Review

SARS-CoV-2 infection in animals: Patterns, transmission routes, and drivers

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A B S T R A C T

The severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) is more widespread in animals than previously thought, and it may be able to infect a wider range of domestic and wild species. To effectively control the spread of the virus and protect animal health, it is crucial to understand the cross-species transmission mechanisms and risk factors of SARS-CoV-2. This article collects published literature on SARS-CoV-2 in animals and examines the distribution, transmission routes, biophysical, and anthropogenic drivers of infected animals. The reported cases of infection in animals are mainly concentrated in South America, North America, and Europe, and species affected include lions, white-tailed deer, pangolins, minks, and cats. Biophysical factors influencing infection of animals with SARS-CoV-2 include environmental determinants, high-risk landscapes, air quality, and susceptibility of different animal species, while anthropogenic factors comprise human behavior, intensive livestock farming, animal markets, and land management. Due to current research gaps and surveillance capacity shortcomings, future mitigation strategies need to be designed from a One Health perspective, with research focused on key regions with significant data gaps in Asia and Africa to understand the drivers, pathways, and spatiotemporal dynamics of interspecies transmission.

1. Introduction

Since December 2019, the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) has emerged as a global pandemic [1], leading to around 676 million confirmed human cases and over 6.9 million deaths worldwide as of March 10, 2023 [2]. The initial outbreak was reported at the Huanan Seafood Market in Wuhan, China [3], where wild animals traded in the market were suspected to be responsible for the initial infection and subsequent spread of SARS-CoV-2 [4].

The origin of SARS-CoV-2 remains unknown, but current evidence suggests that it may have evolved from animal hosts such as bats [5,6] and pangolins [7], both of which are natural reservoirs for SARS-CoV-2-like coronaviruses. A meta-transcriptomic study identified several SARS-CoV-2-associated and SARS-CoV-associated viruses in 411 bat samples collected from Yunnan Province, China [8]. The bat-CoV RaTG13 was found to share 96% genomic similarity with SARS-CoV-2,

while the pangolin-CoV was detected with 91.02% and 90.55% genomic similarity to SARS-CoV-2 and bat-CoV RaTG13, respectively [9, 10]. The receptor binding domain of the pangolin virus protein has five essential amino acids identical to those of SARS-CoV-2, which could make pangolins susceptible to intermediate hosts in the evolution of the virus [11]. Molecular epidemiological studies suggest that the emergence of SARS-CoV-2 was likely the result of multiple zoonotic spillover events [12]. However, little is known about the spatiotemporal pattern and underlying factors of animal outbreaks of SARS-CoV-2 before the pandemic.

There is increasing evidence of transmission of SARS-CoV-2 between humans and animals. Cases of infection have been reported in various domestic and wild species such as lions [13], white-tailed deer [14], pangolins [15], minks [16], and cats [17]. A mink-adapted SARS-CoV-2 variant virus was found in a high-density mink farm in Denmark, leading to zoonotic spillover [18]. Infected hamsters in a pet store in Hong Kong

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transmitted the pathogen to the store staff [19], highlighting the potential for animal–human transmission. As the virus continues to circulate in animals, it is difficult to predict how potential mutations might emerge and what evolutionary changes they might lead to.

The announcement of the end of the SARS-CoV-2 pandemic may have been premature, as the Omicron variant is highly transmissible yet causes milder symptoms [20]. While this may suggest a potentially stable and predictable pattern of transmission, some experts disagree, pointing to Omicron's greater mutability and lower lethality than previous strains [21]. They suggest that the virus may persist as a public health threat for decades to come, necessitating continued vaccination efforts for future generations due to its potential to infect animals and mutate further. Moreover, even if the virus were eliminated in human populations, SARS-CoV-2 could continue to pose a risk to human health and domestic and wild animals through hidden reservoirs in wildlife [22]. Therefore, continued research is crucial for understanding the transmission and evolution of the virus, developing effective public health measures, and safeguarding against potential animal-to-human spillovers.

Taking a One Health approach to combat SARS-CoV-2 requires a comprehensive framework that incorporates an understanding of the socio-ecological processes driving the epidemic pattern and synergistic strategies to promote population, animal, and environmental health. Thanks to improved scientific communication and data sharing, researchers can now monitor the real-time progression of SARS-CoV-2 in human populations [5]. However, a more thorough comprehension of the establishment of SARS-CoV-2 in animals and the factors contributing to pathogen transmission between humans and animals is still needed. This study reviews the current literature on animal infections with SARS-CoV-2 to gather the latest evidence on both biophysical and anthropogenic drivers of disease emergence, identify gaps in current knowledge, and explore potential management strategies from a One Health perspective. The results of this review can provide policy makers with decision support for developing guiding policies that manage the risk of SARS-CoV-2 outbreaks in animals.

2. Method

A systematic review was conducted using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses framework (Fig. 1).

They searched the Web of Science core databases, EmBase, and PubMed for papers published between December 2019 and December 2022 using the search terms ("SARS-CoV-2" [Title/Keywords/Abstract/]) AND ("animal" [Title/Keywords/Abstract/]). During the screening phase, two groups of reviewers screened the abstracts in parallel, and disagreements about inclusion were resolved through consensus. Clinical trials of SARS-CoV-2 treatment drugs or viral genetic sequencing analysis were excluded. To gather spatial data on animal outbreaks, the review team downloaded all animal SARS-CoV-2 situation reports from the World Organization for Animal Health (WOAH) up to August 2022, which contained information on animal species, location, and the date of diagnosis (Table S1).

The initial search yielded 7,621 abstracts, with 2,567 duplicates, leaving 5,054 articles for screening. Among these, 4,584 papers were excluded due to a lack of relevance. Information on 388 animal infection records was collected from WOAH reports (Table 1). In total, 485 studies were selected from the databases, and were classified according to

Table 1
Reported animal infections with SARS-CoV-2 worldwide based on WOAH reports.

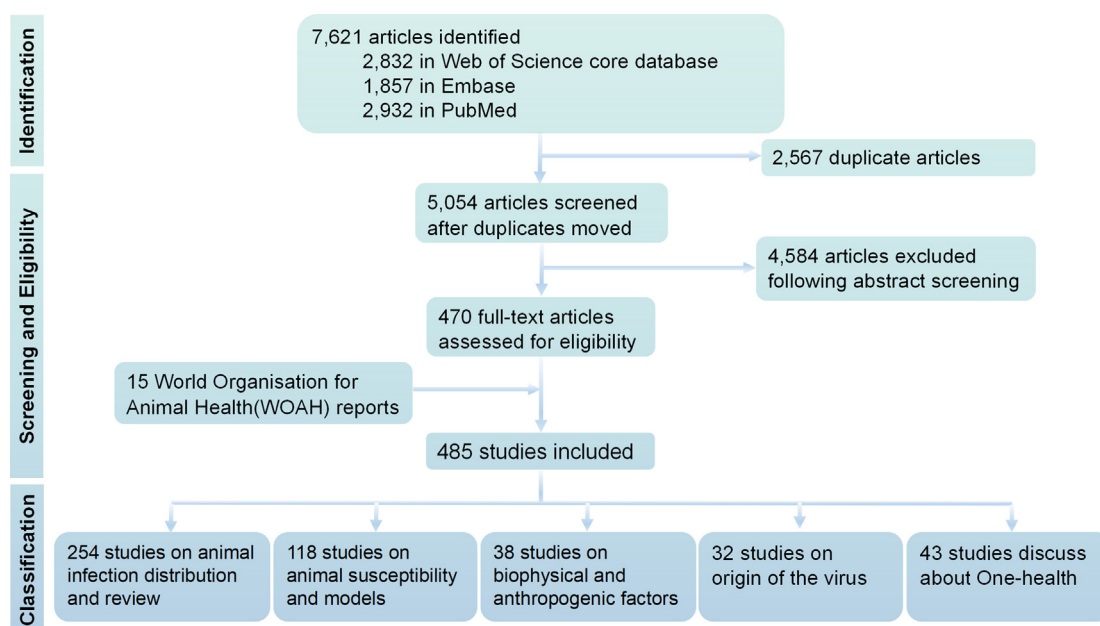| Country/region	Species number	Sum cases	Animals (no of cases)
Greece	3	15,640	Cat (2), Mink (12), Mustelidae (15,626)
Netherlands	1	9,013	Mink (9,013)
Lithuania	2	543	Mink (538), Mustelidae (5)
Canada	4	284	Cat (3), Dog (1), Mustelidae (253), White-Tailed deer (27)
United States of America	14	171	Binturongs (1), Canadian lynxes (1), Cat (47), Dog (29), Gorilla (13), Lion (22), Mustelidae (1), Otter (6), Puma (1), Snow Leopards (10), South American Coatis (1), Spotted Hyenas (2), Tiger (28), White-Tailed deer (8)
Spain	4	143	Cat (2), Gorilla (5), Lion (4), Mink (132)
Brazil	2	38	Cat (17), Dog (21)
Switzerland	2	34	Cat (23), Dog (11)
Hong Kong, China	3	29	Cat (9), Cricetidae (11), Dog (9)
Argentina	4	27	Cat (6), Dog (19), Puma (1), Tiger (1)
Italy	3	23	Cat (1), Mink (2), Mustelidae (20)

Fig. 1. Flow diagram of review steps.

research methodology, including animal infection distribution and review, animal susceptibility and models, biophysical and human factors, viral origin, and One Health global recommendations. The findings were synthesized narratively, focusing on the distribution of infected animals, susceptible animals, and environmental factors.

3. Results and discussion

3.1. On the global distribution of the SARS-CoV-2 virus in animals

According to the review, the first cases of SARS-CoV-2 infection in animals were reported in early 2020, and both companion animals and their owners have been diagnosed with COVID-19. In Hong Kong, a 17-year-old Pomeranian and a two-year-old German shepherd dog were diagnosed positive between February and March 2020 [23,24]. In Belgium, the first case of SARS-CoV-2 infection in domestic cats was reported in March 2020 [25]. The cat showed symptoms of respiratory and digestive dysfunction, and PCR results confirmed the presence of viral RNA in the cat's feces and vomit. The cat was suspected to have contracted the virus from its owner, who had traveled to northern Italy. Another early case of infection in a cat was reported in Hong Kong in late March, but the cat did not show any signs of the disease.

The SARS-CoV-2 transmission events have not only been limited to domestic animals but also include wild animals. At the Bronx Zoo in New York, several felines tested positive for the virus, including two Malayan tigers, two Amur tigers, and three African lions. All of them experienced mild respiratory symptoms and recovered after a week. It was believed that the source of infection could be the infected zoo staffs [13]. SARS-CoV-2 was also detected in small-clawed otters at an aquarium in Georgia, USA, and antibodies to SARS-CoV-2 were found in serum samples taken from white-tailed deer in four US states [26]. Multiple wildlife species have been infected with SARS-CoV-2, and the virus continues to expand its host range. While the current cases of animal infection are sporadic, their numbers continue to rise. Symptoms following infection with the novel coronavirus vary among species. For instance, infected beavers in Mongolia exhibited symptoms such as coughing and runny noses. Ferrets with infections have displayed signs like fever and diminished appetite. In contrast, white-tailed deer that tested positive in the United States showed no signs of illness.

The WOAH's animal outbreak reports (until August 2022) show that cases of animal infections are mainly concentrated in South America, North America, and Europe (Fig. 2). The US reported the most diverse cases, with 171 cases across 14 species. Greece has reported the most cases involving 3 species (cat, mink, and mustelidae), and a total of 15,626 infected animals have been reported in mustelidae. The Netherlands reported 9,013 infected minks, while Lithuania reported 538 cases in minks and 5 cases in mustelidae. In Asia, China reported the most cases of animal infections, covering cats, dogs, and hamsters, with a total of 29 cases. However, the review notes that although other regions have not reported data to the WOAH, this does not necessarily mean that animal infections are absent in those regions.

Our review highlights that the high prevalence and wide geographic distribution of SARS-CoV-2 in the human population increases the chances of the virus encountering new host species and spreading across species. To prevent spillover infections between species, it is important to have a comprehensive understanding of the viral reservoir, transmission modes, viral evolution, and pathogenic mechanisms. Domestic and wild animals are currently affected by infections, but it remains unknown whether virus variants are more commonly found in wild animals. Further research is necessary to determine the zoonotic potential and likelihood of cross-species transmission between wild and domestic animals.

3.2. Possible transmission routes leading to animal infection

In most cases, transmission of SARS-CoV-2 to animals is suspected to occur through direct contact with infected humans or asymptomatic carriers [13]. Laboratory experiments have indicated that the virus can be transmitted to animals through airborne droplets. Cats are susceptible to airborne infection, and infected cats may transmit the virus to healthy cats living together through respiratory droplets or airborne routes [17]. However, there is no evidence of fecal-oral, blood, vertical, or other transmission routes between humans and animals. An investigation of dog and cat infections on mink breeding farms showed some evidence of cross-species transmission among animals [27]. The source of infection in the dogs remains uncertain, but the cat samples yielded whole-genome sequences clustered with sequences from minks on the same farm. Infected cats and dogs on farms may pose a spillover risk to humans. While most infected cats and ferrets are asymptomatic, the illness is still contagious and can act as a silent source of transmission at the human–animal interface [28].
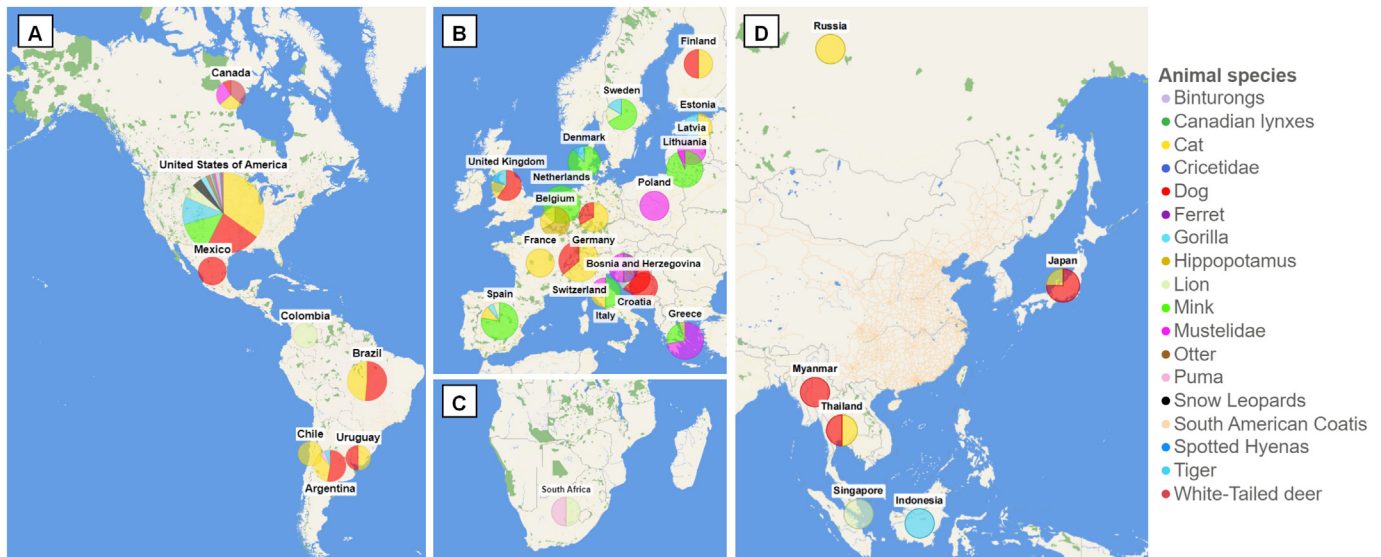

Fig. 2. Global distribution of SARS-CoV-2 infection in animals according to the World Organization for Animal Health. SARS-CoV-2, severe acute respiratory syndrome coronavirus 2.

Another potential route for transmission of SARS-CoV-2 to animals is through contact with contaminated surfaces and objects (Fig. 3). The primary route of transmission appears to be by coughing or sneezing and contact with saliva or other bodily secretions. The persistence of the virus on surfaces may increase the likelihood of transmission, and the virus can survive for up to 72 h on plastic and stainless steel [29]. While it is possible for pets to become infected through contact with contaminated surfaces, it is challenging to directly infect animals through simple touch since their hair can attract and trap the virus. There have been cases of American minks in Eastern Spain occasionally infected by the virus found in wastewaters [30]. A recent hypothesis suggests that SARS-CoV-2 may spread along a natural host–environmental agent–human pathway [31]. The widespread infection among humans poses a risk to animal species that interact with humans, and the potential for cross-species transmission could lead to the emergence of harmful recombinant SARS-CoV-2 strains. Therefore, more epidemiological and genetic studies are needed to investigate the variation and find ways to slow and eventually eradicate transmission within and between species.

3.3. Biophysical factors determining pathogen survival and dynamics

Biophysical factors, such as environmental conditions, can affect the population dynamics of zoonotic pathogens and their host animals, thus impacting the risk of pathogen transmission (Fig. 4). Research examining the relationship between these factors and pathogen ecology may aid in reducing public health risks through landscape management, planning, and design. However, among the studies reviewed, only 7.84% (38 of 485) highlighted the impact of biophysical factors on SARS-CoV-2 infection in animals.

3.3.1. Environmental determinants of viral survival and transmission

SARS-CoV-2 can persist in water, soil, and air, with a potential to cause animal infections. Previous studies have suggested a link between environmental factors such as temperature, humidity, ultraviolet rays, and air quality and human cases of SARS-CoV-2 [32]. Higher temperatures appear to be effective in suppressing the spread of the virus, and

there is a higher risk of indoor airborne transmission in dry environments with 40% relative humidity than humid environments with >90% humidity [33]. Solar irradiance can also limit the spread of SARS-CoV-2, with fewer cases reported in regions with higher temperatures and stronger solar radiation [34]. While the number of cases exhibits a weakly positive correlation with barometric pressure, precipitation, diurnal temperature, sulfur dioxide, and ozone [35], wind speed is rarely significantly associated with the number of infected people, with exceptions such as decreased numbers during intense windy days [36,37].

Coronaviruses have limited ability to migrate from soil to other environments, but can survive in soil due to its high water content and low temperature [38]. High relative humidity above 6 °C can hinder the transmission of HCoV 229E and HCoV OC43, which have similar properties to SARS-CoV-2 [39]. Acidic soils can also inactivate SARS-CoV-2 due to the unfolding of its nucleocapsid proteins at around pH 5.0 and denaturation at pH 2.7. However, the transmission capacity of the virus in different soils has not been demonstrated due to the difficulty and lack of data on SARS-CoV-2 occurrence in soil. The potential risk of virus transmission in soil highlights the need for a better understanding of the types of soil that receive sewage and the plants that grow there [40].

The SARS-CoV-2 virus survives longer in environments with lower temperatures and lower relative humidity. There is a moderate negative correlation between the number of virus multiplications and temperatures above 25 °C [41]. Cold, dry climates in temperate regions of the world may promote the spread of the virus, suggesting seasonality in virus transmission [29]. Low temperatures and dryness can weaken the human immune system and increase the stability of viral molecules, promoting virus transmission and respiratory infection [35]. Short-term exposure to air pollutants, such as $PM_{2.5}$, PM_{10}, and nitrogen dioxide, has been positively correlated with newly confirmed cases during the pandemic [42]. However, changes in weather or air pollution alone are not enough to sustain the spread of SARS-CoV-2.

The survival of SARS-CoV-2 in water can also promote zoonotic transmission. SARS-CoV-2 RNA has been detected in wastewater in Australia and the USA [43]. A study conducted in a hot spring park in Uruguay found SARS-CoV-2 in 13% of the studied samples, which
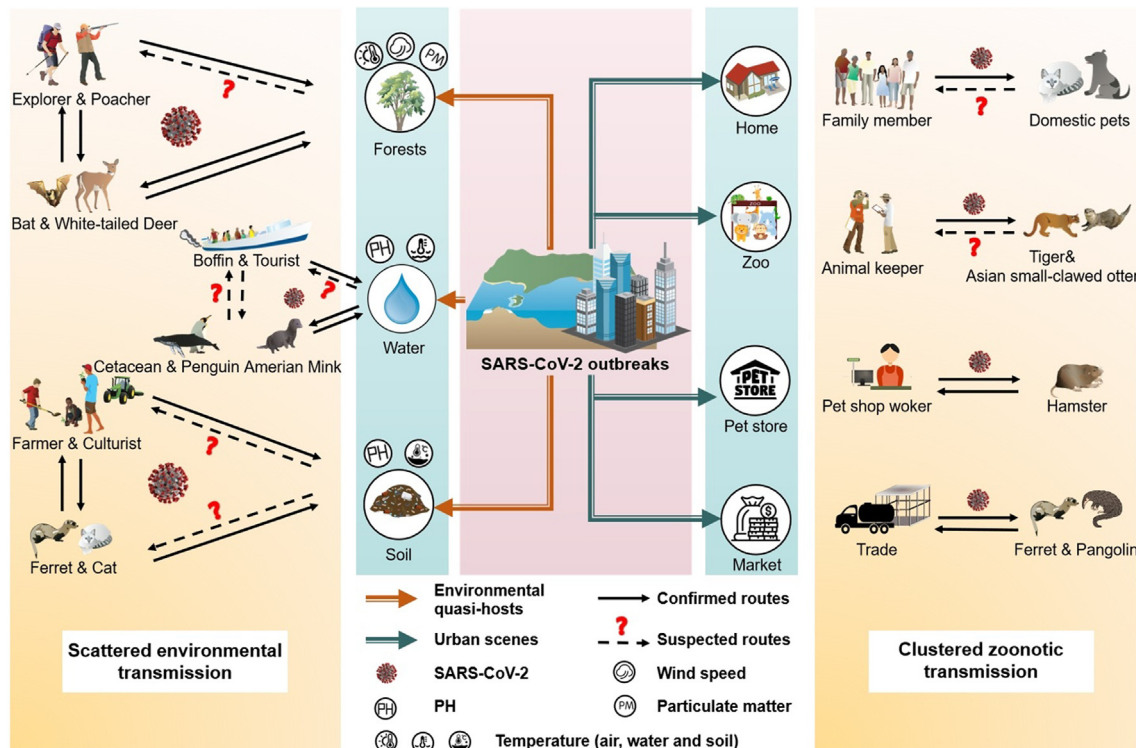

Fig. 3. Potential transmission pathways and associated species of SARS-CoV-2. Source for icons: Integration and Application Network (ian.umces.edumedia-library).
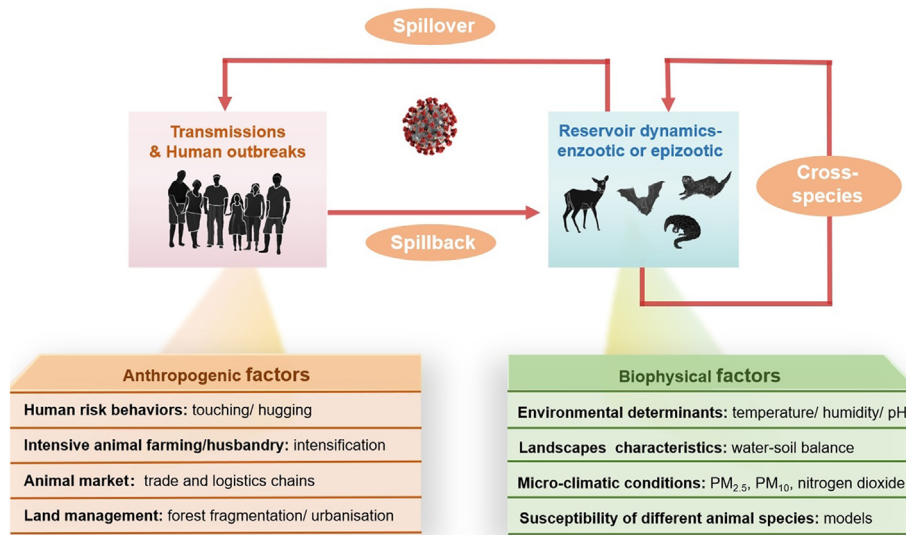
Fig. 4. Possible impacts of anthropogenic and biophysical factors on pathogen transmission.

included swimming pool water, wastewater, and surface water [44]. A free-ranging mink in Spain that tested positive for SARS-CoV-2 is believed to have contracted the virus through contaminated waterways [30]. Research conducted in northeast Ohio showed that white-tailed deer in urban areas had a higher likelihood of getting infected [14], possibly due to both direct and indirect contact with infected sources such as garbage, backyard feeders, and bait stations, as well as interaction with polluted rivers [45].

3.3.2. Pathogen genotypes and competence of animal as reservoir

Farmed, companion, and wild animals living in populations have reported relatively high outbreaks of SARS-CoV-2, according to the WOAH data. Mustelids had the highest number of cases, with 15,925 infected animals in 24 outbreaks in eight countries, followed by mink with 9,717 cases in 84 outbreaks in seven countries. Companion animals, particularly cats, were frequently reported, with a total of 114 cat outbreaks reported in 21 countries worldwide, and 105 dog outbreaks reported in 16 countries. However, as the WOAH data were reported on a voluntary basis, there may be unnoticed and unreported incidences of infection in wildlife animals with low human contact.

Laboratory experiments can be conducted to verify the susceptibility of different animal species to SARS-CoV-2, allowing for the establishment of animal disease models and indications of potential animal sources of human infection. SARS-CoV-2 contains a functional furin cleavage site in its spike protein, which may expand its host range and influence pathogenesis [46]. SARS-CoV-2 infects cells by binding its spike protein to the angiotensin-converting enzyme-2 (ACE2) receptor. Bats, mink, ferrets, and cats have a higher proportion of cells carrying both ACE2 and protease for SARS-CoV-2 replication, while it is lower in pigs, very rare in dogs, and absent in chickens and ducks [47]. Pigs, chickens, and ducks are not susceptible to SARS-CoV-2, and serum tests from these animals are negative for viral RNA. The ACE2 receptors responsible for binding to SARS-CoV-2 spike proteins are nearly identical in pigs, ferrets, cats, orangutans, monkeys, and humans. Most Old World primates and a large number of distantly related mammalian species are likely susceptible to SARS-CoV-2. However, a combination of comparative genomic approaches and protein structural analysis of ACE2 receptors suggests a very low risk of SARS-CoV-2 infection in a range of fish, amphibians, reptiles, and birds [48].

Source and recipient hosts with high genetic similarity also exhibit similarities in body physiology and cellular receptors [49]. This suggests that high similarity in cellular receptors between host species can facilitate the spillover of viral pathogens, as it increases the chances of the

virus interacting with new host cells. Host genetic factors also play a role in determining the ability of viruses to replicate in new hosts, establish infection and spread in new populations [50]. One study suggests that SARS-CoV-2 is highly deficient in CpG among all known type B coronaviruses, which may relate to new intermediate hosts. It is hypothesized that after ingestion of bat meat by the intermediate host dog, the virus evolved by reducing CpG levels in the canine gut, contaminating the respiratory system, and eventually becoming a severe human pathogen by evading ZAP-mediated immune response [51]. However, this view lacks conclusive evidence. Establishing effective animal models is necessary to address various scientific questions, including pathogenesis studies, vaccine development, and assessing the risk of viral spillover.

Finally, there is no evidence suggesting that SARS-CoV-2 or any other similar coronavirus, such as SARS or MERS, can be transmitted by mosquitoes or ticks. This is because the virus would need to replicate in mosquitoes or ticks to be transmitted to humans [52].

Table 2 presents the current evidence of natural and laboratory infections with SARS-CoV-2 in animals. We have selected 12 animal species to enhance our understanding of COVID-19 transmission between humans and animals, both in controlled and wild environments. Companion animals, such as domestic cats and dogs, due to their widespread global presence and close human interaction, were chosen. Susceptible farmed animals, including American minks, ferrets, snow leopards, and otters, exhibiting a high incidence of infections, were included. Hamsters, confirmed as potential transmitters of the virus to humans, merit special attention. Additionally, we considered tigers, lions, pumas, western lowland gorillas, and white-tailed deer, as they have reported infections in zoos and substantial wild populations.

3.4. Anthropogenic factors contributing to human-animal contact rate

A range of anthropogenic factors, including changes in ecological disturbances, landscape pattern, human behavior, and public health strategies, can increase the frequency of contact between human and wildlife populations, contributing to the risk of cross-species virus transmission [99]. In the examined animal studies on SARS-CoV-2, only 5% of them focused on human factors.

3.4.1. Human behaviors and animal exposure risk

The distribution and prevalence of SARS-CoV-2 in humans can affect the outbreak of the virus in species with high contact with humans, particularly companion animals. Factors such as higher household densities, residential building densities, recent immigration, essential

Table 2
Current evidence on natural and laboratory infection with SARS-CoV-2 in animals.

Species	Natural infection					Laboratory infection		
	Human–animal transmission confirmed	Animal–human transmission confirmed	Intra and interspecies transmission confirmed	Place/route of infection	Reference	Laboratory infection confirmed	Species susceptibility	Reference
American mink (*Neovison vison*)	Yes	Yes	Yes	River near farm; zoo	[18,53–56]	Yes	high	[57]
Domestic cat (*Felis catus*)	Yes	Not reported	Yes	Household; airborne transmission	[58–70]	Yes	high	[17,28,71–74]
Domestic dog (*Canis lupus familiaris*)	Yes	Not reported	Not reported	Household; airborne transmission	[24,58,64,65, 70,75–79]	Yes	mild	[17,71]
Ferret (*Mustela putorius furo*)	Yes	Not reported	Yes	Household	[80–82]	Yes	high	[17,83–90]
Tiger (*Panthera tigris*)	Yes	Not reported	Not reported	Zoo	[13]	Not tested		
Lion (*Panthera leo*)	Yes	Not reported	Not reported	Zoo	[13]	Not tested		
Snow leopard (*Panthera uncia*)	Yes	Not reported	Not reported	Zoo	[91]	Not tested		
Puma (*Puma concolor*)	Yes	Not reported	Not reported	Zoo	[92]	Not tested		
Western lowland gorilla (*Gorilla gorilla*)	Yes	Not reported	Yes	Zoo	[93]	Not tested		
Otter (*Aonyx cinereus*)	Yes	Not reported	Yes	Zoo	[94]	Not tested		
White-tailed Deer (*Odocoileus virginianus*)	Yes	Not reported	Yes	Zoo	[14,26,95]	Yes	high	[96,97]
Hamster (*Cricetidae*)	Yes	Yes	Yes	Pet store	[19]	Yes	high	[98]

workers, and educational attainment are linked to a higher risk of testing positive for the virus [100]. Additionally, greater urbanization, labor force participation, and income could lead to increased prevalence of SARS-CoV-2 [101]. Human activities heavily influence the introduction and outbreaks of SARS-CoV-2 in pets, with possible routes of transmission including respiratory droplets, saliva, touching pets' noses or mouths with infected hands [102], or even simply hugging them [99]. The European region has an estimated 90 million households with companion pets, including more than 110 million cats, 90 million dogs, 50 million birds, 30 million small animals, and 15 million aquatic animals [103]. A recent study suggests that the emergence of SARS-CoV-2 in carnivore pets such as cats, dogs, and ferrets can be attributed to factors such as diagnostic tools availability and quality, human density in proximity to pets, and current knowledge of the pathogen [104]. However, there is currently no fine-level data on the population sizes of some pets, such as ferrets, across different regions, which make it difficult to evaluate and monitor their infection risk.

Certain occupational and travel behaviors may contribute to local and transboundary outbreaks of SARS-CoV-2 in animals. Some professions that come into close contact with wildlife, such as forestry workers, pest control workers, and tourists, may potentially cause transmission of the virus to wild animals [105]. The risk of human-to-animal transmission is considerable when an infected person is in close proximity to a susceptible animal. There are concerns that frequent visits by tourists and researchers to Antarctica could expose susceptible wildlife species, such as penguins, to the virus and that the cold conditions could facilitate the spread of the virus [106].

Pollution-related activities deserve more attention in relation to the potential transmission of SARS-CoV-2. Reverse zoonotic transmission of the virus may occur through indirect contact, particularly through fecal transmission [45]. While the role of fecal-oral and fecal-respiratory transmission routes for SARS-CoV-2 is not yet clear, studies have detected high levels of the virus in urban effluent, indicating high fecal shedding of the virus from infected individuals [107]. There may be a risk of SARS-CoV-2 fecal-oral transmission in developing countries that frequently use sewage-contaminated water for irrigation due to the persistent activity of the virus or its RNA in wastewater. However, some studies indicate that the likelihood of infection through sewage-contaminated water or food is extremely low, suggesting that waterways are unlikely to be an important route of transmission [108].

3.4.2. Livestock/wildlife management and intensity of contacts

Domestic animals can act as 'amplifier hosts', spreading pathogens they pick up from wild animals and then infecting humans through frequent and close contact [109]. The intensification of livestock production, driven in part by population growth, dietary changes, and increased demand for animal products [110], has received much attention in relation to zoonotic diseases. Intensive livestock farms may excel at biosecurity because they are generally more isolated geographically and better protected from pathogens through veterinary control and management procedures. However, these farms are often located in peri-urban areas where there is close contact with natural habitats and frequent interactions between humans, domestic animals, and wildlife [111]. We noted a specific outbreak of SARS-CoV-2 on a mink farm in the Netherlands in mid-April 2020. Further sampling of stray cats around the farm showed the presence of antibodies against SARS-CoV-2 in seven cats and the presence of viral RNA in one cat [54], indicating potential transmission of the virus between animals and humans.

Recent studies highlighted the potential for cross-border virus transmission through the animal trade [112]. Animal trading markets and pet stores are particularly concerning because they facilitate interaction between humans, domestic animals, and wild species. There have been reports of SARS-CoV-2 transmissions from hamsters kept in a pet store in Hong Kong [19]. Illegal trade in certain wildlife species, such as Common palm civets, horseshoe bats, Chinese ferret-badgers, and ferrets in the Chinese market, is also believed to be associated with the spread of the virus [113]. Banning the animal trade would not be a feasible solution, as it would only divert the trade to the black market. Instead, better regulation and enhanced monitoring of trade in wildlife species between countries is needed to establish robust disease control mechanisms and reduce the risk of transporting pathogens over long distances. This would further help control human exposure throughout the trade and logistics chains [114].

Finally, we found that the current studies of SARS-CoV-2 in animals related to land management only focus on bats [115], despite the fact that land use change can impact the dynamics of wildlife exposure and susceptibility to pathogen infection through various mechanisms. Land use change can facilitate pathogen shedding or excretion from wildlife and create novel contact opportunities that facilitate pathogen spread between species [116]. The interdependence of human, animal, and ecosystem health has been demonstrated over the past three decades by viruses like the Ebola virus, influenza A (pandemic H1N1, H7N9) virus,

Middle East respiratory syndrome coronavirus, Hendra virus, and Nipah virus [117].

3.5. Knowledge gaps

Our review of the available literature has identified several gaps in our understanding of the animal-to-human transmission of SARS-CoV-2 that require further research. These gaps can be summarized as follows.

(1) The patterns of animal infections are still not well understood, and there are significant data gaps in some key regions. According to the WOAH reports, animal infections are concentrated in Europe and America, which may be due to their well-established animal welfare systems and monitoring networks. As an illustration, the United States Department of Agriculture collected samples from white-tailed deer in Illinois, New York, Michigan, and Pennsylvania. In contrast, Asia and Africa have reported fewer cases, and the medical conditions for animal rescue in some areas are poor. China is the first region where population cases appeared, with a high population density and a high frequency of contact between humans and animals, but there are few related reports.

(2) Most of the animals that can be tested for susceptibility to SARS-CoV-2 in the laboratory are small domestic animals such as minks and domestic cats, and there is no report on the susceptibility of large-scale animal experiments. Lions and tigers in zoos, as well as free-ranging white-tailed deer, have been known to be infected. There is an urgent need to monitor these animal populations in the wild, which remains a gap due to technical difficulties and lack of attention.

(3) The role of animal logistics networks, driven by economic interests, in the transmission of transboundary pathogens such as SARS-CoV-2 remains poorly understood. With only one case of live virus isolated from a cold-chain product, the evidence for cold-chain transmission is suggestive rather than absolute. Studies on the persistence of SARS-CoV-2 have been conducted under experimental conditions. However, the actual cold chain transport environment is more complex than laboratory simulations. In areas where wildlife smuggling and trade are prevalent, the people involved have frequent contact with wild animals in the jungle, and local sewage or other domestic pollutants are not properly treated.

(4) Our understanding of the drivers, pathways, and spatiotemporal dynamics of animal-to-human transmission is also limited. Despite a few reported cases of animal-to-human transmission, such as a case of a hamster infecting a pet shop clerk in Hong Kong, there are significant gaps in our understanding of the transmission pathways between animal species and humans.

3.6. Limitations and research directions

This study has three primary limitations. Firstly, the concentration of reported animal infections in Europe and America introduces a potential regional bias into the analysis. The well-established animal welfare systems and monitoring networks in these regions may have contributed to more effective case detection and reporting, possibly influencing the findings. Secondly, although the paper thoroughly examines anthropogenic and biophysical factors linked to animal infections, it falls short of precisely quantifying the extent of their impact. Lastly, the paper predominantly concentrates on identifying associations between factors and animal infections, rather than delving into causation or offering predictive models. Consequently, its capacity to provide specific guidance for disease prevention is somewhat limited.

In the realm of policy, there is a need for in-depth consideration of how to conduct animal conservation work in regions with limited monitoring capabilities, tailored to the specific local context. Regarding anthropogenic and biophysical factors, future exploration of their influencing factors can leverage machine learning and other methods. In-depth research explorations can help to improve our understanding of the animal-to-human transmission of SARS-CoV-2 and

inform evidence-based interventions to prevent and mitigate future outbreaks.

3.7. One Health as management strategies

The One Health initiative recognizes the intrinsic links between human, animal, and environmental health and aims to prevent and mitigate health risks at their interface. The environment is a fundamental component of public health, and greater attention to environmental factors is essential for promoting health and well-being within societies.

In the context of the SARS-CoV-2 pandemic, the changing landscape of human behavior underscores the need for veterinarians to adapt their roles in mitigating the risks of zoonotic transmission and promoting ecosystem health. By adopting a One Health approach, veterinarians can play a crucial role in safeguarding animals, humans, and their environment from transboundary infections. A One Health framework can also mitigate the economic impacts of pandemics on animal populations and the food supply chain. Anthropogenic environmental changes, such as population growth, urbanization, and transportation networks [118], have proven to be significant drivers of zoonotic disease emergence. Applied research is essential for advancing our understanding of the source and transmission dynamics of emerging diseases, which can inform evidence-based recommendations for promoting animal and human health. This deeper understanding can also help to reduce unwarranted stigma and discrimination toward animals [119].

Early detection of pathogens in the environment, wildlife, and domestic animals is critical for effective One Health surveillance. Given the current state of the SARS-CoV-2 pandemic, there is an urgent need to apply the One Health approach as a means of building resilience against future pandemics. Therefore, it is necessary to develop sustainable mitigation strategies from a One Health perspective to address the complex public health challenges related to zoonotic diseases. Only through such collaborations can we build a more resilient future for all.

4. Conclusion

This study provides a comprehensive review of the current literature on the patterns, transmission routes, and drivers of SARS-CoV-2 outbreaks in animals. Based on the results of available monitoring reports, animal infections of SARS-CoV-2 have been reported mainly in South America, North America, and Europe, with bats being proposed as the natural reservoir of the virus. However, the precise intermediate host and transmission pathways remain uncertain. In addition to domestic animals, free-ranging, captive, or farmed wild animals, such as big cats, minks, ferrets, North American white-tailed deer, and great apes, have been observed to be infected with SARS-CoV-2. Notably, farmed minks and pet hamsters have been confirmed to be capable of transmitting the SARS-CoV-2 virus to humans.

Despite a limited number of reported cases of animal-to-human transmission, substantial gaps persist in our understanding of the transmission pathways between animal species and humans. Symptoms resulting from SARS-CoV-2 infection exhibit variation across diverse animal species. Furthermore, the ongoing mutations of the virus pose a formidable challenge to the preservation of endangered animals, underscoring the significance of vigilant monitoring and dedicated conservation efforts.

This paper's novelty lies in its comprehensive analysis of the biophysical and anthropogenic factors influencing SARS-CoV-2 infections in animals. It offers a broader perspective on zoonotic disease transmission and its implications for global animal health conservation, paving the way for further research in this critical area. It highlights the impact of climate, population density, and landscape changes on different transmission routes of the virus. Sites involving human–animal interaction, such as markets and farming of susceptible animals, are considered focal areas for pathogen transmission. The increase in recreational activities

and wildlife–human contact worldwide may also contribute to the rapid spread of the virus.

To fully implement the One Health concept, there is a need for a further understanding of SARS-CoV-2 transmission pathways in shared spaces between humans and animals and the development of management strategies to prevent intra- and inter-species transmission. The study's identification of key animal species and biophysical and anthropogenic factors could assist in developing and implementing prevention strategies to interrupt cross-population transmission routes and prevent the evolution of pathogen reservoirs in the biosphere.

Author contributions

R.Y. contributed to writing the original draft, and writing, reviewing & editing of the manuscript. R.Y. and X.Y. collected the data and interpreted the findings. S.L. conceived and supervised the study, did analyses, interpreted the findings, and edited the manuscript. S.X. contributed to conceptualization and reviewing & editing of the manuscript. Y.G., B.P. and R.D. accessed and verified the data. All authors were responsible for the decision to submit the manuscript for publication.

Declaration of competing interests

The authors declare no conflicts of interest.

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.eehl.2023.09.004.

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