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Spatial-temporal risk factors in the occurrence of rabies in Mexico

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Abstract

Rabies is a zoonotic disease that affects livestock worldwide. The distribution of rabies is highly correlated with the distribution of the vampire bat *Desmodus rotundus,* the main vector of the disease. In this study, climatic, topographic, livestock population, vampire distribution and urban and rural zones were used to estimate the risk for presentation of cases of rabies in Mexico by co-Kriging interpolation. The highest risk for the presentation of cases is in the endemic areas of the disease, *i.e.* the States of Yucatán, Chiapas, Campeche, Quintana Roo, Tabasco, Veracruz, San Luis Potosí, Nayarit and Baja California Sur. A transition zone for cases was identified across northern Mexico, involving the States of Sonora, Sinaloa, Chihuahua, and Durango. The variables topography, vampire distribution, bovine population and rural zones are the most important to explain the risk of cases in livestock. This study provides robust estimates of risk and spread of rabies based on geostatistical methods. The information presented should be useful for authorities responsible of public and animal health when they plan and establish strategies preventing the spread of rabies into rabies-free regions of México.

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Introduction

Rabies is a zoonotic, lethal disease caused by the rabies virus (RABV) a member of the *Lyssavirus* genus of RNA viruses in the *Rhabdoviridae* family. The virus is present worldwide, causing thousands of deaths in humans each year (León *et al.,* 2021; Benavides *et al*., 2020). It is transmitted by the vampire bat *Desmodus rotundus* and has become an emerging public health problem; the number of cases in humans due to vampire bites has increased lately (Oliveira *et al*., 2022). The number of rabies cases in livestock species, such as cattle, goats, sheep, horses and swine have also increased (León *et al.,* 2021; Ortega-Sánchez *et al*., 2022). The presence of *D. rotundus* from northern Mexico to northern Argentina and Chile makes it endemic in subtropical and tropical areas. Different studies report that populations of this bat are located in areas with high density of cattle, which constitute their main source of food; thus, agricultural zones with cattle population offer them a secure source of food (Benavides *et al*., 2020). In Latin America, the role of dogs in the transmission of RABV is now strongly contained due to vaccination coverage and epidemiological surveillance. Mexico is the first country of Latin America declared free of human rabies transmitted by domestic dogs by the World Health Organization (WHO), an accomplishment not only due to the massive vaccination of dogs, but also owed to prophylactic measures in humans exposed to the RABV. Currently, *D. rotundus* is the principal reservoir and transmitter of the RABV to domestic animals and humans in this country (CENAPRECE, 2018; Aréchiga-Cerballos *et al*., 2022).

The estimated economic loss in livestock due to rabies in Mexico is more than USD 2.6 million per year (Zarza *et al*., 2017).

This cost includes the indirect outlays, such as vaccination of people, post-exposure treatment and running national programs to prevent dissemination plus the farmers' loss caused by animal deaths (Shwiff *et al*., 2007; Anderson *et al*., 2014). In Mexico, rabies is endemic along the Pacific coast, from the southern part of the State of Sonora to the State of Chiapas, and along the coast of the Gulf of Mexico from the State of Tamaulipas to the State of Quintana Roo (Johnson *et al*., 2014; Martínez, 2020). Lately, the disease has been reported in areas previously considered free in the central part of Mexico (Zarza *et al*., 2017; Bárcenas-Reyes *et al*., 2019; Ortega-Sánchez *et al*., 2022).

Dissemination of rabies to new regions has been the focus of recent studies (Benavides *et al.,* 2020); environmental, anthropogenic and climate changes have been reported to play an important role in the distribution of *D. rotundus* leading to increased rabies in livestock (Streicker *et al*., 2012; Meza *et al*., 2022; Ulloa *et al*., 2020). Most of these studies use databases obtained by epidemiological surveillance programs subjected to spatial-temporal analysis with geographic information systems (GIS) and species distribution models, such as the maximum entropy model (MaxEnt) as used by Sarsenbay *et al*. (2016) and Giannakopoulos *et al*. (2016). This has been useful for predicting possible climatic scenarios for the presence of the vector and its relation to the occurrence of cases in cattle (Lee *et al*., 2012; Brito-Hoyos, 2013; Streicker *et al*., 2016a; Acha & Alba, 2018; Orlando *et al*., 2019). Other studies have applied geostatistical methods such as ordinary Kriging and co-Kriging to interpolate regionalized variables for the estimation of predictive values of the spatial distribution of rabies also in cattle in non-sampled settings. These tools are useful; especially when sampling is biased due to site attributes (Bárcenas-Reyes *et al*., 2019; Rocha *et al*., 2020; Ortega Sánchez *et al*., 2022). Recent studies in Mexico based on ordinary Kriging and co-Kriging found that the number of cases in cattle coincide with the distribution of the vampire bat at regional spatial scales, and that the number of counties affected increased at maximum average temperatures around 29.5°C as well as at minimum average temperatures around 16.5°C (Bárcenas-Reyes *et al.*, 2015; Bárcenas-Reyes *et al*., 2019).

An analysis performed with 1,872 cases of rabies in cattle based on MaxEnt and the dispersal capacity of *D. rotundus* in relation to the perceived climate change with regard to temperature and precipitation predicts that *D. rotundus* will lose 20% of its current distribution between 2050 and 2070, and that the northern and central regions of Mexico will instead become suitable habitats for *D. rotundus* (Zarza *et al*., 2017). However, the use of MaxEnt can generate different predictions if the study area changes, with the possibility that results can be significantly affected if they lack quantitative justification of the adjustment of the climatic variables obtained from WorldClim (Escobar, 2016). It must also be considered that when the georeferenced cases are used, the number of cases may not be representative of the population of cases in a region due to limitations and scopes of operation and administration of epidemiological control and surveillance campaigns between one year and another (Maxwell *et al*., 2017; Hayes & Piaggio, 2018; Shipley *et al*., 2019).

Recently, a study based on ordinary Kriging, where the number of cases in different livestock and wildlife species were interpolated, showed that the distribution of cases in bats reported by the Mexican National Epidemiological Surveillance System (SIVE) correlates with the distribution of cases in different livestock and wild species (Ortega-Sánchez *et al*., 2022). These authors also revealed seasonal patterns of rabies cases in livestock and showed that the correlation held even in areas with environmental conditions not appropriate for the reservoir bat.

It is well known that, due to the continuous human invasion of areas occupied by vampire bats, the number of cases in livestock and humans is increasing (Aréchiga-Ceballos *et al*., 2010; Streicker *et al*., 2016b; Seetahal *et al*., 2020). However, the impact of some biogeographical factors and the dispersal capacity of *D. rotundus* is still unclear. Therefore, we wished to identify risk factors in detail and provide the best estimates of the occurrence of rabies cases in different livestock species in endemic and non-endemic areas based on national data on climatic, landscape and livestock populations between 2010 and 2019.

Materials and Methods

Information georeferenced by county of 3,469 cases of rabies in different livestock species (bovine, sheep and goat) and wildlife (hematophagous bats, insectivorous bats, cervid, fox, buffalo, coati and skunks) for the years 2010-2019 from 29 States of Mexico (Figure 1) was included in the study. The information was kindly provided by the National Service of Health, Safety and Agrifood Quality (SENASICA by its Spanish acronym). Cases were confirmed by indirect immunofluorescence, the official diagnostic test of the national campaign for the prevention and control of rabies in cattle and livestock species (Mexican Official Standard NOM-067-ZOO-2007). Wildlife cases were included because some species are considered RABV reservoirs and reporting is mandatory in accordance with official regulations.

The predictor variables (PV) used in this study were: i) climatic factors (CLF), such as annual average precipitation (AP), maximum average temperature (T_{Max}) and minimum average temperature (T_{Min}); ii) topographic factors (TOF), such as landscape orography (OR), mines (MI) and bridges & tunnels (BT); iii) demographic factors (DEF), such as rural population (Rp) and urban population (Up); iv) population distribution of *D. rotundus* bats in Mexico (VBBP); and v) livestock population factors, such as bovines (BP), sheep (SP) and goats (GP); all PVs were georeferenced with decimal coordinates. Information on the variables used is listed in Table 1.

Climatic data were obtained from the official website of the National Water Commission (CONAGUA by its Spanish acronym), Topographic and demographic information was obtained in shapefile format from the National Commission for the Knowledge and Use of Biodiversity (CONABIO by its Spanish acronym). Population distribution data for *D. rotundus* were obtained from the database of common vampire bat reports (Van de Vuurst *et al.,* 2022) and information livestock population was obtained from the Agrifood and Fisheries Information System (SIAP by its Spanish acronym).

To check for normality of the predictor variables, an exploratory analysis of data was performed (Paz-Gómez & Taboada, 1996; Goovaerts, 1997; Wakernaguel, 1998; Ekwaru & Veugelers, 2018). No variable in the dataset was normal, so a natural logarithm transformation was used to accomplish normality (Webster & Oliver 2007, Fuenzalida *et al*., 2015). Transformation was made with the geostatistical package ArcMap v.10.3 (ESRI, Redlands, CA, USA). To obtain values for each sample point separately for each variable, the geostatistical methods Kriging and co-Kriging from the geostatistical package ArcMap v.10.3 as desctibed by

Castellanos *et al*. (2019) were used. Joint variable values were produced through cross-validation by semivariograms. The spatial correlation between the dependent variable and the independent ones was determined by geographical weight regression using a multiple linear regression model. This operation produced interpolated surfaces that envisaged values at unmeasured places (Agyeman *et al*., 2022; Baffoe-Twum *et al*., 2022).

The thirteen PVs, experimental semivariograms were performed and the initial variance and covariance parameters adjusted to validate that the single and the crossed semivariograms had linear combinations (Benito, 2012; Baffoe-Twum *et al*., 2022). The validation of the calculation of the adjusted cross-variogram models is shown in Table 2. Based on the parameters defined, a fitted spherical model was chosen because the variables showed linear behaviour near the origin. The mathematical function for the adjusted model was the following:

$$\gamma(h) = EP + Sill_1 Mod_1(\alpha x_1 \alpha y_2) + Sill_2\ Mod_2\ (\alpha x_1 \alpha y_2) + \ldots \qquad \text{Eq. 1}$$

where *h* is the number of cases with a distance separated between the estimated value and the known value; *EP* the spherical model summation; *Sill Mod* the plateau value; *α* the range value; and *γ* the value of the theoretical semivariogram between the values of location 1

Figure 1. Map of Mexico with the geographic location of its 32 states.

Table 1. Number of observations in Mexico by type of predictor variable used for the period 2010-2019.

ID	Predictor variable (PV)	Name of institution	Time period	Observation (no.)	Source
1	NC	SENASICA	2010-2019	659	https://www.gob.mx/senasica
2	AP	CONAGUA	2010-2019	2,457	https://www.gob.mx/conagua
3	T_{Max}	CONAGUA	2010-2019	2,457	https://www.gob.mx/conagua
4	T_{Min}	CONAGUA	2010-2019	2,457	https://www.gob.mx/conagua
5	OR	CONABIO	2018	567	https://www.gob.mx/conabio
6	MI	CONABIO	2013	6,500	https://www.gob.mx/conabio
7	BT	CONABIO	2014	13,463	https://www.gob.mx/conabio
8	Rp	CONABIO	2016	187,722	https://www.gob.mx/conabio
9	Up	CONABIO	2016	4,525	https://www.gob.mx/conabio
10	VBBP	Published data	1878-2021	7,427	Van de Vuurst et al., 2022
11	BP	SIAP	2019	2,392	https://www.gob.mx/siap
12	SP	SIAP	2019	2,198	https://www.gob.mx/siap
13	GP	SIAP	2019	1,784	https://www.gob.mx/siap

NC, number of cases; AP, annual average precipitation; T_{Max}, maximum average temperature; T_{Min}, minimum average temperature; OR, landscape orography; MI, mines; BT, bridges and tunnels; Rp, rural population; Up, urban population; VBBP, distribution of D. rotundus bats in Mexico; BP, bovine population; SP, sheep population (SP); GP, goat population.; SENASICA, National Service of Health, Safety and Agrifood Quality; CONAGUA, National Water Commission; CONABIO, National Commission for the Knowledge; SIAP, Agrifood and Fisheries Information System.

and location 2.

The spatial correlation of the interpolated variable NC with 13 PVs and the combination among themselves was calculated with the co-Kriging method to evaluate the best adjusted global model with the crossed and the simple semivariograms. The mathematical function for the adjusted model was the following:

$$(G/h) = Co + C1 + Mod1\,(\alpha x1\ \alpha x1) + C2 + Mod2\,(\alpha x2\ \alpha y2) + \ldots \qquad \text{Eq. 2}$$

where *G/h* is the experimental semivariogram obtained from the number of pairs of sample points separated by a distance interval; *Co* the nugget effect; and *Co* + *Cn* the plateau value related to the range *α* of each model *Mod* (Wackernagel, 1998).

The prediction for cases by multivariate and univariate analysis that explains the risk was performed for individual cross-validations, where the mean square error measured the amount of error between the observed and the predicted datasets. The risk maps for presence of cases of rabies were generated with climatic, livestock population-related, topographic and demographic parameters with logarithmic transformation using the spherical model (SphM) with a direction angle of up to 45º with co-Kriging using the software ArcMap v 10.3.

Results

The 3,469 cases of rabies reported in Mexico between 2010-2019 occurred in 1, 633 out of 2,471 counties. Table 3 shows the number of cases, the number of counties affected with cases per year, the T_{Max}, the T_{Min} and the AP for the years 2010 to 2019. It can be observed that the number of counties affected increased in 2012 and onwards, with T_{Max} ranging from 28.4ºC and 29.0ºC, T_{Min} from 14.0ºC to 15.0ºC and the AP from 1,064 to 1,092 mm. As expected, the highest number of cases was observed in livestock species in geographic areas that have temperature and precipitation values suitable for *D. rotundus.*

Figure 2 shows four risk estimation maps obtained by co-Kriging for the presence of cases in each of the four groups of the PVs. It can be observed that the highest case numbers fell in four regions: The Southeast (Tabasco, Chiapas and the South of Veracruz), the Huasteca (parts of San Luis Potosí, Querétaro, Guanajuato, Hidalgo and Tamaulipas), Nayarit and the Yucatán Peninsula. Areas with few case reports included the State of Baja California Sur, the northern part of Chihuahua and Sierra Alta of Sonora in the north-western part of the country. The well-known association between livestock population density and the number of rabies cases can be seen in Figure

Table 2. Statistics of co-Kriging analysis of the number of rabies cases in relation to the climatic and livestock variables in Mexico 2010-2019.

Semi-variogram	Variable combination	Nugget	Sill	Model	Major range	Minor range
$\Upsilon 10^{2}$	AP _ AP	1.34	0.30	Spherical	7.69	3.66
$\Upsilon 10^{-1}$	TMax _ TMax	0.01	0.009	Spherical	7.99	4.31
$\Upsilon 10^{-1}$	T Min _ TMin	13.90	0.57	Spherical	22.62	7.57
$\Upsilon 10$	BP _ BP	0.69	1.25	Spherical	3.37	1.12
$\Upsilon 10^{-1}$	SP _ SP	0.67	0.20	Spherical	4.61	1.54
$\Upsilon 10^{-1}$	GP_ GP	1.57	4.67	Spherical	12.32	6.59
$\Upsilon 10^{-1}$	NC _ AP	0.76	0.011	Spherical	12.74	7.28
$\Upsilon 10^{-1}$	NC _ TMax	0.74	0.0008	Spherical	13.07	4.36
Υ_{10}	NC _ TMin	0.72	0.008	Spherical	6.64	3.07
Υ_{10}	NC _ BP	0.73	0.151	Spherical	6.68	4.44
Υ_{10}	NC _ SP	0.72	0.081	Spherical	5.55	2.94
Υ_{10}	NC _ GP	0.76	0.030	Spherical	15.84	6.34
Υ_{10}	NC _ OR	0.75	0.045	Spherical	4.63	2.46
Υ_{10}	NC _ MI	0.78	0.115	Spherical	8.91	5.24
$\Upsilon 10^{3}$	NC _ BT	0.35	0.005	Spherical	0.001	1.59
$\Upsilon 10^{-1}$	NC _ RZ	0.78	0.036	Spherical	22.36	7.46
$\Upsilon 10^{3}$	NC _ UZ	1.004	0.189	Spherical	0.008	0.004
Υ_{10}	NC _ CLF	0.76	0.002	Spherical	2.67	2.26
Υ_{10}	NC _ LPF	0.72	0.72	Spherical	5.18	3.24
Υ_{10}	NC _ TOF	0.75	0.009	Spherical	4.06	4.06
$\Upsilon 10^{1}$	NC _ DEF	0	0.368	Spherical	0.27	0.16
Υ_{10}	NC _ VBBP	0.71	0.22	Spherical	4.68	4.68
$\Upsilon 10^{-1}$	NCLP _ CLF	0.77	0.0006	Stable	12.09	12.09
Υ_{10}	NCLP _ LPF	0.71	0.136	Spherical	3.98	3.98
$\Upsilon 10^{-1}$	NCLP _ TOF	0.79	0.29	Stable	17.17	17.17
$\Upsilon 10^{-1}$	NCLP _ DEF	0.71	0.27	Spherical	2.09	2.09
Υ_{10}	NCLP _ VBBP	0.70	0.s44	Spherical	3.35	3.35

AP, annual average precipitation; TMax, average maximum temperature; TMin, average minimum temperature; BP, bovine population; SP, sheep population; GP, goat population; NC, Number of cases; MI, mines; BT, bridges and tunnels; RZ, rural zone; UZ, urban zone; CLF, climatic factors; LPF, livestock population factors; TOF, topography factors; DEF, demographic factors; VBBP, vampire bat and cattle population; NCLP, number of cases in livestock population.

2B. Topographical factors, such as mines, tunnels and bridges, showed the highest risk for case increases (10-15 cases), which coincided with high estimated risk in livestock populations (Figure 2B) in the regions Chiapas, the Yucatán Península, northern Veracruz, the Huasteca, Guerrero and Nayarit (Figure 2C). Figure 2D shows the demographic factors in south-eastern Mexico, the Huastecas and the State of Nayarit in the western region, *i.e.* the regions with the highest risk for occurrence of livestock cases (9-15 cases). These areas have a greater number of rural counties with populations greater than 2,500 people where the population trend is increasing. Close to 54% of the areas there are destined for grazing and forestry activities (Orlando *et al*., 2019; INEGI, 2023).

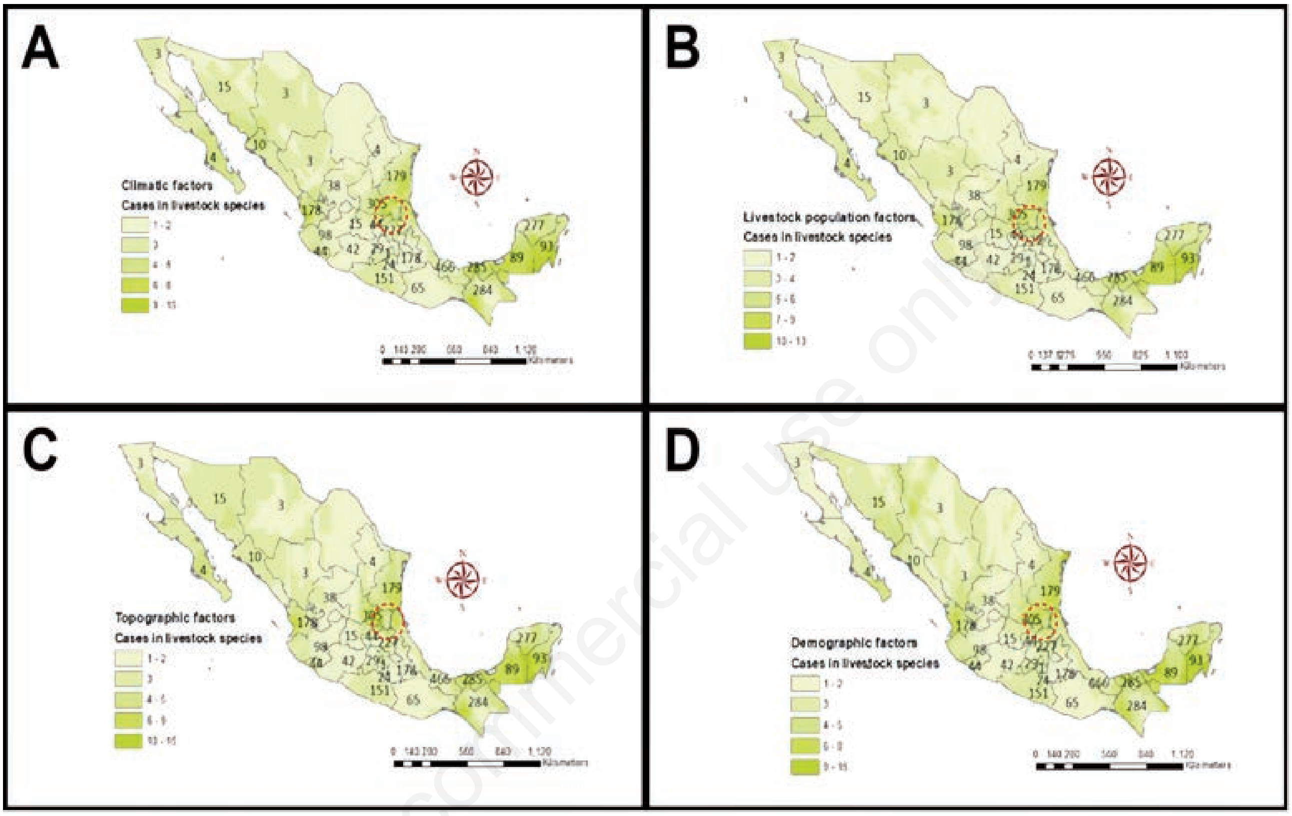

Figure 2. Risk of rabies in livestock species by co-Kriging interpolation. The number of cases in each state is given according to: **A**) climatic factors; **B**) livestock populations; **C**) topographic factors; **D**) demographic factors. Darker colour shades mean higher risk of infection. The dotted red circle marks Huasteca Potosina region.

Table 3. Annual numbers of rabies cases in wildlife and livestock species in relation to county and climatic variables in Mexico 2010-2019.

Year	Number of cases	Affected counties	Average T_{Max} (°C)	Average T_{Min} (°C)	Average AP (mm)
2010	172	81	27.9 (3.75)	14.0 (4.45)	1,379 (93.74)
2011	58	26	28.9 (4.72)	14.4 (4.25)	1,064 (78.09)
2012	326	159	28.4 (3.6)	14.3 (5.05)	1,064 (100.87)
2013	364	178	29.0 (3.46)	15.3 (4.48)	1,205 (103.69)
2014	487	218	28.6 (3.75)	15.0 (5.15)	1,107 (95.94)
2015	500	209	28.8 (3.92)	15.5 (5.18)	1,042 (103.53)
2016	460	228	29.2 (3.96)	15.3 (4.72)	980 (96.89)
2017	402	185	29.3 (4.26)	15.0 (4.86)	1,147 (95)
2018	409	188	28.9 (3.85)	14.8 (5.37)	1,092 (82.95)
2019	291	161	30.0 (3.98)	15.0 (5.21)	986 (83.84)

AP, average precipitation; T_{Max}, maximum average temperature; T_{Min}, minimum average temperature; the numbers in parentheses are standard deviations (SD); the total number of observations for T_{max}, T_{Min} and AP were 3,469.

The models obtained from the interpolation of cases in the different livestock species with each PV group were: 0.7728*Nugget (+0.26297^Spherical 12.095) for climatic variables; 0.7191*Nugget (+0.20020^Spherical 3.9887) for livestock populations; 0.0*Nugget (+0.26463^Spherical 4.8463) for topographic variables and 0.71257*Nugget (+0.0.14463^Spherical 2.097) for demographic factors. The value of the mean square error of the case risk prediction performed for individual cross-validations obtained by a multivariate analysis comparing the robustness of the models by co-Kriging were 1.08 for CLF, 1.06 for LPF, 1.05 for TOF and 1.02 for DEF (the individual data not shown).

Figure 3 shows four patterns of risk estimation maps obtained with co-Kriging for the presence of cases of rabies in all species, both domestic and wildlife (cattle, goats, sheep, horses, pig, haematophagous bats, insectivorous bats, cervids, foxes, buffaloes, coati and skunks), for each of the PV groups. It was observed that the Huasteca Potosina (the dotted red circle in the Figure) is the region with the highest risk for the case occurrence, more cases and the only area in which the annual frequency of the occurrence of cases is not constant. In addition, non-endemic regions, such as the states of Tamaulipas and Nuevo León, were found to have the highest risk for the occurrence of rabies in livestock. The estimated risk with the TOF and LPF clearly marks a transverse zone dividing the endemic and the non-endemic areas. This zone stretches from the Sinaloa State in Mexico's West to the northern part of Tamaulipas in the East. Thus, it represents areas where the presence of new cases can be expected although such reports have not yet appeared.

The models obtained from the interpolation for the number of cases of rabies in different livestock species with each set of variables were: 0.76674*Nugget (+0.15077^Stable 2.67) for climatic variables; 0.72858*Nugget (+0.19076^Spherical 5.1859, 3.2469, 93.9) for livestock populations; 0.75079*Nugget (+0.17219^Stable 4.0642, 1.49) for topographic variables and 0.0*Nugget (+0.78011^Spherical 0.27549, 0.10172, 153.5, 0.2) for demographic factors. Figure 4A shows two risk maps obtained with co-Kriging for the estimated presence of rabies based on the distribution of vampire bats, cattle population and wild species, with Figure 4B giving the risk when wildlife species are not taken into account. It was observed that the spatial behaviour of the number of cases associated with the groups of the spatiotemporal variables LPF and VBBP is different. In particular, map A reveals that there are some areas with fewer cases reported in livestock but still with a clear risk due to presence of both vector and livestock. This was observed in the Huasteca region, where areas with high numbers of cases (dark colour in the figure) radiate transversely from East to West and also to northern states. This pattern was not observed in map B, although it represents regions with a higher number of cases of rabies in livestock. Map A was obtained with the model 0.71856*Nugget (+0.19789^Spherical 4.6803, 1.5628, 87.9) and Map B with the model 0.70696*Nugget (+0.20609^Spherical 3.3558).

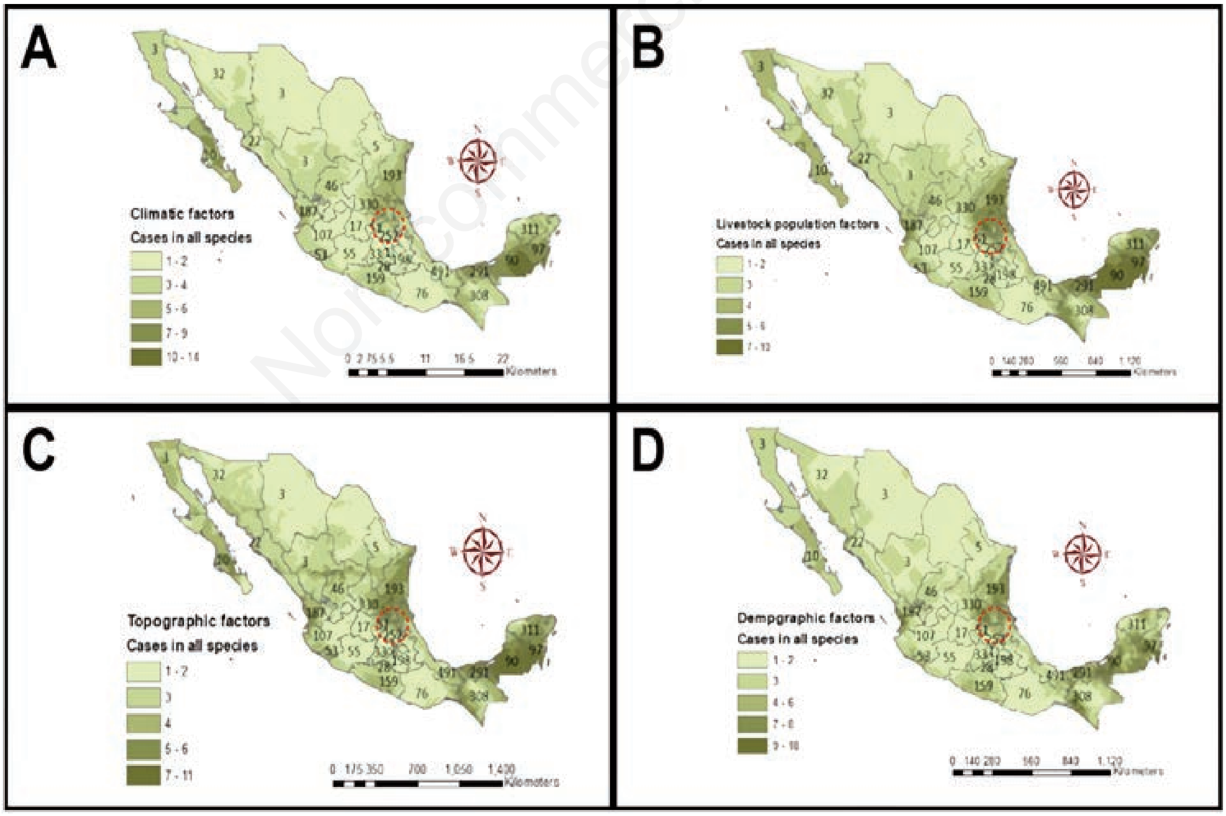

Figure 3. Risk of rabies in livestock and wildlife species by co-Kriging interpolation. The number of cases in each state is given according to: **A**) climatic factors; **B**) livestock populations; **C**) topographic factors; **D**) demographic factors. States in darker colour shades mean higher risk of infection. The dotted red circle marks the Huasteca Potosina region.

Discussion

Our study identified relevant interactions between the number of rabies cases in domestic species (cattle, goats and sheep) with four PV groups in Mexico based on co-Kriging interpolation. The results show that the south-eastern region (Yucatán Península and Huasteca Potosina) not only has the highest number of cases, but also the highest risk of more cases (9-15 cases). This may be due to the fact that the temperatures of this region (21-32°C) favour the distribution of *D. rotundus*, particularly that it never gets colder than 10°C (Bárcenas-Reyes *et al*., 2019, Franco-Molina *et al*., 2021). These are also the Mexican areas with the highest populations of vampire bats and livestock species. The states of Nuevo León, Sonora, Sinaloa and Chihuahua, on the other hand, are traditionally non-endemic areas, with no risk of more than 1-3 cases. They are characterized by environmental conditions that do not represent a high risk for the spread of the disease in domestic species. More cases at the national level in the design, with need for implementation of control measures should therefore not be assumed (Velasco-Villa *et al*., 2002; Jaramillo-Reyna *et al*., 2020).

The regions with the highest risk of receiving more cases (10-13 cases) are Chiapas, Yucatán Península, northern Veracruz, the Huasteca, Guerrero and Nayarit, which together have 41% of the cattle population, 43% of the sheep population and 26% of the goat population of the national livestock population in grazing meadows and pastures year to year (SIAP, 2022). This is lower than the livestock population of the northern states of Nuevo León, Sonora, Sinaloa and Chihuahua (Jurado-Guerra *et al*., 2021), which all use stabled livestock management and where the future risk of presenting more cases therefore is low (1-4 cases). The considerable movement of unvaccinated animals in natural pastures is an important risk factor as they are not protected against RABV infection (Galarde-López *et al*., 2020) when coinciding with the mating and breeding seasons of *D. rotundus* bats (Zortéa & Calaça, 2018; Ortega-Sánchez *et al*., 2022). The presence of livestock can be considered a predictor for demography, immunological profiles and risk of RABV infection in vampire bats that in turn is a risk factor for rabies outbreaks in endemic areas (Bárcenas-Reyes *et al*., 2017; Becker *et al*., 2018).

The association with mines, tunnels and bridges shown in Figure 2 depends on natural or artificial shelters resulting from anthropogenic changes that are now occupied by rabies virus-infected *D. rotundus* close to livestock herds (Rocha *et al*., 2020; Pimentel *et al*., 2022). Our results suggest that the movement of infected bats and establishment of their colonies in shelters close to livestock herds (Mantovan *et al*., 2022) should be considered a risk factor for new cases due to the fact that the prevalence of rabies in larger bat colonies (usually <1%) can increase as 70% of bats generate antibodies (Dzikwi *et al*., 2010). In contrast, the lower risk of have more cases in States of Nuevo León, Sonora, Sinaloa and Chihuahua (1-2 cases) may be due to lack of suitable microclimates in both natural or artificial shelters to host bat colonies (Lanzagorta-Valencia *et al*., 2020). Therefore, the risk of new cases there may depend on factors such as mobilization of infected livestock from endemic areas (Tidman *et al*., 2022). This does not rule out the existence of viable shelters at local scales that represent a risk for the establishment of the vector, which climate change could make a source of RABV infection in future years for livestock or other wildlife as well as humans in current non-endemic areas (Benavides *et al*., 2020). It is known that rabies is maintained in rural areas due to the presence of *D. rotundus* close to livestock herds to which they transmit RABV (Rupprecht *et al*., 2018), a fact which is consistent with our study. The demographic factors indicating the regions with the highest risk for the occurrence of rabies cases in livestock (Figure 2D) confirm that *D. rotundus* can feed on livestock blood and adapt to areas with human activities (Stricker *et al*., 2016a). Even though it has been observed at regional spatial scales that *D. rotundus* avoids biting cows resting in places where there is intense human activity (Lanzagorta-Valencia *et al*., 2020), our results show that this bat attacks cattle in areas close to human settlements in areas with developing agro-silvo-pastoral activities (Torres-Mejía *et al*., 2022).

The risk maps showing the interactions of cases occurring in all species (livestock and wildlife) and the PVs revealed new areas of the country with risk of having more cases. That the estimated number of case occurrences was less than those that only considered cases in livestock species as a response variable is in agreement with the spatial epidemiology study by Chen (2022) on the spatial trend of cases in livestock he feels can be used as sentinel. It would then be an excellent tool for rabies-monitoring in reservoirs as potential transmitters of RABV to humans. In addition, we found the co-Kriging method useful in estimating the number of expected cases and identifying risk areas in places lacking data or

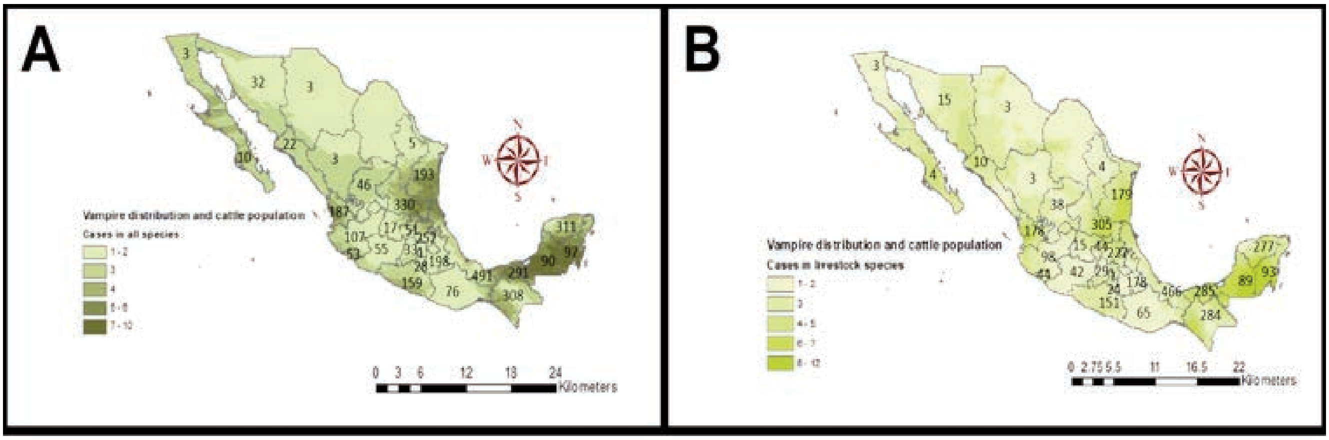

Figure 4. Risk of rabies according to the distribution of cattle and D. rotundus. The number of cases in each state is given for; A) wild and livestock species; B) livestock animals. States in darker colour shades mean higher risk of infection.

yet to be sampled (Bárcenas-Reyes *et al*., 2019). This could be the reason for few notifications of rabies cases occurring in bats or other wildlife, either due to inferior quality of the sample for diagnosis, difficult access to localities or lack of knowledge of the disease during epidemiological surveillance exercises (Aréchiga-Cerballos *et al*., 2022),

Our results suggest that the spread of rabies cases to new regions has been due to intersectional movements of infected bats (Streicker *et al*., 2012) from south-eastern Mexico to the central and western parts of the country. Figure 3A shows that this increases the risk for the occurrence of cases in any species in areas that do not necessarily have macroclimates with ranges of maximum and minimum temperatures and precipitation levels tolerated by *D. rotundus* (Bárcenas-Reyes *et al*., 2019; Torres-Mejía *et al*., 2022). It can thus be a risk with regard to the spread of RABV in reservoirs in non-endemic areas such as Baja California Sur, Sonora, Northern Sinaloa, Chihuahua, Durango, Zacatecas, Coahuila and Nuevo León, a fact that needs immediate consideration by the National epidemiological surveillance systems (Morgan *et al*., 2020).

According to the risk map for the presence of more cases in any livestock and wildlife species related to livestock population factors and the number of reported *D. rotundus* sightings (see Figures 3B and 4B), the high-risk zones were found to be south-eastern Mexico, the Huasteca and the western part of the State of Nayarit, which all coincide with those identified as carrying rabies risk for cattle; however, two new high-risk regions were identified here: Baja California and Baja California Sur (7-10 cases). In addition, it demonstrated a transverse intersection line from the State of San Luis Potosí to southern Sinaloa with an estimated risk of 1-4 cases. This was also observed in Mexico with TOF, DEF and sightings of *D. rotundus* (see Figures 3C, 3D and 4A), suggesting that wildlife is now the main risk for the spread of RABV infection into currently disease-free areas of Mexico. Occasional cases should therefore not be neglected and underreporting in livestock and wildlife species should be avoided (Aréchiga-Cerballos *et al*., 2022). Indeed, for every reported rabies case, 10 are not reported (Escobar, 2004; Zarza *et al*., 2017). This highlights a potential limitation of our study: the use of second-hand information may have an under-reporting bias; there is commonly less reports of rabies in wildlife than in livestock in Mexico (Aréchiga *et al*., 2022; Ortega-Sánchez *et al*., 2022). In this way, the occurrence of cases in wildlife correlates more with the low quantity of samples than with a real natural phenomenon for rabies in wildlife (Bouslama *et al*., 2020; García-Hernández *et al*., 2022).

Vaccination of cattle and other domestic animal species is mandatory when moving animals from controlled zones to rabies-free zones. Animals need to be vaccinated at least 30 days before and must have an animal health certificate (NOM-ZOO-067-2007) warranting that the animals are free of this disease. However, it is possible that some animals are moved without these requirements and thus contribute to the spread of the disease (Mantovan *et al*., 2022). Although it would have been useful to include information about movement of animals and vaccine coverage in our study, this information is not available in Mexico. However, our results provide useful information for authorities responsible for public and animal health for establishing preventive measures to stop the spread of rabies, e.g., the use of a sentinel tool for rabies monitoring in reservoirs and potential transmitters of RABV to animals and humans. It would also be useful to establish buffer zones between endemic and free areas, with monitoring for the presence of the RABV in wildlife. Above all, the control of animal movement is crucial.

Conclusions

The presence of risk for the occurrence of rabies cases in different livestock species in Mexico has been estimated with multivariate geostatistical methods including dense sets of climatic variables, demographic topography, geographic distribution of livestock populations and sightings of *D. rotundus* bats. This study revealed that on a national scale, the topographic conditions and the variations in livestock populations specific to each region form a hidden pattern, with intersections between endemic regions and other regions that contribute to transmission of RABV including the vector, livestock species and wildlife.

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