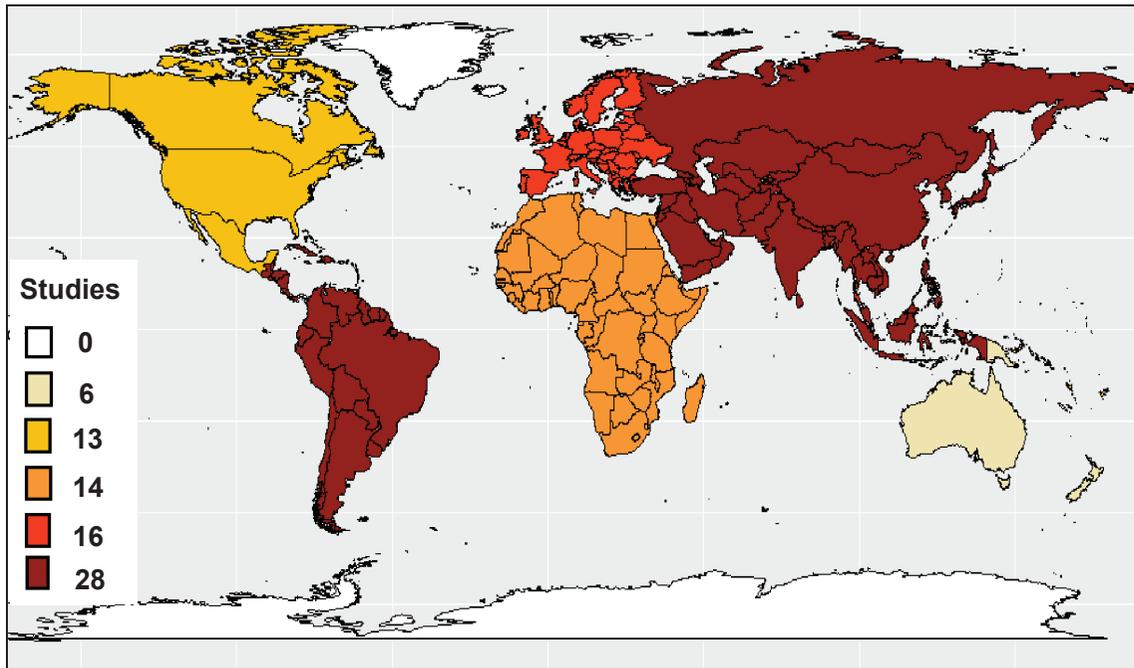
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Cover Image: Forest clearance for intensive agriculture in highland regions of Peninsular Malaysia. Photo credit: Connor Butler

1399x787mm (72 x 72 DPI)

# What do we know about the effects of anthropogenic land-use change on the spread of mammalian zoonotic diseases?



- Systematic review of 137 studies.
- Key hosts, like bats, are under-studied.
- Urbanisation most studied, effects of agricultural intensification beyond livestock under-studied.
- Need for studies linking host ecology and responses with pathogen ecology and disease spread.