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REVIEW

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What do studies in wild mammals tell us about human emerging viral diseases in Mexico?

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Abstract

Multiple species of viruses circulate in wild mammals, some of them potentially causing zoonosis. Most of the suspected viral zoonotic diseases affecting human patients remain unidentified with regard to their aetiological agent. The aim of this study is to summarize the state of knowledge of the viral richness associated with wild mammals in Mexico throughout 1900–2018 and their relationship with human cases. We compiled two databases, one of them containing all available published studies on potentially zoonotic viruses in wild mammals and another with human cases related to zoonotic viruses. The database on wild mammals covers the period of 1900–2018; the human case database spans 2000–2013. We calculated the richness of viral potential zoonotic agents and evaluated their geographical distribution. We found 262 records of 42 potential zoonotic viral species associated with 92 wild mammal species in 28 states across Mexico. Records of human viral cases were only found in 29 states, which did not overlap with the reports in wild mammals. We detected 25.6% (42/164) of viral zoonotic agents reported worldwide. This analysis opens a relevant topic of discussion for public health attention.

KEYWORDS
historical analysis, hosts, Mexican wild mammals, reservoirs, virus, zoonosis

1 | INTRODUCTION

Viruses are one of the most diverse groups of microorganisms and also one of the most difficult to study, given their small size and their dependence on host cells (Lefkowitz, Davidson, Sabanadzovic, Siddell, & Simmonds, 2017; Zhang, Shi, & Holmes, 2018; Zhang, Wu, Shi, & Holmes, 2018). The inventory of viral species has increased exponentially in recent decades with the advent of new research tools such as molecular tests and massive parallel sequencing (e.g. metagenomics, Zhang, Shi, et al., 2018). According to the latest review by The International Committee on Taxonomy on Viruses (Lefkowitz et al., 2017), a total of 4,843 species of viruses have been recognized. However, estimations show more than 1.6 millions of mammalian and waterfowl viruses in 25 families that can cause human infections (Carroll et al., 2018). To now, approximately 75% of all known species infect eukaryotic cells, and only 164 viral species are considered as zoonotic species (Taylor, Latham, & Woolhouse, 2001).

Most of these viral diseases are zoonosis (which have gained widespread attention given their mortality rate and lethality, in some cases) circulating in wildlife, and particularly in wild mammals (Cleaveland, Laurenson, & Taylor, 2001; Daszak, Cunningham, & Hyatt, 2000; Han, Kramer, & Drake, 2016). Given our close contact with mammalian groups such as rodents, bats and ungulates, we can assume that many of these

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viral pathogens recorded in wildlife populations can come into contact and spread into human populations under particular circumstances. Some examples of this include SARS [Severe acute respiratory syndrome] (Chan & Chan, 2013), hantavirus (Byers, 2018) and rabies (Begeman et al., 2018).

It is noteworthy that in Mexico the Ministry of Health has reported an important number of patients with suspected viral diseases without identification of the aetiological agent (CENAVECE, 2013). For this reason, the aim of this study was to summarize the state of knowledge of the viral richness associated with wild mammals in Mexico and the possible relationship with human cases recorded in the country.

2 | MATERIAL AND METHODS

2.1 | Species occurrence database

We compiled a database of all the published studies we could identify through a literature search that focused on potential human zoonotic viral species associated with wild mammals in Mexico during the period of 1900–2018. We consider as potential zoonotic viral species those which belong to the viral families of viral species listed by Taylor et al. (2001). For this step, an exhaustive literature research, using the following specialized databases: BioOne, Elsevier, HighWire, Iris, JSTOR, PubMed, Scopus, SpringerLink, Wiley Online, Web of Science and Zoological Records, was carried out. For this, a combination of several keywords: "virus", "wild", "mammals", "pathogens" and "Mexico" were used. Only those papers that met all of the following specifications were considered: (a) studies on wild mammals that occur and were sampled in Mexico, (b) viral species identification (at least at genus level) and (c) viral agent considered as zoonotic or potentially zoonotic.

The following information was recorded from each study:

- Family, genus and species of potential zoonotic viruses. The nomenclature used is in accordance with the 10th report of The International Committee on Taxonomy of Viruses' review (Lefkowitz et al., 2017).
- Order, family, genus and species of the mammalian host. Mammalian nomenclature was updated following the most recent taxonomical review for both terrestrial (Ramírez-Pulido, González-Ruíz, Gardner, & Arroyo-Cabrales, 2014) and marine mammals (Ceballos & Arroyo-Cabrales, 2012).
- Disease caused by the viral species, and whether it has been reported as human disease based on ICD-10 (WHO, 2008).
- Locality and collection date.

We gathered spatial coordinate data for the reported localities or geo-referenced all localities from studies which did not provide spatial coordinates using the Fallingrain electronic catalogue for localities (http://www.fallingrain.com/world/index.html), and corroborated with Google Earth software, following the best practices for geo-referencing described in Chapman and Wieczorek (2006).

2.2 | Human disease records

We obtained data of human cases with viral zoonotic diseases reported in Mexico during 2000–2013 from the 'National Health Information System [Sistema Nacional de Información en Salud] (SINAIS)' published by the Mexican Ministry of Health [Secretaría de Salud] (CENAVECE, 2013). The SINAIS concentrates the relation of hospital intakes and discharges registered by the Ministry of Health of Mexico. These records correspond only to patients who were hospitalized, in which the sex, age, district, the disease causing the admission and the possible associated pathologies according to the international classification of diseases (WHO, 2008) were recorded. However, the database does not specify the method of identification of the pathogen (e.g. serology, molecular biology). The data do not include names or personal identification data of individual patients.

All reports obtained from the SINAIS database were classified in accordance with the International Statistical Classification of Diseases and Related Health Problems [ICD-10] (WHO, 2008). All the cases were geo-referenced to locality level based on the 'Catalogue of Keys from the Federal States, Municipalities and Localities' [Catálogo Único de Claves de Áreas Geoestadísticas Estatales, Municipales y Localidades] (INEGI, 2013), a nationwide database of spatially comparable and interoperable geo-statistical units.

2.3 | Database analyses

For wild mammals in Mexico, we evaluated the richness of potential zoonotic viral species obtained from passive or active surveillance in wild mammals through simple frequencies analyses. Graphics were done using GraphPad Prism v. 6 (GraphPad Software). A similar analysis was done for the human case database.

To estimate how many species we expected to record in Mexico, we calculated a species accumulation curve with the R package *vegan* (Oksanen et al., 2016) with a rarefaction method.

First, we performed a descriptive spatial analysis to summarize the overall spatial distribution of viral species recorded from wild mammals and across human populations using QGIS 2.18.9, a free and open-source GIS, using the open-access layers provided by the 'National Commission for the Knowledge and Use of Biodiversity' [Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, CONABIO] [http://www.conabio.gob.mx/informacion/gis/]. To calculate the incidence rate per state of viral species recorded in wild Mexican mammals, we used the mammalian richness per state calculated by Ceballos and Oliva (2005).

For the human cases, we calculated the incidence rate per 1,000,000 inhabitants per state, using the total population size per state reported by the 'Single Information System for Epidemiological Surveillance, General Directorate of Epidemiology, Ministry of Health' [Sistema Único de Información para la Vigilancia Epidemiológica, Dirección General de Epidemiología, Secretaría de Salud] (SUIVE, 2019).

With the geo-referenced coordinate data for the collecting localities of the mammalian hosts and the centroid coordinates of the geo-statistical locality polygons for the human records, we could investigate co-distribution as a point process. We followed Wheeler, Worden, and McLean (2016) and implemented a random relabelling permutation approach of the cross-K function. This method allows us to test whether there is a spatial patterning or association between wild mammal virus records and human viral cases. The cross-K function is the bivariate version of Ripley's K function and can be used to characterize point patterns and determine whether they are clustered, dispersed or randomly distributed (Dixon, 2002). To test co-distribution under a realistic null hypothesis, we kept the point locations fixed, but randomly assigned each one to be either a wild mammal viral record or a human case under the same marginal frequencies. This test is appropriate for instances in which sampling is biased or uneven (Wheeler et al., 2016). We called functions from the R packages *spatstat* (Baddeley, Turner, & Rubak, 2018), *sp* (Pebesma et al., 2018) and *rgdal* (Bivand et al., 2018) to run this test.

2.4 | Sampling and reporting bias

We compared our data with known spatial and taxonomic patterns of research effort in mammalogy in Mexico, drawn from a review of 2,527 abstracts for work presented at 11 meetings of the Mexican Society of Mammalogy between 1991 and 2014 (Briones-Salas, Ramos, & Santiago, 2014). This study identified geographic and taxonomic variations in research effort on Mexican mammals in relation to patterns of species diversity, to local demographics and to the distribution of research institutions.

3 | RESULTS

We obtained 371 records, each one represents the mammalian host and its associated viral species per locality and study. From these records, 262 were identified at species level and the remaining 109 were identified at genus level (Colunga-Salas et al., 2019).

From the 262 species-identified records, 42 species of potentially zoonotic viruses were identified from 52 published scientific articles (Table S1), which corresponded to 0.87% (42/4,843) of the worldwide virus richness and 25.6% (42/164) of potential zoonotic viruses. From all families recorded in Mexico, *Coronaviridae* exhibited the highest number of records in Mexico with 14, followed by *Flaviviridae* and *Hantaviridae* with six species each (Table 1). On the other hand, 52.4% (22/42) of all viral potential zoonotic species detected in Mexico are currently in validation process and could be considered as new species by the ICTV (Tables 1 and S1).

The species accumulation curve is increasing without a clearly defined asymptote (Figure 1). Moreover, studies on viruses associated with Mexican wild mammals were scattered and not systematic, and it was not until the early 1990s that more studies focusing on these taxa and the report of new species increased exponentially (Figure 2a,b).

We recorded a total of 91 species of potential mammalian hosts (89 wild species and two peri-domestic wild mammals [*Mus musculus*, the house mouse and *Rattus rattus*, the black rat]) from 21 families of seven orders (Table 2). Rodentia had the highest number of studies with 24, followed by Chiroptera (23), Carnivora (19), and Artiodactyla and Didelphimorphia with three each. In contrast, the last two orders with the lowest number of studies were Lagomorpha with two studies and Cetacea with a single record. These represent 58.3% (7/12) of all mammalian orders present in Mexico. These results are in line with overall patterns of research effort in Mexico for mammalian orders, where bats, rodents and carnivores are the most studied groups. However, our results do not reflect the vast amount of research on white-tailed deer in the country.

When analysing the database, we found that *Rhabdoviridae* and *Togaviridae* are the two most recorded viral families found in the 85.7% (6/7) of the Mexican mammalian orders with data available, since *Rabies lyssavirus* (*Rhabdoviridae*) and *Venezuelan equine encephalitis virus* (*Togaviridae*) were the most common species recorded in Mexico (see: Colunga-Salas et al., 2019). In contrast, seven viral families were restricted to a single mammalian order (for Rodentia: *Arenaviridae* and *Hantaviridae*; for Chiroptera: *Coronaviridae* and *Paramyxoviridae*; for Artiodactyla: *Hepeviridae*; and for Cetacea: *Herpesviridae*) representing the 50% (6/12) of all viral families (Figure 3).

The most frequently reported techniques for viral exposure were serological tests (37 studies of the 52 obtained = 71%), such as ELISA, fluorescent antibody tests and haemagglutination–inhibition tests, followed by molecular techniques [*e.g.* PCR and RFLP] (22/52 = 42%); meanwhile, other techniques (isolation, electron microscopy and Seller's method) were used much less frequently (6/52 = 12%). It is noteworthy that only in three studies, the method used was not specified (Figure S1).

Geographically, the states with the highest incidence rate (per 100 mammalian species) of viral species associated with wild mammals were Mexico City (53.96), Coahuila (48.59) and Baja California (31.25). The states with the lowest rate were Quintana Roo (1.21), Oaxaca (1.04) and Nayarit (1.03). Meanwhile, the states with no reports were Querétaro, Tabasco and Tlaxcala (Figures 4 and 6a; Table S3). If we consider the richness of potential viral zoonotic species, the states with the highest number of species are Campeche with 10 viral species and Mexico City with seven species. The states with the lowest number of potential zoonotic viral species correspond to those with the fewest records (Aguascalientes, Nayarit and Quintana Roo), with only one viral species recorded. The geographic distribution of studies and records does not follow known patterns of research effort related to species diversity nor species richness. Other abiotic factors may be involved, such as population size, funds and the number of research centres. For example, Mexico City is not particularly rich in mammals, but it is the capital and the venue for several major research institutions and other public health infrastructure (e.g. the Institute of Epidemiological Diagnosis and

TABLE 1 Number of viruses' species reported in Mexico compared with the number of species reported by the ICTV (2017)

Family	Total species of virus (ICTV, 2017)	Virus in Mexico	New species	
			Viral species	Reference
Arenaviridae	41	3	*Ocozocoautla de Espinosa virus*	Cajimat, Milazzo, Bradley, and Fulhorst (2012)
			Real de Catorce virus	Inizan et al. (2010)
Coronaviridae	39	14	*Alphacoronavirus* (*group 1*)	Anthony et al. (2013)
			Alphacoronavirus (*group 2*)	Anthony et al. (2013)
			Alphacoronavirus (*group 4*)	Anthony et al. (2013)
			Alphacoronavirus (*group 5a*)	Anthony et al. (2013)
			Alphacoronavirus (*group 5b*)	Anthony et al. (2013)
			Alphacoronavirus (*group 6*)	Anthony et al. (2013)
			Alphacoronavirus (*group 7*)	Anthony et al. (2013)
			Alphacoronavirus (*group 8*)	Anthony et al. (2013)
			Betacoronavirus (*group 9*)	Anthony et al. (2013)
			Betacoronavirus (*group 10*)	Anthony et al. (2013)
			Betacoronavirus (*group 11a*)	Anthony et al. (2013)
			Betacoronavirus (*group 11b*)	Anthony et al. (2013)
			novel *Alphacoronavirus* (*group 3*)	Anthony et al. (2013)
			A novel betacoronavirus (presumably group C)	Bentim-Goés et al. (2013)
Flaviviridae	89	6	*Pegivirus* PMX 1376	Quan et al. (2013)
			Pegivirus PMX 1641	Quan et al. (2013)
			Pegivirus PMX 1615	Quan et al. (2013)
Hantaviridae	41	6	*Four Corners virus*	Deardorff et al. (2011)
			Playa de Oro virus	Chu, Owen, Sánchez-Hernández, Romero-Almaraz, and Jonsson (2008)
			Rio Grande virus	Hjelle et al. (1995)
Hepeviridae	5	1	–	–
Herpesviridae	90	1	–	–
Paramyxoviridae	55	1	–	–
Parvoviridae	137	2	–	–
Peribunyaviridae	53	2	–	–
Rhabdoviridae	135	4	–	–
Togaviridae	32	2	–	–
Total	788	42	22	

Note: New species were determined as those species not included in the last ICTV report, and with molecular information in their original publication.

Reference (Instituto de Diagnóstico y Referencia Epidemiológicos [InDRE]). The reasons for the high incidence rate in wild mammal-associated virus research records for Baja California Sur could be the low mammalian diversity related to its area, and the bias as a result of the very high sampling and capture effort made in the respective works, as in the case of Coahuila (see Colunga-Salas et al., 2019).

Regarding viral zoonotic human cases, during the period of 2000–2013, 198 confirmed cases were registered in 29 states (Mexico City, Querétaro and Tlaxcala were the only three states that never reported cases). Regarding the incidence rate per (1,000,000 inhabitants), the states with the highest rate of reported zoonotic cases were Nuevo Leon (10.91), followed by Colima (5.01), Quintana Roo (4.43) and Sonora [3.96] (Figures 5 and 6b; Table S4).

We found that the distributions of human cases were not spatially related to the distribution of wild mammals harbouring the zoonotic virus. The observed K_r distance function lies within the 99% simulation band and mirrors the mean of the simulation bands almost exactly, suggesting that the spatial records for human cases are spatially random conditional on where viruses were detected in wild mammals (Figure 7).

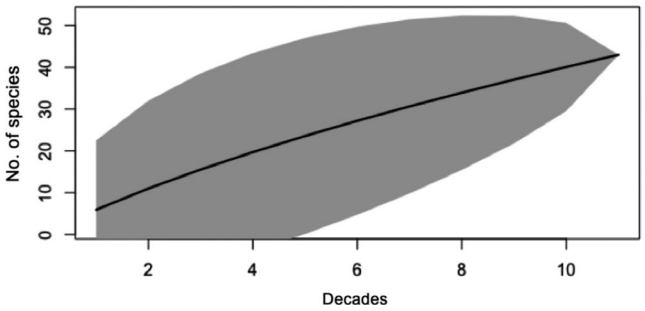

FIGURE 1 Species accumulation curve. The curve was obtained with rarefaction index, and it shows an increasing curve, which means that the inventory of virus species in Mexico is too far to reach the asymptote

4 | DISCUSSION

This is the first attempt to compile all studies published with Mexican wild mammals and their viral potential zoonotic pathogens since 1900–2018. We found that a small number of papers focused on viral infections in wild mammals. The first records of a zoonotic virus detected on wild mammals in Mexico were established by Téllez-Girón (1937, 1944), who isolated *Rabies virus* from the vampire bat (*Desmodus rotundus*) in the state of Michoacán.

Since the 1980s, the number of publications has been increasing exponentially, focusing on detecting the viral agent, as well as analysing their ecological, genetical and evolutionary aspects (Davis, Nadin-Davis, Moore, & Hanlon, 2013; Kariwa et al., 2012; Saasa et al., 2012; Scherer, Dickerman, Fiandra, Chia, & Terrian, 1971; Suzán & Ceballos, 2005).

Broadly, the study and publications on viruses of wild mammals linked to human viral disease outbreaks have focused mainly on *Rabies virus* (Belotto, Leanes, Schneider, Tamayo, & Correa, 2005; de Mattos et al., 1999) and *Venezuelan equine encephalitis virus*. Yet, in this latter case, only three wildlife studies for this pathogen have been carried out after an outbreak in the 1980s (Adams et al., 2012; Deardorff et al., 2011; Estrada-Franco et al., 2004). However, those studies were not associated with human population.

Rodents and bats (Rodentia and Chiroptera) are often incriminated as the main reservoirs of viral-emerging agents in wildlife

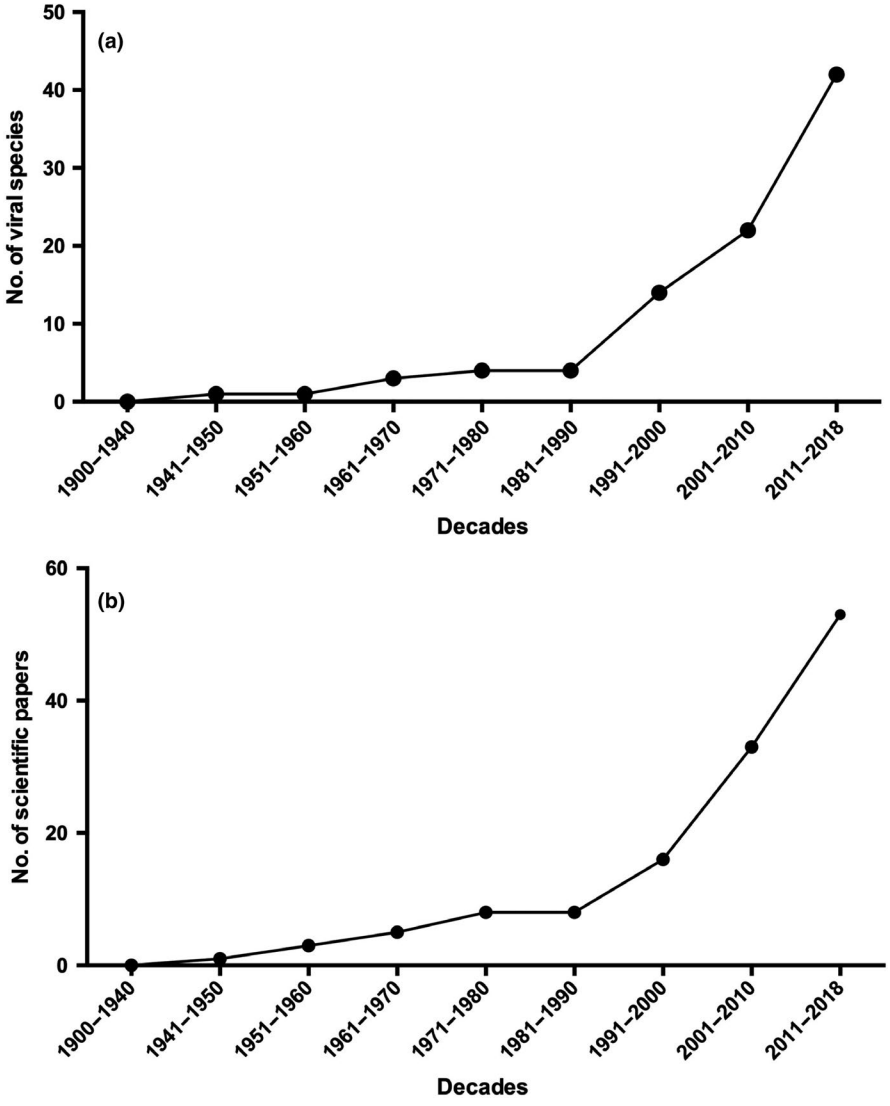

FIGURE 2 Records of virus associated with wild Mexican mammals. (a) Number of published scientific papers per decade, (b) accumulative records of viral species associated with wild mammals. In both cases, the records start to increase in 1990 decade

TABLE 2 Mammalian host species of potential zoonotic viral species recorded from previous studies done in Mexico

Order	Family	Species
Artiodactyla	Cervidae	*Mazama pandora*
		Odocoileus virginianus
	Tayassuidae	*Tayassu pecari*
Carnivora	Canidae	*Canis latrans*
		Urocyon cinereoargenteus
		Vulpes macrotis
	Felidae	*Lynx rufus*
		Panthera onca
		Puma concolor
	Mephitidae	*Conepatus leuconotus*
		Conepatus semistriatus
		Mephitis mephitis
		Spilogale gracilis
		Spilogale putorius
	Mustelidae	*Mustela frenata*
		Taxidea taxus
	Procyonidae	*Bassariscus astutus*
		Nasua narica
		Procyon lotor
	Ursidae	*Ursus americanus*
Cetacea	Delphinidae	*Tursiops truncatus*
Chiroptera	Vespertilionidae	*Eptesicus fuscus*
		Lasiurus cinereus
		Myotis velifer
		Rhogeessa parvula
	Phyllostomidae	*Artibeus jamaicensis*
		Carollia perspicillata
		Carollia sowelli
		Carollia subrufa
		Dermanura phaeotis
		Dermanura tolteca
		Dermanura watsoni
		Desmodus rotundus
		Glossophaga commissarisi
		Glossophaga morenoi
		Glossophaga soricina
		Leptonycteris yerbabuenae
		Lonchorhina aurita
		Micronycteris microtis
		Sturnira hondurensis
		Sturnira parvidens
		Trachops cirrhosus
	Mormoopidae	*Mormoops megalophylla*
		Pteronotus davyi
		Pteronotus parnellii
	Molossidae	*Nyctinomops laticaudatus*
		Nyctinomops macrotis
		Tadarida brasiliensis
Didelphimorphia	Didelphidae	*Didelphis marsupialis*
		Didelphis virginiana
		Philander opossum
Lagomorpha	Leporidae	*Lepus californicus*
		Sylvilagus audobonii
		Sylvilagus brasiliensis
Rodentia	Agoutidae	*Dasyprocta punctata*
	Cricetidae	*Baiomys musculus*
		Baiomys taylori
		Megadontomys thomasi
		Neotoma albigula
		Neotoma leucodon
		Neotoma mexicana
		Neotoma micropus
		Onycomys leucogaster
		Oryzomys alfaroi
		Oryzomys chapmani
		Oryzomys mexicanus
		Oryzomys texensis
		Peromyscus aztecus
		Peromyscus beatae
		Peromyscus eremicus
		Peromyscus hylocetes
		Peromyscus leucopus
		Peromyscus levipes
		Peromyscus maniculatus
		Peromyscus megalops
		Peromyscus melanotis
		Peromyscus mexicanus
		Reithrodontomys megalotis
		Reithrodontomys microdon
		Reithrodontomys sumichrasti
		Sigmodon hirsutus
		Sigmodon hispidus
		Sigmodon mascotensis
		Sigmodon toltecus
	Dasyproctidae	*Cuniculus paca*
	Heteromyidae	*Chaetodipus nelsoni*
		Dipodomys merriami
		Heteromys irroratus
	Muridae	*Mus musculus*
		Rattus rattus
	Sciuridae	*Otospermophilus variagatus*

Note: All species were updated according to the last taxonomic reviews of Ramírez-Pulido et al. (2014) and Ceballos and Arroyo-Cabrales (2012).

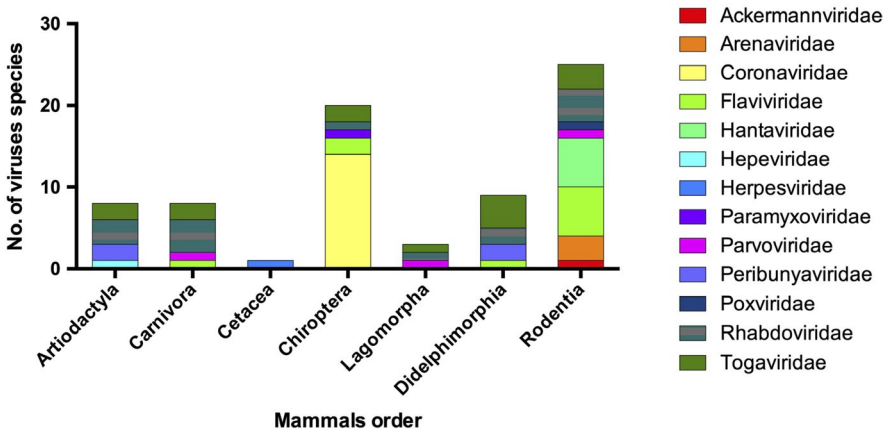

FIGURE 3 Viral richness per virus family in each mammal order. Rodentia and Chiroptera orders are the most studied and show the highest record of viral species in the wildlife inventory. Cetacea is the only one with one species recorded [Colour figure can be viewed at wileyonlinelibrary.com]

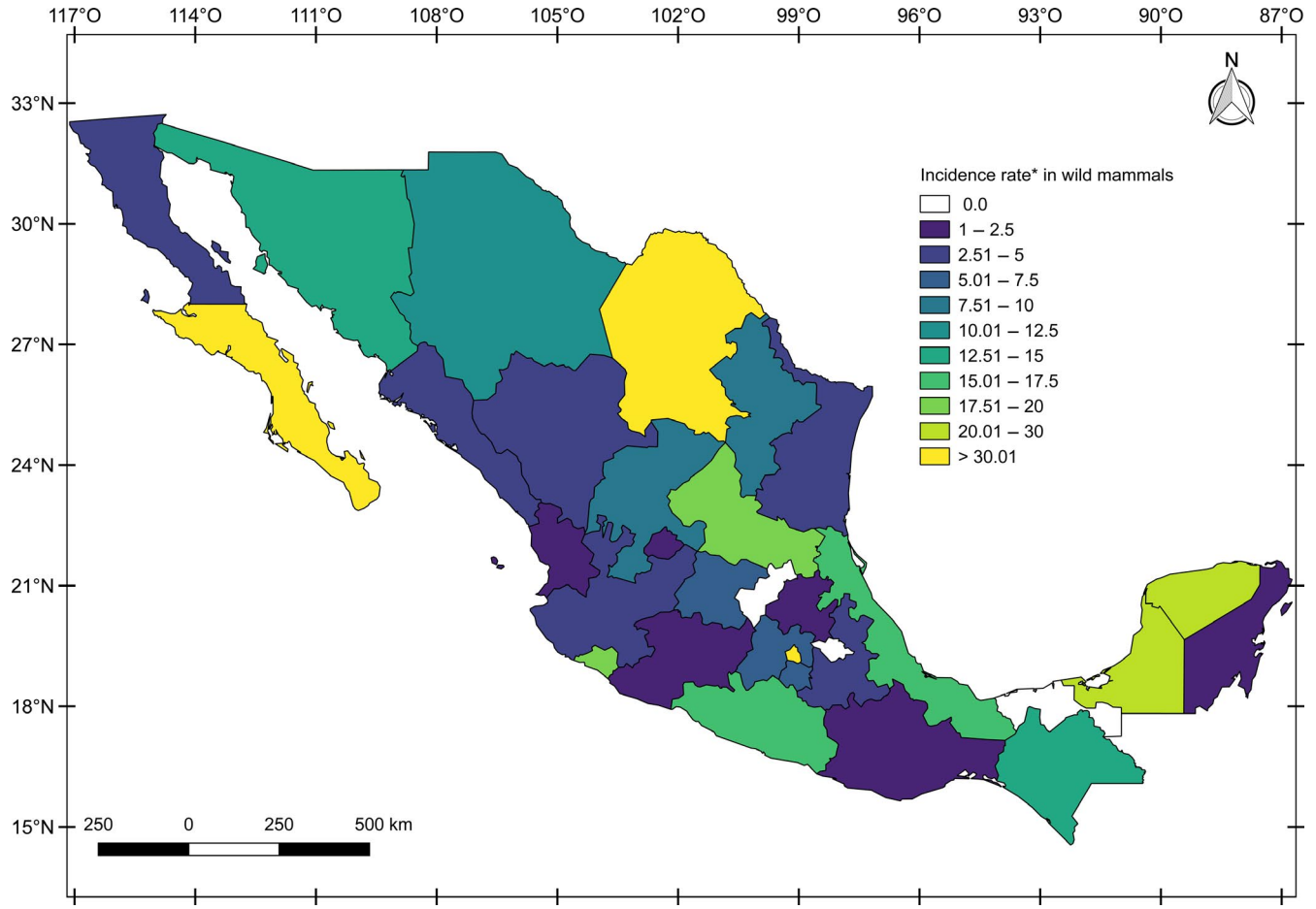

FIGURE 4 Incidence rate of viral species associated with wild Mexican mammals. Colour intensity of states corresponds to incidence rate calculated (for data, see Table S2). *Rate per 100 mammalian species [Colour figure can be viewed at wileyonlinelibrary.com]

(Calisher, Childs, Field, Holmes, & Schountz, 2006; Han et al., 2016; Luis et al., 2013; Mills & Childs, 1998; Plyusnin & Sironen, 2014; Taylor et al., 2001). That reason could lead to even more studies on those mammalian orders, leaving many orders unattended.

Carnivora take up the third place in the number of reported wild mammals associated with zoonotic viruses. The reason for this can be attributed to the close relationships of some species with humans, their ease of sampling and their historical importance as *Rabies virus* reservoirs. On the other hand, five orders (Cingulata, Soricomorpha, Sirenia, Pilosa and Primates) have never been described as possible reservoirs of any potential zoonotic viruses in Mexico. Their possible role as reservoirs needs to be assessed, especially in Primates, where important zoonotic virus species have been recorded worldwide [e.g. *Ebola virus*, *Marburg virus*, *Herpes B virus* and *Hepatitis virus*] (Huff and Peter, 2003; Bermejo et al., 2006; Swanepoel et al., 2007; Thi et al., 2016; de Carvalho-Dominguez-Sousa et al., 2018).

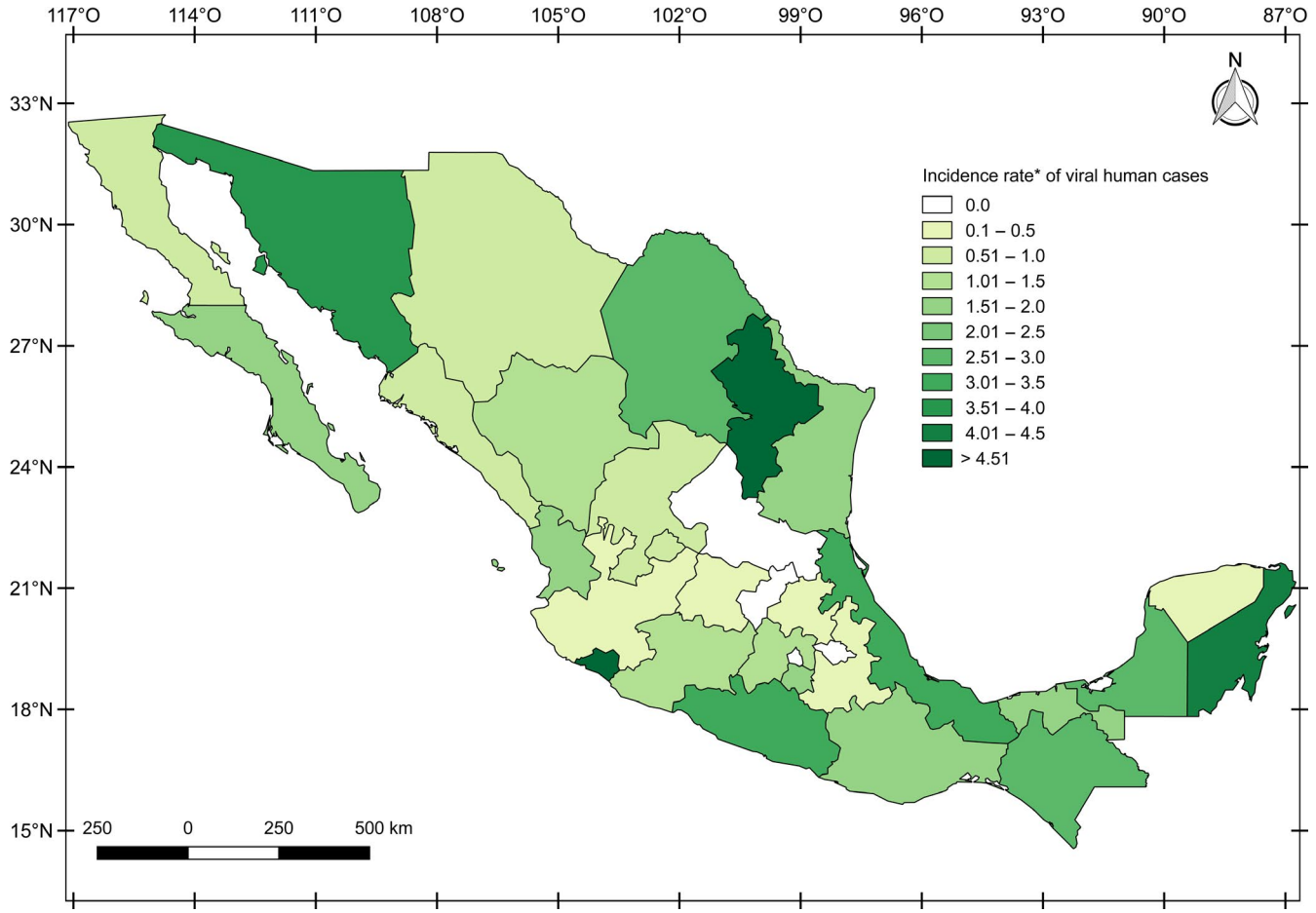

FIGURE 5 Incidence rate of confirmed viral human cases from 2000 to 2013. Colour intensity of states corresponds to incidence rate calculated (for data, see Table S2). *Rate per 1,000,000 inhabitants [Colour figure can be viewed at wileyonlinelibrary.com]

Until the decade of 2000, *Hantaviridae* family was restricted to Rodentia, (Padula et al., 2004; Schmaljohn & Hjelle, 1997; Torres-Pérez et al., 2004); however, since the early 2000s, recent discoveries found some hantavirus species in Indian shrews [order: Soricomorpha] (Klempa et al., 2007; Zhang, 2014) and American and European bats (Sabino-Santos et al., 2018; Straková et al., 2017; Těšíková, Bryjová, Bryja, Lavrenchenko, & Goüy de Bellocq, 2017; Zhang, 2014). This new information opens the possibility to assess the role of North American shrews and bats as host of hantavirus species. On this point, it is important to note that in Mexico Soricomorpha comprises 38 species (Ramírez-Pulido et al., 2014), distributed along the entire national territory, and some of them distributed into isolated patches (Carraway, 2007), all of these features, could lead to a high hantavirus richness.

We clearly identified well-defined periods in which research on zoonotic viruses was focused on specific species, particularly, during the 1990s and 2000s when studies focused on rabies. Meanwhile, during the last decade the *Hantaviridae* family has been the most studied taxon.

Since the 1980s, the knowledge of viruses associated with wild mammals has been increasing, perhaps due to the improvement of detection techniques, followed by the development of several serological and molecular tests, since they are straightforward, sensitive and specific (Schochetman, Ou, & Jones, 1988; Weigle, Murphy, & Brunell, 1984; Zambon, Hays, Webster, Newman, & Keene, 2001). However, it is important to note that not all serological tests are specific, due to unspecific or cross-reaction with antibodies among other related viral species (Gónzalez-Barrio & Ruiz-Franco, 2019). To avoid that, we consider necessary to use molecular techniques as confirmatory tests.

It is also important to emphasize the high number of potential new species recorded in Mexico; in the case of the *Cororonaviridae* family, all species recorded until now in Mexico are likely new species, since phylogenetic analyses show that these species form separate clades (Anthony et al., 2013). The same occurs with the genus *Pegivirus*, where at least three different lineages of that genus are clearly identified from Bayesian phylogenetic analysis (Quan et al., 2013).

Geographically, Veracruz and Chiapas were the states with the highest species richness of zoonotic virus associated with wild mammals and human cases. This can be related to the high wild mammal richness and the environmental conditions of both states, and in particular to their weather conditions, which can be an important driver for the proliferation of the invertebrate vectors of viral agents, given

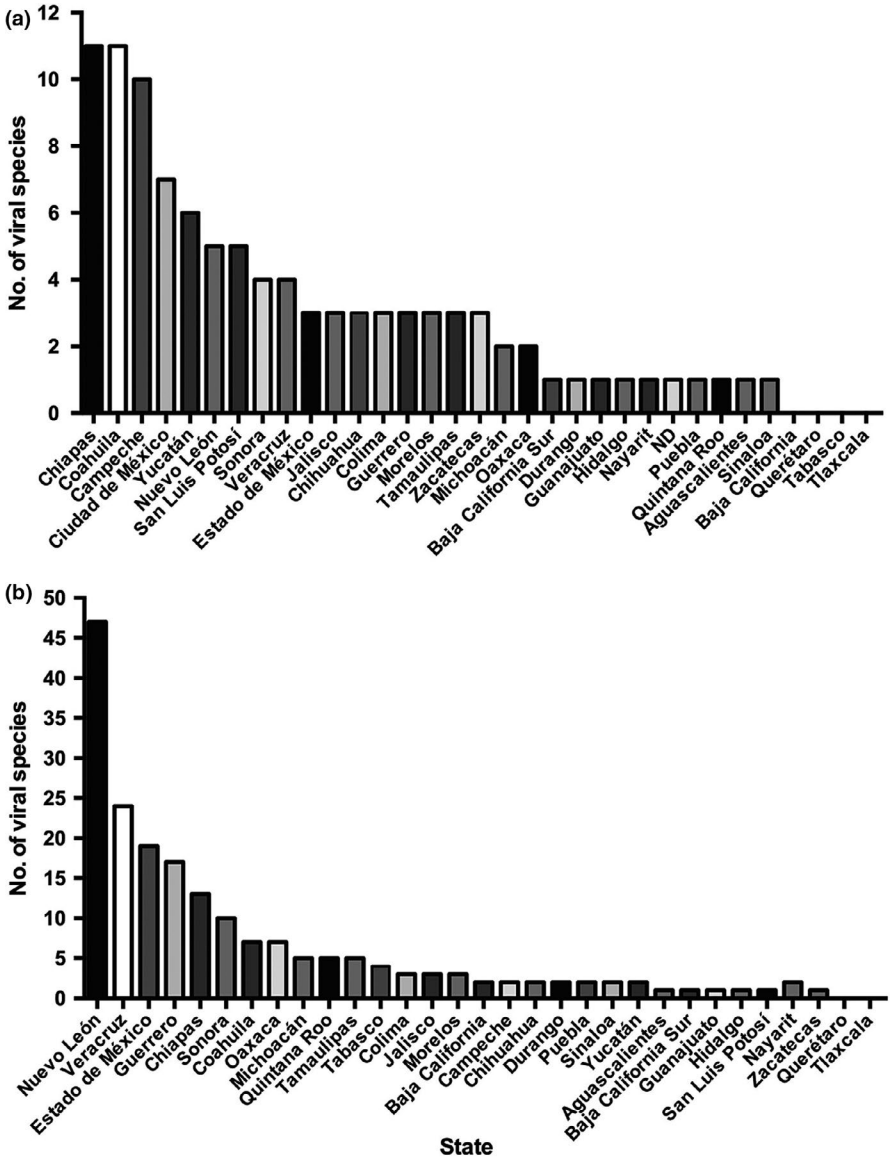

FIGURE 6 Number of potentially zoonotic virus per state of Mexico. (a) Number of potential zoonotic viral species detected in wild mammals per state, (b) number of human viral cases per state

the vast areas of tropical forest and montane ecosystems where vectors are often found (Ceballos & Oliva, 2005; González-Christen, 2008; Krasnov, Shenbrot, Khokhlova, & Degen, 2004; Retana & Lorenzo, 2002).

We found that records of human cases seem to be spatially unrelated to viruses in wild mammals. This may be because most viral human cases were not fully confirmed and most of them were notified as unspecified viral fever or as unspecified arthropod-borne viral fever (Table S4). Additionally, there are fundamental differences in how human cases and wildlife records are reported and sampled spatially. Despite known roadside bias in wild mammal sampling, wild mammal records are more likely to come from less urbanized landscapes than reports for human cases, which are tied more closely with health infrastructure in or close to human settlements. Our method for testing co-distribution accounts for distance and could potentially overcome these biases, but larger-scale simulation-based studies may be needed to accurately measure the sensitivity of this approach to sampling biases.

The species accumulation curve is increasing, and an asymptote is not clearly defined, indicating biased sampling during the last century. This information is related to the unfinished worldwide inventory of viruses and specifically in Mexico, where the systematic inventory of biodiversity only began in the early 2000s (CONABIO, 2008). Clearly, more information on zoonotic virus infections is necessary to improve clinical diagnosis and health services in Mexico. It is noteworthy that at least 42 of the 164 (25.6%) species of zoonotic virus reported worldwide are circulating in mammals in the country. It is noteworthy that at least, in human viral cases, only 17% (33/199) were diagnosed showing the aetiological agent (Table S1) (CENAVECE, 2013). Therefore, it is critically important to enhance the surveillance of infecting zoonotic viruses in patients, since until now dengue fever is the only disease for which reporting is mandatory.

It is essential to increase sampling efforts and enhance studies in more mammal species and states, in order to increase our knowledge about the biology, systematics, ecology and epidemiology of

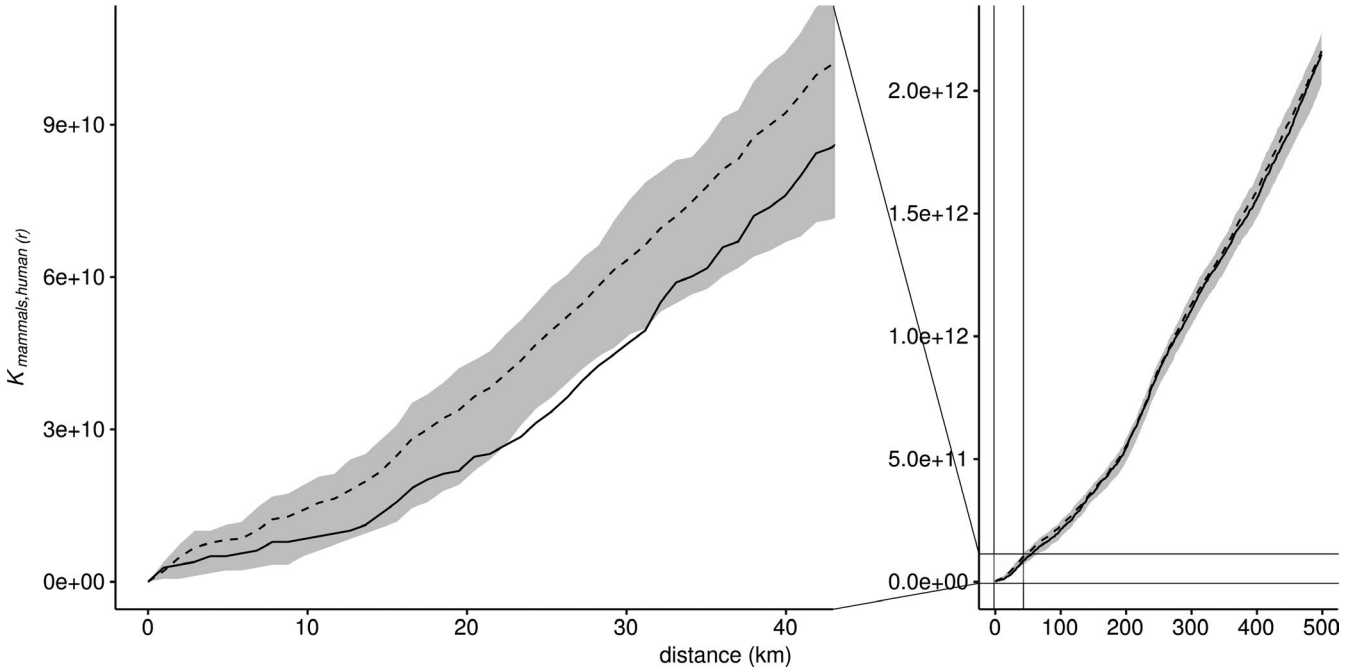

FIGURE 7 Cross-K statistics. Grey band represents simulated 99% confidence intervals based on 999 permutations where the point labels for human cases or wild mammal virus detection were randomly reallocated. The dark solid line shows the observed statistic. If the black line is above the grey band, it means the points are clustered at that distance, and if the black line is below the grey band, it means the points have fewer pairs than expected by chance at that distance

viral agents circulating in Mexico. This can be used for the development of surveillance policies by health and environmental authorities. Furthermore, it is important to consider that areas with higher biodiversity rates are also considered a buffer to prevent the spillover of infectious diseases to human and domestic animals. Usually, the disruption of these ecosystems is the cause of the viral emergence; for this reason, the implementation of buffer zones and plans for sustainable exploitation should be the main axes for government decision-makers.

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CONFLICT OF INTEREST

The authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest, non-financial interest in the subject matter or materials discussed in this manuscript.

AUTHOR CONTRIBUTIONS

Pablo Colunga-Salas, Sokani Sánchez-Montes and Estefania Grostieta contributed equally to database compilation and analysed the wildlife and human viral cases, wrote and reviewed the manuscript. Luis Darcy Verde-Arregoitia performed, analysed and discussed the statistical analyses. He also made substantial contributions to manuscript. Martín Yair Cabrera-Garrido reviewed and updated the mammalian species and made contributions to manuscript. Ingeborg Becker made substantial contributions to manuscript and reviewed early versions. Livia León-Paniagua contributed to identifying and updating the mammalian species, and contributed substantially with the manuscript.

ETHICAL STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. No ethical approval was required as this is a review article with no original research data.

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SUPPORTING INFORMATION

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