Scientific Reports https://doi.org/10.1038/s41598-026-60843-w

Article in Press

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Received: 11 December 2025

Accepted: 30 June 2026

Published online: 06 July 2026

Cite this article as: Furlan M.E., Hayman D.T.S., Wada M. *et al.* Optimizing human rabies prevention in Brazil through spatial prioritization and a One Health approach. *Sci Rep* (2026). https://doi.org/10.1038/s41598-026-60843-w

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Optimizing human rabies prevention in Brazil through spatial prioritization and a One Health approach

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Abstract

Agricultural expansion and urbanization create fragmented landscapes that alter resources for wildlife. These changes influence populations of key pathogen reservoirs, affecting zoonotic disease risk. In the Neotropics, common vampire bats (*Desmodus rotundus*) often benefit from fragmented areas where cattle pastures replace their native habitat with cattle acting as a food source and contributing to their population growth and geographic expansion. Because *D. rotundus* is a key reservoir of the rabies virus, understanding its distribution is essential for anticipating and mitigating rabies risk. We analyzed priority areas for rabies prevention across Brazil's 5,570 municipalities using vulnerability, exposure, and hazard indicators, including *D. rotundus* potential distribution, human rabies cases, rabies in dogs and cats, and environmental and socioeconomic descriptors available from the Brazilian government and open datasets. Using spatial prioritization methods, we ranked municipalities to identify priority areas for prevention and control. From 2001 to 2024, an average of six human rabies cases occurred annually in 1.15% of municipalities (N=81). For cats and dogs (N=240), cases occurred in 2.19% of municipalities, not overlapping with human cases. Priority areas included the municipalities of Ouricuri (Pernambuco), Viseu (Pará), and several cities in Maranhão, including those where no cases were reported. These findings can support targeted One Health interventions by identifying municipalities with elevated structural and historical susceptibility to rabies risk, supporting 2030 rabies-elimination goals.

Keywords: Lyssavirus; Chiroptera; zoonoses; risk assessment; hazard; species distribution modeling; One Health.

Introduction

Rabies is one of the oldest known zoonoses. It is a fatal infection of the central nervous system caused by viruses belonging to the genus *Lyssavirus*[1], transmitted through saliva from infected animal bites. Rabies is a neglected tropical disease[2] with the burden falling mainly on children under 15 years old in poor rural populations (WHO, 2024). The rabies virus (RABV), the most common *Lyssavirus*, is present in more than 150 countries, and approximately 59,000 people die from this disease every year worldwide (WHO, 2024), and its main host has changed over the years. In Latin America, until the early 2000s, domestic dogs were the main transmitters of the virus. Although still present in several countries, canine rabies has decreased in recent decades, mainly due to mass vaccination programs in dogs and cats[3]. Currently, rabies transmission to people is from several wild mammal species, but vampire bats are the primary source, as they are natural reservoirs of the virus[4]. Rabies causes serious socioeconomic impacts and poses a public and veterinary health threat, resulting in substantially high human and livestock rabies deaths in Latin American countries[3].

In Neotropical regions, the conversion of natural forests at alarming rates for agricultural expansion has generated highly fragmented landscapes[5,6]. Human activities can cause drastic changes in the types, abundance, and distribution of resources available for biodiversity, as landscape change leads to habitat loss for many species[7,8]. Changes in resources can also have significant consequences on disease transmission, modifying demographic processes, and interactions between animals and host immunity, leading to increased or decreased risk of threats to human and animal health[9]. Bats (order Chiroptera) are hosts to a number of known emerging viral zoonoses[10] and are impacted by anthropogenic actions on land cover and use[11,12]. Common vampire bats (*D. rotundus*) are highly specialized, feeding on the blood of mammals, but are known to be able to adapt their dietary preferences from wildlife to livestock[13,14]. The increase in livestock farming has created a new, abundant, and reliable food source, which has driven population growth and increased the range expansion of vampire bats[15,16]. In Brazil, the locations where RABV outbreaks have been reported are mostly in environments altered by humans, such as cattle farming or deforestation for economic reasons like gold and timber exploration[17,18]. In addition, poor housing conditions and access to health services make populations vulnerable[17,19,20]. Brazil has achieved a 10 year absence of dog-transmitted rabies to humans, a success achieved due to the "Programa Regional de Eliminação da Raiva" from the "Organização Pan-Americana da Saúde (OPAS)", yet rabies still occurs in Brazil in dogs, cats, humans, and wildlife[21].

The objective of this study was to map zoonotic rabies risk and prioritize high-risk areas in Brazil by integrating ecological, epidemiological, and socioeconomic dimensions of transmission risk. Using a One Health perspective—a collaborative, multisectoral, and transdisciplinary approach that recognizes the interconnections among human, animal, and environmental health—we developed a parsimonious and reproducible framework to inform local One Health actions using the best available data[22]. Because *D. rotundus* is an important wildlife reservoir of rabies virus (RABV) in Latin America, we estimated its potential distribution using habitat suitability models and integrated this with additional variables across three risk components—hazard, exposure, and vulnerability—including human and animal rabies cases, landscape characteristics, and socioeconomic indicators. By combining multiple components of rabies transmission risk, our approach aims to identify spatial patterns associated with both wildlife- and domestic animal-linked transmission pathways. Our results can support rabies prevention by informing locally optimized effective mitigation strategies and public health policies.

Results

Habitat suitability models

We compiled a total of 107,134 occurrences of *D. rotundus* (Figure S3) from different locations across its entire distribution in the Americas. Results outside Brazil are presented to illustrate model consistency across the species' broader range but are not used in downstream analyses.. After cleaning the data, we used 5,660 occurrences of the species with high quality to adjust the models (Figure 1). Habitat suitability model prediction maps for *D. rotundus* in the Neotropical region are shown in Figure 1. The best-supported model (ΔAICc = 0) used a regularization multiplier of 0.5 and LQHPT feature classes. It achieved an AUC of 0.80, a Boyce index of 1, and a TSS of 0.47 at a threshold of 0.51. We presented a continuum prediction map to show gradient-suitable areas (Figure 1A) and a binary map (suitability values above the threshold) to specify potential presence and absence, which were used to summarize the potential distribution in municipalities (Figure 1B). The areas most suitable for *D. rotundus* are concentrated in many Brazilian regions, such as the Northeast, Southeast, South, and Midwest, with some patches of highly suitable areas in the North (Figure 1A). Suitability areas occur in both forested areas and anthropized areas, including urban areas (Figure 1B). In addition to Brazil, our model predicted suitable areas in north-central Argentina, almost all of Paraguay and Bolivia, and along Ecuador, Peru, Colombia, and Venezuela. The entire Neotropical region of Central America was also predicted, as well as the main Caribbean islands, such as Cuba and the Antilles. However, we highlight low values and rarify suitable areas in the central Amazon basin.

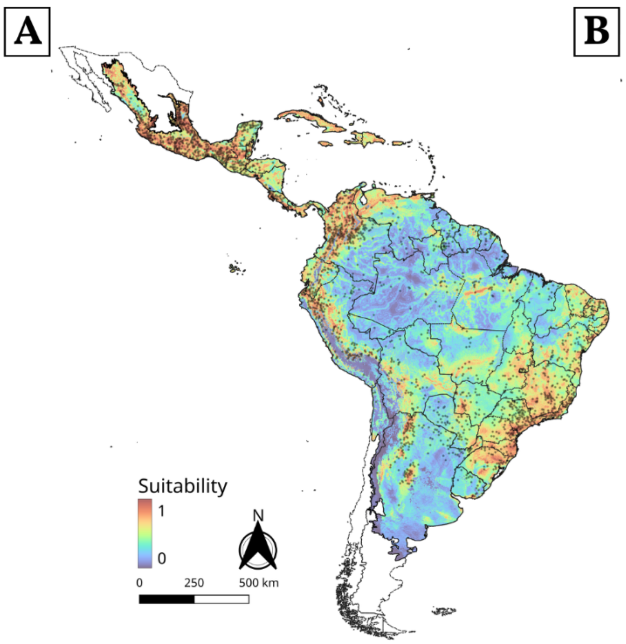
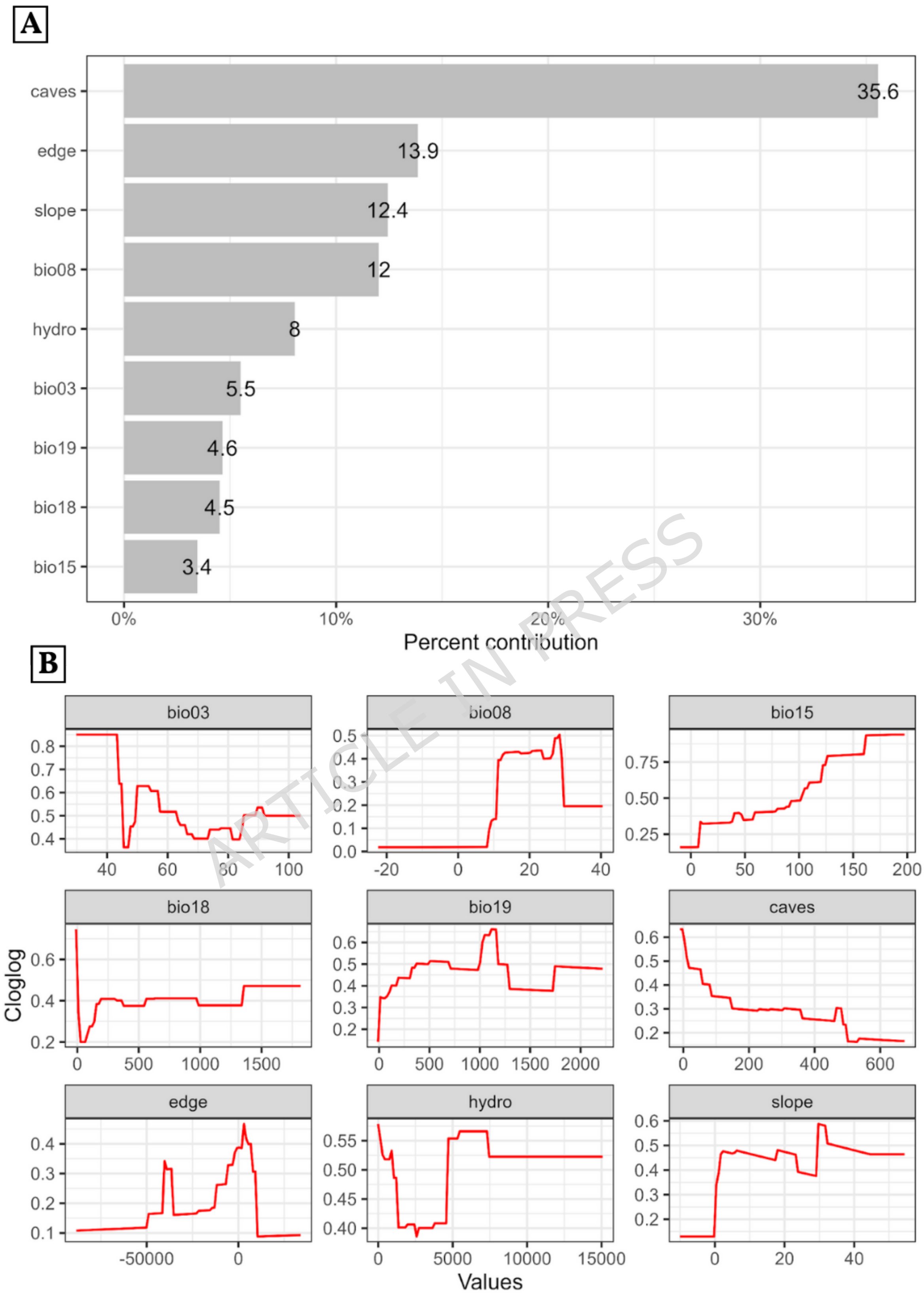


Figure 1. Results of the habitat suitability model for *Desmodus rotundus* in the Neotropics. (A) Continuous model and (B) Binary model (threshold = 0.51). The black dots on the maps represent records of the species occurrences. The continuous suitability map was used to derive the binary map based on the selected threshold, which was subsequently used for aggregation at the municipal level.

The most important environmental variables for predicting the potential distribution of *D. rotundus* were distance from karst caves (35.6%), distance from forest edges (13.9%), slope (12.45%), BIO8—average temperature of the wettest quarter (12%), distance from hydrology (8%), BIO3—isothermality (5.5%), BIO19—precipitation in the coldest quarter (4.6%), BIO18—precipitation in the hottest quarter (4.5%), and BIO15—seasonality of precipitation (3.4%) (Figure 2A). These results show the importance of caves and steep slopes, which may contain more caves or shelters, as refuges and habitats for the species, as well as forest edges as preferred habitats, as described for other species (e.g.[23]). Suitability is greater for values closer to caves, decreasing with increasing distance from caves (Figure 2B; caves). For the edge distance variable, suitability values are higher for values close to zero, indicating a preference for forest edge habitats by *D. rotundus* (Figure 2B; edge). Finally, for the slope variable, suitability values are higher for higher values of this variable, indicating that more rugged terrain is more suitable for the species (Figure 2B; slope).



A
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8
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Percent contribution
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Figure 2. Importance and response of environmental variables. (A) Importance of variables in percentage (Maxent's permutation importance) and (B) marginal response curves to variables based on suitability (cloglog transformation, which approximates the probability of occurrence) and each variable. Variables represent the following: bio03—isothermality, bio08—mean temperature of wettest quarter, bio15—precipitation seasonality, bio18—precipitation of warmest quarter, bio19—precipitation of coldest quarter, caves—Euclidean distance from caves (positive values outside from the caves), edge—Euclidean distance from forest edges (positive values outside from the edge, negative values inside from the edge, and zero is the edge), hydro—Euclidean distance from hydrography (positive values outside from hydrography), and slope—rise or fall of the land surface based on topography.

Domestic animal and human rabies

In domestic animals, between 2015 and 2023, 240 cases of rabies in canids and felids were reported in Brazil (27 cases per year; Figure 3A and B). The highest number of reported cases occurred in canids, with 187 records in Brazil (Figure 3A). Most cases occurred in the Northeast region (N=85; 45.5%), followed by the Midwest (N=77; 41.2%), Southeast (N=17; 9.1%), North (N=4; 2.1%), and South (N=4; 2.1%) regions. There was a high number of cases in the municipality of Corumbá in Mato Grosso do Sul, with 57 confirmed cases in 2015 and one case in 2016. There were fewer reported cases (N=53) in felids (Figure 3B), which predominated in the Northeast region (N=24; 45.3%), followed by the Southeast (N=18; 34.0%), South (N=7; 13.2%), Central-West (N=3; 5.7%), and North (N=1; 1.9%) regions.

From 2001 to 2024, 145 cases of human rabies were reported in Brazil (Figure S8), with an average of approximately six cases per year in 81 Brazilian municipalities (Figure 3C). Most municipalities of Brazil (4488 of 5571) have no reported cases of rabies and are not neighbors of historically rabies-free municipalities. Human cases were most common in the Northeast region (N = 70; 48.3%), followed by the North (N = 53; 36.6%), Southeast (N = 16; 11.0%), Central-West (N = 5; 3.5%), and South (N = 1; 0.7%) regions. Together, the North and Northeast regions accounted for 85% of rabies cases in Brazil during the study period. Most cases occurred in the states of Pará (N = 45; 31.0%), Maranhão (N = 43; 29.7%), and Minas Gerais (N = 11; 7.6%).

The highest number of human rabies cases occurred in Turiaçu in the state of Maranhão (N = 16), followed by the municipalities of Portel (N = 15), Augusto Corrêa (N = 13), Melgaço (N = 10), and Viseu (N = 5), with the latter four municipalities located in the state of Pará. During the study period, of the 145 cases of human rabies, 85 (59%) were transmitted by bats, 30 cases (21%) by canids, and 20 cases (15%) were transmitted by other animals, including felines, nonhuman primates, and herbivores. Another 10 human cases (7%) available in the data were left blank and/or ignored the transmitting animal.

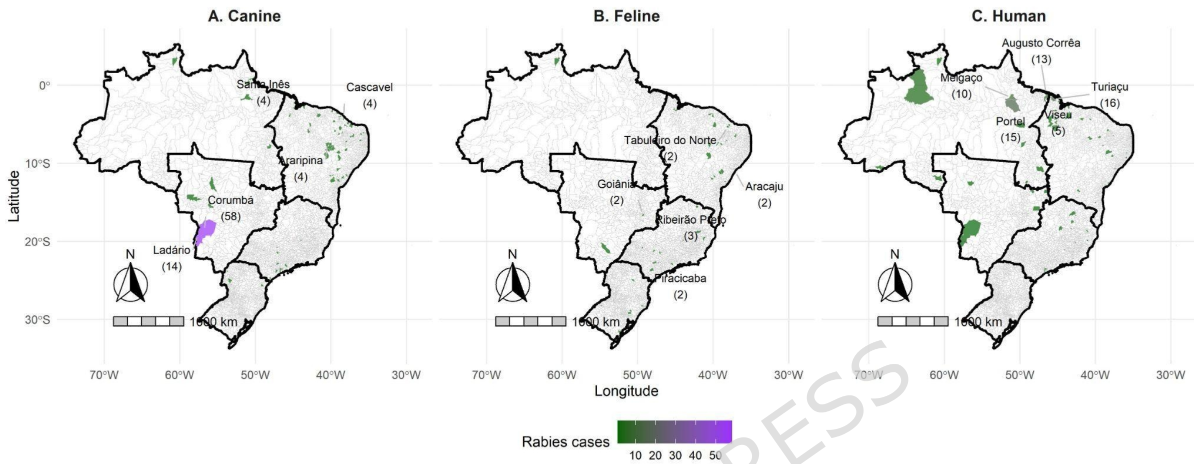

Figure 3. Geographic distribution of municipalities reporting confirmed rabies cases. (a) In dogs, (b) in cats from 2015 to 2023, and (c) in humans from 2001 to 2024. The display shows the five cities with the highest number of cases . Rabies was reported and confirmed in a total of 203 municipalities, including cats, dogs, or humans (Figure S4). The bold lines represent the five Brazilian regions for visual purposes (North, Northeast, Central-West, Southeast, and South).

Spatial prioritization

Correlation analyses revealed weak linear relationships among the three risk components, with a small positive Pearson’s correlation (r = 0.096) with exposure and vulnerability (r = 0.013), but a weak negative correlation with hazard (r = –0.061). Among the risk components, hazard and vulnerability were moderately negatively correlated (r = –0.333), while exposure was weakly negatively correlated with hazard (r = –0.199) and weakly positively correlated with vulnerability (r = 0.077).

Human rabies was confirmed in 81 Brazilian cities. Cities with reported human rabies cases and our risk component classification totaled 19 cities with reported human rabies cases. Another 565 cities were flagged as having a high rating in one of the three risk components, but rabies has not been confirmed in the municipality. Finally, 61 cities tested positive for rabies but were not classified in the highest 200 for any risk component.

Maps showing the rescaled average of hazard, vulnerability, and exposure of rabies throughout the Brazilian territory, integrating data related to the occurrence of rabies cases, socioeconomic and landscape variables are presented in Figure S10. The highest risk is dispersed in Brazil, but particularly in some areas of the center-south, especially parts of Minas Gerais, São Paulo, and some areas of the north and northeast. The highest levels of vulnerability are concentrated mainly in the North and areas of the Northeast and Midwest, especially in the states of Amazonas, Roraima, Acre, Rondônia, Pará, part of Maranhão, and Mato Grosso do Sul. Low vulnerability characterizes the Southeast, South, and certain areas of the Midwest. The highest levels of exposure are located mainly in the North and Northeast regions, with a focus on the states of Pará, Maranhão, and parts of Amazonas and Bahia. Some parts of the Southeast and Midwest regions have a medium exposure to rabies, such as the states of Minas Gerais, Mato Grosso, and Mato Grosso do Sul, while the South has low levels of exposure.

The clustered pattern for rabies presence was captured in our spatial prioritization risk index (Figure 4, Figure S4) for both contextual weights used in our risk index very similarly (weight equal to 0.5: Moran'I statistic= 0.073, Expected- =-0.0001, z-score = 92.31, AUC = 0.93), so we present the results for weight = 0.5 in the main text. The highest priority cities (very high, N=19) for rabies prevention actions are in Pernambuco (N=8), Maranhão (N=4), Bahia (N=3), São Paulo (N=2), Ceará (N=1), and Rio Grande do Norte (N=1). including 31 cities where no rabies was reported to date (Table 1). For high priority, 52 cities were listed, including mostly cities from Maranhão (n=15), Bahia (N=14) and Ceará (N=8) and other states, including Pernambuco (N=6), Rio Grande do Norte (N=4), São Paulo (N=4) and Pará (N=1). Most cities in Brazil were considered very low ranking in prioritization (N=4356), while 952 were considered low risk and 191 had an average ranking. Spatial prioritization results for all municipalities' data are available in Table S2.

Table 1. High (N=52) and very high (N=19) priority municipalities for One Health actions aiming at rabies prevention in Brazil. Cities are ordered alphabetically and by rank, rabies detection, and priority class based on available data up to 2024.

Municipality	State	Rabies detection	Priority
Bodocó	Pernambuco	1	Very high
Campinas	São Paulo	1	Very high
Capela do Alto Alegre	Bahia	1	Very high
Granito	Pernambuco	1	Very high
Ipubi	Pernambuco	1	Very high
Moreilândia	Pernambuco	1	Very high
Ouricuri	Pernambuco	1	Very high
Parnamirim	Pernambuco	1	Very high
Paulínia	São Paulo	1	Very high
Quijingue	Bahia	1	Very high
Santa Cruz	Pernambuco	1	Very high
Santa Inês	Maranhão	1	Very high
Santa Luzia	Maranhão	1	Very high
Viana	Maranhão	1	Very high
Governador Dix-Sept Rosado	Rio Grande do Norte	0	Very high
Jaguaribe	Ceará	0	Very high
Pintadas	Bahia	0	Very high

Serrita	Pernambuco	0	Very high
Tufilândia	Maranhão	0	Very high
Araci	Bahia	1	High
Arame	Maranhão	1	High
Araripina	Pernambuco	1	High
Cândido Mendes	Maranhão	1	High
Hortolândia	São Paulo	1	High
Ipirá	Bahia	1	High
Jaguariúna	São Paulo	1	High
Limoeiro do Norte	Ceará	1	High
Pé de Serra	Bahia	1	High
Quixeré	Ceará	1	High
Santa Filomena	Pernambuco	1	High
São Gonçalo do Amarante	Ceará	1	High
São João Batista	Maranhão	1	High
São José de Ribamar	Maranhão	1	High
São Vicente Ferrer	Maranhão	1	High

Senador Elói de Souza	Rio Grande do Norte	1	High
Tucano	Bahia	1	High
Viseu	Pará	1	High
Altamira do Maranhão	Maranhão	0	High
Amapá do Maranhão	Maranhão	0	High
Aracati	Ceará	0	High
Baraúna	Rio Grande do Norte	0	High
Camaçari	Bahia	0	High
Caucaia	Ceará	0	High
Dormentes	Pernambuco	0	High
Exu	Pernambuco	0	High
Grajaú	Maranhão	0	High
Itaipava do Grajaú	Maranhão	0	High
Januário Cicco	Rio Grande do Norte	0	High
Juquitiba	São Paulo	0	High
Macaíba	Rio Grande do Norte	0	High
Mairi	Bahia	0	High

Marajá do Sena	Maranhão	0	High
Monção	Maranhão	0	High
Nova Fátima	Bahia	0	High
Olinda Nova do Maranhão	Maranhão	0	High
Paulista	Pernambuco	0	High
Paulo Ramos	Maranhão	0	High
Pedro do Rosário	Maranhão	0	High
Pentecoste	Ceará	0	High
Ribeira do Pombal	Bahia	0	High
Rodelas	Bahia	0	High
Rosário	Maranhão	0	High
Russas	Ceará	0	High
Santa Quitéria	Ceará	0	High
São José do Jacuípe	Bahia	0	High
São Sebastião do Passé	Bahia	0	High
Sátiro Dias	Bahia	0	High
Serra Preta	Bahia	0	High

Simões Filho	Bahia	0	High
Sumaré	São Paulo	0	High
Trindade	Pernambuco	0	High

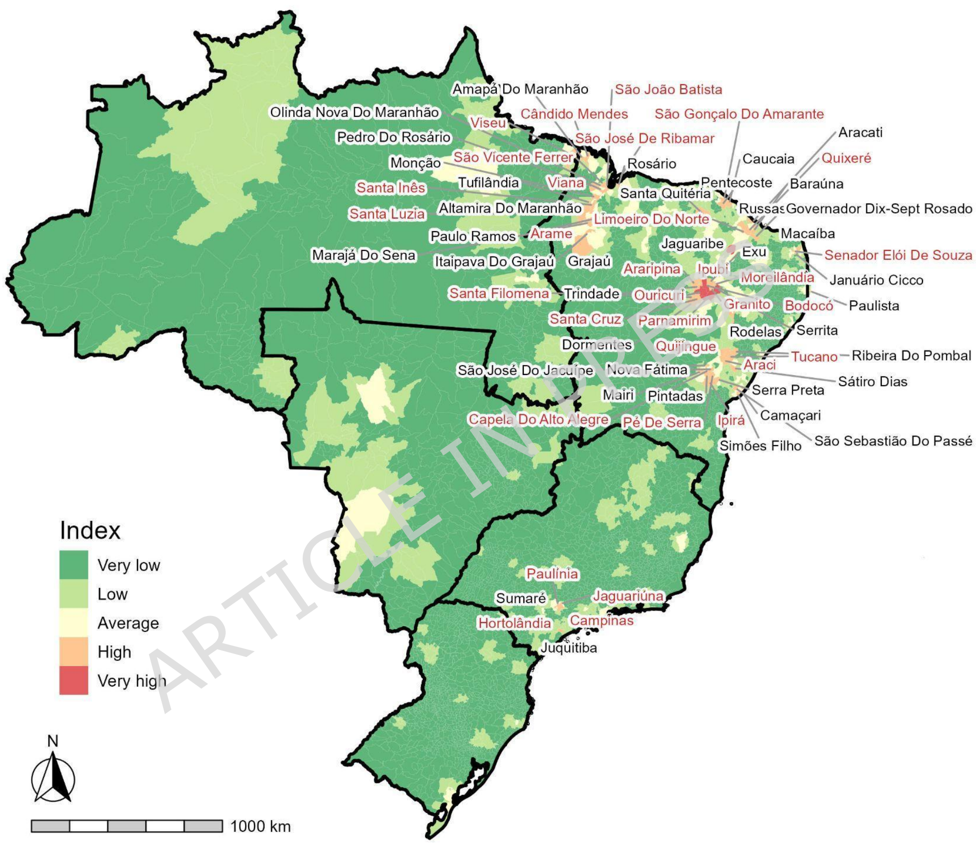

Figure 4. Spatial Prioritization Index for rabies prevention in Brazilian cities. Labeled cities are the ones ranking high and very high. Labels in red are the ones ranking high or very high where rabies has been historically detected based on data up to 2024.

Discussion

This study inferred the potential distribution of the bat *Desmodus rotundus* using habitat suitability models, based on data on the occurrence of the species and environmental and landscape variables. Based on this prediction, we evaluated the risk components of rabies, dividing them into vulnerability, exposure, hazard, and historical risk. While our analysis focuses on a composite risk framework, we acknowledge that rabies transmission in Brazil involves multiple viral variants maintained in partially independent transmission cycles across wildlife, domestic animals, and humans, which may vary regionally in their relative importance, reflecting the complexity of rabies dynamics in Brazil. The spatial prioritization index integrates variables from different time periods and should therefore be interpreted as a composite measure of structural and historical susceptibility to rabies risk, rather than a time-specific estimate of current transmission risk. The results, however, allowed us to generate spatial prioritization maps, aiming to support the development of more effective One Health strategies for the prevention and control of rabies at the municipal level.

The habitat suitability model for *D. rotundus* showed results similar to other studies found in the literature (e.g.[16]), indicating a preference for warm and humid climatic conditions, characteristic of tropical and subtropical regions, and consistent with the ecological requirements of the species. It was observed that areas of high suitability are concentrated in forested regions and in highly anthropized landscapes, such as those associated with extensive livestock farming and deforestation, as demonstrated by the edge distance variable, reinforcing the ecological plasticity of the species and its adaptation to human-modified environments[5,24]. This relationship is important for identifying areas of potential risk for RABV transmission.

However, it is important to highlight the limitations of the model. The species occurrence data presented a significant information gap in the northern region of the country, which may have affected the accuracy of predictions in this area since the Amazon is a geographical center of the species distribution range[25]. Occurrence records in this region are often spatially biased toward river networks due to logistical constraints on sampling, which may influence relationships with hydrological variables included in the model[26]. In addition, the variable distance from caves was used as a proxy for shelters, but this type of formation is rare in the Amazon rainforest, and in this region, *D. rotundus* uses, for example, tree hollows as shelter[18]. The variable was a factor not incorporated into the model, which probably underestimated the habitat suitability for the species in this region. Moreover, ecological factors such as lower livestock densities and the predominance of intact forest habitats may also reduce local colony density or detectability compared to more anthropized regions, further contributing to uncertainty in model predictions for the Amazon. Despite this, it is still possible to estimate species distribution patterns with a certain degree of certainty[27]. A further limitation is the potential temporal mismatch between occurrence records (1970–present) and dynamic landscape variables such as forest edge, which have changed rapidly and unevenly across the Neotropics due to deforestation; consequently, some associations may reflect historical rather than current conditions[28,29].

The analysis of human rabies cases from 2001 to 2024 showed that, although classified as a rare disease, rabies was reported annually, except for 2014 when no notifications were recorded. Cases were concentrated in the North and Northeast regions of the country, matching previous reports that link *D. rotundus* reservoir dynamics to a high rabies prevalence in these locations[17,18,30–32].

Records of rabies transmitted by bats to humans in the Brazilian Amazon constitute the highest number of cases among the regions of the country, distributed mainly among the mesoregions of Northern Maranhão (Turiaçu), Marajó (Portel and Melgaço), and Northeastern Paraná (Viseu and Augusto Corrêa). We observed that in these locations, the epidemiological profile is characterized by: i) most cases occur in rural communities; ii) the population lives in precarious conditions; iii) localities undergoing changes in the type of production process, such as deforestation for mining; iv) there is limited access to health services and a lack of information on prophylactic treatment; and v) there is a lack of information on the risk of transmission due to contact with wildlife. In addition, bat attacks and bites are considered normal in the daily lives of most residents of these communities[17,31,33]. These patterns are largely consistent with a sylvatic transmission cycle dominated by vampire bats but differ from other regions of Brazil, where human exposure may more often involve domestic animals or non-hematophagous bat-associated variants. These municipalities had low human development indices, with significant portions of the population residing in rural areas[34]. Housing in these communities is located in remote areas, where people live in precarious and unprotected dwellings, such as houses without doors or windows, and it is common to find residences without masonry walls[17,35]. These conditions increase the risk of exposure to any animal, including bats, which, consequently, can increase the risk of transmission of zoonoses.

Outbreaks of rabies in humans have been associated with abrupt structural changes, such as logging, deforestation, and the removal of livestock[3,18]. Such changes alter the composition of species available as food sources for vampire bats, bringing them closer to humans, who consequently receive more bites[18,36]. In contrast to this scenario, the introduction of livestock farming may reduce attacks on humans, since *D. rotundus* prefers the blood of cattle, as they are considered easy prey[37]. However, such practices may increase the population of *D. rotundus*, causing a positive feedback effect that will increase feeding on humans.

There is a lack of knowledge about the sylvatic transmission cycle of rabies, particularly the role of wildlife reservoirs such as bats and the mechanisms of spillover to humans, which may contribute to normalization of bat bites, underestimation of risk, and delays in seeking post-exposure prophylaxis[38]. There is also a lack of knowledge about rabies prevention, among the population, who are unaware of the prophylactic regimen and the risks of rabies, and among those who do not complete the regimen, as reported in different cases[35]. There is also a lack of knowledge among local health professionals, who do not always consider rabies in the differential diagnosis, allowing the disease to develop and no longer be treatable[39,40]. Furthermore, ensuring access to post-exposure prophylaxis is difficult in remote areas. In some locations (e.g., Portel and Viseu, municipalities in Pará), travel, although time-consuming, is facilitated by river or road routes, while in other locations, logistics are considerably more difficult[31,35,41].

Our spatial prioritization model considering the risk components of rabies—hazard, vulnerability, and exposure—indicated a high correlation between these three factors, mainly in the northern region of the country, although the municipality rankings vary between components. This overlap signals an increased transmission risk in the region, matching the distribution of the rabies cases observed in our study. In contrast, other regions of the country tend to exhibit only one of the components with less intensity, which also requires attention, since once infected and left untreated, rabies is fatal but may require less investment and focus on fewer components.

Underreporting of rabies cases and incomplete data were a plausible limitation in our study, and we acknowledge the implications for these. For some variables, the treatment of missing values as zeros may introduce bias if missingness reflects incomplete reporting rather than true absence, and results should be interpreted with this caveat in mind. Underreporting stems from the combination of barriers to accessing health services and the possible failure to seek care due to lack of awareness of the risks and prophylactic protocol[33]. It also includes deficiencies in epidemiological surveillance systems, often marked by incomplete or inconsistent reports[42], and clinical underdiagnosis, since the initial symptoms of rabies are nonspecific and can be confused with other neurological conditions[43,44]. With that said, we are not able to test the validity of the missing-data values we had in our analysis, and this evidence supports our decision to use a spatial prioritization for creating our rank. Even though, for instance, many municipalities in Maranhão have no rabies detected, they ranked highly in our index and are following similar trends of social neglect and neglected tropical diseases reported to date[45]. The use of a single-year (2020) land-use layer constrains the SDM to a static representation of landscape structure, which may not fully capture historical or ongoing land-use dynamics; therefore, model outputs should not be interpreted as representing either historical habitat conditions or fully current landscape configurations. A further potential limitation is that our framework does not explicitly distinguish between different rabies transmission cycles or viral variants, instead treating using proxy variables as components that indicate higher or lower risk (bat host occurrence as a main hazard component for the main bat-variant transmission cycles potentially limiting inference for the role of insectivorous bats and dog vaccination coverage as a crucial component for eliminating dog-variant transmission) as a composite outcome; while this enables national-scale prioritization, it may mask important contextual differences between regions. Nevertheless, because we selected components most relevant to viral circulation, we consider our prioritization workflow broadly applicable, while acknowledging that systematic, integrated surveillance of infection in non-hematophagous bats and other mammals remains unlikely to be feasible but see (Duarte et al. 2020).

Regional inequalities in health infrastructure contribute to greater difficulty in diagnosis and reporting in rural and remote areas, as documented in the eastern Amazon[46]. Furthermore, problems with filling out notification forms and the resulting incomplete data are recurrent, limiting the epidemiological characterization of the disease[47]. Taken together, these elements show that official figures may substantially underestimate the actual burden of rabies.

Current rabies control strategies, which include capturing and poisoning bats and destroying their natural shelters with explosives, have proven not only ineffective but also potentially harmful in terms of increasing viral spread, as individuals tend to migrate to other areas[48]. Such measures are harmful because they drastically impact entire cave ecosystems, which are home to a diversity of bat species (pollinators, insectivores, frugivores, carnivores, and hematophages) and other animals essential for maintaining ecological functions[20,49]. Furthermore, these actions affect and diminish the crucial ecosystem services provided by bats, which have direct and positive implications for agriculture, for example[50,51].

It is common for vampire bats to be presented only as dangerous carriers of RABV, without any differentiation or information about prevention or about why and how these animals are increasingly coming into contact with humans. Although many negative myths persist historically, little is said about the invasion, destruction, and fragmentation of their natural habitats resulting from agricultural expansion, mining, and urbanization[18]. These factors are crucial to understanding the increased risks of zoonoses and the increasingly widespread geographical distribution of this species and should be central elements in public and political debate[49].

Although *D. rotundus* plays an important role in our spatial prioritization analysis as a hazard component, we highlight how our results can contribute to One Health actions for complying with the global strategic plan to eliminate human deaths from canine rabies by 2030[52]. Bats can infect dogs, establishing a pathway of secondary transmission to humans; however, this occurs alongside other transmission cycles, including urban dog-mediated rabies and spillover from both hematophagous and non-hematophagous bats, which may operate with differing dynamics across regions[53]. Other species of mammals also likely play a role in RABV maintenance (see Figure S8)[54]. Future work could extend our approach by developing regionally stratified or cycle-specific models that explicitly account for interactions between wildlife reservoirs, domestic animals, and humans when complete surveillance data is available.

Rabies does not respect political or administrative boundaries, and we must break down several barriers to achieve the goal of controlling this zoonosis, benefitting from the One Health approach. This includes barriers between sectors of society and government agencies, between public knowledge, and between countries that border Brazil and have cases of rabies in these locations[55]. It is important to improve health education focused on rabies for the population and health professionals, in addition to equitable access to the health and surveillance system[56].

The results of this study have direct implications for public health risk management and One Health action prioritization by providing a list of priority municipalities based on historic rabies risk components. We recommend that surveillance actions continue to focus on areas with a history of cases, but also target those identified as high and very high risk in our analyses, even in the absence of previous rabies records. A preventive approach with communication and awareness campaigns and capacity building is vital to foster discussions about the zoonotic risk of rabies in these locations[57].

Future efforts should continue promoting multidisciplinary approaches to better understand and address rabies risk[43]. It is imperative that this dialogue actively includes communities living in risk areas, integrating their local knowledge and needs for the development of effective and culturally appropriate prevention strategies in conjunction with other segments of the public and private sectors of society.

This study emphasizes that the occurrence of rabies risk is a complex phenomenon that extends beyond the mere presence of the viral reservoir. It is evident that the vulnerability, exposure, and risk of populations, determined by socioeconomic conditions and anthropogenic environmental changes, can be crucial factors in determining priority areas for rabies control. Given our far-from-complete overlap between cities reporting rabies in humans, dogs, and cats, future efforts can tailor risk components after more local input and validation of the components used. The prioritization maps generated together with the list of municipalities at risk provide a start for developing strategic tools for directing surveillance and resources to these locations.

We reinforce the adoption of a One Health approach because once we understand the complexity of zoonosis and all the components that surround it, effective strategies must be multisectoral, such as joint work between professionals from different areas[57,58]. Future actions and research should integrate the community and improve models and data that overcome gaps in the north and northeast of Brazil, aiming not only to control the disease but also its socioeconomic and ecological drivers. Due to the limitations of our model, considering the current data, future work could explore region-specific models to better capture local transmission dynamics. Thus, with the integration of multiple data sources and approaches, our results can effectively contribute to and direct efforts toward the sustained elimination of the disease in Brazil.

Methods

Bat occurrence data and environmental variables

We compiled *D. rotundus* occurrence records from different sources and databases, including speciesLink (specieslink.net), SALVE/ICMBio (salve.icmbio.gov.br), the Brazilian Biodiversity Information System (SiBBr) (sibbr.gov.br), Atlantic Bats[59], DarkCideS 1.0[60], and a database of common vampire bat reports[61]. In addition, we used the R *spocc* package[62] to download data from the Global Biodiversity Information Facility (gbif.org), VertNet (vertnet.org), and iDigBio (idigbio.org). After integrating the occurrence data, we had a total of 107,134 occurrences. Then, we cleaned the occurrences based on the following criteria: (i) temporal filtering (excluding records prior to 1970), (ii) low spatial accuracy filtering (excluding records with fewer than three decimal places in latitude/longitude), (iii) filtering based on the Neotropical boundary[63], and the historical distribution of the species[64], (iv) invalid record filtering (removing duplicate records, invalid reference system coordinates, and records with zero coordinates); and (v) rarefaction to 20 km resolution to reduce model overfitting. A spatial rarefaction distance of 20 km was applied to reduce spatial sampling bias and model overfitting, representing a compromise between retaining sufficient occurrence data and minimizing spatial autocorrelation at the scale of environmental predictors. Furthermore, this is also estimated to be the value of the species' home range[65–67]. Data cleaning was performed using the R packages *CoordinateCleaner*[68] and *spThin*[69].

We used five classes of predictor variables for each unique point of bat occurrence: climatic, topographic, hydrographic, landscape, and cave-related. The climatic variables (19 bioclimatic variables) were obtained from WorldClim v.2.1[70] which represents long-term climatic averages for the period 1970–2000. For the topographic variables, we downloaded elevation, slope, and aspect data from EarthEnv (earthenv.org/topography)[71]. We also downloaded hydrographic data from EarthEnv and calculated the nearest Euclidean distance (km) from freshwater ecosystems[72]. We also used a landscape structure metric for edge habitats, considering only the forest class for the year 2020[73] as a static proxy for landscape structure. We calculated the nearest Euclidean distance (km) from the vegetation class, with increasing positive values representing the distance outward from the edge and increasing negative values representing the distance inward from the edge, where a value of zero represents the edge itself. Finally, we used Euclidean distance (km) data from karst and caves considering any possible cave or karst where bats could roost[23]. All variables were adjusted for the extent of the Neotropical region, with a spatial resolution of 30 arc-seconds (~1 km). These variables represent long-term environmental conditions, and therefore the SDM reflects climatic suitability rather than short-term or current environmental variability.

Natural host distribution modeling

We used the maximum entropy (MaxEnt) machine learning algorithm[74] with automated hyperparameter tuning and evaluation[75]. MaxEnt is one of the most widely used machine learning algorithms for fitting habitat suitability models using presence-only data, and it almost always demonstrates robust performance, even with a limited number of occurrences[74]. To reduce multicollinearity among predictor variables, we performed a Variance Inflation Factor (VIF) analysis, considering only variables with VIF < 2 for model fitting, using the R package *usdm*[76]. We generated 10,000 randomly sampled background points and tested different combinations of hyperparameters, resulting in a total of 60 models. We varied two hyperparameters: (i) Regularization Multiplier (RM)—determines the penalty associated with the inclusion of variables or their transformations in the model; and (ii) Feature Classes (FC)—determines the potential shape of the marginal response curves. These models were constructed by combining 10 RM values (ranging from 0.5 to 5 in increments of 0.5) with six types of FC (L, LQ, H, LQH, LQHP, and LQHPT, where L = linear, Q = quadratic, H = hinge, P = product, and T = threshold).

To evaluate model performance, we applied a quadruple spatial partitioning block method. Models were fitted and evaluated using the R package *ENMeval* 2.0.4[75], which facilitates model fitting, evaluation, and comparison to identify optimal hyperparameter settings. This fitting process typically results in models that balance fit quality (i.e., minimizing overfitting) and predictive power[77,78]. We selected the best model based on the lowest ΔAICc value and evaluated model performance using the Area Under the Curve (AUC), Boyce scores, and True Skill Statistics (TSS), the latter using the threshold of maximum sensitivity and specificity. The SDM was calibrated across the Neotropical region to capture the full environmental niche of the species and reduce edge effects, while subsequent analyses and interpretations were restricted to Brazil.

Rabies data

We compiled data on human rabies cases between 2001 and 2009 from the Notifiable Diseases Information System (SINAN) (https://portalsinan.saude.gov.br). The same data, but between 2010 and 2024, were compiled directly from the Ministry of Health website, since the most recent data were not yet available on SINAN as of March 2025, when they were compiled (www.gov.br/saude/pt-br/assuntos/saude-de-a-a-z/r/raiva/raiva-humana). These data was separated by municipality and year of occurrence. Two rabies cases for 2025 were available as of January 13, 2025, but were not used because they were still subject to change, and other cases may have arisen during this study.

Data on domestic dog and cat cases were collected from the Ministry of Health website[79] for the years from 2015 to 2024, where they were separated by Federal Units/Municipality and year of occurrence, available to the public, and for wild and rural animal cases (cattle, horses, bats, raccoons, non-human primates, and wild canids) for the years 2002 to 2024, in which they were separated only by Federated Units and year of occurrence (Figure S5).

During the preliminary analysis of rabies data, some questions arose regarding the source of human data: (i) the data were compiled from two different sources (SINAN and the Ministry of Health), and some data were inconsistent between the years 2010 and 2021. Therefore, we chose to use SINAN data only between 2001 and 2009, and we used Ministry of Health data for subsequent years until 2024; (ii) we found a previously published article[32] and noted that rabies data for the year 2000 were used, but these data are not included in publicly available databases, reducing the number of rabies cases we have to use in our analyses. After this preliminary analysis, we verified the reliability of the data using news reports and The Ministry of Health provided reports and epidemiological bulletins to address the discrepancies initially found.

We also observed a gap in human rabies cases regarding the animal that caused the transmission of the rabies virus between 2007 and 2009. Therefore, news reports, epidemiological bulletins, and graphs provided by the Ministry of Health[80] were also used to complete this data set, and we obtained a complete set of data on rabies in humans and the attacking species between 2001 and 2024 as our historical risk for human rabies. In addition, we gathered curated data on rabies in cats and dogs to create a composite historical hazard dataset.

Socioeconomic and landscape data

We compiled socioeconomic data from articles and information published online that we deemed relevant to our analysis, considering the risk factors for rabies. We compiled data on the percentage of poor people, child population, Municipal Human Development Index (IDHM), GINI Index, Municipal Human Development Index for Education, and percentage of inadequate walls for the year 2010 from the Atlas of Brazil. We also compiled data on population density, rural and urban population, indigenous population, average number of years of schooling, and literacy rate for the year 2022 from the 2022 Demographic Census. We also compiled data on total health expenditures between 2000 and 2024; expenditures on epidemiological surveillance; and expenditures on basic health between 2013 and 2015 from the Public Health Budget Information System. We compiled data on the National Rabies Vaccination Campaign between 2012 and 2017 from the National Immunization Program Information System, focusing on dogs and cats. Finally, we compiled data on motorized travel time to the nearest hospital for 2019 from the article by Weiss et al. (2020).

For landscape structure data, we compiled data on the percentage of pastureland for the year 2023 from MapBiomas Brasil; cattle population data for the year 2023 from the Agricultural Census; and data on the density of secondary roads for the year 2022 from the Brazilian Institute of Geography and Statistics (IBGE) (Figure S5). All of these data was organized at the municipal level for all of Brazil, for which we also incorporated the average habitat suitability values from our habitat suitability model for *Desmodus rotundus* generated with the MaxEnt algorithm.

Data integration

After compilation, we verified and cleaned all socioeconomic and landscape structure data, standardizing column names and integration codes for the municipal and state administrative codes and providing detailed metadata, as some tables had to be manually transcribed from PDF to Excel®. After data integration, we consolidated our data into the Brazilian municipality vector using R 4.5.1[81]. For one coastal city in Rio Grande do Sul (Imbé), no information for SDMs was available, so we imputed data with its closest neighbor's host suitability (Novo Barreiro, suitability = 0.7). For one municipality, we had an uncommon spatial pattern: the municipality of Ladario, in Mato Grosso do Sul, was located within a complete perforation of the

Corumbá municipality. In this case, the Ladário municipality neighborhood was attributed to Corumbá.

Spatial prioritization index: factor selection and assessment

We grouped these data (rabies, socioeconomic, and landscape structure data) into four categories. These categories were proposed because we worked with the One Health approach (Figure S7)[57], which recognizes the interconnection between human health, animal health, and the environment. To do this analysis, we need to understand the risk factors, exposure, vulnerability, and historical risk of the disease. The first category was **exposure**—we included variables considered to influence the probability of contact and subsequent infection by a zoonotic agent (e.g., when there are more inadequate walls for housing, there is a greater possibility of rabies transmission by *D. rotundus*, as they can serve as shelter and they are more likely to attack, and this is linked to the poor living conditions of rural communities[30,82]). The second category was **vulnerability**—we included variables considered to influence the probability of a given exposure to a hazard resulting in a zoonotic disease outbreak (e.g., when there is a higher literacy rate, there is less chance of contracting rabies, since education is an important factor, given that many people were not even aware of the risks of rabies[30]). The third category was **hazard**—we included variables that influence the relative quantity of zoonotic infectious agents available, acting as potential sources of a zoonotic disease outbreak (e.g., when there is a higher habitat suitability value for *Desmodus rotundus*, there is a higher risk of rabies virus transmission since it is the reservoir of the rabies virus[30]). Finally, the **historical hazard category** refers to cases of rabies that occurred between 2001 and 2024.

We verified the completeness of these data (Figure S6) and then proceeded to transform the NAs into zeros for the data so that we could quantitatively evaluate the correlations and variance inflation factor (VIF). We performed a variance inflation factor (VIF) analysis, eliminating variables that led to VIF values greater than 2 (similar to the absolute value > 0.7 for rho in Spearman's correlation analysis). The NAs in the rabies data were assumed to be true zeros in our analysis. One possible caveat in the health expenditure data is that completeness is around ~80%, but no municipality where rabies was present (our main target) had any expenditure value defined as NA. Therefore, we proceeded with the analysis and flagged our municipalities that had NA values for these variables in the prioritization analysis results. Thus, we retained extensive data coverage for Brazil, while the variables in green that had few NA values are cases such as islands and very small municipalities that were not covered by any reference raster (e.g., travel time).

Based on current literature, we selected 21 risk factors associated with rabies transmission based on their fit as risk components and data availability at the municipality level: three hazard factors, one historical hazard factor, eight exposure components, and ten vulnerability components (Table 2). After that, we selected data based on VIF, whereas after removing collinearity effects, the final input variables for each component were a total of 17 variables across three components: hazard (variable names: sdm_cont_mn, CATTLE_POP, CANINE_VACCINATED), historical hazard (prior human rabies cases), exposure (WALL, HAB_KM2, PRural, roads_density_km, CHILDREN, PIndig, pasture_pct), and vulnerability (HOSPITAL_TRAVEL_TIME, GINI_INDEX, RT_LITE, SPENDING_HEALTH, SPENDING_EPIDEMIO_SURV, SPENDING_BASIC_CARE). For dog vaccination coverage and literacy, we inverted the variable since we assume that greater vaccination coverage is negatively associated with risk. After gathering the final covariates for each component, we ran an exploratory correlation analysis across the three components to understand their intersections.

Table 2. Rabies risk components for spatial prioritization index development.

Category	**Variable**	**Description and rationale**	**Data source**	**Period covered**
Exposure	Inadequate walls	% households in a city with inadequate walls	Atlas do desenvolvimento humano	2010
Exposure	Human Population density / km2	Potential contact between people and vectors	Censo demográfico	2022
Exposure	Number of total human population / urban human population	Potential contact between people and hazard components	Censo demográfico	2022
Exposure	Number of rural population	Potential contact between people and vectors	Censo demográfico	2022
Exposure	Secondary road density	This layer represents a proxy for both	IBGE	2023

	(km)	connectivity and mobility. Secondary road length has been positively associated with rabies risk [83]		
Exposure	Children's population	Number of children between 0 and 14 years old	Atlas do desenvolvimento humano	2010
Exposure	Indigenous population	More exposure in remote areas	Censo demográfico	2022
Exposure	Pasture	Percentage of pasture	MapBiomas Brasil	2023
Hazard	Vampire bat current presence	Key reservoir host in rural areas at the Wildlife-Domestic-Human Interface	Our models	2025
Hazard	Cattle population	Potential attractor for vampire bats at the Wildlife-Domestic-Human Interface	Censo agropecuário	2017
Hazard	Dog immunisation coverage *(-1)	Dog-mediated human rabies reduction	DATASUS	2012-2017
Vulnerability	Travel time to hospital	Travel time to healthcare is measured in motorized minutes at a spatial resolution of 1 km	Weiss et al.	2019
Vulnerability	Gini Index	It measures the degree of income concentration in a given group	Atlas do desenvolvimento humano	2010
Vulnerability	Percentage of Poor People	Per capita household income below the poverty line adopted by the World Bank	Atlas do desenvolvimento humano	2010
Vulnerability	Municipal Human Development Index	It is a composite measure of indicators from three dimensions of human development: longevity, education and income.	Atlas do desenvolvimento humano	2010

Vulnerability	Municipal Human Development Index - Education	It is the combination of two variables - average years of schooling of the population aged 25 or older and expected years of schooling	Atlas do desenvolvimento humano	2010
Vulnerability	Literacy Rate *(-1)	Expresses the minimum educational status of the population	Censo demográfico	2022
Vulnerability	Average Number of Years of Study	Associated with lower awareness of rabies	Censo demográfico	2022
Vulnerability	Spent on Epidemiological Surveillance by the Ministry of Health (Figure S1, Figure S2)	Availability of life-saving treatment	SIOPS	2013-2015
Vulnerability	Spent on Basic Care by the Ministry of Health (Figure S1)	Availability of life-saving treatment	SIOPS	2013-2015
Vulnerability	Total Health Expenditure by the Ministry of Health (Figure S1)	Availability of life-saving treatment	SIOPS	2000-2024
Historical hazard	Historical rabies presence	Prior human cases	SINAN e Ministério da Saúde	2001-2024

Analysis of risk components

Prior to the spatial prioritization analysis, as a first exploratory data analysis, we developed a naive, aspatial analysis, considering that all input components for risk are weighted equally, based on risk components selected from the One Health approach. The hazard-exposure-vulnerability framework was operationalized to capture complementary dimensions of rabies risk, recognizing that some variables may reflect interacting ecological, socioeconomic, and institutional processes. While some conceptual overlap between exposure and vulnerability is unavoidable in complex socio-ecological systems, variables were grouped based on their primary functional role in influencing contact rates (exposure), susceptibility and response capacity (vulnerability), and pathogen presence or amplification (hazard). With that, we flagged municipalities that were highly ranked in terms of human rabies hazard, exposure, and vulnerability by creating a rank containing the top-200 cities for each component. This seemed adequate considering the number of human rabies-positive cities (N=81) and the plausibility of under-reporting (Figure S9).

Then, we proceeded to evaluate whether rabies cases in humans could be considered proxies for cat and dog rabies, but the spatial overlap was weak. Because of that, we flagged as contextual hazard cities where any rabies case (human, dog, or cat) would be detected as a proxy for historical viral circulation. We did not add data for herbivores because it is incomplete at the municipal level. Historical rabies in Brazil is rare, but human, cat, and dog cases tend to cluster spatially, with Moran's I indicating statistically significant spatial autocorrelation ($I = 0.08$, $z = 10.24$, $p < 0.001$), although the magnitude of clustering was weak. With that, we proceeded to define spatial effects on our spatial prioritization formula and test for sensitivity of weights for the contextual factors. We added to our composite index the three core risk components and local contextual modifiers (rabies presence history in cats, humans, or dogs and adjacency). That means a municipality with low values for risk components could still attain a high overall score merely for being next to or having a past case. Therefore, our composite index indicates a baseline risk based on our expected rationale, which is amplified by historical and spatial contexts. After generating the index, we displayed ROC curves to verify omission and commission for rabies presence according to two different contextual weights (0.5 and 1).

Municipalities with prior rabies cases (historical hazard > 0) were flagged as high-priority regardless of their component values. To account for potential spatial spillover, we incorporated neighborhood effects by connecting municipalities through a contiguity-based adjacency matrix derived from municipal shapefiles. Municipalities adjacent to those with historical cases (in humans, cats, or dogs) were assigned an elevated rabies priority. We developed a spatial prioritization index by combining three scaled risk components (exposure, hazard, and vulnerability) with historical and neighborhood risk contributions based on continuous and immediate spatial contiguity across cities. This approach ensures that municipalities with historical cases, their neighbors, and those scoring highly across the three components are spatially prioritized. The resulting spatial priority index was classified into five categories (very low, low, medium, high, and very high) for interpretability.

We additionally labeled the “very high” priority municipalities according to which historical cases occurred (human, dog, cat, multiple, or all) to provide context for spatial priority patterns. We used human, cat, and dog rabies cases as proxies for historical risk (rather than human cases alone) because the overlap among municipalities with human, dog, and cat rabies was very low. Using only human cases would therefore inadequately represent historical risk. Notably, only Boa Vista reported cases in all three hosts, with most human and dog cases not overlapping, followed by cases in cats (Fig. S4). Fernando de Noronha and Ilha Bela, the only municipalities without neighbors (pure islands), were deemed to have zero historical risk because they reported no cases, independent of adjacent municipalities.
Our spatial prioritization index formula is defined as follows:

$$\text{Spatial prioritization index}_i = \underbrace{\frac{1}{3}\left(\text{exposure}_i + \text{hazard}_i + \text{vulnerability\_average}_i\right)}_{\text{risk components}} + \underbrace{0.5 \cdot \text{hazard}_i}_{\text{historical contribution}} + \underbrace{0.5 \cdot \frac{1}{|N(i)|} \sum_{j \in N(i)} \text{hazard}_j}_{\text{neighbor contribution}} \quad (1)$$

We reapplied a Moran’s test to check if our index captures the contextual hazard factors without overweighting them for the two weights tested (and 0.5 and 1). We then proceeded to plot our spatial prioritization map, applying a color legend for Jenks natural breaks, seeking to highlight similar values together while maximizing the differences between groups, focusing on municipalities at high risk that should be prioritized for prevention actions. Because historical rabies occurrence is incorporated as a contextual component of the index, evaluation metrics such as AUC should not be interpreted as measures of predictive performance, but rather as indicators of spatial coherence between the index and known patterns of disease occurrence. Finally, this index combines variables from different time periods and therefore reflects a composite of historical, structural, and environmental conditions rather than a strictly time-specific representation of current rabies risk.

Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information. The dataset analyzed during the current study is included in the following: https://github.com/dudadkc/Projeto_Morcegos.

Ethics declaration

This study used exclusively secondary data complying with the Transparência Pública Brasil and open-access databases (e.g., SINAN, Ministry of Health, GBIF, and other biodiversity repositories). All data were aggregated at the municipal or broader spatial level and did not contain any personally identifiable or sensitive individual-level information. As such, this study did not require approval from an institutional ethics or research committee, in accordance with applicable guidelines for research using publicly available data. The authors declare no competing interests.

Acknowledgements

We thank the anonymous reviewers for their insightful and constructive feedback, which significantly improved the clarity and quality of this work.

MEF was supported by undergraduate grants #2024/07056-6 and #2024/20504-8, São Paulo Research Foundation (FAPESP). MEF thanks FAPESP, Universidade Estadual Paulista (UNESP), the Laboratory of Spatial Ecology and Conservation at UNESP, and the Molecular Epidemiology and Public Health Laboratory at Massey University for their support. RLM is supported by an Australian Research Council Australian Laureate Fellowship (FL240100037) funded by the Australian Government. RLM thanks the Mabs Melville Bequest at The University of Sydney and the Morris Trust for Animal and Human Health and the Massey Foundation at Massey University for their support. MHV was supported by grants #2022/01899-6, #2024/19865-6, and #2025/15581-6, São Paulo Research Foundation (FAPESP).

Funding

This study was financed by the São Paulo Research Foundation (FAPESP), process numbers #2024/07056-6 and #2024/20504-8. RLM is supported by an Australian Research Council Australian Laureate Fellowship (FL240100037) funded by the Australian Government. RLM thanks the Mabs Melville Bequest at The University of Sydney and the Morris Trust and Massey Foundation at Massey University for their support. DTSH was supported by the Percival Carmine Chair in Epidemiology and Public Health. MHV was supported by grants #2022/01899-6, #2024/19865-6, and #2025/15581-6, São Paulo Research Foundation (FAPESP).

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