Since January 2020 Elsevier has created a COVID-19 resource centre with free information in English and Mandarin on the novel coronavirus COVID-19. The COVID-19 resource centre is hosted on Elsevier Connect, the company's public news and information website.

Biochemical and Biophysical Research Communications 538 (2021) 2–13

Contents lists available at ScienceDirect

Biochemical and Biophysical Research Communications

journal homepage: www.elsevier.com/locate/ybbrc

Biodiversity loss and COVID-19 pandemic: The role of bats in the origin and the spreading of the disease

Sara Platto [a, b, *], Jinfeng Zhou [a], Yanqing Wang [a], Huo Wang [a], Ernesto Carafoli [c]

[a] China Biodiversity Conservation and Green Development Foundation, Beijing, China
[b] Department of Biotechnology, College of Life Sciences, Jianghan University, Wuhan, China
[c] Venetian Institute of Molecular Medicine, University of Padova, Italy

ARTICLE INFO

Article history:
Received 11 October 2020
Accepted 14 October 2020
Available online 16 October 2020

Keywords:
Biodiversity loss
Dilution effects
Amplification effect
Bat CoVs
Bat meat consumption
Alphacoronavirus
Betacoronavirus

ABSTRACT

The loss of biodiversity in the ecosystems has created the general conditions that have favored and, in fact, made possible, the insurgence of the COVID-19 pandemic. A lot of factors have contributed to it: deforestation, changes in forest habitats, poorly regulated agricultural surfaces, mismanaged urban growth. They have altered the composition of wildlife communities, greatly increased the contacts of humans with wildlife, and altered niches that harbor pathogens, increasing their chances to come in contact with humans. Among the wildlife, bats have adapted easily to anthropized environments such as houses, barns, cultivated fields, orchards, where they found the suitable ecosystem to prosper. Bats are major hosts for αCoV and βCoV: evolution has shaped their peculiar physiology and their immune system in a way that makes them resistant to viral pathogens that would instead successfully attack other species, including humans. In time, the coronaviruses that bats host as reservoirs have undergone recombination and other modifications that have increased their ability for inter-species transmission: one modification of particular importance has been the development of the ability to use ACE2 as a receptor in host cells. This particular development in CoVs has been responsible for the serious outbreaks in the last two decades, and for the present COVID-19 pandemic.

1. HOW biodiversity loss affects epidemics insurgence

The global impact of COVID-19 has reached more than 200 countries causing over a million of deaths (data of September 2020). Bats have been identified as the reservoirs of the current coronavirus, and it is believed that the spillover of the virus to humans was caused by the consumption of these Chiroptera. However, the current global disease emergence could have been the result of a convergence of three factors: (1) the diversity of wildlife microbes in a region (the *zoonotic pool*) [1]; (2) the effects of environmental changes on the prevalence of pathogens in wild populations; and, (3) the frequency of human and domestic animals contacts with wildlife reservoirs of potential zoonoses [2]. In general, biodiversity has been linked to reduced pathogen transmission through the so called *dilution effect*, which occurs when in a niche there is a variety of host species that negatively affect pathogen persistence by acting as *buffering species* [3,4]. However, the dilution effect does not appear to be universal, but depends on the animal community composition, host and pathogen ecologies, and the scale at which the system is examined [5–7]. For example, the biodiversity' dilution effect will occur if increased species diversity leads to decreased host population density, that will reduce the contact rates, and therefore the transmission rate (β) (Fig. 1). Conversely, an amplification effect could occur if increased diversity leads to increased host density, with higher contact rates, and/or transmissibility [3,6–10] (Fig. 1).

Disruptive, extrinsic pressures in regions of high zoonotic potential where host or pathogen richness is already particularly high could trigger spillover to human hosts [11–14]. For example, the last 40 years have been characterized by a great decline of the environment in Southeast Asia (SEA), which has lost approximately 30% of its forest surface mainly caused by increased agricultural exploitation, and poorly managed urban growth [25]. The demographic growth in SEA has generated a great pressure on land use, with the most common activity being farming, logging, and hunting [15]. Anthropogenic pressure causes fragmentation of forest habitats,

* Corresponding author. Department of Biotechnology, College of Life Sciences, Jianghan University, Wuhan, China.
E-mail addresses: saraplatto@cbcgdf.org (S. Platto), jz@cbcgdf.org (J. Zhou), v52@cbcgdf.org (Y. Wang), linda.wong@cbcgdf.org (H. Wang), Ernesto.carafoli@gmail.com (E. Carafoli).

https://doi.org/10.1016/j.bbrc.2020.10.028
0006-291X/

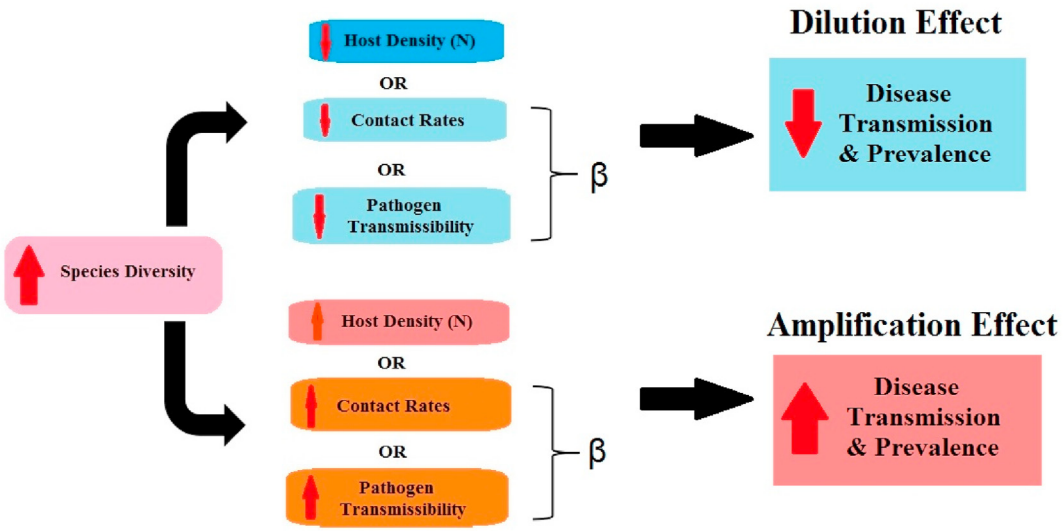

Fig. 1. Conceptual diagram of how biodiversity *dilution* and *amplification* effects affect the transmission and prevalence of a directly transmitted disease (Modified from Angela et al. [10]).

with the formation of patches, where the interfaces between them are called ecotones - "*transitory zones between adjacent ecological systems where biological and ecological processes are concentrated and intensified*" [16–19]. The expansion of the ecotonal areas through human activities such as farmland, and settlements can alter pathogen niches by bringing together humans, vectors, and reservoir hosts (wildlife or domestic) thus increasing contact, and the risk of transmission [17,19,20]. Evidence for an association between disease emergence and ecotones has been documented for several zoonoses such as Nipah virus encephalitis, influenza, rabies, hantavirus pulmonary syndrome [19,21–23].

Bat species are among the most numerous wildlife mammals that easily adapt to anthropized rural and urban environments. In these anthropized environments, bats can find niches compatible with their roosting and hunting needs: house lights attract a large number of insects at night, offering easy prey for insectivorous bats, while houses and barns offer shelter for cave-dwelling bats, while orchards and fields attract frugivorous bats [24–27]. These changes of the structure of the wildlife communities are characterized by low biodiversity, with an increase of the synanthropic species (a wild animal that lives in close contact with humans) population density that can elevate the contact rates, and thus increase the risk of pathogen transmission to humans [28–31]. This attractive effect of anthropized environments on bats with differing biological needs results in a higher concentration of bat-borne viruses, which increases the risk of transmission of viruses through direct contact with urine and feces, or through domestic animal infection [24–27,32–34]. The crowding and comingling of different host species will increase the number of pathogen genomes which will favor the production of strains that are more virulent and more adaptable to the new hosts through mutation, and recombination mechanisms [25,35].

Evidence suggests that many pathogens are transmitted between their animal reservoirs and humans but fail to be transmitted from human to human, or do so at rates that do not allow pathogen establishment within the human population. This condition has been termed *viral chatters* a seemingly common phenomenon of repeated transmission of viruses to humans, most of which fail to develop to a human-to-human transmission [36]. High rates of viral chatters will increase the diversity of viruses, and sequence variants moving into humans, raising the probability of transmission of a pathogen that can successfully replicate, and ultimately adapt to human environment [36–38]. This could be the way in which COVID-19 has emerged.

Bats are considered to play a key role in the evolution of coronaviruses, being the major reservoirs of alphacoronaviruses (αCoV) and betacoronaviruses (βCoV) [39,40]. Bats have been originated 64 millions years ago, a time spam that might have allowed the development of co-evolutionary processes between these Chiroptera and different virus species [25,41]. This phenomenon might have also favored the development of a strong correlation between bat ecology and coronaviruses diversity [25,42]. Moreover, the long co-evolutionary processes between bats and coronaviruses might have also contributed to the constitution of a vast pool of viruses with high opportunities of cross-species mixing, that has favored the development of strains with the ability to infect a vast range of hosts [43,44,62].

2. WHY are bat suitable reservoirs of coronaviruses?

Bats are members of the order Chiroptera and are the only mammals capable of sustained flight. There are approximately 1,230 species of bats, making these animals the second most numerous mammals after the rodents [45–47]. Bats fulfill many ecological roles from that of pollinators of fruit-bearing trees, playing a role in the processes of reforestation, to that of significant predators of insects, in particular crop pests and nuisance insect species [45].

Bats host more zoonotic viruses and more total viruses per species than rodents, and significantly higher proportion of zoonotic viruses than all other mammalian orders [44]. These viruses include, but are not limited to, various species of the genus Lyssavirus, henipaviruses, coronaviruses (e. g. SARS-CoV, MErs-CoV, COVID-19), and filoviruses such as several species of the Ebola virus [48–53].

2.1. Bat adaptation to viruses

Bats are the only flying mammals and this function has been accompanied by genetic changes to their immune system as a consequence of their metabolic rate. For example, bats produce large amounts of reactive oxygen species (ROS), and in response, have modulated genes to limit oxidative stress [54], which may result in reduced viral replication and pathogenesis [55]. Bat have high metabolic rate, compared to other animals. For example, metabolic rate in a running rat is 7-fold, and in a flying bird is 2-fold, while in bat

can reach 15/16-fold [56]. Filoviruses such as Marburg and Ebola can replicate at the bat flight temperatures of 37–41 C°, indicating that the elevation in temperature does not affect their replication [56]. On the other hand, bats can also display a daily torpor with a decrease of the body temperature which might be a strategy to interfere with the optimal virus replication [56]. Moreover, bats display a unique interferon system (IFN) that might explain their ability to coexist with pathogens [57]. In general, mammals possess a large IFN locus that comprises a family of IFN-α genes expressed only following an infection. Conversely, in bats only three IFN-α are expressed, but constantly and constitutively [57]. This could be a highly effective system for controlling viral replication, which helps explaining bats' resistance to viruses. In addition, bats lack the known PYHIN (PYRIN and HIN domain-containing) genes within the inflammasome pathway [54,58]. Natural killer immunoglobulin-like receptors (KIRs) are absent or significantly reduced in some surveyed bat species, potentially limiting disease and damage following infection [54,58]. Moreover, bats have very limited bone marrow or lack it at all, with the consequence of a low or absent production of B-cells, making bats asymptomatic carriers [54,58]. Another characteristic is their commensal relationship with the viruses [59]. The pool of viruses identified in the bats' enteric samples may help their microbiome to enhance immunity [60]. All these factors can work in combination, and they can explain how, for example, diverse pools of CoV quasi-species can survive in bat populations [61].

2.2. Virus genetic variability in bats

The aspects that permit virus persistence in bats also contribute to their diversity and to the potential emergence of new viral species. As a result of flight for short periods of time, bats can accumulate ROS species which may have mutagenic effects. In the case of coronaviruses, the accumulation of ROS species could potentially overwhelm proofreading repair and/or altering viral polymerase fidelity, leading to virus species diversity, and therefore to cross-species transmission [62]. The constitutive expression of the IFN in bats may favor the selection of viral mutation that possess enhanced resistance to the antiviral defense pathways, providing a replication advantage after cross species transmission [57]. On the other hand, the absence of key inflammatory mediators in bat species provides no selective pressure to minimize these responses [58], which will favor a massive and pathogenic inflammation response in a new host as seen with both SARS-CoV, MERS-CoV [63,64], and COVID-19 infections in humans. In addition, virus recombination in bats are also common. The recombination frequency of coronaviruses, which can be as high as 25% for the entire genome [65], could make bats important reservoirs for coronavirus recombination and virus evolution, much like birds and pigs are for influenza viruses. Furthermore, the majority of recombination events identified in coronaviruses isolated from bats suggest recombination hot-spots around the spike gene [66,67].

2.3. Virus maintenance in a bat colony

Social organization in bats contributes to the maintenance of virus in the population. Bats are gregarious animals, living in colonies composed by thousands of individuals that often belong to more than one species [25]. For example, cave dwelling bats are characterized by multi-species association which shows higher frequency during maternity periods [25,68]. The transmission of the viruses in the bats' colonies can occur through different ways depending on the bat and virus species considered i.e. aerosols, contact with feces, urine, blood, or other body fluids, or by bite [25,69].

Factors that can cause viral fluctuations within a bat colony can be the presence of high number of susceptible individuals, and stressful events. The inflow of susceptible bats into the colonies occur with the new births, or with the immigration of naïve animals from neighboring colonies, or with the expiration of immunity in previously infected individuals. These events can cause virus spreading within the colony and therefore keep the infection at high rates [69–71].

Stress-induced immunosuppression events in the bat population can increase susceptibility for contracting and shedding viruses. For example, a recent study demonstrated that secondary infection with the white-nose syndrome fungus (*Pseudogymnoascus destructans*) in bats increases CoV replication [72]. Weather conditions can also influence virus shedding and therefore possible spillovers. Inclement weather such as low precipitation can act as stressors, especially when associated with lack of food resources that can impair the immune system of the bats, causing increased susceptibility to pathogenic agents [73,74]. In fact, during rainy season roost sites may be limited for foliage-roosting bats, increasing the contact between individuals and thus more opportunities for pathogen transmission [73,74]. Therefore, seasonality might be an important driver of viral infections, including extreme weather conditions such as El Niño [75]. Precisely, the emergence of Nipah virus was also driven by the severe weather condition caused by El Niño. During dry season, when food resources are limited, bat are in poor body condition and might be less immunocompetent. Thus, individuals may become more susceptible to acquire viral infections in the subsequent rainy season [75]. For example, the year 2019 was characterized by El Niño, which even though was considered mild in comparison with previous events, it might have affected the insurgence of COVID-19.

2.4. Distribution of bat coronaviruses

The high diversity of bat species provides a great variety of cell types and receptors. Bats are found to be hosts of at least 30 different CoVs with complete genome sequences [76–87], and many more if those without genome sequences are included [88–97]. Bat coronaviruses are classified into four genera, Alphacoronavirus, Betacoronavirus, Gammacoronavirus (ɣCoVs) and Deltacoronavirus (δCoVs). Within Betacoronavirus, they can be further subclassified into lineages A, B, C and D [98]. In 2018, these four lineages were reclassified as subgenera of Betacoronavirus, and renamed as *Embecovirus* (previous lineage A), *Sarbecovirus* (previous lineage B), *Merbecovirus* (previous lineage C) and *Nobecovirus* (previous lineage D) [99]. In addition, a fifth subgenus, *Hibecovirus* was also included [99] (Fig. 2).

Among the four genera, only αCoVs and βCoVs have been found in bats, leading to the conclusion that bat CoVs are the ancestors for αCoVs and βCoVs, whereas bird CoVs are the ancestors for ɣCoVs and δCoVs [100]. Interestingly, for the βCoVs only those from subgenera *Sarbecovirus* (SARS-related CoVs), *Merbecovirus* (Ty-BatCoV HKU4, Pi-BatCoV HKU5, Hp-BatCoV HKU25, MERS-related CoVs), Nobecovirus (Ro-BatCoV HKU9 and Ro-BatCoV GCCDC1) and *Hibecovirus* (Bat Hp-betaCoV Zhejiang 2013) have been detected in bats so far [78,81,82,86,87,99,101], while several βCoVs from the subgenus *Embecovirus* (Murine CoV and ChRCoV HKU24) have also been discovered in rodents [78,99].

Both αCoVs and βCoVs have higher detection rates in bats' intestinal and fecal samples, making these animals' excretions the major environmental source for the shedding of CoVs in spillover events [76,102–105]. For example, the conditions encountered in a wet market would be favourable to the infection of new hosts. In these places, animals of various species, including live bats, are kept in cages stored one above the other, with continuous contamination of food and water with excretions. The presence of a variety of animal species is also characterized by a great availability of

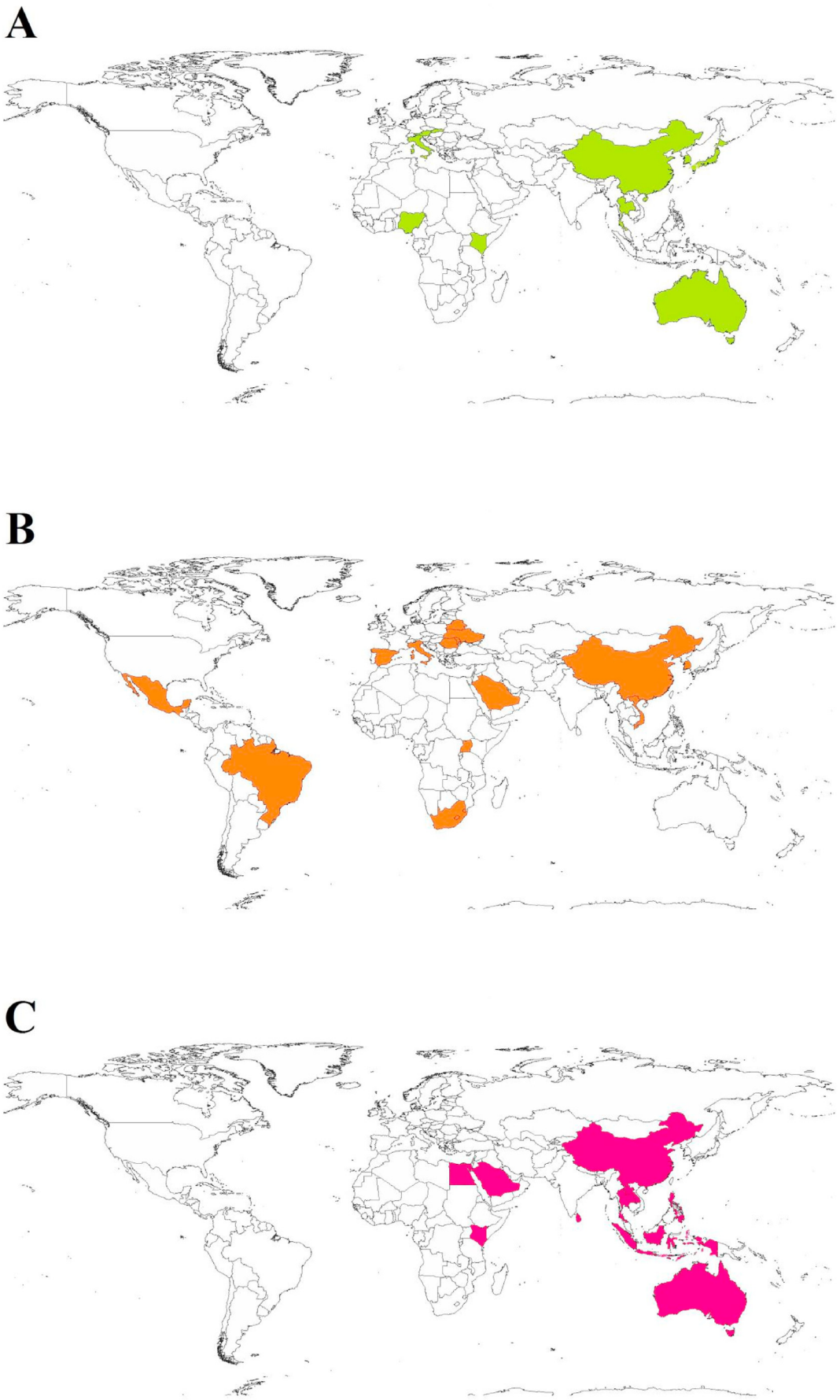

Fig. 2. Geographic distribution of bat CoVs from the genus Betacoronavirus. **A**: light green regions represent the countries with the presence of bat CoV from *Sarbecovirus*. **B**: orange regions represent the countries with the presence of bat CoV from *Merbecovirus*. **C**: purple regions represent the countries with the presence of bat CoV from *Nobecovirus* (modified from Wong et al. [181]).

different cell receptors that viruses can use to enter in a new host.

In general, αCoVs and βCoVs have been detected in bats in Asia, Europe, Africa, North and South America and Australasia [76,77,83,92,97,104–112], with αCoVs being more widespread and with higher detection rate compared to βCoVs (Fig. 3).

SARS-like-CoV are present in different bat species but all belong to the family *Rhinolophidae* and *Hipposideridae* [101]. In China, horseshoe bat species (*Rhinolophus spp.*) are widely distributed, and are also the most frequent SARS-like-CoV carriers throughout the nation [66,76,101,102,113–123]. In fact, the largest population of completely sequenced bat's SARS-like CoVs were found in Chinese horseshoe bats (*Rhinolophus sinicus*) [66,76,111,123] (Fig. 4). It is also interesting to note that geographic factors also contribute to the diversity of SARS-like-CoVs. Precisely, the majority of SARS-like-CoVs are found in Yunnan province (China), and they share higher nucleotide identity (90–95%) with human SARS-CoV, while those found in southeast China, Korea and Europe shared only 77–90% genome nucleotide identity [66,115,124,125]. A similar situation also occurred with COVID-19. In this case, a SARS-like-CoV, RaTG13, was identified in *Rhinolophus affinis* from Yunnan province, and it showed an identity of 96.2% with COVID-19 [126]. Yunnan province is an ecological niche where many different species of horsheshoe bats (*Rhinolophus spp.*) reside, and it is the geographical region with the highest diversity of bat SARS-like-CoVs with many recombination events among the various strains [66,101,115]. It is interesting to notice that all strains of SARS-like-CoV capable of using human ACE2 as receptors were found in *Rhinolophus sinicus* and *affinis* only from Yunnan province, while other SARS-like-CoVs that cannot use human ACE2 were distributed in multiple provinces including Hubei province where Wuhan is located [66,113,114,117]. In addition, the ORF8 protein, that is important for interspecies transmission in CoVs, was found in viruses that were carried by *Rhinolophus ferrumequinum* and *sinicus* only from Yunnan province [66,115].

Thus, it was suggested that SARS-CoV most likely originated from Yunnan *Rhinolophis* bats via recombination events among existing SARS-like-COVs. Could these types of events also happened for COVID-19? Could the virus have jumped to humans in remote areas of South China, and then spread by human-to-human infection to the rest of the population? This hypothesis would be compatible with the fact that most of the hunting and guano collection activities are located in south China, and Southeast Asia, with higher probability of multiple spillovers, and therefore viral chatters that might have lead to the emergence of the new virus.

Bats have also the ability to harbor more than one species of virus at the same time, which might allow the CoVs to incorporate genes from other viral families through recombination events [113,127]. Examples of the coexistence of more than one virus in the same bat are: bat CoV 1 and HKU8–CoV [113,127]; HKU2-CoVs (SADS-CoV, the virus that caused the outbreak in pigs in 2016 in South China), and SARSr-CoVs [76,128]; two or more distinct genotypes of HKU9-CoVs [76]; HKU9-CoVs and a new identified bat filovirus (Mengla virus) that is phylogenetically related to the Ebola and Marburg viruses [129,130].

2.5. The coronaviruses machinery for successful spillover and emergence

Fidelity and gene acquisition in CoVs allow these viruses to alter key viral factors to overcome species barriers without sacrificing the function of other important elements [131]. Coronavirus genomes are the largest known RNA genomes (26–32 kilobases), and still being able to maintain functional components that allow it to be viable. The COVID-19 contains 4 structural proteins [132–137] and 16 non structural proteins (nps) [132]. In order to allow the emergence of new CoVs, these proteins must provide sufficient changes to overcome species barrier, maintaining, at the same time, key viral functions [132–137]. Two of the structural proteins (E and M) form the envelope of the virus, one (the N-nucleocapsid protein) binds the genomic RNA of the virus, the fourth, the S-glycoprotein, is the trimeric protein that forms the typical protrusions from the surface of the virus that have given to it the "*corona*" name. It is perhaps the most important structural protein, as its task is the recognition of the ACE2 receptor of the host cell, and its interaction with it, that are the necessary steps that promote the penetration of the virus into the host cell. Importantly, the actual penetration of the virus demands the "priming" of the S-protein by host cell proteases that cleave to S-protein into S1 and S2 segments, exposing a sequence in the latter that fuses it with the plasma membrane of the host cell [138]. Mutations at S1 level, and adaptations within the new hosts are critical factors to ensure the emergence of new CoVs and pathogenesis [138]. Once the COVID-19 is incorporated of host cell, its RNA genome is liberated into its cytoplasm and reaches the ribosomes of the endoplasmic reticulum, where its open reading frames are translated into two proteins that are cleaved by cell proteases to yield the 16 nps [132]. One of them (nps 12) is the RNA-dependent RNA polymerase that, with the assistance of nps 7 and nsp 8 will synthesize the new RNA of the infecting virus. The function of the invading virus has additional complexities: for instance, a recent study has found that accessory proteins can also be taken from other pathogens [86]. Variations in the accessory proteins can create variability in infection characteristics and severity across CoVs' families [139,140]. For example, a novel CoV (Ro-BatCoV GCCDC1) was found to contain 30 protein that were omologues to those of a known reovirus gene. This suggests the possibility of recombination activities even between viral families [139,140]. Therefore, CoVs have the ability to acquire proteins that allow them to survive in natural hosts and emerge as new ones [139,140].

3. Tracing bat coronaviruses spillover hotspots

Nine months after the onset of the epidemic in Wuhan, the city is still considered the place where the virus originated, even though a phylo-epidemiological study carried out by the Centre of Integrative Conservation (Xishuangbanna Tropical Botanical Garden) indicated that the COVID-19 found at Huanan market (Wuhan) could have been imported from other places [141]. According to the initial findings, the cause of the emergence of the current epidemic is the consumption of bats. Bat hunting practice is widespread in South China, Southeast Asia, Africa, and some Pacific Islands, and targets at least 167 species of bats [142]. In addition, guano extraction from bat caves, or harvested in bat farms is also a widespread activity, and the product is used as fertilizer in several countries, including Thailand, Indonesia, Vietnam, Cambodia, Mexico, Cuba, and Jamaica [112]. Bat excretions have been found to present high levels of α-CoV and β-CoV, and therefore guano extraction must be considered a concern for public health [76,102,103,105,112,143], and a risk for virus spillover [112,144].

In this chapter, we will review the practices of guano collection, bat hunting, and farming in Asia, and the related studies on coronavirus strains encountered in bats used for these activities.

Indonesia. Bat hunting is a very common practice in Indonesia which has caused the decimation of some bat species such as flaying foxes (genus *Pteropus* and *Acerodon*). The bushmeat trade favors flying foxes because of their large body size and tendency to aggregate in large colonies, which increases the ease of capture [143]. In some regions smaller bat species were hunted because flying foxes were no longer present [145]. Bats are not considered an endangered species by the Indonesian Government, and the law allows the hunting and trading of these animals with a legal permit [146,147]. Before the bushmeat market reached its current form in Indonesia, local villagers

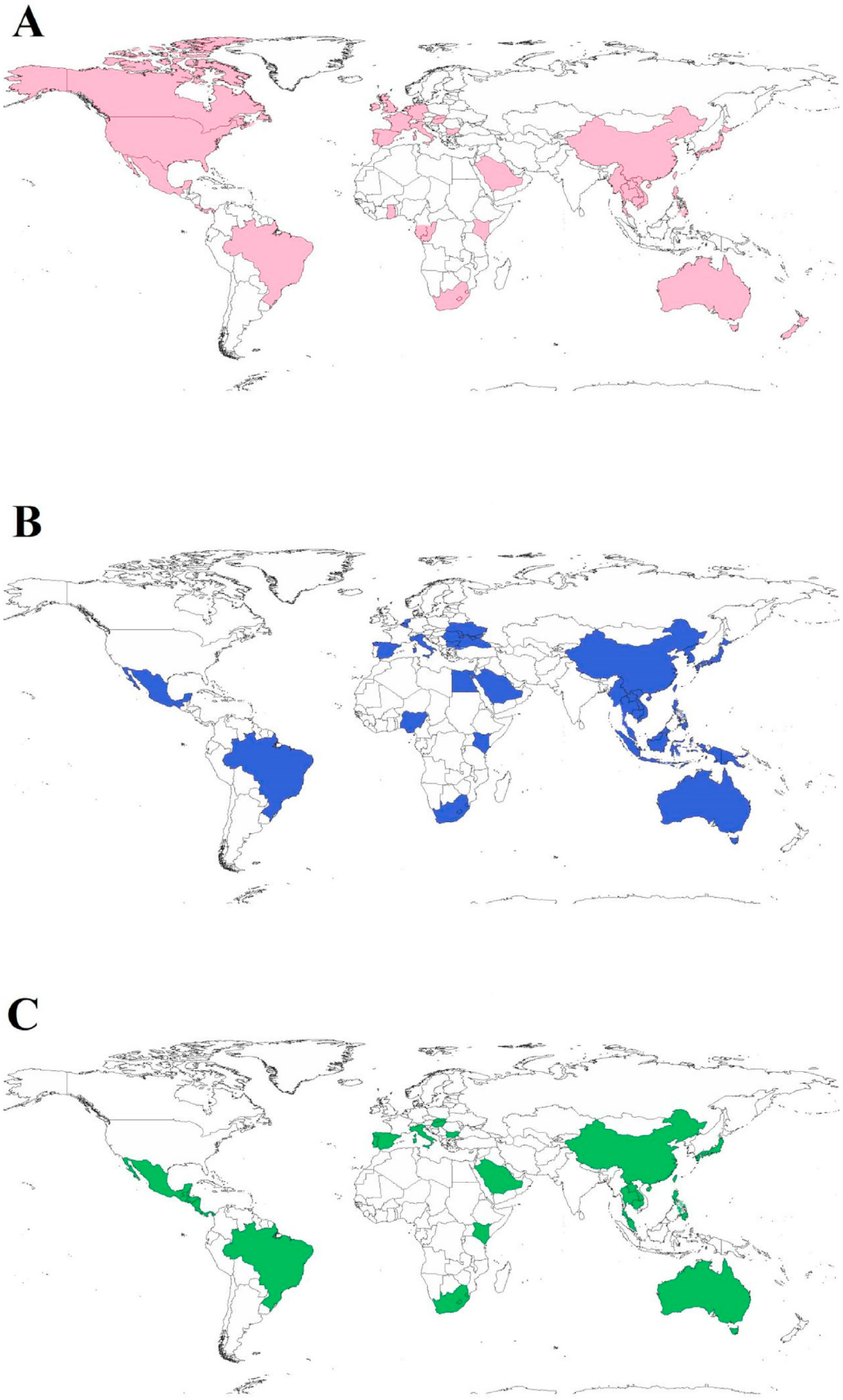

Fig. 3. Geographic distribution of αCoVs and βCoVs. **A**: pink regions represent the countries where αCoVs were discovered. **B**: blue regions indicate the countries where βCoVs were discovered. **C**: green regions represent the countries where both αCoVs and βCoVs were discovered (modified from Wong et al. [181]).

often hunted flying foxes for private consumption, or to sell them in traditional markets. Now bats are also available in some modern supermarkets in the cities [148]. In general, all the bats that reach the markets are already dead, but some places sell live individuals [148]. It is estimated that approximately 45–75 flying foxes are sold each day, with an increase to 150–450 on weekends [151]. The period of highest sale intensity if that of Christmas and New Year Festivities, when approximately 1000 flying foxes are sold [148]. Bat are kept in cages with other wild animals such as endemic black macaques (*Macaca nigra*), pythons from Kalimantan (*Python reticulatus* or *P. curtus*) [149], water monitors (*Varanus salvator*), Sulwaesi wild pigs (*Sus celebensis*), and Bornean bearded pigs (*Sus barbatus*) [150,151]. These conditions can exacerbate the spillover of viruses from bats to other animals facilitating the transmission to humans. In particular, the presence of Old World monkeys such as macaque in association with bats could potentially facilitate the transmission of CoVs from the primates to humans, considering the genetic similarities between the two species [152].

Vietnam. A survey performed by Huong et al. [153] from 2009 to 2014 assessed coronavirus spillover risk from different wildlife supply chains (rat and bat farms, and other wildlife animal farms) destined for human consumption [154]. In addition, guano farms were also sampled to assess the possibility of spillovers considering that bat artificial roosts are erected in gardens or backyards of the farms with the presence of other farm animals such as duck, goat, chicken, and pigs [154]. The survey included 6006 registered wildlife farms across 12 provinces with approximately one million wild animals including rodents, primates, civet cats, wild boar, Oriental rat-snakes, deer, crocodiles, and softshell turtles. Ninety-five percent of the farms held 1–2 species of wildlife, and 70% of them also raised domestic animals on the same premises [154]. These farms sell wild meat to urban restaurants of all the country, and also supply international markets [155]. Commercial wildlife farming in Viet Nam is part of the expanded international trade of wildlife that is thought to have contributed to global epidemics, such as SARS and now COVID-19 [153,156–158].

Six distinct taxonomic units of coronaviruses corresponding to bat coronavirus 512/2005, Longquan aa coronavirus, avian infectious bronchitis virus (IBV), murine coronavirus, PREDICT_CoV-17, and PREDICT_CoV-35 were detected from the study of Huong et al. [153]. Phylogenetic analysis showed that among the six coronaviruses detected, PREDICT_CoV-35 and bat CoV 512/2005 clustered within the Alphacoronaviruses, while PREDICT_CoV-17, Longquan aa CoV, and murine CoV clustered within the Betacoronaviruses. The virus identified within the Gammacoronavirus genus was avian IBV [153]. Both PREDICT_CoV-17 and PREDICT_CoV-35 were detected previously in bats in Viet Nam, Cambodia, and Nepal, which confirms that coronaviruses are capable of infecting distantly related hosts [41]. The finding of the same virus in different bat species raises the question of whether they co-roost and/or share viruses through contact during other activities. Moreover, the presence of the same virus in bat species in multiple neighboring countries supports the hypothesis that viruses distribution is correlated with their bat hosts distribution [41,124,144] (Fig. 4).

Bat coronavirus 512/2005 was frequently found in co-infection with PREDICT_CoV-35 [153], while three types of coronaviruses (Longquan aa CoV, murine CoV, and IBV) were found in rats. The presence of a bat CoV and a poultry CoV in rats can be explained by the presence of multiple species on the wildlife farms, which may facilitate viral recombination leading to the emergence of new viruses [66,127]. The transit of multiple animal species through the supply chain offers opportunities for inter- and intra-species mixing. Animals confined in overcrowded cages with poor nutrition can increase stress which contribute to shedding of coronavirus and amplification of the infection through the supply chain for human consumption, including close direct contact with traders, butchers, cooks, and consumers [159,160].

Moreover, a high proportion of bat feces were found positive to coronaviruses at bat guano farms, indicating the potential risk of bat guano farmers, their families, and their animals being exposed to the viruses [66,127].

Cambodia and Lao PDR. In Cambodia and Laos several thousand bats per day are sold in the markets [161]. Bat are also exported from these countries to markets in Thailand [162]. In Cambodia and Laos, small farmers also practice artificial bat roosting in their backyard farms for guano collection, with other domestic animals sharing the same environment. A study conducted by Lacroix et al. [163] found a significant diversity of CoVs in bats both in Cambodia and Laos. For example, it was reported that *Pipistrellus* bats hosted both αCoV and βCoV, a finding that raises concern since this species is very common is rural and urban areas [80,164–167]. In addition, the health risk in Cambodia is worsened by the fact that *Pipistrellus* bats are also hunted for food, beside being used for guano extraction [166,167]. Furthermore, hunters, restaurant workers, and farmers have been reported to be bitten by bats, and to have been exposed to their urine and feces. Farmers, who wear no protective equipment or clothing, collect guano in tarpaulins or nets laid beneath the bats' roosts, and are regularly urinated and defecated upon. The risk of contamination by direct contact with urine and feces must therefore be considered [163]. In fact, a study conducted by Wacharapluesadee et al. [111] identified HKU1 betacoronavirus in a non-hill individual with high level of occupational exposure to guano.

Thailand. Bats are hunted for consumption also in Thailand. They can be easily found in restaurants in Bangkok, and in the daily markets in north-east regions of the country [143,162]. Some bats may be transported from Laos, indicating cross-border trades. Bats play a cultural role in Thailand, including medicinal, religious, and culinary functions [168]. A survey conducted by Suwannarong et al. [169] reported the highest bat consumption in the Northern region of Thailand (Chiang Mai and Chiang Rai at the border with Burma and Laos). Surveyed people responded that they had consumed bats at least one time in the previous 6 months. Bats were mostly obtained from caves, purchased in local markets, or hunted by locals [169].

Philippines. In Philippines over 1500 bat caves have been recorded. Most hunters kill only a few bats per trip, but those operating at roost sites take hundreds in a single hunt [170]. In the country, bats are mostly hunted for food, but bats' caves are also frequently visited for guano extraction [171,172]. Locals and some indigenous groups usually hunt larger species of bats such as fruit and large hipposiderids bats for protein source and trade. A clear indication of bat hunting and exploitation in caves is the presence of carcasses and bones of bats, and coconut torches that may have been used to smoke the caves [143].

China. The bat meat trade is mainly found in the Southern China, where bat can be traded locally and regionally. Some restaurants in Guangdong and Guanxi provinces offer bat dishes on the menu [143]. Bats are not a protected species in China, and during the last 30 years the population of these animals has shown a 60% decline, mainly caused by bat cave exploitation for tourism, and poaching by locals [173]. Surveys carried out in Guangdong province between 2005 and 2012 revealed the consumption of bats by the majority of the respondents [174,175]. Live bats were found to be sold at wet-markets in Guangzhou and Gaozhou (Guangdong province) [174]. In addition, cases of dead bats found in oyster sauce containers were reported by customers. The oyster sauce was produced by a factory in Guangdong province. The presence of the bats in the processed food was incidental, probably caused by the animals roosting in the production areas, and falling inside the containers [176]. Whole bats, body parts, or desiccated feces are also used in the Chinese Traditional Medicine, which raise great health concerns [177].

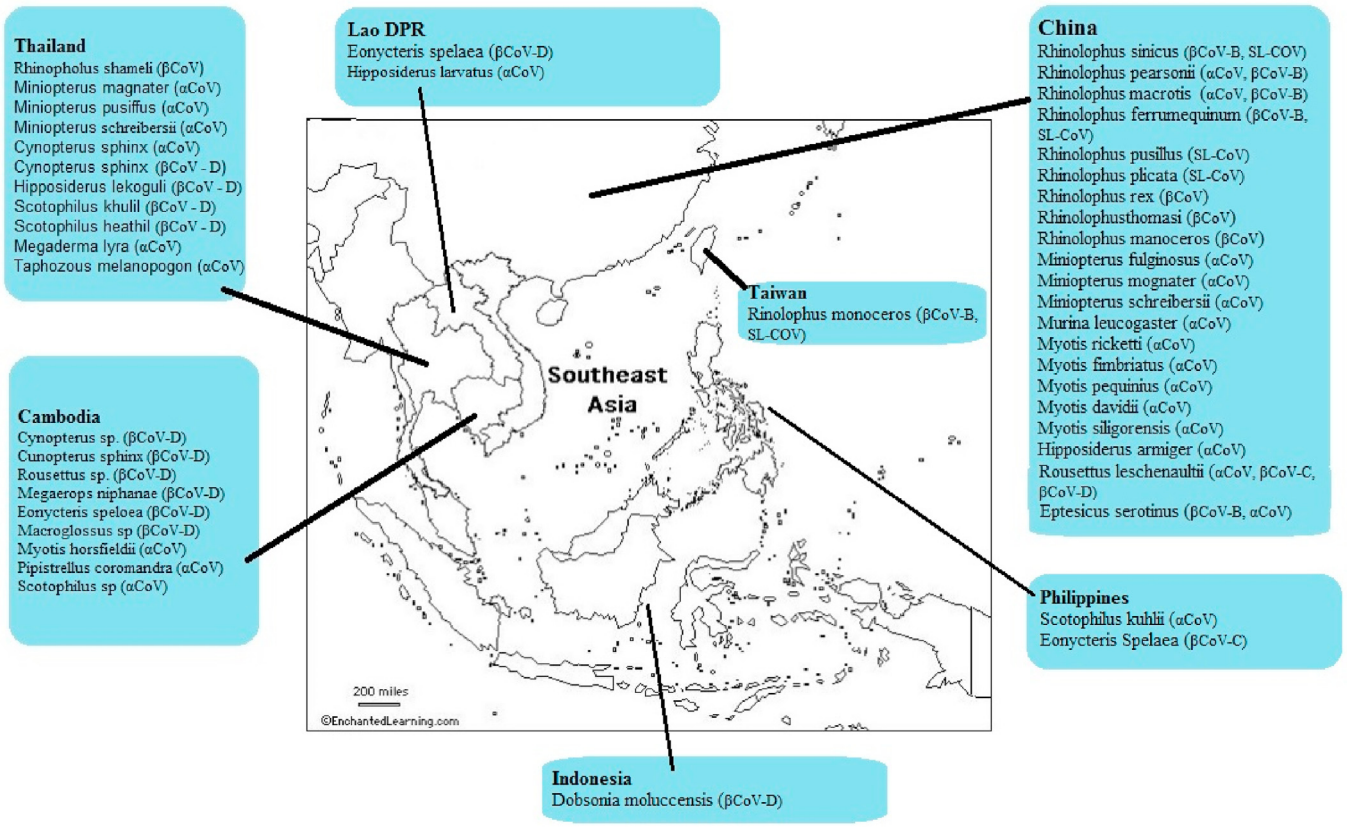

Fig. 4. Distribution of the types of coronaviruses in several Asian countries along with the bat species from which they have been isolated (modified from Afelt et al. [25]).

3.1. Malaysia and Nepal

Bat are regarded as luxury meat in Malaysia with most vendors selling 200–300 bats per season [178]. In Nepal, bats are also used as food by the local communities [143].

3.2. A general point

A final comment is in order at the end of this contribution: bats are kept in the markets with other animals species, which could amplify the spillover events. Among the animals sold at the markets, there are Old World monkeys such as macaques. In a recent study Damas et al. [179] have examined the ACE2 receptors from 410 vertebrates (fishes, amphibians, birds, reptiles, and mammals) to predict their ability to bind COVID-19 spike proteins. The ability of the vertebrates was classified as low, medium, and high. The 18 species classified as "very high" were all Old World monkeys, whose S-protein binding residues in the ACE2 receptors were identical to those of humans. Among these primates, Rhesus macaque (*Macaca mulatta*) is the only known species infected with COVID-19, and showing symptoms similar to those in humans [179]. Macaques of the species *Macaca fascicularis* and *Macaca nigra* are the most common primate traded in Cambodia, Malaysia, Philippines, and Indonesia to be sold in laboratories, and is also used for consumption in South China [152]. Therefore, an hypothesis for an intermediate host could be propose here. Even though different SARS-like-CoVs have the ability to use ACE2 as entry receptors, thus arguing against the necessity for them of an intermediate host to reach humans [113,120], macaques might be proposed as likely susceptible hosts for COVID-19. This hypothesis could be further supported by the fact that these primates are kept in markets in association with bats, raising serious concerns on the probable spillovers from these animals to humans.

4. Conclusions

Anthropogenic changes such as deforestation, habitat fragmentation, land-use, agricultural development, and uncontrolled urbanization can impact the transmission of infectious disease from animals to humans by altering the biodiversity's *dilution effect*. These changes also alter pathogens' niches, and the movements of hosts and vectors preparing the general ground that favors the emergence of infectious diseases. The pathogenic dynamics of CoVs only demand a host as the permanent reservoir, and albeit not necessarily, an intermediate host. In Southeast Asia, the permanent reservoir of CoVs are the bats, which in this region are commonly consumed as food. Evolution has shaped the metabolic properties of bats and their immune system in ways that have made them insensitive to the pathogenic effects of CoVs. The CoVs themselves have also undergone evolutionary changes that have increased their pathogenic potential: one of particular importance in the present pandemic, and in previous outbreaks (SARS-CoV), has been the ability to use the ACE2 receptors of target cells to invade them. The presence of multiple animals species in the markets in SEA and South China, including bats, produces a high density of possible susceptible hosts, which creates an *Amplification Effect Zone* increasing the probability of spillovers. Macaques are most frequently encountered primates in these markets, and are also raised in farms in different SEA Countries to be sold to laboratories, or for food consumption in particular in South China. Considering that macaques have a close phylogenetic relationship with humans [180], it might be easier for CoV to use them as intermediate hosts

for the spillover of the virus to humans. Therefore, the possibility that macaques used in the wildlife trade chain could be intermediate hosts for COVID-19 should be given serious consideration.

Declaration of competing interest

I declare no conflict of interest.

Acknowledgments

I would like to thanks all the collaborators of China Biodiversity Conservation and Green Development Foundation (CBCGDF) for the help in researching the material.

References

[1] S. S Morse, Examining the origins of emerging viruses, in: S.S. Morse (Ed.), Emerging Viruses, Oxford University Press, New York, 1993, pp. 10–28.
[2] N.D. Wolfe, P. Daszak, A.M. Kilpatrick, D.S. Burke, Bushmeat hunting, deforestation, and prediction of zoonoses emergence, Emerg. Infect. Dis. 11 (12) (2005) 1822–1827.
[3] F. Keesing, R.D. Holt, R.S. Ostfeld, Effects of species diversity on disease risk, Ecol. Lett. 9 (2006) 485–498.
[4] F. Keesing F, L.K. Belden, P. Daszak, A. Dobson, C.D. Harvell, R.D. Holt, P. Hudson, A. Jolles, K.E. Jones, C.E. Mitchell, S.S. Myers, T. Bogich, R.S. Ostfeld, Impacts of biodiversity on the emergence and transmission of infectious diseases, Nature 468 (2010) 647–652.
[5] C.L. Wood, A. McInturff, H.S. Young, D. Kim, K.D. Lafferty, Human infectious disease burdens decrease with urbanization but not with biodiversity, Philos. Trans. R. Soc. Lond. B Biol. Sci. 372 (2017) 1–22.
[6] D.J. Salkeld, K.A. Padgett, J.H. Jones, A meta-analysis suggesting that the relationship between biodiversity and risk of zoonotic pathogen transmission is idiosyncratic, Ecol. Lett. 16 (2013) 679–686.
[7] C.L. Wood, K.D. Lafferty, Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission, Trends Ecol. Evol. 28 (2013) 239–247.
[8] C.L. Wood, K.D. Lafferty, G. Deleo, H.S. Young, P.J. Hudson, A.M. Kuris, Does biodiversity protect humans against infectious disease? Ecology 95 (2014) 817–832.
[9] A.M. Kilpatrick, D.J. Salkeld Dj, G. Titcomb, M.B. Hahn, Conservation of biodiversity as a strategy for improving human health and well-being, Philos. Trans. R. Soc. Lond. B Biol. Sci. 372 (2017) 1–31.
[10] D.L. Angela, A.J. Kuenzi, J.N. Mills, Species diversity concurrently dilutes and amplifies transmission in a zoonotic host–pathogen system through competing mechanisms, Proc. Natl. Acad. Sci. Unit. States Am. 115 (31) (2018) 7979–7984, https://doi.org/10.1073/pnas.1807106115.
[11] B.A. Jones, D. Grace, R. Kock, S. Alonso, J. Rushton, M.Y. Said, D. McKeever, F. Mutua, J. Young, J. McDermott, D. Udo, Zoonosis emergence and agro-ecological change, Pfeiffer Proceedings of the National Academy of Sciences 110 (21) (2013) 8399–8404, https://doi.org/10.1073/pnas.1208059110.
[12] M.Q. Benedict, R.S. Levine, W.A. Hawlwy, L.P. Lounibos, Spread of the tiger: global risk of invasion by the mosquito *Aedes albopictus*, Vector Borne Zoonotic Dis. 7 (2007) 76–85.
[13] E.A. Gould, S. Higgs, Impact of climate change and other factors on emerging arbovirus diseases, Trans. R. Soc. Trop. Med. Hyg. 103 (2009) 109–121.
[14] J.A. Patz, S.H. Olson, C.K. Uejio, H.K. Gibbs, Disease emergence from global climate and land use change, Med. Clin. 92 (2008) 1473–1491.
[15] J.M. Hassell, M. I Begon, M.J. Ward, E.M. Fèvre, Urbanization and disease emergence: dynamics at the wildlife–livestock–human interface, Trends Ecol. Evol. 32 (1) (2017) 55–67, https://doi.org/10.1016/j.tree.2016.09.012.
[16] E.C. Ellis, N. Ramankutty, Putting people in the map: anthropogenic biomes of the world, Front. Ecol. Environ. 6 (2008) 439–447.
[17] W.K. Reisen, Landscape epidemiology of vector-borne diseases, Annu. Rev. Entomol. 55 (2010) 461–483.
[18] D.S. Wilcove, C. H McLellan, A. P Dobson, Habitat fragmentation in the temperate zone, in: E. Soulé (Ed.), Conservation Biology, the Science of Scarcity and Diversity, Sinaure Associates, 1986, pp. 237–256.
[19] D. Despommier, B.R. Ellis, B.A. Wilcox, The role of ecotones in emerging infectious diseases, EcoHealth 3 (2006) 281–289.
[20] H.E. Brown, M. Diuk-Wasser, T. Andrealis, D. Dish, Remotely-sensed vegetation indices identify mosquito clusters of West Nile virus vectors in an urban landscape in the northeastern United States, Vector Borne Zoonotic Dis. 8 (2008) 197–206.
[21] T. Goldberg, T.R. Gillespie, I.B. Rwego, E.L. Estoff, C.A. Chapman, Forest fragmentation as cause of bacterial transmission among nonhuman primates, humans, and livestock, Uganda, Emerg. Infect. Dis. 14 (2008) 1375–1382.
[22] R.J. Eisen, G.E. Glass, L. Eisen, J. Cheek, R.E. Enscore, P. Ettestad, K. L Gage, A spatial model of shared risk for plague and hantavirus pulmonary syndrome in the southwestern United States, Am. J. Trop. Med. Hyg. 77 (2007) 999–1004.
[23] M.B. E.S Gurley Hahn, J. H Epstein, M.S. Islam, J.A. Patz, P. Saszak, S.P. Luby, The role of landscape composition and configuration on Pteropus giganteus roosting ecology and Nipah virus spillover risk in Bangladesh, Am. J. Trop. Med. Hyg. 90 (2014) 247–255.
[24] R. K Plowright, P. Eby, P.J. Hudson, I.L. Smith, D. Westcott, W. L Bryden, D. Middleton, P.A. Reid, R.A. McFarlane, G. Martin, G.M. Tabor, L.F. Skerratt, D.L. Anderson, G. Crameri, D. Quammen, D. Jordan, P. Freeman, L.F. Wang, J.H. Epstein, G.A. Marsh, N.Y. Kung, H. McCallum, Ecological dynamics of emerging bat virus spillover, Proc. Biol. Sci. 282 (2015) 20142124, https://doi.org/10.1098/rspb.2014.2124.
[25] A. Afelt, R. Frutos, C. Devaux, Bats, coronaviruses, and deforestation: toward the emergence of novel infectious diseases? Front. Microbiol. 9 (702) (2018) 1–5, https://doi.org/10.3389/fmicb.2018.00702.
[26] K.E. Reuter, A.R. Wills, R.W. Lee, E. E Cordes, B.J. Sewall, Using stable isotopes to infer the impacts of habitat change on the diets and vertical stratification of frugivorous bats in Madagascar, PloS One 11 (2016), e0153192, https://doi.org/10.1371/journal.pone.0153192.
[27] M.G. Walsh, A. Wiethoelter, M.A. Haseeb, The impact of human population pressure on flying fox niches and the potential consequences for Hendra virus spillover, Sci. Rep. 7 (2017) 8226, https://doi.org/10.1038/s41598-017-08065-z.
[28] S. Davis, E. Calvet, Fluctuating rodent populations and risk to humans from rodent-borne zoonoses, Vector Borne Zoonotic Dis. 5 (2005) 305–314.
[29] K.L. Evans, S.E. Newson, K.J. Gaston, Habitat influences on urban avian assemblages, Ibis 151 (2009) 19–39, https://doi.org/10.1111/j.1474-919X.2008.00898.x.
[30] P.S. Warren, E. Shochat, W.A. Marussich, Trophic dynamics in urban communities, Bioscience 55 (5) (2005) 399–407, https://doi.org/10.1641/0006-3568, 055[0399:TDIUC]2.0.CO;2.
[31] J.A. Galbraith, J.R. Beggs, D.N. Jones, M.C. Stanley, Supplementary feeding restructures urban bird communities, Proc. Natl. Acad. Sci. U.S.A. 112 (2015) e2648–e2657.
[32] H.J. Han, H.L. Wen, C.M. Zhou, F.F. Chen, L.M. Luo, J.W. Liu, X.J. Yu, Bats as reservoirs of severe emerging infectious diseases, Virus Res. 205 (2015) 1–6, https://doi.org/10.1016/j.virusres.2015.05.006.
[33] A. Lacroix, V. Duong, V. Hul, S. San, H. Davun, K. Omaliss, S. Chea, A. Hassanin, A.,W. Theppangna, S. Silithammavong, K. Khammavong, S. Singhalath, Z. Greatorex, A.E. Fine, T. Goldstein, S. Olson, D.O. Joly, L. Keatts, P. Dussart, A. Afelt, R. Frutos, P. Buchy, Genetic diversity of coronavirus in bats in Lao PDR and Cambodia, Infect. Genet. Evol. 48 (2017a) 10–18, https://doi.org/10.1016/j.meegid.2016.11.029.
[34] A. Lacroix, V. Duong, V. Hul, S. San, H. Davun, K. Omaliss, S. Chea, A. Hassanin, A.,W. Theppangna, S. Silithammavong, K. Khammavong, S. Singhalath, Z. Greatorex, A.E. Fine, T. Goldstein, S. Olson, D.O. Joly, L. Keatts, P. Dussart, A. Afelt, R. Frutos, P. Buchy, Diversity of bat astroviruses in Lao PDR and Cambodia, Infect. Genet. Evol. 47 (2017b) 41–50, https://doi.org/10.1016/j.meegid.2016.1.
[35] S.J. Schrag, P. Wiener, Emerging infectious disease: what are the relative roles of ecology and evolution, Trends Ecol. Evol. 10 (1995) 319–324.
[36] N.D. Wolfe, W.M. Switzer, J.K. Carr, V.B. Bhullar, V. Shanmugam, U. Tamoufe, A.T. Prosser, J.N. Torimiro, A. Wright, E. Mpoudi-Ngole, F.E. McCutchan, D.L. Birx, T.M. Folks, D.S. Burke, W. Heneine, Naturally acquired simianretrovirus infections in central African hunters, Lancet 363 (9413) (2004) 932–937.
[37] C. Apetrei, P.A. Marx, Simian retroviral infections in human beings, Lancet 364 (2004) 137–138.
[38] B.H. Hahn, G.M. Shaw, K.M. de Cock, P.M. Sharp, AIDS as a zoonosis: scientific and public health implications, Science 287 (2000) 607–614.
[39] J.F. Drexler, V.M. Corman, C. Drosten, Ecology, evolution and classification of bat coronaviruses in the aftermath of SARS, Antivir. Res. 101 (2014) 45–56.
[40] B. Hu, X. Ge, L. Wang, Z. Shi, Bat origin of human coronaviruses, Virol. J. 12 (221) (2015) 1–10, https://doi.org/10.1186/s12985-015-0422-1.
[41] S.J. Anthony, C.K. Johnson, D.J. Greig, S. Kramer, X. Che, H. Wells, A.L. Hicks, D.O. Joly, N.D. Wolfe, P. Daszak, W. Karesh, W.I. Lipkin, S.S. Morse, P. Consortium, J.A.K. Mazet, T. Goldstein, Global patterns in coronavirus diversity, Virus Evol 3 (2017) vex012, https://doi.org/10.1093/ve/vex012.
[42] E.C. Teeling, M.S. Springer, O. Madsen, P. Bates, S.J. O'Brien, W.J. Murphy, Molecular phylogeny for bats illuminates biogeography and the fossil record, Science 307 (2005) 580–584.
[43] C.H. Calisher, J.E. Childs, H.E. Field, K.V. Holmes, T. Schountz, Bats: important reservoir hosts of emerging viruses, Clin. Microbiol. Rev. 19 (2006) 531–545.
[44] A.D. Luis, D.T. Hayman, T.J. O'Shea, P.M. Cryan, A.T. Gilbert, J.R. Pulliam, J.N. Mills, M.E. Timonin, C.K. Willis, A.A. Cunningham, A.R. Fooks, C.E. Rupprech, J.J.L. Wood, C.T. Webb, A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? Proc. Biol. Sci. 280 (2013) 20122753.
[45] T.H. Kunz, E. Braun de Torrez, D. Bauer, T. Lobova, T.H. Fleming, Ecosystem services provided by bats, Ann. N. Y. Acad. Sci. 1223 (1) (2011) 1—38, https://doi.org/10.1111/j.1749-6632.2011.06004.x.
[46] J. Schipper, J.S. Chanson, F. Chiozza, N.A. Cox, M. Hoffman, V. Katariya, et al., The status of the world's land and marine mammals: diversity, threat, and knowledge, Science 322 (5899) (2008) 225—230, https://doi.org/10.1126/science.1165115.
[47] N.B. Simmons, Personal communication. American museum of natural

history, New York, in: V. Elangevan, M. Kumar, Diversity (Eds.), Roost Selection and Ecological Importance of the Bats of Uttah Pradesh, International Day for Biological Diversity, 2015, p. 44—50.
[48] C.H. Calisher, J.E. Childs, H.E. Field, K.V. Holmes, T. Schountz, Bats: important reservoir hosts of emerging viruses, Clin. Microbiol. Rev. 19 (3) (2006) 531—545, https://doi.org/10.1128/CMR.00017-06.
[49] J.S. Mackenzie, Emerging zoonotic encephalitis viruses: lessons from Southeast Asia and Oceania, J. Neurovirol. 11 (5) (2005) 434—440, https://doi.org/10.1080/13550280591002487.
[50] T. Omatsu, S. Watanabe, H. Akashi, Y. Yoshikawa, Biological characters of bats in relation to natural reservoir of emerging viruses, Comp. Immunol. Microbiol. Infect. Dis. 30 (5–6) (2007) 357—374, https://doi.org/10.1016/j.cimid.2007.05.006.
[51] W.H. van der Poel, P.H. Lina, J.A. Kramps, Public health awareness of emerging zoonotic viruses of bats: European perspective, Vector Borne Zoonotic Dis. 6 (4) (2006) 315—324, https://doi.org/10.1089/vbz.2006.6.315.
[52] G. Wibbel, S. Speck, H. Field, Methods for assessing diseases in bats, in: T.H. Kunz, S. Parsons (Eds.), Ecological and Behavioural Methods for the Study of Bats, Johns Hopkins University Press, Baltimore, MD, 2009, pp. 775—794.
[53] S. Wong, S. Lau, P. Woo, K.Y. Yuen, Bats as a continuing source of emerging infections in humans, Rev. Med. Virol. 17 (2) (2007) 67—91, https://doi.org/10.1002/rmv.520.
[54] M.L. Reshi, Y.C. Su, J.R. Hong, RNA viruses ROS-mediated cell death, Int J Cell Biol (2014) 1—16. 467452.
[55] T.J. O'Shea, P.M. Cryan, A. Andrew, A.A. Cunningham, A.R. Fooks, D.T.S. Hayman, A.D. Luis, A.J. Peel, R.K. Plowright, J.L.N. Wood, Bat flight and zoonotic viruses, Emerg. Infect. Dis. 20 (2014) 741—745.
[56] P. Zhou, M. Tachedjian, J.W. Wynne, V. Boyd, J. Cui, I. Smith, et al., Contraction of the type I IFN locus and unusual constitutive expression of IFNalpha in bats, Proc. Natl. Acad. Sci. U. S. A. 113 (2016) 2696—2701.
[57] M. Ahn, J. Cui, A.T. Irving, L.F. Wang, Unique loss of the PYHIN gene family in bats amongst mammals: implications for inflammasome sensing, Sci. Rep. 6 (2016) 21722.
[58] J.W. Wynne, L.F. Wang, Bats and viruses: friend or foe? PLoS Pathog. 9 (2013), e1003651.
[59] E.S. Barton, D.W. White, J.S. Cathelyn, K.A. Brett-McClellan, M. Engle, M.S. Diamond, V.L. Miller, H.W. Virgin, Herpesvirus latency confers symbiotic protection from bacterial infection, Nature 447 (2007) 326—329.
[60] K. Kapp, J. Maul, A. Hostmann, P. Mundt, J.C. Preisset al, Modulation of systemic antigen-specific immune responses by oral antigen in humans, Eur. J. Immunol. 40 (2010) 3128—3137.
[61] S. Seronello, J. Montanez, K. Presleigh, M. Barlow, S.B. Park, J. Choi J, Ethanol and reactive species increase basal sequence heterogeneity of hepatitis C virus and produce variants with reduced susceptibility to antivirals, PloS One 6 (2011), e27436.
[62] V.D. Menachery, R.L. Graham, R.S Baric, Jumping species—a mechanism for coronavirus persistence and survival, Curr. Opin. Virol. 23 (2017) 1—7, https://doi.org/10.1016/j.coviro.2017.01.002.
[63] E. de Wit, N. van Doremalen, D. Falzarano, V.J. Munster, SARS and MERS: recent insights into emerging coronaviruses, Nat. Rev. Microbiol. 14 (2016) 523—534.
[64] R.S. Baric, K. Fu, M.C. Schaad, S.A. Stohlman, Establishing a genetic recombination map for murine coronavirus strain A59 complementation groups, Virology 177 (1990) 646—656.
[65] B. Hu, L.P. Zeng, X.L. Yang, X.Y. Ge, W. Zhang, B. Li, et al., Discovery of a rich gene pool of bat SARS-related coronaviruses provides new insights into the origin of SARS coronavirus, PLoS Pathog. 13 (2017), e1006698.
[66] Y. Tao, M. Shi, C. Chommanard, K. Queen, J. Zhang, W. Markotter, I.V. Kuzmin, et al., Surveillance of bat coronaviruses in Kenya identifies relatives of human coronaviruses NL63 and 229E and their recombination history, J. Virol. 91 (5) (2017) 16, https://doi.org/10.1128/JVI.01953-16, e01953.
[67] C.K. Willis, R.M. Brigham, Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat, Behav. Ecol. Sociobiol. 62 (2007) 97—108.
[68] J. Serra-Cobo, M. López-Roig, M. Seguí, L.P. Sánchez, J. Nadal, et al., Ecological factors associated with European bat Lyssavirus Seroprevalence in Spanish bats, PloS One 8 (5) (2013), e64467.
[69] B. Amengual, h. Bourhy, m. López-Roig, J. Serra-Cobo, Temporal dynamics of European bat Lyssavirus type 1 and survival of Myotis myotis bats in natural colonies, PloS One 6 (2007) e566.
[70] E.L. Delwart, Viral metagenomics, Rev. Med. Virol. 17 (2007) 115—131, https://doi.org/10.1002/rmv.532.
[71] C.M. Davy, M.E. Donaldson, S. Subudhi, N. Rapin, L. Warnecke, J.M. Turner, T.K. Bollinger, C.J. Kyle, N.A.S. Dorville, E.L. Kunkel, et al., White-nose syndrome is associated with increased replication of a naturally persisting coronaviruses in bats, Sci. Rep. 8 (2018) 15508, https://doi.org/10.1038/s41598-018-33975-x.
[72] G. Brearley, J. Rhodes, A. Bradley, G. Baxter, L. Seabrook, D. Lunney, Y. Liu, C. McAlpine, Wildlife disease prevalence in human-modified landscapes, Biol. Rev. 88 (2013) 427—442.
[73] I. Smith, L.F. Wang, Bats and their virome: an important source of emerging viruses capable of infecting humans, Current Opinion in Virology 3 (2013) 84—91.
[74] K.B. Chua, B.H. Chua, C.W. Wang, Anthropogenic deforestation, El Niño and the emergence of Nipah virus in Malaysia, Malays. J. Pathol. 24 (2002) 15—21.
[75] S.K.P. Lau, K.S.M. Li, Y. Huang, C.T. Shek, H. Tseet al, Ecoepidemiology and complete genome comparison of different strains of severe acute respiratory syndrome-related Rhinolophus bat coronavirus in China reveal bats as a reservoir for acute, self-limiting infection that allows recombination events, J. Virol. 84 (2010) 2808—2819.
[76] S.k. Lau, P.C. Woo, K.S. Li, Y. Huang, M. Wang, C.S. Lam, H. Xu, R. Guo, K.H. Chan, B.J. Zheng, et al., Complete genome sequence of bat coronavirus HKU2 from Chinese horseshoe bats revealed a much smaller spike gene with a different evolutionary lineage from the rest of the genome, Virology 367 (2007) 428—439.
[77] S.K.P. Lau, L. Zhang, H.K.H. Luk, L. Xiong, X. Peng, K.S.M. Li, et al., Receptor usage of a novel bat lineage C betacoronavirus reveals evolution of Middle East respiratory syndrome-related coronavirus spike proteins for human dipeptidyl peptidase 4 binding, J. Infect. Dis. 218 (2018) 197—207.
[78] S.K. Lau, K.S. Li, A.K. Tsang, C.T. Shek, et al., Recent transmission of a novel alphacoronavirus, bat coronavirus HKU10, from Leschenault's rousettes to pomona leaf-nosed bats: first evidence of interspecies transmission of coronavirus between bats of different suborders, J. Virol. 86 (2012) 11906—11918.
[79] P.C. Woo, S.K. Lau, K.S. Li, R.W. Poon, B.H. Wong, H.W. Tsoiet al, Molecular diversity of coronaviruses in bats, Virology 351 (2006) 180—187.
[80] P.C. Woo, M. Wang, S.K. Lau, H. Xu, R.W. Poon, et al., Comparative analysis of twelve genomes of three novel group 2c and group 2d coronaviruses reveals unique group and subgroup features, J. Virol. 81 (2007) 1574—1585.
[81] S.J. Anthony, K. Gilardi, V.D. Menachery, T. Goldstein, B. Ssebide, R. Mbabazi, I. Navarrete-Macias, E. Liang, et al., Further evidence for bats as the evolutionary source of Middle East Respiratory Syndrome coronavirus, mBio 8 (2) (2017) 17, https://doi.org/10.1128/mBio.00373-17, e00373.
[82] X.L. Yang, B. Hu, B. Wang, M.N. Wang, Q. Zhang, W. Zhang, et al., Isolation and characterization of a novel bat coronavirus closely related to the direct progenitor of severe acute respiratory syndrome coronavirus, J. Virol. 90 (2015) 3253—3256.
[83] L. Yang, Z. Wu, X. Ren, F. Yang, J. Zhang, G. He, J. Dong, et al., MERS-related betacoronavirus in Vespertilio superans bats, China, Emerg, Inf. Disp. 20 (2014) 1260—1262.
[84] A. Moreno, D. Lelli, L. De Sabato, G. Zaccaria, A. Boni, E. Sozzi, A. Prosperi, et al., Detection and full genome characterization of two beta CoV viruses related to Middle East respiratory syndrome from bats in Italy, Virol. J. 14 (239) (2018) 1—11.
[85] C. Huang, W.J. Liu, W. Xu, T. Jin, Y. Zhao, J. Song, Y. Shi, et al., A bat-derived putative cross-family recombinant coronavirus with a reovirus gene, PLoS Pathog. 12 (9) (2016), e1005883, https://doi.org/10.1371/journal.ppat.1005883.
[86] V.M. Corman, N.L. Ithete, L.R. Richards, M.C. Schoeman, W. Preiser, C. Drostenet al, Rooting the phylogenetic tree of Middle East respiratory syndrome coronavirus by characterization of a conspecific virus from an african bat, J. Virol. 88 (2014) 11297—11303.
[87] P. De Benedictis, S. Marciano, D. Scaravelli, P. Priori, B. Zecchin, I. Capua, I. Monne, G. Cattoli, Alpha and lineage C betaCoV infections in Italian bats, Virus Gene. 48 (2014) 366—371.
[88] M. Bourgarel, D.M. Pfukenyi, V. Boue, L. Talignani, N. Chiweshe, F. Diop, A. Caron, G. Matope, D. Misse, F. Liegeois, Circulation of alphacoronavirus, betacoronavirus and paramyxovirus in hipposideros bat species in Zimbabwe, Infect. Genet. Evol. 58 (2018) 253—257.
[89] D. Lelli, A. Papetti, C. Sabelli, E. Rosti, A. Moreno, M.B. Boniotti, Detection of coronaviruses in bats of various species in Italy, Viruses 5 (2013) 2679—2689.
[90] A. Falcon, S. Vazquez-Moron, I. Casas, C. Aznar, G. Ruiz, F. Pozo, P. Perez-Brena, J. Juste, C. Ibanez, et al., Detection of alpha and betacoronaviruses in multiple Iberian bat species, Arch. Virol. 156 (2011) 1883—1890.
[91] S. Tsuda, S. Watanabe, J.S. Masangkay, T. Mizutani, P. Alviola, N. Ueda, K. Iha, S. Taniguchi, H. Fujii, et al., Genomic and serological detection of bat coronavirus from bats in the Philippines, Arch. Virol. 157 (2012) 2349—2355.
[92] C.S. Smith, C.E. de Jong, J. Meers, J. Henning, L. Wang, H.E. Field, Coronavirus Infection and Diversity in Bats in the Australasian Region, EcoHealth vol. 13 (2016) 72—82.
[93] C.V. Carrington, J.E. Foster, H.C. Zhu, J.X. Zhang, et al., Detection and phylogenetic analysis of group 1 coronaviruses in South American bats, Emerg, Inf. Disp. 14 (2008) 1890—1893.
[94] J. Suzuki, R. Sato, T. Kobayashi, T. Aoi, R. Harasawa, Group B betacoronavirus in rhinolophid bats, Japan, J. Vet. Med. Sci. 76 (2014) 1267—1269.
[95] A. Lacroix, V. Duong, V. Hul, S. San, H. Davun, K. Omaliss, et al., Genetic diversity of coronaviruses in bats in Lao PDR and Cambodia, Infect. Genet. Evol. 48 (2017) 10—18.
[96] Y. Tao, M. Shi, C. Chommanard, K. Queen, J. Zhang, W. Markotter, I.V. Kuzmin, E.C. Holmes, S. Tong, Surveillance of bat coronaviruses in Kenya identifies relatives of human coronaviruses NL63 and 229E and their recombination history, J. Virol. 91 (5) (2017) 16, e01953.
[97] R.J. De Groot, S.C. Baker, R. Baric, L. Enjuanes, A.E. Gorbalenya, K.V. Holmes, S. Perlman, L. Poon, P.J.M. Rottier, P.J. Talbot, et al., Family coronaviridae, in: A.M.Q. King, M.J. Adams, E.B. Carstens, E.J. Lefkowitz (Eds.), Virus Taxonomy, Classification and Nomenclature of Viruses. Ninth Report of the International Committee on Taxonomy of Viruses, first ed., Elsevier Academic Press, San Diego, CA, USA, 2011, pp. 806—828.
[98] ICTV Taxonomy History, Cornidovirineae, 2019. https://talk.ictvonline.org/

taxonomy/p/taxonomy-history?taxnode_id=20186105.
[99] P.C. Woo, S.K. Lau, C.S. Lam, C.C. Lau, A.K. Tsang, J.H. Lau, R. Bai, J.L. Teng, C.C. Tsang, M. Wang, et al., Discovery of seven novel Mammalian and avian coronaviruses in the genus deltacoronavirus supports bat coronaviruses as the gene source of alphacoronavirus and betacoronavirus and avian coronaviruses as the gene source of gammacoronavirus and deltacoronavirus, J. Virol. 86 (2012) 3995–4008.
[100] Z. Wu, L. Yang, X. Ren, G. He, J. Zhang, J. Yang, Z. Qian, J. Dong, L. Sun, Y. Zhu, et al., Deciphering the bat virome catalog to better understand the ecological diversity of bat viruses and the bat origin of emerging infectious diseases, ISME J. 10 (2016) 609–620.
[101] S.K.P. Lau, P.C.Y. Woo, K.S.M. Li, Y. Huang, H.W. Tsoi, B.H.L. Wong, S.S.Y. Wong, et al., Severe acute respiratory syndrome coronavirus-like virus in Chinese horseshoe bats, Proc. Natl. Acad. Sci. U.S.A. 102 (2005) 14040–14045.
[102] K.P. Dhondt, B. Horvat, Henipavirus infections: lessons from animal models, Pathogens 2 (2013) 264–287.
[103] S. Subudhi, N. Rapin, T.K. Bollinger, J.E. Hill, M.E. Donaldson, C.M. Davy, L. Warnecke, et al., A persistently infecting coronavirus in hibernating Myotis lucifugus, the North American little brown bat, J. Gen. Virol. 98 (2017) 2297–2309.
[104] S. Watanabe, J.S. Masangkay, N. Nagata, S. Morikawa, T. Mizutani, S. Fukushi, P. Alviola, T. Omatsu, N. Ueda, et al., Bat coronaviruses and experimental infection of bats, the Philippines, Emerg. Infect. Dis. 16 (2010) 1217–1223.
[105] J. Jeong, C.S. Smith, A.J. Peel, R.K. Plowright, D.H. Kerlin, J. McBroom, H. McCallum, Persistent infections support maintenance of a coronavirus in a population of Australian bats (Myotis macropus), Epidemiol, Infect 145 (2017) 2053–2061.
[106] R.J. Hall, J. Wang, M. Peacey, N.E. Moore, K. McInnes, D.M. Tompkins, New alphacoronavirus in Mystacina tuberculata bats, New Zealand, Emerg. Infect. Dis. 20 (2014) 697–700.
[107] S.J. Anthony, R. Ojeda-Flores, O. Rico-Chavez, I. Navarrete-Macias, C.M. Zambrana-Torrelio, M.K. Rostal, J.H. Epstein, T. Tipps, et al., Coronaviruses in bats from Mexico, J. Gen. Virol. 94 (2013) 1028–1038.
[108] K. Fischer, V. Zeus, L. Kwasnitschka, G. Kerth, M. Haase, M.H. Groschup, A. Balkema-Buschmann, Insectivorous bats carry host specific astroviruses and coronaviruses across different regions in Germany, Infect. Genet. Evol. 37 (2016) 108–116.
[109] E. Monchatre-Leroy, F. Boue, J.M. Boucher, C. Renault, F. Moutou, M. Ar Gouilh, M.,G. Umhang, Identification of alpha and beta coronavirus in wildlife species in France: bats, rodents, rabbits, and hedgehogs, Viruses 9 (2017) 364.
[110] S. Wacharapluesadee, P. Duengkae, A. Rodpan, T. Kaewpom, P. Maneeorn, B. Kanchanasaka, S. Yingsakmongkon, et al., Diversity of coronavirus in bats from Eastern Thailand, Virol. J. 12 (57) (2015) 1–7.
[111] S. Wacharapluesadee, C. Sintunawa, T. Kaewpom, K. Khongnomnan, K.J. Olival, J.H. Epstein, A. Rodpan, et al., Group C betacoronavirus in bat guano fertilizer, Thailand, Emerg, Inf. Disp. 19 (2013) 1349–1351.
[112] X.Y. Ge, N. Wang, W. Zhang, B. Hu, B. Li, Y.Z. Zhang, J.H. Zhou, et al., Coexistence of multiple coronaviruses in several bat colonies in an abandoned mineshaft, Virol. Sin. 31 (2016) 31–40.
[113] X.Y. Ge, J.L. Li, X.L. Yang, A.A. Chmura, G.J. Zhu, J.H. Epstein, J.K. Mazet, B. Hu, W. Zhang, C. Peng, et al., Isolation and characterization of a bat SARS-like coronavirus that uses the ACE2 receptor, Nature 503 (2013) 535–550.
[114] S.K. Lau, Y. Feng, H. Chen, H.K. Luk, W.H. Yang, K.S. Li, Y.Z. Zhang, et al., Severe acute respiratory syndrome (SARS) coronavirus ORF8 protein is acquired from SARS-related coronavirus from greater horseshoe bats through recombination, J. Virol. 89 (2015) 10532–10547.
[115] W.D. Li, Z.L. Shi, M. Yu, W.Z. Ren, C. Smith, J.H. Epstein, H.Z. Wang, G. Crameri, Z.H. Hu, H.J. Zhang, et al., Bats are natural reservoirs of SARS-like coronaviruses, Science 310 (2005) 676–679.
[116] B. He, Y. Zhang, L. Xu, W. Yang, F. Yang, Y. Feng, L. Xia, L.J. Zhou, J.,W. Zhen, Y. Feng, et al., Identification of diverse alphacoronaviruses and genomic characterization of a novel severe acute respiratory syndrome-like coronavirus from bats in China, J. Virol. 88 (2014) 7070–7082.
[117] X.C. Tang, J.X. Zhang, S.Y. Zhang, P. Wang, X.H. Fan, L.F. Li, G. Li, B.Q. Dong, W. Liu, C.L. Cheung, et al., Prevalence and genetic diversity of coronaviruses in bats from China, J. Virol. 80 (2006) 7481–7490.
[118] W. Ren, W.D. Li, M. Yu, P. Hao, Y. Zhang, P. Zhou, S.Y. Zhang, G.P. Zhao, Y. Zhong, S.Y. Wang, et al., Full-length genome sequences of two SARS-like coronaviruses in horseshoe bats and genetic variation analysis, J. Gen. Virol. 87 (2006) 3355–3359.
[119] J.F. Yuan, C.C. Hon, Y. Li, D.M. Wang, G.L. Xu, H.J. Zhang, P. Zhou, L.L.M. Poon, T.T.Y. Lam, et al., Intraspecies diversity of SARS-like coronaviruses in Rhinolophus sinicus and its implications for the origin of SARS coronaviruses in humans, J. Gen. Virol. 91 (2010) 1058–1062.
[120] X.L. Yang, B. Hu, B. Wang, B.,M.N. Wang, Q. Zhang, W. Zhang, L.J. Wu, X.Y. Ge, et al., Isolation and characterization of a novel bat coronavirus closely related to the direct progenitor of severe acute respiratory syndrome coronavirus, J. Virol. 90 (2016) 3253–3256.
[121] D. Hu, C.Q. Zhu, L.L. Ai, T. He, Y. Wang, F.Q. Ye, L. Yang, C.X. Ding, et al., Genomic characterization and infectivity of a novel SARS-like coronavirus in Chinese bats, Emerg. Microb. Infect. 7 (2018) 154.
[122] L. Yang, Z.Q. Wu, X.W. Ren, F. Yang, G.M. He, J.P. Zhang, et al., Novel SARS-like betacoronaviruses in bats, China, 2011, Emerg. Infect. Dis. 19 (2013) 989–991.
[123] J.F. Drexler, F. Gloza-Rausch, J. Glende, V.M. Corman, D. Muth, M. Goettsche, A. Seebens, M. Niedrig, S. Pfefferle, S. Yordanov, et al., Genomic characterization of severe acute respiratory syndrome-related coronavirus in European bats and classification of coronaviruses based on partial RNA-dependent RNA polymerase gene sequences, J. Virol. 84 (2010) 11336–11349.
[124] S. Lee, S.D. Jo, K. Son, I. An, J. Jeong, S.J. Wang, Y. Kim, W. Jheong, J.K. Oem, Genetic characteristics of coronaviruses from Korean bats in 2016, Microb. Ecol. 75 (2018) 174–182.
[125] H. Zhou, H. Chen, T. Hu, J. Li, H. Song, Y. Liu, et al., A novel bat coronavirus closely related to SARS-CoV-2 contains natural insertions at the S1/S2 cleavage site of the spike protein, Curr. Biol. 30 (11) (2020) 2196–2203.
[126] D.K. Chu, J.S. Peiris, H. Chen, Y. Guan, L.L. Poon, Genomic characterizations of bat coronaviruses (1A, 1B and HKU8) and evidence for co-infections in Miniopterus bats, J. Gen. Virol. 89 (2008) 1282–1287.
[127] P. Zhou, H. Fan, T. Lan, X.L. Yang, W.F. Shi, W. Zhang, Y. Zhu, Y.W. Zhang, Q.M. Xie, S. Mani, et al., Fatal swine acute diarrhoea syndrome caused by an HKU2-related coronavirus of bat origin, Nature 556 (2018) 255–258.
[128] X.L. Yang, C.W. Tan, D.E. Anderson, R.D. Jiang, B. Li, W. Zhang, Zhu, X.F. Lim, P. Zhou, X.L. Liu, et al., Characterization of a filovirus (Mengla virus) from Rousettus bats in China, Nat. Microbiol. (2019), https://doi.org/10.1038/s41564-018-0328-yPMID:30617348.
[129] Y. Luo, B. Li, R.D. Jiang, B.J. Hu, D.S. Luo, G.J. Zhu, B. Hu, H.Z. Liu, Y.Z. Zhang, et al., Longitudinal surveillance of betacoronaviruses in fruit bats in yunnan province, China during 2009–2016, Virol. Sin. 33 (2018) 87–95.
[130] S. Crotty, C.E. Cameron, R. Andino, RNA virus error catastrophe: direct molecular test by using ribavirin, Proc. Natl. Acad. Sci. U. S. A. 98 (2001) 6895–6900.
[131] M.R. Denison, R.L. Graham, E.F. Donaldson, L.D. Eckerle, R.S. Baric, Coronaviruses: an RNA proofreading machine regulates replication fidelity and diversity, RNA Biol. 8 (2011) 270–279.
[132] K.M. Peck, C.L. Burch, M.T. Heise, R.S. Baric, Coronavirus host range expansion and middle east respiratory syndrome coronavirus emergence: biochemical mechanisms and evolutionary perspectives, Annu Rev Virol 2 (2015) 95–117.
[133] G. Lu, Q. Wang, G.F. Gao, Bat-to-human: spike features determining 'host jump' of coronaviruses SARS-CoV, MERSCoV, and beyond, Trends Microbiol. 23 (2015) 468–478.
[134] M.M. Becker, R.L. Graham, E.F. Donaldson, B. Rockx, A.C. Sims, T. Sheahan, R.J. Pickles, D. Corti, R.E. Johnston, et al., Synthetic recombinant bat SARS-like coronavirus is infectious in cultured cells and in mice, Proc. Natl. Acad. Sci. U. S. A. 105 (2008) 19944–19949.
[135] V.D. Menachery, B.L. Yount Jr., K. Debbink, S. Agnihothram, L.E. Gralinski, J.A. Plante, et al., A SARS-like cluster of circulating bat coronaviruses shows potential for human emergence, Nat. Med. 21 (2015) 1508–1513.
[136] V.D. Menachery, B.L. Yount Jr., A.C. Sims, K. Debbink, S.S. Agnihothram, L.E. Gralinski, R.L. Graham, et al., SARS-like WIV1-CoV poised for human emergence, Proc. Natl. Acad. Sci. U. S. A. 113 (2016) 3048–3053.
[137] A.L. Totura, R.S. Baric, SARS coronavirus pathogenesis: host innate immune responses and viral antagonism of interferon, Curr Opin Virol 2 (2012) 264–275.
[138] X.M. Zhang, K.G. Kousoulas, J. Storz J, The hemagglutinin/esterase gene of human coronavirus strain OC43: phylogenetic relationships to bovine and murine coronaviruses and influenza C virus, Virology 186 (1992) 318–323.
[139] A. Klausegger, B. Strobl, G. Regl, A. Kaser, W. Luytjes, R. Vlasak, Identification of a coronavirus hemagglutinin-esterase with a substrate specificity different from those of influenza C virus and bovine coronavirus, J. Virol. 73 (1999) 3737–3743.
[140] W.B. Yu, G.D. Tang, L. Zhang, R.T. Corlett, Decoding the evolution and transmissions of the novel pneumonia coronavirus (SARS-CoV-2/HCoV-19) using whole genomic data, Zool. Res. 41 (2020) 247–257.
[141] J. Schipper, J.S. Chanson, F. Chiozza, N.A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A.S.L. Rodrigues, S.N. Stuart, H.J. Temple, J. Baillieet al, The status of the world's land and marine mammals: diversity, threat, and knowledge source, Science New Series 322 (5899) (2008) 225–230.
[142] S. Mickleburgh, K. Waylen, P. Racey, Bats as bushmeat: a global review, Oryx 43 (2) (2009) 217–234, https://doi.org/10.1017/S0030605308000938.
[143] A.C. Breed, J. Meers, I. Sendow, K.N. Bossart, J.A. Barr, I. Smith, et al., The distribution of 671 henipaviruses in southeast Asia and Australasia: is wallace's line a barrier to Nipah 672 virus? Schnell MJ editor, PloS One 8 (2013), e61316, https://doi.org/10.1371/journal.pone.0061316.
[144] S. Heinrichs, Sulawesi Fruit Bat Conservation and EducationCampaign. Unpublished Report for Fauna & Flora International 100% Fund, Fauna & Flora International, Cambridge, UK, 2004.
[145] S. Broad, T. Mulliken, D. Roe, Nature and extent of legal illegal trade in wildlife, in: S. Oldfield (Ed.), The Trade in Wildlife: Regulation for Conservation, Earthscan Publications Ltd., UK, 2003, pp. 3–20.
[146] C.R. Shepherd, The bird trade in Medan, north Sumatra: an overview, Birding ASIA 5 (2006) 16–24.
[147] S.M. Sheherazade, S.M. Tsang, Quantifying the bat bushmeat trade in North Sulawesi, Indonesia, with suggestions for conservation action, Glob. Ecol. Conserv. 3 (2015) 324e330.
[148] R.B. Stuebing, A checklist of the snakes of Borneo, Raffles Bull. Zool. 39 (1991) 324–362.

[149] E.J. Milner-Gulland, E.J. Clayton, The trade in babirusa sand wild pigs in North Sulawesi Indonesia, Ecol. Econ. 42 (2002) 165–183.
[150] S. Churchill, Australian Bats, Jacana Books, CrowsNest, 2008.
[151] A.A. Eudey, The crab-eating macaque (Macaca fascicularis): widespread and rapidly declining, Primate Conserv. 23 (2008) 129–132.
[152] N.Q. Huong, N.T.T. Nga, N.V. Long, B.D. Luu, et al., Coronavirus Testing Indicates Transmission Risk Increases along 1 Wildlife Supply Chains for Human Consumption in Viet Nam, 2013-2014, https://doi.org/10.1101/2020.06.05.098590doi. BioRix preprint 2020.
[153] FAO (Food and Agriculture Organization of the United Nations), Wildlife Farming in Viet Nam: Southern Viet Nam's Wildlife Farm Survey Report in a Glance, 2014. http://www.fao.org/3/a-az118e.pdf.
[154] S.I. Roberton, T. Tran, F. Momberg, Hunting and Trading Wildlife: an Investigation into the Wildlife Trade in and Around the Pu Mat National Park, Nghe an Province, Vietnam, SFNC Project Management Unit, Nghe An, Vietnam, 2003.
[155] L. Swift, P.R. Hunter, A.C. Lees, D.J. Bell, Wildlife trade and the emergence of infectious diseases, EcoHealth 4 (2007) 25–30, https://doi.org/10.1007/s10393-006-0076-y.
[156] CBNRM Learning Institute, Emerging Trends, Challenges and Innovations for CBNRM in Cambodia, CBNRM 2nd. Advanced Persistent Threat, Phnom Penh, 2009. https://static1.squarespace.com/static/593a250a15d5dbd460e153ad/t/593f6abcf7e0ab6a55576 40e571/1497328395206/Emerging+trends-challenges-and-innovations-English-2009.pdf.
[157] N.M. Furey, Designing homes for tropical bats. Scientists explore artificial roosts for rebuilding forests, Bats 30 (2012) 7–9.
[158] Z.F. Greatorex, S.H. Olson, S. Singhalath, S. Silithammavong, et al., Wildlife trade and human health in Lao PDR: an assessment of the zoonotic disease risk in markets, PloS One 11 (2016), e0150666, https://doi.org/10.1371/journal.pone.015066.
[159] N. Huber, V. Marasco, J. Painer, S.G. Vetter, F. Göritz, P. Kaczensky, et al., Leukocyte coping capacity: an integrative parameter for wildlife welfare within conservation interventions, Front Vet Sci 6 (2019) 1–10, https://doi.org/10.3389/fvets.2019.00105.
[160] C. M Francis, A. Guillen, M.F. Robinson, Order Chiroptera: bats, in: Wildlife in Lao PDR, Status Report (Compilers J.W. Duckworth, R.E. Salter & K. Khounboline), IUCN, Wildlife Conservation Society and Centre for Protected Areas and Watershed Management, Vientiane, Lao PDR, 1999, pp. 225–235.
[161] M.F. Robinson, Observation on the wildlife trade at the daily market in Chiang Khan, northeast Thailand, Nat. Hist. Bull. Siam Soc. 42 (1994) 117–120.
[162] A. Lacroix, V. Duong, V. Hul, S. San, H. Davun, et al., Genetic diversity of coronaviruses in bats in Lao PDR and Cambodia, Infect. Genet. Evol. 48 (2017) 10–18.
[163] X.c. Tang, J.X. Zhang, S.Y. Zhang, P. Wang, X.H. Fan, L.F. Li, G. Li, B.Q. Dong, W. Liu, C.L. Cheung, K.M. Xu, et al., Prevalence and genetic diversity of coronaviruses in bats from China, J. Virol. 80 (2006) 7481–7490.
[164] K. Fischer, V. Zeus, L. Kwasnitschka, G. Kerth, M. Haase, M.H. Groschup, A. Balkema-Buschmann, Insectivorous bats carry host specific astroviruses and coronaviruses across different regions in Germany, Infect. Genet. Evol. 37 (2016) 108–116.
[165] H.J. Stibig, F. Stolle, R. Dennis, C. Feldkötter, Forest cover change in Southeast Asia—the regional pattern, JRC Sci. Tech. Rep. EUR 22896 (2007) 1–52.
[166] J. Broadhead, R. Izquierdo, Assessment of Land Use, Forest Policy and Governance in Cambodia, FAO-Regional Office for Asia and the Pacific, Thailand, 2010.
[167] K. Suwannarong, S. Schuler, Bat consumption in Thailand, Infect. Ecol. Epidemiol. 6 (2016) 29941, https://doi.org/10.3402/iee.v6.29941.
[169] K. Suwannarong, S. Chanabun, P. Kanthawee, Sa Khiewkhern, P. Boonyakawee, K. Suwannarong, C. Saengkul, N. Bubpa, A. Amonsin, Risk factors for bat contact and consumption behaviors in Thailand: a quantitative study, BMC Publ. Health 20 (841) (2020) 1–13, https://doi.org/10.1186/s12889-020-08968-z.
[170] G.E. Shively, Poverty, technology, and wildlife hunting in Palawan, Environ. Conserv. 24 (1997) 57–63.
[171] K.C. Tanalgo, J.A.G. Tabora, Cave-dwelling bats (mammalia: Chiroptera) and conservation concerns in south central mindanao, Philippines, J. Threat. Taxa 7 (2015) 8185–8194, https://doi.org/10.11609/jott.1757.7.15.8185-8194.
[172] K.C. Tanalgo, M.J.M. Achondo, B.L.P. Bretaña, L.R. Fernadez-Casim, J.A.G. Tabora, Wing ecomorphology and flight performance of bats in pisan caves, kabacan, north cotabato, Philippines, Asian Journal of Biodiversity 3 (2015) (2011) 13–125.
[173] L. Zhang, G. Zhu, G. Jones, S. Zhang, Conservation of bats in China: problems and recommendations, Oryx 43 (2009) 179–182.
[174] Q. Zhou, C. Yuelin, Guangzhou bat and bat cultural investigation (广州蝙蝠与"蝠"文化调查), Guangdong Agricultural Sciences 4 (2012).
[175] C. Zhang, Y. Wu, Analysis of Guangzhou citizen's cognition and eating condition of bats and birds, Sichuan J. Zool. 26 (1) (2007).
[176] Beiwan New Vision Network. https://www.takefoto.cn/viewnews-2292269.html, 2020.
[177] T.M. Wassenaar, Y. Zou, 2019_nCoV/SARS-CoV-2: rapid classification of betacoronaviruses and identification of Traditional Chinese Medicine as potential origin of zoonotic coronaviruses, Lett. Appl. Microbiol. 70 (2020) 342–348.
[178] M.S. Fujita, M.D. Tuttle, Flying foxes (Chiroptera: pteropodidae): threatened animals of key ecological and economic importance, Conserv. Biol. 5 (1991) 455–463, https://doi.org/10.1111/j.1523-1739.1991.tb00352.x.
[179] J. Damas, G.M. Hughes, K.C. Keough, C.A. Painter, N.S. Persky, et al., Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates, Proc Natl Acad Sci U S A 117 (36) (2020) 22311–22322, https://doi.org/10.1073/pnas.2010146117.
[180] K.A. Phillips, L. Karen, J.P. Bales, J.P. Capitanio, A. Conley, et al., Why primate models matter, Am. J. Primatol. 76 (9) (2014) 801–827, https://doi.org/10.1002/ajp.22281.