

# Chapter 8

## Bats, Pathogen Diversity and Rabies in a Changing Neotropic Landscape



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### 8.1 Introduction

There are misconceptions that have led to the underestimation of bats' ecological roles, even though bats are essential to the health of natural and modified ecosystems (Kalka et al. 2008; de Carvalho-Ricardo et al. 2014; Medellín et al. 2017; Kemp et al. 2019). More than one-third of all bat species assessed by the International Union for Conservation of Nature (IUCN) are classified as threatened or data deficient, and more than half have unknown population trends (Fenton et al. 2020). According to the most recent IUCN Red List, 77 species are endangered. In addition, at least 988 of the approximately 1400 known bat species require immediate conservation measures and additional research (Frick et al. 2020). Due primarily to their nocturnal and cryptic behaviors, we are unable to accurately evaluate the ecosystem services bats provide. The primary hazards to bats are habitat degradation, roost damage, and hunting (Frick et al. 2020). In addition, bats are erroneously stigmatized in many regions of the world, and the current acute respiratory syndrome COVID-19 has generated fear to the point where it is endangering bat populations (Fenton et al. 2020; Rocha et al. 2021).

Most of the research on pathogens in bats has focused on the diversity and distribution of medically significant emergent pathogens, such as Ebola, Hendra, Nipah, Marburg, and multiple coronaviruses (Epstein et al. 2006; Woo et al. 2006; Smith

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et al. 2011; Hayman 2016). Bats are significant reservoirs of numerous viruses (Streicker and Gilbert 2020), but their unique function as hosts of zoonotic viruses relative to other mammalian taxa is questionable. While some studies assert that bats host more zoonotic viruses per species than other mammalian orders, such as rodents (Luis et al. 2013; Olival et al. 2017), more recent research has demonstrated that the number of zoonotic pathogens found in bats is largely a function of host species diversity and that the proportion of zoonotic pathogens varies little among mammalian orders (Mollentze and Streicker 2020).

Rabies is the most significant zoonosis transmitted by bats in Latin America due to its global distribution, human cases, a wide range of potential reservoirs, and veterinary and economic cost implications, representing a public and animal health concern for which local governments allocate substantial funds for control and eradication programs. In the case of dog-transmitted rabies, these programs have been successful, notably in urban areas, but programs focused on bat eradication have not been effective (Rupprecht et al. 2002; Viana et al. 2023). Bat-mediated transmission of rabies virus only occurs in North, Central, and South America. It is believed that rabies has existed in tropical America since pre-Columbian times and is transmitted primarily by hematophagous vampire bats. However, recent phylogenetic reconstructions indicate that the rabies virus in the Americas is unlikely to have originated from vampire bats. Now that diagnostic techniques have advanced, it is possible to comprehend the dynamics of bat-rabies; nevertheless, a transdisciplinary approach that considers the ecology and habitat use of the main reservoir, the common vampire (*Desmodus rotundus*), is needed.

The risk of zoonoses of wild origin has led to several programs that sample wildlife to discover new viruses and assess their zoonotic potential (Olival et al. 2017). These programs include the PREDICT project (Kelly et al. 2017), the Global Virome Project (Carroll et al. 2018), and SpillOver: Virus Risk Ranking (Grange et al. 2021). The first two programs focused on conducting targeted surveillance to detect emerging viral pathogens with zoonotic potential, with the goal of preventing emerging diseases and possible pandemics. On the other hand, SpillOver is an open-source tool that evaluates the potential of wild-origin viruses for zoonotic transmission.

It has been observed that there is a significant bias in the investigation of emerging infectious disease events, with greater infectious disease surveillance efforts in wealthy and developed countries in Europe, North America, Australia, and parts of Asia compared to developing countries located in tropical regions. These areas are described as hotspots for the emergence of infectious diseases due to their high human population density and greater mammalian diversity. In other words, economic and scientific resources for pathogen detection and surveillance are located in nations that have a low probability of pathogen emergence (Jones et al. 2008). This is also the case for pathogen research in the order Chiroptera, where regions in Latin America and parts of Asia have comparatively few characterized viruses despite their bat abundance (Olival et al. 2012, 2017; Szentivanyi et al. 2023).

The economic losses resulting from zoonotic outbreaks are significant. The World Bank estimates that six zoonotic outbreaks (Nipah virus, West Nile virus,

severe acute respiratory syndrome, highly pathogenic avian influenza virus, bovine spongiform encephalopathy, and Rift Valley fever) from 1997 to 2009 caused \$80 billion in losses, equivalent to \$6.7 billion per year. In 2016, Fan et al. estimated that a pandemic with the potential to harm 720,000 people could result in \$570 billion in annual economic costs. In 2017, Daszak et al. estimated that the total damage caused by emerging infectious diseases of zoonotic origin over the next 50 years could reach \$3.6 trillion, considering the global frequency of pandemics, mortality rates from emerging infectious diseases, and gross domestic product. According to Dobson et al. (2020), the COVID-19 pandemic was expected to reduce the global gross domestic product by \$5.6 trillion by 2020.

Opposed to the mentioned economic effects, the World Bank estimated that upgrading public health and animal health systems in developing countries to meet World Health Organization (WHO) and Organization for Animal Health (OIE) standards would cost between \$1.9 and \$3.4 billion per year. In contrast, the PREDICT Project, which began in 2009 and lasted for 10 years, spent \$200 million per year to enhance global capabilities to detect viruses with pandemic potential. The Global Virome Project, a 10-year initiative to discover, characterize, and evaluate 70% of viral diversity, is estimated to cost \$1.2 billion annually (Dobson et al. 2020). This initiative focuses on collecting samples from key zoonotic reservoirs, such as bats, in highly biodiverse tropical developing countries with limited capacity to respond to public health crises (Carroll et al. 2018). Preventive measures to avert pandemics, including wildlife trade monitoring, reduction of spillovers, control and early detection, halving the rate of deforestation, and terminating the bushmeat trade in China, are estimated to cost between 22 and 31.2 billion annually (Dobson et al. 2020).

As the demand for natural resources rises worldwide, land-use change in tropical and subtropical ecosystems is occurring at an unprecedented rate (Song et al. 2018). Several recent zoonotic infections have been linked to land-use change; however, little is known about the connection between changing land use and the rise of diseases (Gibb et al. 2020). Several authors have suggested that land-use change may increase the risk of disease emergence by promoting human–animal interactions or by influencing pathogen diversity, either directly by changing the prevalence and/or diversity of pathogens or indirectly through impacts on host assemblages (Bradley et al. 2008; Vittor et al. 2009; Murray and Daszak 2013; Rulli et al. 2017). However, empirical research examining the impact of land-use change on pathogen assemblages in Neotropical bats remains limited.

## 8.2 Methodology

A comprehensive search of the Web of Science Core Collection for current information on parasite ecology in Neotropical bats from 1990 to 2021 was conducted. The initial search focused on pathogen groups (viruses, bacteria, and parasites), bats (bats, Chiroptera), and the Neotropical region (Neotropics, South America, and Latin America). Review articles and laboratory/experimental investigations reporting

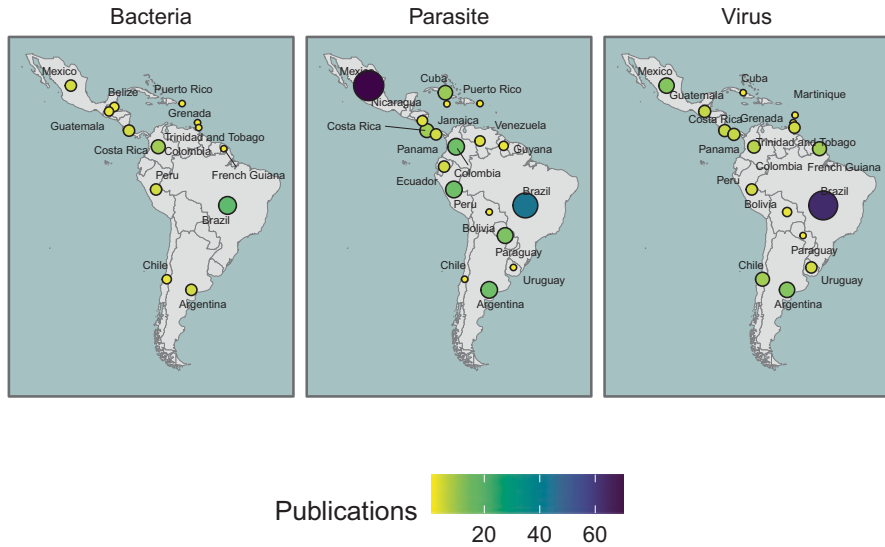
pathogens were excluded from the study. The second search was conducted to identify studies that demonstrate how anthropogenic (fragmentation, land use, landscape, urban, habitat perturbation) and ecological (temperature, latitude, altitude, precipitation, humidity, climate change, functional traits) factors are associated with the prevalence and diversity of each pathogen group. A database was constructed where a single observation consisted of a pathogen reported in a single bat species. Bat family, bat species, year, pathogen type (virus, bacteria, or parasite), pathogen family, and country where the report was made were collected.

The bias in the surveillance of pathogens with zoonotic potential may be due to the high costs associated with identifying and sampling wild species. Therefore, an analysis was conducted to investigate the relationship between gross domestic expenditure on research and development as a percentage of gross domestic product and detection and sampling effort to assess pathogen richness in Neotropical bat species. The goal was to determine whether these factors could affect the surveillance of viral pathogens in bats and how this could impact research and viral surveillance efforts. Information was collected on gross domestic expenditure on research and development (R&D), bat-associated viral richness, and bat richness in Latin America and the Caribbean.

The indicator of gross domestic expenditure allocated to research and development (R&D), expressed as a percentage of gross domestic product (GDP), was utilized to assess the participation of various nations in epidemiological surveillance. This indicator can be used to evaluate and analyze scientific research and experimental development activities (United Nations 2017). It was obtained from the World Bank's databank (World-Bank 2022), analyzing data from 1996 to 2018, as the countries with submissions have records for these years. Since not all countries have entries for all years, the average annual expenditure for each country was calculated. A list of the number of bat species present in each country was prepared using data from the International Union for Conservation of Nature (IUCN 2022). Linear regression analyses were performed between total reported bat viruses per country and gross domestic expenditure on research and development as a percentage of gross domestic product and between bat richness and total reported bat viruses per country. Finally, a literature review was conducted to describe rabies control strategies with emphasis on the ecology of *Desmodus rotundus*, the main species involved in the maintenance and dispersal of the rabies virus.

### 8.3 Bat-Associated Pathogen Diversity in the Neotropics

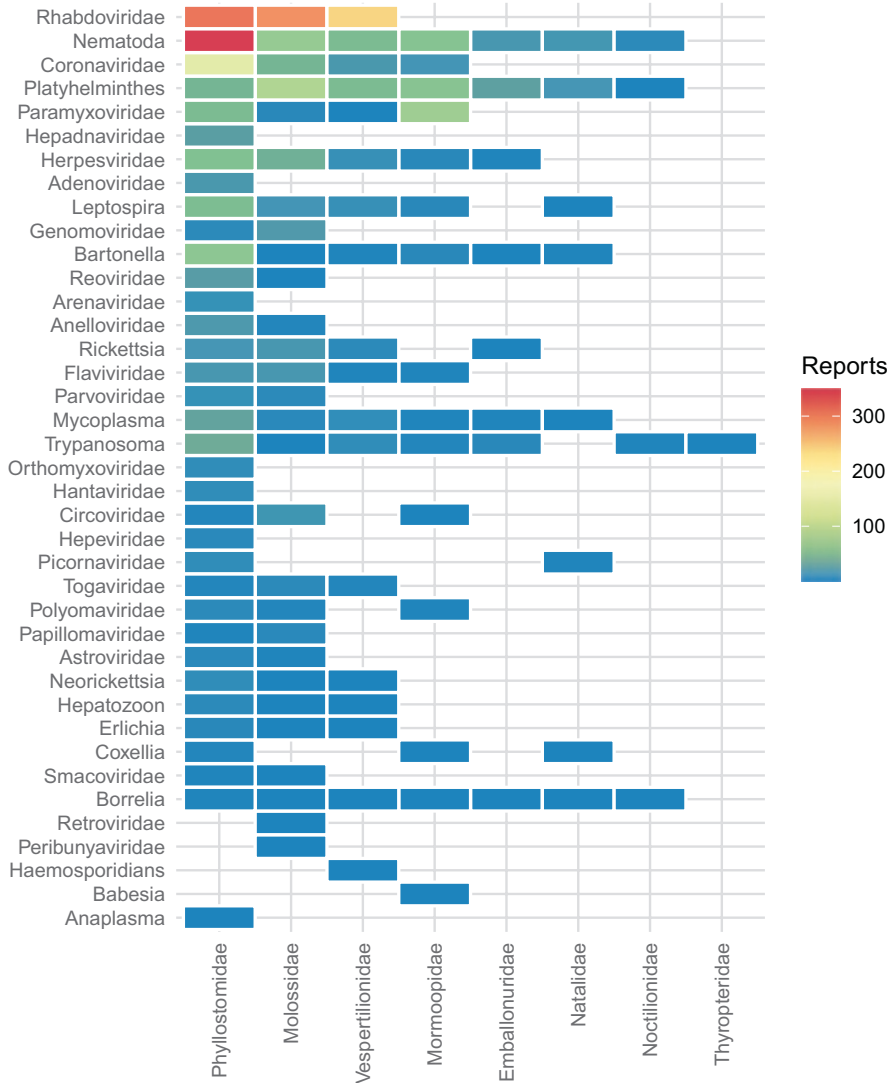
A total of 403 studies were selected. Of these, 24 of 33 existing Latin American and Caribbean countries were represented (Brazil, Peru, Argentina, Colombia, Chile, Ecuador, Mexico, Venezuela, Costa Rica, Dominican Republic, French Guiana, Panama, Guatemala, Bolivia, Uruguay, Jamaica, Trinidad and Tobago, Martinique, Paraguay, Grenada, St. Kitts, Cuba, Nicaragua, and Surinam). Brazil was the country with the highest number of publications (123), followed by Mexico (85),



**Fig. 8.1** Distribution map of the number of publications on pathogens associated with bats

Argentina (29), Colombia (28), Peru (22), Costa Rica (17), Paraguay (13), Chile (11), and Cuba (10) (Fig. 8.1). In terms of groups of pathogens, Brazil, Mexico, Argentina, Costa Rica, Chile, and Peru were the countries that contained publications belonging to all three groups of pathogens on which we aimed to focus in this chapter: Virus, Bacteria, and Parasites (Hemosporidians, *Babesia*, *Hepatozoon*, *Trypanosoma*, and Helminths; Nematoda and Platyhelminthes). Brazil mainly contained publications of viruses such as Rhabdoviridae, Coronaviridae, and Paramyxoviridae but also contained a significant number of publications of pathogenic bacteria (*Bartonella*, *Mycoplasma*, and *Rickettsia*). Regarding parasite publications, Brazil, together with Mexico, has the highest number of publications reporting Nematoda, Platyhelminthes, and *Trypanosoma* parasites.

Apart from containing the highest number of publications, Brazil represented the country with the highest pathogen richness (840), followed by Argentina (220), Mexico (203), Chile (180), Costa Rica (168), and Peru (126). These six countries contained most of the studies that we were able to retrieve. Additionally, our first search revealed that almost all pathogens included in our study (over 1380 parasite observations out of 2214 total pathogen observations) are being recorded and studied in bat species of the family Phyllostomidae (1383), followed by bats of the family Molossidae (675), Vespertilionidae (414), Mormoopidae (247), Emballonuridae (56), Natalidae (38), Noctilionidae (10), and Thyropteridae (1). Most records observed in the family Phyllostomidae belong to Nematoda parasites, followed by the viral families Rhabdoviridae and Coronaviridae (Fig. 8.2). Several pathogens (e.g., *Anaplasma*, Hepeviridae, Hepadnaviridae, Arenaviridae, and Adenoviridae) were found to be uniquely associated with the Phyllostomidae family. Other



**Fig. 8.2** Heatmap of the pathogen diversity associated with bat families

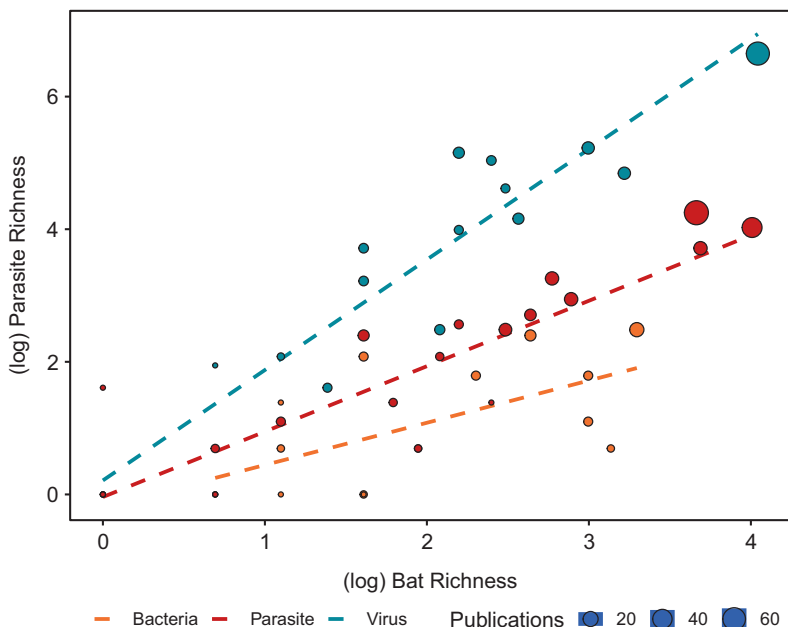
families with exclusive associations were Molossidae with retroviruses and peribunyaviruses, Vespertilionidae with haemosporidians, and Mormoopidae with *Babesia* (Fig. 8.2). The bat species with the highest number of publications were *Desmodus rotundus* (75), *Carollia perspicillata* (58), *Tadarida brasiliensis* (56), *Molossus molossus* (41) and *Artibeus lituratus* (41) (Fig. 8.3). The high number of pathogens associated with these species can be attributed to their widespread distribution; as they are found throughout the majority of the Neotropics, they are considered habitat generalists that are able to tolerate the alteration of their habitat. In particular,



**Fig. 8.3** Number of publications by bat species. Species with more than four publications are shown

*D. rotundus* and *C. perspicillata* are considered bioindicators of altered ecosystems (Medellín et al. 2000). When analyzing the relationship between species richness and the richness of reported pathogens, a strong positive correlation was found between the richness of viruses ( $R^2_{adj} = 0.89, p < 0.001$ ) and parasites ( $R^2_{adj} = 0.85, p < 0.001$ ) and the richness of bats, whereas the positive correlation between bacteria ( $R^2_{adj} = 0.34, p = 0.015$ ) and bats was not as strong (Fig. 8.4).

In the second search, 20 studies were selected where anthropogenic or ecological factors (fragmentation, habitat loss, habitat type, or ecological factors) were



**Fig. 8.4** Relationship between bat richness per country and the number of pathogen reports

examined in relation to the presence, prevalence, or diversity of pathogens. Only six studies correlated anthropogenic variables such as fragmentation, habitat loss, or habitat type with the presence, diversity, and presence of pathogens. Fourteen studies analyzed ecological variables such as host specificity, vegetation cover, functional characteristics, climate, temperature, trophic guilds, population properties, and elevational gradient (Table 8.1). In these 20 studies, the following pathogen types were evaluated: bacteria (*Mycoplasma*), hemoparasites (*Trypanosoma*), helminths (Trematoda, Cestoda, and Nematoda), and viruses (primarily Rabies, Coronaviridae, Herpesviridae, and Hepadnaviridae).

Clearly, there is a bias in the study of viruses associated with bats, while most studies focus on detecting, sequencing, and reporting viruses of medical significance. There are studies that attempt to comprehend the patterns of association and distribution between viral diversity and host diversity (Luis et al. 2013, 2015; Nieto-Rabiela et al. 2018, 2019). It is predicted that viral richness will be higher in species with a trophic frugivorous guild (Luis et al. 2015; Willoughby et al. 2017), that are long-lived (Luis et al. 2013; Guy et al. 2020) and have a larger body size (Maganga et al. 2014), that form large colonies (Turmelle and Olival 2009; Guy et al. 2020) and that have extensive geographical ranges that overlap with those of multiple species (Luis et al. 2013; Maganga et al. 2014; Olival et al. 2017).

There is evidence to suggest that deforestation can increase the prevalence and diversity of viruses in bat hosts. A study conducted in the Atlantic Brazilian Forest provides additional proof. The study identified 13 distinct viral species belonging to



**Table 8.1** Summary of the selected studies that explore the association between anthropogenic/ecological factors and pathogen prevalence/diversity in Neotropical bats

Factor	Region	Parasite Studied	Bat Family	Main findings	References
Anthropogenic	Brazil	Bacteria: <i>Mycoplasma spp</i>	Phyllostomidae	Hemotropic <i>Mycoplasma</i> spp. were identified in one ( <i>Sturnira parvidens</i> ) out of 15 bats tested from forest fragments	Collere et al. (2022)
Ecological	Belize	Bacteria: <i>Mycoplasma spp</i>	Phyllostomidae	Hemoplasmas displayed high genetic diversity and strong host specificity.	Becker et al. (2020)
Ecological	Peru and Belize	Bacteria: <i>Mycoplasma spp</i>	Phyllostomidae	Prevalence was highest in nonreproductive and young individuals, did not differ by country, and was relatively stable over time.	Volokhov et al. (2017)
Anthropogenic	Panama	Hemoparasite: <i>Trypanosoma sp</i>	Phyllostomidae	Trypanosome prevalence was significantly higher in bats from forest fragments than in bats captured in continuous forest.	Cottontail et al. (2009)
Ecological	Mexico	Parasites: Trematoda, Cestoda and Nematoda	Phyllostomidae, Noctilionidae, Molossidae, Vespertilionidae, Emballonuridae	Prevalence and mean intensity of infection values ranged from 7.1% to 100% and from 1 to 56, respectively.	Moguel-Chin et al. (2023)
Anthropogenic	Trinidad and Tobago	Virus: Rabies	Phyllostomidae	Juvenile bats were more likely to be seropositive than adults, suggesting early exposure to the RABV. RVNA was found in bats from both rural and nonrural areas, as well as in both hematophagous and nonhematophagous bat species.	Seetahal et al. (2020)

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Table 8.1 (continued)

Factor	Region	Parasite Studied	Bat Family	Main findings	References
Anthropogenic	Mexico	Virus: Coronaviridae, Herpesviridae, Adenoviridae and Astroviridae	Phyllostomidae, Mormoopidae, Vespertilionidae	A positive relationship was found between the phylogenetic diversity of hosts and viral diversity and with viral richness. Statistical models categorized host species and habitat types that have a higher risk of being associated with a greater viral richness.	Rico-Chávez et al. (2015)
Anthropogenic	Brazil	Virus: Coronaviridae, Herpesviridae, Adenoviridae, Hantaviridae, Paramyxoviridae and Astroviridae	Phyllostomidae, Molossidae, and Vespertilionidae	Deforested sites had a less diverse bat community and higher viral prevalence than forested sites Viral detection was more likely in juvenile males located in deforested sites. Coronaviridae family were detected more frequently in generalist species.	Loh et al. (2022)
Ecological	Panama	Virus: Hepadnavirus	Phyllostomidae	Distribution of TBHBV in bats was significantly affected by forest cover, with higher infection rates in areas with lower forest cover.	Hiller et al. (2019)
Ecological	Uruguay	Virus: Herpesviridae, Rhabdovirus and Pneumovirus	Phyllostomidae, Molossidae, and Vespertilionidae	The viral community in the bat species is more strongly associated with ecological traits of the hosts, rather than their taxonomy. Herpesviruses may be used to track the population dynamics of their hosts, including movement and demographics.	Moreira Marrero et al. (2021)
Ecological	French Guiana	Virus: Rabies	Phyllostomidae	Species' seroprevalence ranged from 0% to 20%, and the risk of seropositivity was higher in bats with a hematophagous diet, living in monospecific colonies and in dense forests. Temporal fluctuations in seroconversions and waning immunity were observed.	de Thoisy et al. (2016)

Ecological	French Guiana	Virus: Nairoviridae, Circoviridae, Retroviridae, Herpesviridae, Papillomaviridae	Phyllostomidae and Molossidae	Viral diversity was shaped by the diet of the bat species, with a high proportion of plant and insect-related viral families for <i>M. molossus</i> and a high proportion of vertebrate-related viral families for <i>D. rotundus</i> .	Salmier et al. (2017)
Ecological/ Anthropogenic	Peru	Virus: Rabies	Phyllostomidae	Seroprevalence of rabies virus (RV) in vampire bats ranged from 3% to 28%, with highest prevalence in juvenile and subadult bats. RV exposure was independent of bat colony size, suggesting an absence of population density thresholds for viral invasion and extinction. Culling campaigns implemented during the study failed to reduce seroprevalence and may have been counterproductive for disease control.	Streicker et al. (2012b)
Ecological	Puerto Rico	Virus: Herpesviridae	Phyllostomidae, Molossidae and Mormoopidae	Reproductively active bats, especially females, have significantly higher viral richness. Host sex significantly affects viral turnover across host populations.	Sjodin et al. (2020)
Ecological	Costa Rica, Panama, Ecuador and Brazil	Virus: Coronaviridae	Phyllostomidae, Noctilionidae, Molossidae, Vespertilionidae and Emballonuridae	The 50 viruses reported represented five different alphacoronavirus RGUs and two betacoronavirus RGUs, and closely related alphacoronaviruses were detected in <i>Carollia perspicillata</i> and <i>C. brevicauda</i> across a geographical distance exceeding 5600 km.	Corman et al. (2013)
Ecological	Argentina	Virus: Rabies	Phyllostomidae	Phylogenetic analysis of N gene sequences from vampire bat-related RABV variants showed a geographical and temporal structure. Multiple introductions of the infection were detected.	Torres et al. (2014)

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Table 8.1 (continued)

Factor	Region	Parasite Studied	Bat Family	Main findings	References
Ecological	Neotropic	Virus: Rabies	Phyllostomidae	Viral evolutionary rates were labile following historical jumps between bat species and nearly four times faster in tropical and subtropical bats compared to temperate species. The association between geography and viral evolution could not be explained by host metabolism, phylogeny, or variable selection pressures, and instead appeared to be a consequence of reduced seasonality in bat activity and virus transmission associated with climate.	Streicker et al. (2012a)
Ecological	Peru	Virus: Rabies	Phyllostomidae	Spatially compartmentalized transmission cycles of rabies virus were observed in vampire bats, but no effects of bat demography or environmental context on seroprevalence were found. Seroprevalence in bats was only weakly correlated with outbreaks in livestock, indicating the challenge of predicting spillover.	Meza et al. (2022)
Ecological	Peru	Virus: Rabies	Phyllostomidae	Gradual spread of RABVs and involvement of different vampire bat subpopulations. New RABV lineages were found in 3 non-vampire bat species, suggesting new virus reservoirs.	Condori-Condori et al. (2013)
Ecological	Peru	Viroma	Phyllostomidae	Viral communities in vampire bats vary significantly and are not consistently predicted by spatial or genetic distances. Viral diversity follows an elevational gradient, is enriched by juvenile-biased age structure, and declines with local anthropogenic food resources.	Bergner et al. (2020)

four viral families known to infect humans with Coronaviridae viruses, the majority of which were generalists. The likelihood of viral detection was higher in young male bats, who were more likely to interact and share food sources with unfamiliar host species, increasing their exposure to potential viruses (Loh et al. 2022). The study demonstrated that despite having fewer bat species, deforested regions maintain higher virus richness. Although the risk of disease was not directly assessed, people living near disturbed forest edges may be particularly vulnerable to zoonotic infections due to increased exposure to disease reservoirs and because deforested areas have higher viral richness. These findings are consistent with a published study that examined the association between bat diversity and the variety of four medically important virus families across an environmental gradient in human-dominated settings in southern Mexico (Rico-Chávez et al. 2015). The generalist species were linked with more viruses than predicted when examining the kind of host response to habitat change, and a positive correlation between the beta diversity of both viral and bat communities and the habitat gradient was found.

The habitat heterogeneity hypothesis (Lawton 1983) postulates a strong relationship between environmental diversity; in this case, phylogenetic host diversity and biological diversity (pathogen diversity) were supported by the significant positive correlation of phylogenetic diversity with viral richness and viral diversity. The findings imply that variables such as fragmentation and habitat loss drive species assemblages, resulting in regions of increased risk for the establishment of zoonotic species (Rubio et al. 2014; Kamiya et al. 2014; Gay et al. 2014). Viral community composition changes throughout the assessed anthropogenic settings revealed a significant dependency on host species change. The study discovered significant rates of turnover in viral populations, validating the perturbation theory, which states that changes in land use alter parasite dynamics in multihost systems by modifying the mode of transmission across species (Murray and Daszak 2013). According to several studies (Lloyd-Smith et al. 2009; Murray and Daszak 2013; Brearley et al. 2013), habitat change causes the exposure of new hosts to a diverse pool of parasites, particularly in locations with high levels of biodiversity.

Future research is needed to determine which characteristics of the host determine microparasite community assemblages, but greater microparasite diversity does not necessarily translate into higher health risks. In fact, the relationship between parasites and host diversity suggests that a pathogen's chances of posing a health risk are only increased in disturbed, deforested environments. Using machine learning, it has been possible to accurately identify reservoir hosts (Plowright et al. 2019; Becker et al. 2022). In addition, data-driven identification of vector species of a wide range of zoonotic diseases has been carried out, evaluating the vectorial capacity of various mosquito and tick species (Yang and Han 2018). Utilizing these predictive tools could assist in prioritizing sampling of bat species and pathogen surveillance. Moreover, combining refined molecular tools (e.g., metagenomic sequencing) with noninvasive collection methods (e.g., eDNA) could not only optimize pathogen surveillance but also contribute to the conservation of the targeted species (Giles et al. 2021).

## 8.4 Investment in Research and Development and Surveillance of Viral Diversity in Bats

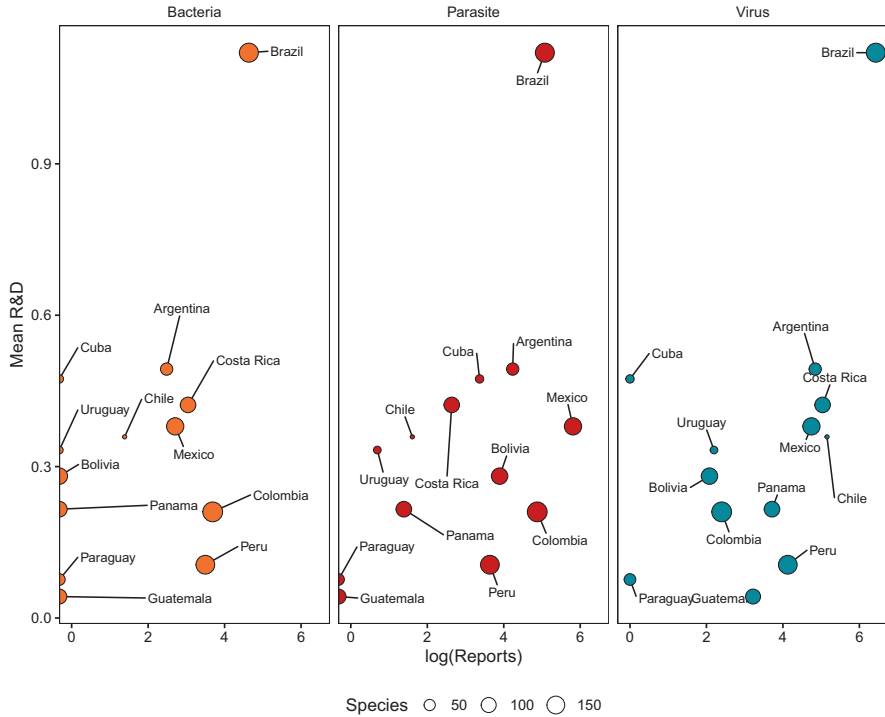
From 1996 to 2018, the World Bank database contains information on gross domestic expenditure on research and development for 15 Latin American countries. The average expenditure varies across the Neotropical region, ranging from 0.042% in Guatemala to 1.12% in Brazil. Among the countries with the greatest bat richness, Brazil (bacteria = 103, parasite = 160, virus = 620) and Mexico (bacteria = 15, parasite = 334, virus = 115) are the only countries with a significant number of pathogen registers, which coincides with their higher R&D expenditure (1.12%). In contrast, Colombia (bacteria = 40, parasite = 131, virus = 11) and Peru (bacteria = 33, parasite = 38, virus = 62), which also have a high diversity of bat species, have very few reports due to minimal pathogen surveillance efforts (Turmelle and Olival 2009; Olival et al. 2017).

The linear regression between total reported bat pathogens per country and gross domestic expenditure on research and development as a percentage of the gross domestic product showed a positive trend (bacteria:  $r = 0.74$ ,  $p < 0.001$ , parasite:  $r = 0.55$ ,  $p < 0.001$ , virus:  $r = 0.88$ ,  $p < 0.001$ ). On the other hand, the relationship between bat richness and total reported bat viruses per country did not show a statistically significant correlation (Fig. 8.5).

Most countries in the region spend less than 0.5% of their GDP on research and development, which translates to a low national investment in the detection and surveillance of bat-associated viruses. Despite the importance of the relationship between bats and viruses, the pathogen diversity described in Latin America depends largely on foreign investment. This highlights the need to prioritize the allocation of resources to the most vulnerable regions, especially those experiencing high rates of land use change, and to direct epidemiological surveillance to areas with a higher likelihood of infectious disease emergence. Encouraging transdisciplinary approaches aimed at both conserving bats and their ecosystems and improving human health should be a priority.

## 8.5 A Multidisciplinary Approach to Bat Rabies Virus in Latin America

Rabies, an acute progressive viral encephalitis (family Rhabdoviridae, genus *Lyssavirus*), is one of the oldest known zoonoses associated with bats, but it continues to pose a threat to public and animal health systems on most continents. The natural history and evolution of lyssaviruses are largely attributed to bats (Rupprecht et al. 2002). Rabies transmitted by *Desmodus rotundus*, commonly known as the common vampire bat, has become an increasingly concerning and previously underestimated threat. It currently represents the leading cause of rabies-related deaths in both humans and livestock in Latin American countries, where canine rabies is on



**Fig. 8.5** Relationship between research and development spending and pathogen richness reported per country

the verge of eradication (Vigilato et al. 2013; Velasco-Villa et al. 2017; Benavides et al. 2017). Among more than a dozen lyssaviruses associated with bats, rabies virus (RABV) is the most significant member and species of the genus from a public health perspective. It is unknown how RABV spreads to new hosts and why spill-over events typically result in one-time infections as opposed to sustained infections. Due to the frequency of interaction between conspecifics, it is hypothesized that host taxonomy and social behavior play a role in RABV persistence (Hughes et al. 2005). Species barriers also limit the host range of the rabies virus (Streicker et al. 2010).

Although measuring the human health burden of RABV is difficult due to the geographic isolation of infected communities and underreporting, the rates of bat depredation on humans and the associated rabies mortality can be alarming. Surveys indicate that in high-risk areas, 23–88% of residents are bitten by *D. rotundus*, causing the death of 1–7% of the local human population during epidemics. Agricultural losses are also substantial, with tens of thousands of livestock being killed by RABV annually, resulting in a cost of more than \$30 million USD before accounting for underreporting and recurring investments in surveillance, diagnostics, and prevention (Benavides et al. 2017).

In Latin America, efforts to control and prevent RABV have led to the establishment of various programs, including surveillance, livestock vaccination, pre- and postexposure human prophylaxis, and bat eradication (Johnson et al. 2014). The only method currently employed to reduce RABV transmission within the reservoir is the eradication of bats to reduce their population density. Theoretically, eradication of disease reservoirs is most effective when pathogen transmission rates are dependent on host density, with a critical density threshold below which the pathogen cannot be maintained by the population (Lloyd-Smith et al. 2005). However, the elimination of vampire bat colonies has not had a significant effect on reducing the circulation of the virus; in contrast, there is evidence that this type of program could favor the persistence of RABV in local populations (Choisy and Rohani 2006; Viana et al. 2023).

Several countries, such as Belize, Costa Rica, Ecuador, Guatemala, Mexico, Paraguay, and Peru, have reported an increase in the rate of RABV cases over the past decade, which requires a review of control and prevention strategies and the incorporation of multidisciplinary strategies, such as landscape management, new forms of livestock management, and the development of bat vaccines (Benavides et al. 2020).

### **8.5.1 Landscape Features and the Presence of *Desmodus rotundus***

There is substantial evidence that human activities influence the dynamics and distribution of animal populations (Lewis et al. 2021). Although these effects are typically detrimental to wild animal species (Chase et al. 2020), livestock production has benefited vampire bat populations in Latin America, the primary reservoir of RABV (Fenton et al. 1992; García-Morales et al. 2013). The common vampire bat (*Desmodus rotundus*) is one of three hematophagous bats found in the Neotropics. It mainly feeds on livestock, with a preference for cattle, frequently choosing juveniles, weak individuals, or those dozing at the herd's perimeter (Johnson et al. 2014; Anderson et al. 2014), while occasionally feeding on humans. The other two species, the hairy-legged vampire bat (*Diphylla ecaudata*) and the white-winged vampire bat (*Diaemus youngi*), primarily feed on birds and other wildlife (Fenton and Kunz 2003; Mayen 2003).

Understanding the factors that influence the geographic distribution and regional movement of *D. rotundus* is crucial to comprehending the RABV risk. *D. rotundus* is distributed throughout tropical and subtropical Latin America, from northern Mexico to northern Argentina and Chile (Lee et al. 2012). It inhabits diverse ecosystems, including tropical rainforests, coastal deserts, xeric shrublands, and montane regions as high as 3600 m (Lee et al. 2012). At large spatial scales, temperature, altitude, and precipitation are important factors influencing bat presence and rabies risk, whereas, at local scales, factors such as livestock density, human-induced



forest fragmentation, and density/proximity of highways and rivers appear to be important (Lee et al. 2012; de Andrade et al. 2016). In the past decade, efforts have been made to investigate and better understand the population ecology and the influence of local landscape characteristics on the abundance and bite rates of *D. rotundus* on livestock.

The highest levels of forest loss and fragmentation in the Neotropics are currently associated with forest conversion into extensive pastures used for cattle raising, which appears to be the most important factor in explaining the abundance of *D. rotundus* in sites dominated by a pasture matrix (Sanchez-Gomez et al. 2022). It has been found that *D. rotundus* tends to be more abundant at sites that are embedded within pasture matrices with high levels of forest fragmentation. This pattern was characterized by a large number of agricultural areas and high landscape heterogeneity (Bolívar-Cimé et al. 2019; Sanchez-Gomez et al. 2022). In contrast, the abundance of *D. rotundus* tends to be considerably lower at sites with extensive fragments of continuous forest, nonfragmented forest or in areas with very low levels of fragmentation, where there are no easily accessible food sources for this hematophagous bat, such as cattle and other types of domestic livestock (Medellín et al. 2000).

This pattern suggests that *D. rotundus* is highly opportunistic when searching for food, as it frequently approaches rural areas with human settlements, where corrals, chicken coops, and pig farms, which typically contain confined animals, represent valuable and easily accessible food resources (Bobrowiec 2012). Thus, vampire bat populations are favored by their adaptability to human-altered environments, and they thrive in landscapes with high concentrations of cattle and other domestic livestock raised for human consumption (Bobrowiec et al. 2015). Therefore, the vampire bat is an excellent indicator species of human habitat disturbance or land-use change resulting from cattle husbandry in the Neotropics (Medellín et al. 2000).

It is known that *D. rotundus* prefers to fly using linear elements of the landscape, although no preference has been found for one type of element. However, it has been suggested that the use of linear elements of the landscape as a reference for flight is influenced by the level of contrast between the linear feature and the open areas. Moreover, food abundance is a factor promoting the use of linear features by insectivorous bats (Ávila-Flores and Sánchez Gómez 2019).

Studies indicate that the detection range of objects, including experimental “prey,” is limited for *D. rotundus* through the use of echolocation, scent, thermoreception, and passive hearing of sounds emitted by prey. The role of vision in *D. rotundus* prey detection is uncertain, but it is suggested that their visual detection of prey decreases as the distance from their flight paths increases. This implies that *D. rotundus* is more likely to commute near wooded areas because they have greater prey availability. Domestic animals kept near wooded areas and *D. rotundus* roosting sites are the most vulnerable to hematophagous bat attacks. These findings have strong implications for livestock management in tropical regions, as production animals resting near linear landscape features are at higher risk of attacks by *D. rotundus* (Ávila-Flores and Sánchez Gómez 2019).

### 8.5.2 Effectiveness of Bat Culling on Rabies Prevalence

Reducing wildlife populations by lethal methods is a common strategy for preventing the spread of pathogens into human or domestic animal populations (Velasco-Villa et al. 2017). Lower densities of susceptible organisms are believed to reduce the incidence of infection in the reservoir and, consequently, the risk of transmission to other species. In extreme cases, reservoir populations may fall below a critical threshold that triggers pathogen extinction (Benavides et al. 2017). While culling has been effective in managing some host–pathogen systems, its effectiveness in other systems has been hampered by the underestimation of ecological complexity (Vigilato et al. 2013). Therefore, understanding the factors that contribute to the success or failure of culls in reducing disease transmission is essential for improving their efficacy, promoting investments in alternatives for disease control, such as vaccination or reproductive suppression, or increasing the attractiveness of such investments.

Few studies have modeled the effect of bat culling on the prevalence and circulation of the rabies virus in bat populations, and even fewer empirical studies have tested the effect of this type of management on the prevalence (Benavides et al. 2016, 2017; Viana et al. 2023). One of these studies conducted in Peru found that a large, geographically synchronized cull was associated with widespread reductions in vampire bat populations but had negligible effects on the occurrence or intensity of spillover to local livestock (Viana et al. 2023). Although preventive culls halted the virus's spread, culls in regions with active viral circulation had the opposite impact, accelerating the spread of rabies across the landscape. These findings support that the long-term maintenance of rabies through spatial processes limits the efficacy of culling as currently practiced. They also provide a rare empirical example of perturbation effects, in which changes in reservoir host behavior following incomplete eradication compromise spillover management by promoting pathogen spatial spread. The authors observed a reduction in the population density of the common vampire and a decrease in the rate of bites to livestock, but there was no reduction in the transmission of rabies to livestock. Rabies is only ephemerally present in individual bat colonies and can spread at low bat densities due to virus-induced behavioral changes that facilitate biting (Benavides et al. 2020). The social disruption caused by bat control may facilitate the spread of rabies by increasing bat dispersal (Blackwood et al. 2013). If culls reduce population immunity by preferentially removing adult immune individuals or if vacated niche space increases juvenile survival or immigration of naive individuals (Choisy and Rohani 2006), additional complications may arise. While empirical data remain limited, a comparison of seroprevalence between *D. rotundus* colonies with varying histories of culling suggests that culling is associated with higher rather than lower rabies seroprevalence in bats (Streicker et al. 2012b).

Additionally, population size is unrelated to rabies incidence, and there are no population thresholds below which rabies cannot invade. This emphasizes the

importance of analyzing epidemiological and genomic data alongside real-world culls to provide fundamental insights into the determinants of viral maintenance within bat reservoirs and to assess how ecological and behavioral responses of bats to culling translate into pathogen spillover risk and spatial spread (Benavides et al. 2020).

### 8.5.3 Vaccination in Bats

The vaccination of reservoirs is a fundamental component of human rabies prevention for all nonbat reservoirs (Hampson et al. 2015; Benavides et al. 2019). Vaccines have been effectively applied to both canines and wild carnivores. One effective approach to combat wildlife rabies in some European regions and the dog/coyote rabies virus variant in the United States has been the use of oral rabies vaccine baits containing an attenuated recombinant vaccinia virus vector vaccine expressing the rabies virus glycoprotein gene (VRG) (Maki et al. 2017). A long-term oral rabies vaccine barrier program in the United States is preventing the spread of the raccoon rabies virus variant (Maki et al. 2017). However, to date, there is no official vaccination program against rabies in free-living bats, largely due to the difficulties caused by their ecology and immunology, especially in the common vampire bat. In laboratory experiments, recombinant viral vaccines using vaccinia (Almeida et al. 2005) and raccoon pox (Stading et al. 2016, 2017) vectors have been shown to be immunogenic and protective in hematophagous and insectivorous bats. Since both vectors are already used in large-scale campaigns targeting wildlife, their safety and lack of virulence reversion in nontarget species have been extensively evaluated (Brochier et al. 1991; Rocke et al. 2017). Alternatively, transmissible vaccines are being developed, which have a greater potential for spread, ensuring that the potential negative effects of a genetically modified microorganism in wild populations are minimized (Nuismer et al. 2016).

A recent experiment used spatiotemporally replicated deep sequencing to parameterize competing epidemiological mechanistic models of *D. rotundus* betaherpesvirus (DrBHV), a candidate vector for a vaccine against vampire bat-transmitted rabies (Griffiths et al. 2023). The study determined that lifelong infections with cycles of latency and reactivation, along with high transmission rates, are required to explain patterns of DrBHV infection observed in feral bats. Simulations demonstrated that inoculating a single bat with a DrBHV-vectored rabies vaccine could immunize greater than 80% of a bat population, thereby reducing the magnitude, frequency, and duration of rabies outbreaks by 50–95% (Griffiths et al. 2023).

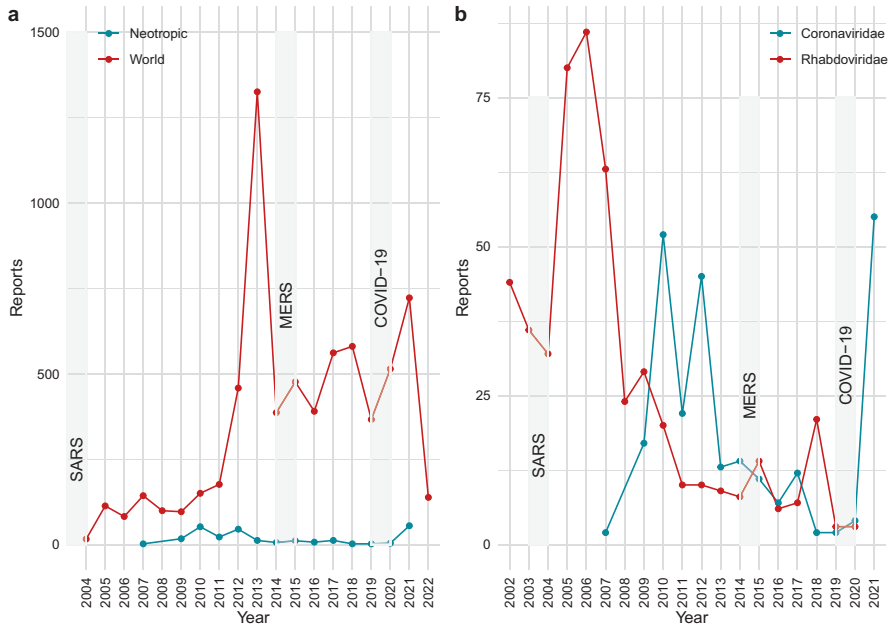
Important next steps include investigating the dynamics of vaccine spread in the environment through field trials. However, even if vaccination of bats reduced rabies transmission, the deleterious effects of bat bites on humans and livestock would necessitate enhanced bat population management strategies (Benavides et al. 2020).

## 8.6 Impact of Bat-Virus Relationships on the Conservation of Latin American Bats

The natural link of bats with the night and darkness, in combination with their peculiar external appearance, has historically produced fear, aversion, or even repugnance in many people around the world. In many cultures, associating bats with evil, death, and magic has reinforced negative emotions and feelings toward bats. In the last century, the identification of bats as reservoirs of the rabies virus and the association of bat guano with the growth of *Histoplasma* fungus contributed to creating the popular notion that bats are synonyms of disease and danger. Not surprisingly, direct attacks on bat colonies and destruction of bat roosting sites were the most important causes of human-induced bat mortality during the nineteenth and twentieth centuries (O’Shea et al. 2016).

In tropical regions of Latin America, the public image of bats has been further deteriorated by the association of common vampire bats with the transmission of the rabies virus to cattle. The inefficient culling campaigns promoted by Latin American governments to control bovine paralytic rabies have contributed to reinforcing the idea that killing wild animals is the best option to reduce zoonotic disease transmission. In addition to the annual killing of dozens of thousands of common vampire bats under official culling campaigns, individuals of other species of bats have been erroneously poisoned or attacked by untrained people to control bovine paralytic rabies (Saldaña-Vázquez et al. 2013). In fact, direct kills and roost destruction are, at present, the main causes of multiple-mortality events of bats in Latin America (O’Shea et al. 2016).

In 2019, the emergence of COVID-19 raised the concern of bat biologists and conservationists (Fenton et al. 2020) because the causative pathogen (SARS-CoV-2) was closely related (96.2% genome sequence identity) to the RaTG13 coronavirus found in *Rhinolophus affinis* from Yunnan Province in China (Zhou et al. 2020). The only suggestion that this coronavirus could have a bat origin triggered a cascade of news in traditional media and social networks that put bats in the global spotlight (Cerri et al. 2022). By then, there was growing evidence that bats harbor a great diversity of viruses, including many SARS-like coronaviruses, and more research was generated to identify new bat-virus associations (Fig. 8.6). The worry of being infected by SARS-CoV-2 renewed the fear, aversion, and repugnance of bats in many people around the world (Lu et al. 2021). In Latin America, at the beginning of the pandemic, there were sound cases of attacks to bat colonies and roosts that resulted in the death of many individuals (e.g., <https://phys.org/news/2020-03-peru-blamed-coronavirus.html>). Further studies demonstrated that SARS-CoV-2 was sufficiently different from any coronavirus present in bats (or any other mammal) so that it should be considered a human-specific virus (Boni et al. 2020). To date, available information does not allow us to identify the precise origin of SARS. CoV-2 (Fenton et al. 2020). However, most scientists agree that the activities of modern human societies set the stage for the emergence of COVID-19 and other zoonotic



**Fig. 8.6** Temporal trend of coronavirus reports in bats. The years of the beginning of the outbreaks of severe acute respiratory syndrome (SARS), Middle East respiratory syndrome (MERS), and COVID-19 are highlighted. **(a)** Trend of reports in the Neotropics and the rest of the world; **(b)** trend of reports of rabies virus and coronaviruses in the Neotropical region

diseases. In particular, it has been suggested that the risk of pathogen spillover has increased in recent times by (at least), (1) the reduction in the disease's dilution effect due to biodiversity loss, (2) the increase in contacts between people, domestic animals, and free-living wildlife due to habitat loss and land-use change, and (3) the accelerated exchange of native and exotic pathogens (e.g., in local wet markets) due to illegal trade, the appearance of new and distant markets that demand wildlife, and the movement of sick individuals (Fenton et al. 2020; Platto et al. 2021; Córdoba-Aguilar et al. 2021). Both the history of paralytic rabies control and the experience of the COVID-19 pandemic have left important lessons to manage enzootic and emergent zoonotic diseases in Latin America. First, the interaction between bats, domestic animals, and people is strongly mediated by human activities, so preventive or reactive strategies must consider the human dimension. Second, scientists from different disciplines should improve communication to design more integrative strategies. In this sense, the one-health approach might provide a suitable framework for guiding research efforts. Third, official protocols to manage diseases must be based on the best available evidence, so local authorities should maintain open communication channels with scientists.

## 8.7 Conclusions

In this chapter, we identify research opportunities to improve our knowledge of the complex relationship between humans, bats, and pathogens from a one-health perspective. Our review revealed that viruses and parasites are the most studied pathogen groups in bats throughout the Neotropical region. Currently, there is a significant bias in favor of viral research compared to bacterial research in bats. Despite the fact that viruses pose a significant risk to public health and host conservation due to their potential to spread to susceptible species, our understanding of infectious bacterial pathogens in bats is limited. Bats and their ectoparasites harbor potentially zoonotic bacterial pathogens (Mühldorfer 2013; Hornok et al. 2019). It was observed that epidemics caused by viruses genetically related to specific bat viruses have a direct impact on virus detection efforts (Fig. 8.6), reflecting a public health policy-driven bias.

The collected data revealed that Brazil, Mexico, Argentina, Costa Rica, Chile, and Peru had a greater diversity of parasite species than the other analyzed Neotropical countries. This was expected due to the wide diversity of bat species in these countries, but it should also be correlated with the large number of studies we were able to retrieve for these countries. Reduced funding for research in Latin America seems to limit pathogen surveillance based on molecular tools, although international collaboration might facilitate such efforts. In contrast, the use of inexpensive microbiological techniques appears to be an alternative to learning about different kinds of parasites. We encourage the science, agricultural, and health authorities of Latin American countries to increase investment in pathogen surveillance and zoonotic disease diagnostics in bat populations to identify conditions that increase the risk of pathogen or parasite spillover. We identified a variety of anthropogenic and ecological factors that influence the prevalence of pathogens throughout the Neotropics. However, few studies have analyzed anthropogenic factors, with most research focusing on contrasting conserved and altered sites. There is a lack of knowledge regarding the temporal and spatial diversity of pathogens associated with bats.

Due to its significance in public health and its economic effects on livestock production, the rabies virus is the Neotropical region's most studied bat-associated virus. To implement multidisciplinary strategies to prevent and monitor rabies, particularly in regions with high rates of habitat loss, it is necessary to integrate knowledge on population ecology and response to landscape characteristics by bats. There is evidence that the strategy based on vampire bat extermination has not been entirely effective and may, in some cases, contribute to the spread of rabies. Undoubtedly, the integration of multidisciplinary, multi-institutional, and even multinational teams could provide more fruitful results and help to design more effective strategies for disease prevention and control.

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